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CONTEXT-DEPENDENT SPECIES IDENTITY EFFECTS WITHIN A FUNCTIONAL GROUP OF FILTER-FEEDING BIVALVES

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Abstract. We asked whether species richness or species identity contributed more to ecosystem function in a trait-based functional group, burrowing, filter-feeding bivalves (freshwater mussels: Unionidae), and whether their importance changed with environmental context and species composition. We conducted a manipulative experiment in a small river examining the effects of mussel assemblages varying from one to eight species on benthic algal standing crop across two sets of environmental conditions: extremely low discharge and high water temperature (summer); and moderate discharge and water temperature (fall). We found strong species identity effects within this guild, with one species (*Actinonaias ligamentina*) influencing accrual of benthic algae more than other species, but only under summer conditions. We suspect that this effect is due to a combination of the greater biomass of this species and its higher metabolic and excretion rates at warm summer temperatures, resulting in increased nitrogen subsidies to benthic algae. We also found that *Actinonaias* influenced the condition of other mussel species, likely through higher consumption, interference, or both. This study demonstrates that species within trait-based functional groups do not necessarily have the same effects on ecosystem properties, particularly under different environmental conditions.

Key words: biodiversity; Bivalvia; ecosystem function; functional group; species identity; species richness; stream; Unionidae.

Introduction

A critical effort in ecology is to determine the functional role of biodiversity (Jones and Lawton 1995). Biodiversity is perceived to have positive effects on ecosystem functioning through several different mechanisms. Species richness may increase ecosystem function because individual species utilize different niches (niche complementarity) or through synergistic interactions (facilitation), thus increasing the overall contribution of the community to a given ecosystem service (Loreau 2000). Species redundancy, in which different species perform identical ecosystem services, has been proposed to act as an "insurance policy" in the event of species loss or decline (Walker 1995). Species identity effects occur where ecosystem processes are driven by the presence of a singular species whose traits are best adapted to a given environment (Naeem et al. 2002). In natural systems, these different mechanisms can operate concurrently and sometimes counteract one another, leading to weak net effects (Bruno et al. 2005).

Species that are believed to perform similar functions in an ecosystem are typically assigned to functional groups, types, or guilds. Since species in such groups are assumed to be "functionally identical," they are believed to compensate for one another as species are lost or decline in abundance (Petchey and Gaston 2002). This has led to the idea that ecosystem function can be maintained in the event of species loss by maintaining functional group richness (i.e., the number of functional groups) (Walker et al. 1999, Symstad and Tilman 2001), even if the number of species within a functional group is reduced. Problems limiting the applicability of the concept include that functional groups have been inadequately defined for many communities and ecosystems (Wright et al. 2006) and that the degree of functional overlap between species assigned a priori to many guilds has not been adequately quantified (Rosenfeld 2002*a*). Most importantly, we do not have a good understanding of how the functional roles of species change with both abiotic and biotic environmental context (Cardinale et al. 2000, Duffy et al. 2005). For example, apparently redundant species may have different physical and chemical optima, so that their "functional niches" do not overlap when environmental axes are included (Rosenfeld 2002*a*). Species interactions also can affect how species respond to the environment; thus, the manner in which species traits influence ecosystem function may depend on assemblage composition and resulting species interactions (Downing and Liebold 2002, Duffy et al. 2005).

Early studies of biodiversity and ecosystem function focused primarily on terrestrial systems and were restricted to experiments addressing a single trophic level, usually primary producers (Hooper et al. 2005). More recent work has expanded into marine and freshwater systems (Covich et al. 2004, Gessner et al. 2004, Raffaelli 2006) and has examined how biodiversity

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changes at one trophic level can impact processes at other trophic levels (Duffy et al. 2001, 2005, Hillebrand and Cardinale 2004). Freshwater systems, and streams in particular, are losing biodiversity at a more rapid rate than terrestrial or marine systems (Allan and Flecker 1993), primarily through habitat modification (Richter et al. 1997). These habitat changes, including altered flow and temperature regimes, can alter the relative importance of species and their interactions. Freshwater mussels (Bivalvia: Unionoida) are a trait-based guild of primary consumers (long-lived, benthic, burrowing, filter-feeding bivalves) that perform important functions in rivers (Vaughn and Hakenkamp 2001). For example, the ecological processes performed by mussels (e.g., nutrient excretion, biodeposition, bioturbation) can impact both primary producers and consumers through direct and indirect pathways (Spooner and Vaughn 2006, Vaughn and Spooner 2006). Because all unionid mussels filter-feed as adults, and studies have found few differences in either microhabitat preferences or feeding selectivity (Vaughn and Hakenkamp 2001, Strayer et al. 2004), species have been assumed to perform equivalent ecosystem roles; however, this assumption has not been adequately tested. This is an important question because freshwater mussels are a globally imperiled fauna experiencing catastrophic declines in both species richness and overall mussel biomass (Strayer et al. 2004). We need to be able to predict whether members of the mussel guild can compensate for one another as species are lost and how this may vary with environmental conditions and assemblage composition. In a laboratory experiment comparing clearance and nutrient cycling rates of two common mussel species (*Actinonaias ligamentina* and *Amblema plicata*), we found strong biomass effects but few other differences between species (Vaughn et al. 2004). In a year-long field experiment manipulating the same two species, we found that algal and invertebrate colonization rates on the sediment surrounding mussels and on mussel shells of the two species differed (Spooner and Vaughn 2006). However, because unionid mussels commonly occur as multispecies aggregates, studies limited to two species are not predictive of ecosystem functions performed by natural assemblages.

This study asks whether species richness or species identity contributes more to ecosystem function within a trait-based functional group, freshwater mussels, and if their importance changes with environmental context and species composition. We present results of a manipulative field experiment examining the effects of freshwater mussel assemblages varying from one to eight species on benthic algal standing-crop biomass across two sets of seasonal environmental conditions in a small river. We focus on accrual of benthic algae as a response variable for several reasons. First, our previous work with two species showed that mussels stimulate the growth of benthic algae, likely because mussels transfer nutrients from the water column to the benthos and sediment–water interface (Vaughn et al. 2004, Spooner and Vaughn 2006). Second, standing-crop biomass of benthic algae is correlated with benthic primary production, and primary production has been the parameter of choice in many studies of biodiversity and ecosystem function (Hooper et al. 2005), facilitating comparison of our results.

Methods

The experiment was performed in the Kiamichi River, in the Ouachita Uplands of southeastern Oklahoma, USA, a comparatively undisturbed, small river (basin area 4650 km^2; Matthews et al. 2005) with healthy, diverse unionid mussel assemblages (Vaughn et al. 1996). We used a factorial design with 13 species treatments and two environment treatments, with each combination replicated five times. Mussels in the Kiamichi River primarily face two sets of environmental conditions: moderate flow and water temperature throughout much of the year and severely reduced flow combined with high water temperature primarily in late summer and early fall (Spooner and Vaughn 2006). Therefore, we used time as our environment treatment and performed the experiment over two 6-week periods, 18 July through 30 August 2003 (summer) and 26 September through 6 November 2003 (fall). During the summer run of the experiment, mean water depth in the reach with the enclosures was 57 $\pm$ 0.79 cm (mean $\pm$ SE) and mean midday water temperature was 31° $\pm$ 0.18°C. Flow was so low during the summer it often was not measurable with our flow meter; discharge was 12.94 $\pm$ 3.69 cm^2/s. During the fall run of the experiment depth was 61 $\pm$ 1.68 cm, mean temperature was 17° $\pm$ 0.38°C, and discharge was 25022 $\pm$ 6308 cm^2/s.

Many biodiversity experiments have used random subsets of species drawn from a common pool of taxa. This approach is useful for understanding the theoretical consequences of biodiversity loss, but is unrealistic in that it assumes that species are equally abundant and that potential extinction order is random (Solan et al. 2004). In most natural systems, a few species are common and many more are rare, and the common species are most likely to make significant contributions to ecosystem services (Jones and Lawton 1995). Our approach was to mimic as closely as possible actual species composition of mussel beds. Mussel beds in the Kiamichi River have a species richness of 11 $\pm$ 0.75 and are typically dominated by one to several common species with the rest of the species more rare. There are four species that are typically dominant: *Actinonaias ligamentina* (Lamarck 1819), *Amblema plicata* (Say 1817), *Fusconaia flava* (Rafinesque 1820), and *Obliquaria reflexa* (Rafinesque 1820). We used eight species in our experiments, the four common species above in all treatments and four additional more rare taxa, *Ellipsaria lineolata* (Rafinesque 1820), *Lampsilis cardium* (Rafinesque 1820), *Quadrula pustulosa* (Lea 1831), and *Truncilla truncata* (Rafinesque 1820), only in the high-

TABLE 1. Mussel species used in the experiment.

Species	Tribe	Length (mm)	Shell-free dry mass (g)
Actinonaias ligamentina	Lampsilini	108.44 (0.71)	5.99 (0.08)
Amblema plicata	Amblemini	86.57 (0.95)	3.36 (0.11)
Fusconaia flava	Pleurobemini	61.39 (0.49)	1.58 (0.006)
Ellipsaria lineolata	Lampsilini	95.04 (0.27)	4.48 (0.31)
Lampsilis cardium	Lampsilini	105.8 (2.8)	5.69 (0.32)
Obliquaria reflexa	Lampsilini	54.34 (0.34)	1.49 (0.004)
Quadrula pustulosa	Amblemini	61.5 (1.05)	1.59 (0.02)
Truncilla truncata	Lampsilini	43.07 (3.54)	1.64 (0.05)

Notes: Data are given as means and SE (in parentheses). Tribal placement is based on Lydeard et al. (1996), C. Lydeard (*personal communication*), and Davis and Fuller (1981). The experiment was performed in the Kiamichi River, in the Ouachita Uplands of southeastern Oklahoma, USA.

diversity treatments. Our design included a no-mussel control. The chosen species all co-occur in mussel beds in the river and vary in adult size, shell morphology, and phylogeny (Table 1) and thus should encompass the range of ecological attributes occurring in natural mussel assemblages. We used a replacement series design, stocked mussels at the mean density for mussel beds in the Kiamichi River (eight individuals per enclosure, 32 individuals/m^2; Vaughn et al. 1997), and combined species in treatments at equal densities (e.g., in the four-species treatments, two individuals of each dominant species for a total of eight individuals).

We performed the experiment in 65 0.25-m^2 ($50 \times 50 \times 15$ cm) enclosures constructed from 2.33 cm diameter PVC pipe with 2.5 cm diameter wire poultry netting covering the bottom and sides. To control for depth and current velocity, enclosures were placed within one stream reach (50×15 m). To control for effects between enclosures, they were placed ~2 m apart and staggered in a checkerboard fashion (Spooner and Vaughn 2006). Prior to the experiment, sediment was extracted from the riverbed and mixed in 246-L plastic trash cans to homogenize the distribution of invertebrates and algae among treatments. All nonexperimental mussels were removed prior to homogenization, and no mussels except treatment mussels were included in the experiment. Enclosures were buried 15 cm into the streambed and filled with homogenized sediment, so that the sediment in the enclosures was level with the streambed. This design allowed movement of invertebrates and fish in and out of enclosures through both the sediment and water column, but prevented escape by mussels (Spooner and Vaughn 2006). Enclosures were numbered, and treatments were randomly assigned to enclosures.

Mussels were collected at the experiment site, gently cleaned to remove periphyton and other biofilm, weighed (wet mass), their length recorded, and individually marked with a Floy shellfish tag (Floy, Seattle, Washington, USA) attached with gel-type adhesive. At the end of the experiment we remeasured the wet mass of all individual mussels. Mussels were blotted with a towel and left out of the water for 15 min prior to estimating wet mass. Following the experiment a subsample of mussels was collected and their shell-free (tissue) dry mass was measured. We then used shell length − tissue dry mass regressions to estimate the tissue dry mass of all mussels used in the experiment and to determine the tissue dry mass of each enclosure.

To measure benthic algal standing-crop biomass, four standard glass microscope slides (18.75 cm^2) were placed flat side on the sediment in each enclosure for each six-week run to allow colonization by periphyton. While we recognize that the rate of chlorophyll *a* accumulation on slides may underestimate that growing on rocks, it serves our purpose as a relative estimate of the difference among treatments. At the end of each run, the combined four slides from each enclosure were frozen. Chlorophyll *a* was extracted with acetone and measured spectrophotometrically with a correction for pheophyton (ASTM 1995). For all analyses below, we $\ln(x + 1)$-transformed chlorophyll *a* data to meet expectations for normality.

Mussels excrete nitrogen and phosphorus that may be taken up by periphyton (Vaughn et al. 2004); effects of such excretion should be strongest where nutrients are limiting. To determine whether nutrients were limiting at our field site, we measured algal growth (biomass) on nutrient-diffusing substrates (Pringle and Triska 1996) distributed throughout the stream reach where the experiment was conducted. Our substrates consisted of 20-mL scintillation vials filled with agar enriched with N, P, N + P, and a non-enriched control. We had 65 replicates of each nutrient treatment in each season. Vials were covered with a porous silica disc affixed with silicone (Toetz 1999) and buried in the sediment with only the silica disc exposed. Vials were placed in the stream at the end of the second week and removed at the end of the sixth week. Discs were removed from the vials, and chlorophyll *a* was extracted with acetone and measured spectrophotometrically as described above. We used two-way ANOVA with Tukey's post-hoc multiple comparisons, with nutrient and season as treatments, to examine the effects of nutrient supplementation on algal biomass.

We compared algal biomass on the sediment among all 13 species treatments using two-way ANCOVA with species combination and time (season) as treatment variables and enclosure biomass (mussel tissue dry mass) as the covariate. We then examined algal biomass on the sediment with linear regression, with total species richness, densities of the four dominant species, enclosure tissue dry mass, and the proportion of enclosure biomass composed of *Actinonaias* as independent variables and $\ln(\text{chlorophyll } a + 1)$ as the dependent variable.

We compared observed values of chlorophyll *a* on the sediment with that predicted from species' behavior in monocultures. Predicted values were calculated by first determining the mean milligrams of chlorophyll per square centimeter per gram of mussel dry mass for the four species in monoculture. Then, for all paired-species

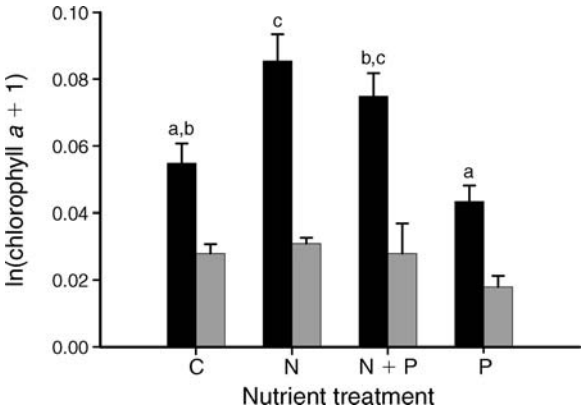

FIG. 1. Mean (+SE) ln(chlorophyll $a + 1$), originally measured in milligrams per square centimeter, on the sediment as a result of the nutrient addition experiment. Key to abbreviations: C, control; N, nitrogen addition; P, phosphorus addition; N + P, nitrogen + phosphorus addition. Black bars are summer treatments, and gray bars are fall treatments. Letters indicate significant differences between treatments. The experiment was performed in the Kiamichi River, in the Ouachita Uplands of southeastern Oklahoma, USA.

and four-species enclosures, we multiplied the monoculture mean by the biomass of a particular species in an enclosure and summed the results to obtain predicted chlorophyll *a* in milligrams per square centimeter for an enclosure. Predicted and observed chlorophyll *a* values were compared using paired *t* tests with Dunn-Sidak corrected alpha.

We estimated net mussel body condition (change in [whole mussel wet mass/shell length]) for each mussel. This ratio is commonly used as a surrogate for growth in slow-growing bivalves (Crosby and Gale 1990). We examined the relationship between mussel species richness and change in mussel body condition for the four common species, again comparing patterns resulting from species mixtures to monoculture means.

RESULTS

Nutrients were limiting at our field site during the summer, but not in the fall (Fig. 1; season, $F_{1,508} = 112.3$, $P < 0.001$; nutrient, $F_{3,508} = 10.81$, $P < 0.001$; season × nutrient, $F_{3,508} = 4.26$, $P = 0.005$). Nutrient limitation in the summer was caused by nitrogen limitation; phosphorus was not limiting in our field experiment (Fig. 1).

Algal biomass on glass slides placed on the sediment was higher in the summer than in the fall, regardless of treatment (Figs. 2 and 3). Algal biomass was significantly different among the 13 species treatments in the summer, but not in the fall (Fig. 2; species combination, $F_{12,101} = 8.80$, $P < 0.001$; season, $F_{1,101} = 71.26$, $P < 0.001$; species × season, $F_{12,101} = 6.28$, $P < 0.001$; biomass, $F_{1,101} = 0.87$, $P = 0.35$). This pattern appears to be driven by the presence of one species, *Actinonaias ligamentina*, rather than by species richness. Algal biomass decreased with increasing species richness in the summer (Fig. 3a), although this relationship was not statistically significant ($R^2 = 0.018$, $P = 0.285$). In

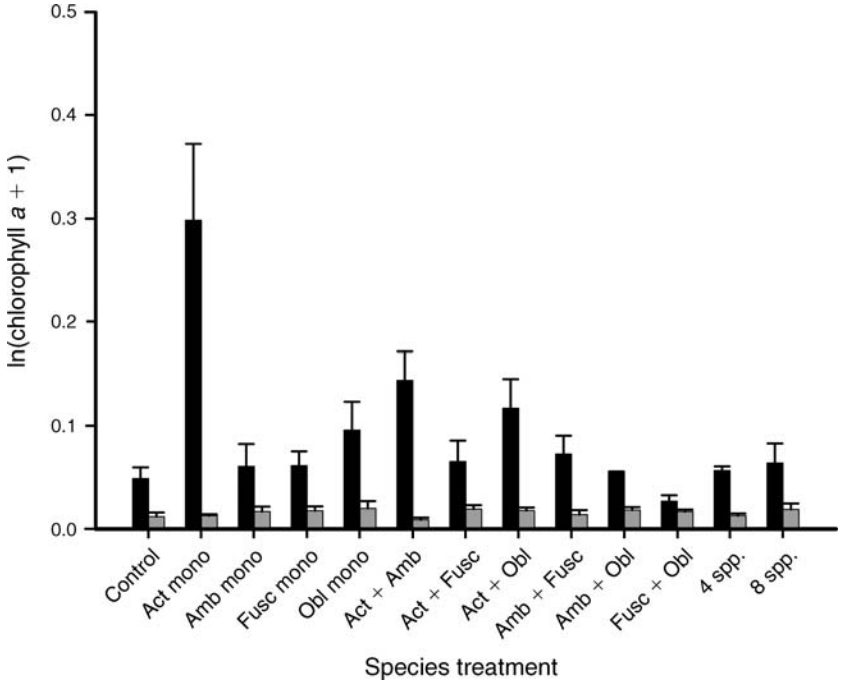

FIG. 2. Mean (+SE) ln(chlorophyll $a + 1$), originally measured in milligrams per square centimeter, on glass slides on the sediment for all mussel species treatments. Black bars are summer treatments, and gray bars are fall treatments. Abbreviations are: Act, *Actinonaias*; Amb, *Amblema*; Fusc, *Fusconaia*; Obl, *Obliquaria*.

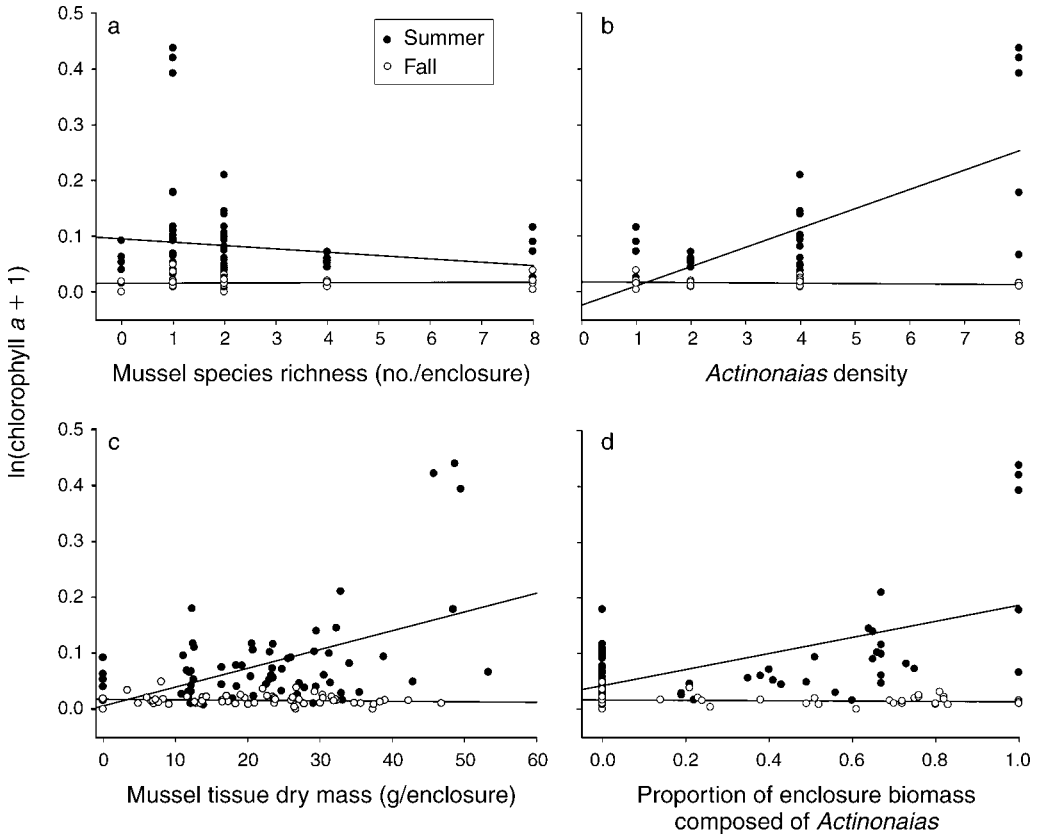

FIG. 3. Observed ln(chlorophyll $a+1$), originally measured in milligrams per square centimeter, on glass slides on the sediment as a function of: (a) mussel species richness (summer, $R^2 = 0.018$, $P = 0.285$; fall, $R^2 = 0.003$, $P = 0.67$); (b) *Actinonaias* density (summer, $R^2 = 0.46$, $P < 0.001$; fall, $R^2 = 0.033$, $P = 0.345$); (c) enclosure tissue dry mass (summer, $R^2 = 0.236$, $P < 0.001$; fall, $R^2 = 0.013$, $P = 0.378$); (d) proportion of enclosure biomass composed of *Actinonaias* (summer, $R^2 = 0.271$, $P < 0.001$; fall, $R^2 = 0.021$, $P = 0.275$).

contrast, algal biomass was generally higher in species mixtures that included *Actinonaias* (Fig. 2). Summer algal biomass significantly increased with increasing *Actinonaias* density (Fig. 3b; $R^2 = 0.46$, $P < 0.001$), but not with increasing densities of *Amblema* ($R^2 = 0.004$, $P = 0.736$), *Fusconaia* ($R^2 = 0.056$, $P = 0.21$) or *Obliquaria* ($R^2 < 0.001$, $P = 0.976$). Strong effects of *Actinonaias* were related to the larger size and higher biomass of this species (Table 1). There was a strong, positive relationship between both the dry mass of mussels in an enclosure (Fig. 3c; $R^2 = 0.236$, $P < 0.001$) and the proportion of *Actinonaias* biomass in an enclosure (Fig. 3d; $R^2 = 0.271$, $P < 0.001$) and summer algal biomass.

In contrast to the summer experiment, in the fall there were no differences in sediment algal biomass among species richness or species density treatments (Figs. 2 and 3), and algal biomass showed no relationship with enclosure dry mass or the proportion of *Actinonaias* dry mass (Fig. 3c, d). Indeed, algal growth on glass slides on the sediment was quite low in the fall and in most cases was little different than the non-mussel controls (Figs. 2 and 3).

In summer, the magnitude of differences between predicted and observed chlorophyll *a* on the sediment was greater in treatments containing *Actinonaias* (Fig. 4, Table 2), with *Actinonaias* mixtures containing less chlorophyll *a* than predicted by an additive model based on monocultures. This pattern was not apparent in the fall (Fig. 4, Table 2).

Effects of species richness on mussel body condition varied across the four common species and in some cases with season (Fig. 5). *Actinonaias* was impacted by strong intraspecific competition as evidenced by increasing body condition with decreasing numbers of *Actinonaias* in enclosures. In addition, intense interspecific competition from *Actinonaias* led to decreased body condition of other species.

DISCUSSION

In this study species identity had a stronger influence on ecosystem function than species richness, with one species (*Actinonaias*) contributing more to ecosystem processes than other species and influencing the condition of other species. Other studies of both primary producers and primary consumers also have found

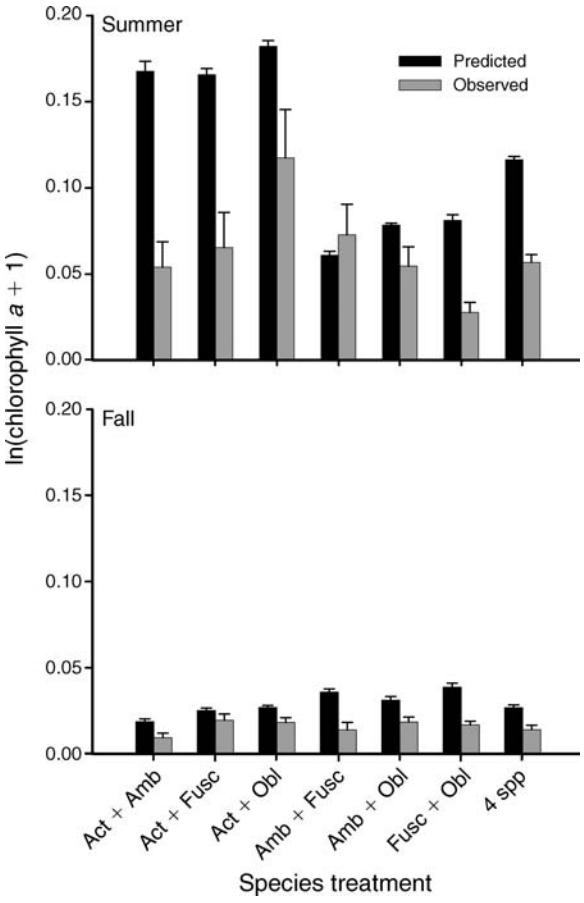

FIG. 4. Predicted and observed ln(chlorophyll $a + 1$) (mean + SE) on glass slides in the sediment × species treatment. Abbreviations are: Act, *Actinonaias*; Amb, *Amblema*; Fusc, *Fusconaia*; Obl, *Obliquaria*.

strong species identity effects and more subtle species richness effects (Symstad et al. 1998, Emmerson et al. 2001). For example, macroalgal species identity strongly influenced primary production in North Carolina subtidal communities (Bruno et al. 2005), and gastropod species identity controlled primary production in Irish intertidal communities (O'Connor and Crowe 2005). In addition, in this study species identity effects were context-dependent, varying across seasons. While fewer studies have been performed across seasons or at a range of environmental conditions, those that have been conducted in this manner have found that species identity effects usually are context-dependent, with species performing differently under different environmental conditions (Liancourt et al. 2005, Norkko et al. 2006).

We found seasonal differences in benthic algal biomass above and beyond effects of mussels. Algal biomass was much higher in summer than in fall across all species composition treatments, including no-mussel controls. This is not surprising since algal growth rates increase with both temperature and insolation (Steinman et al. 2006) and during the summer water temperatures were higher and discharge was much lower, decreasing sediment loads and allowing more light penetration. In addition, discharge at our field site was on average much higher in the fall than in the summer, and this may have dislodged some periphyton from glass slides (Spooner and Vaughn 2006).

The magnitude of effects of *Actinonaias*, our unique species, on benthic primary production was much greater than other species in the summer, even after accounting for their larger size and higher biomass (Table 1). Most likely, this effect is largely a direct result of nitrogen supplied by *Actinonaias* to the periphyton. Nitrogen was limiting at our field site during the summer (Fig. 1), so any nitrogen subsidies to the stream should have enhanced periphyton growth. Field measurements of mussel ammonia excretion rates, at a temperature approximate to conditions during our summer experiment (33°C), showed that while *Actinonaias* is on average 1.64 times larger than *Amblema*, its mass-specific ammonia excretion rate at 33°C is 3.6 times higher and its molar N:P excretion rate is 3.4 times higher (D. E. Spooner and C. C. Vaughn, *unpublished data*). *Actinonaias* is on average 3.8 times larger than *Fusconaia*, but its mass-specific ammonia excretion rate is twice as high (D. E. Spooner and C. C. Vaughn, *unpublished data*). Thus, *Actinonaias* is providing more nitrogen to the benthic algae both because there is more *Actinonaias* biomass present than other mussel species and because this species excretes nitrogen at a much higher rate under summer conditions. There was no effect of any bivalve combinations in fall, likely because mussels affect algal accumulation via alleviation of nutrient limitation and nutrients were not limiting in the fall (Fig. 1).

In summer, mixtures containing *Actinonaias* resulted in accrual of less benthic algae than predicted from an additive model based on monoculture means; i.e., the strong effects of *Actinonaias* were diminished when they were replaced by other species. This implies that the higher biomass of periphyton in treatments with *Actinonaias* is due to *Actinonaias* activities rather than complementarity among species (Fridley 2001). This is likely due to fertilization by *Actinonaias*, as described above, but also to negative interactions of *Actinonaias* with other species. Body condition results support this

TABLE 2. Results of paired t test comparisons for predicted and observed chlorophyll a on the sediment by species treatments (df = 4 for all comparisons).

Treatment	Summer		Fall	
	t	P	t	P
Actinonaias + *Amblema*	−9.406	0.001	−2.52	0.065
Actinonaias + *Fusconaia*	−4.931	0.008	−1.25	0.280
Actinonaias + *Obliquaria*	−2.37	0.077	−2.46	0.069
Amblema + *Fusconaia*	0.688	0.529	−3.97	0.016
Amblema + *Obliquaria*	−2.23	0.089	−3.25	0.031
Fusconaia + *Obliquaria*	−6.37	0.003	−5.86	0.004
Four species	−13.34	0.0002	−4.74	0.018

Note: P values are Dunn-Sidak corrected probabilities.

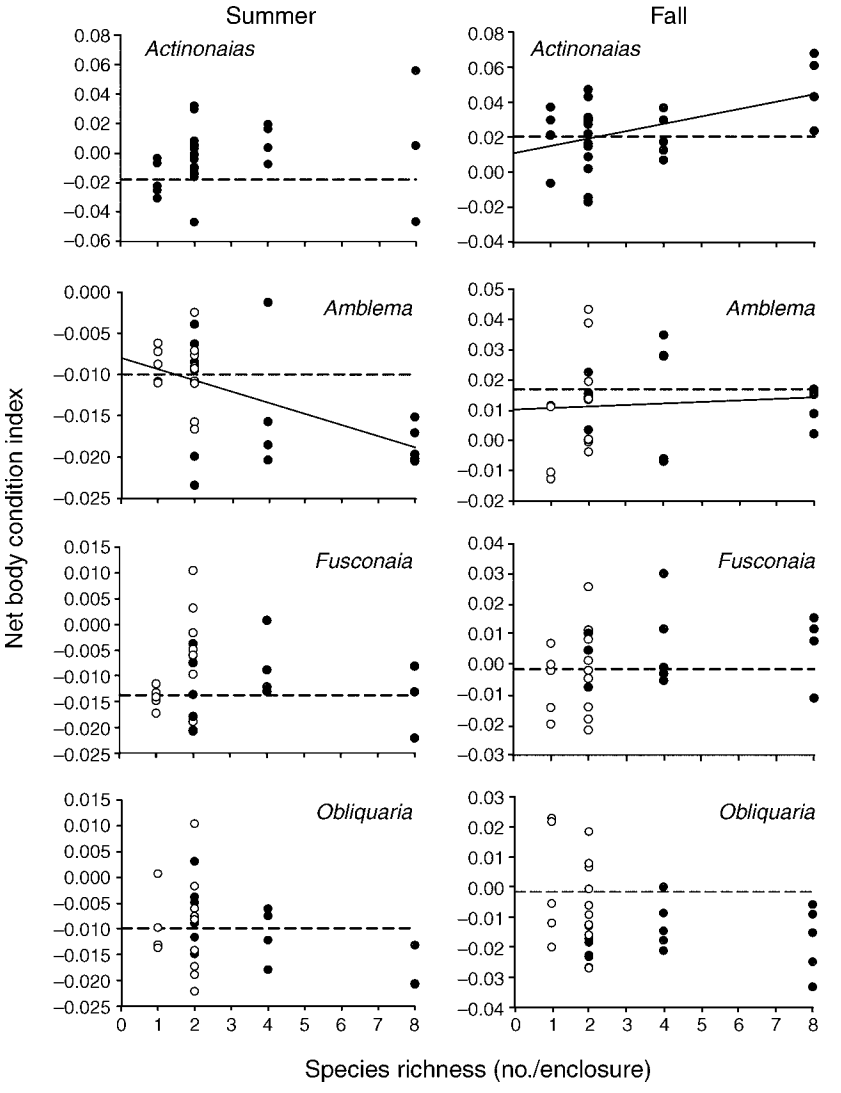

FIG. 5. Net mussel body condition index (change in [wet mass/shell length]) as a function of mussel species richness. Each point represents one enclosure. Shaded data points represent enclosures containing at least one *Actinonaias*, and open data points are treatments without *Actinonaias*. Dashed lines represent monoculture means. *Actinonaias*: summer, $R^2 = 0.06$, $P = 0.218$; fall, $R^2 = 0.234$, $P = 0.008$. *Amblema*: summer, $R^2 = 0.286$, $P = 0.003$; fall, $R^2 = 0.007$, $P = 0.65$. *Fusconaia*: summer, $R^2 = 0.075$, $P = 0.167$; fall, $R^2 = 0.101$, $P = 0.087$. *Obliquaria*: summer, $R^2 = 0.134$, $P = 0.061$; fall, $R^2 = 0.097$, $P = 0.093$.

hypothesis. *Actinonaias* influenced the body condition of other mussel species, and this in turn may have influenced the performance of these species. In summer, all species decreased in condition in enclosures with *Actinonaias*. Decreased condition in the presence of *Actinonaias* indicates that this species may be affecting food resource acquisition by other mussel species, either through higher consumption, interference, or both. *Actinonaias* has higher algal filtration rates than the other species in the study (Vaughn et al. 2004, Spooner and Vaughn 2005) and may be depleting food resources. In addition, in both field and laboratory studies we observed that *Actinonaias* is much more active than other species in the assemblage, moving around and bioturbating the sediment (Spooner and Vaughn 2006; C. C. Vaughn et al., *unpublished data*). These activities may interfere with feeding behavior of both other species and conspecifics. Body condition results also indicate intraspecific competition is occurring in *Actinonaias*: *Actinonaias* body condition decreased with increasing numbers of conspecifics in an enclosure.

Fusconaia behaved differently than other species in the fall, increasing in body condition with increased species richness (and thus decreased *Actinonaias*). Laboratory experiments indicate that *Fusconaia* performs better at cooler fall water temperatures than our other species (Spooner and Vaughn 2005). In addition, we suspect that *Fusconaia* may have been reproductively active and brooding larvae in the fall, which would have increased body mass and thus condition.

A shortcoming of many manipulative biodiversity experiments is that they are by necessity performed at limited spatial scales, but species abundance patterns and functional traits vary over regional scales and environmental gradients (Srivastava and Vellend 2005). Our experiment manipulated three-quarters of the average available species pool and closely approximated species richness and density/biomass of actual mussel beds, making our results robust at an ecological scale (Bolam et al. 2002). However, because our enclosures were designed to be as environmentally uniform as possible, opportunities for exploitation of different niches within this small space may be more limited than in a mussel bed itself, which would bias our design towards finding strong effects from particular species rather than complementarity (Duffy et al. 2001). In the same vein, this study examined only one ecosystem response variable, accrual of benthic algae. Experiments assessing species roles based on a single functional attribute also are biased toward finding strong species identity effects, because species are more likely to have nonoverlapping functional niches in an *n*-dimensional functional space (Rosenfeld 2002*a*, Duffy et al. 2005). We found only weak species richness effects at the spatial scale at which our experiment was conducted; however, as mentioned above, species richness may be important at larger spatial scales with different environmental conditions and different species dominance patterns that correspond with different species traits (Zedler et al. 2001, Rosenfeld 2002*b*).

Actinonaias and *Amblema* alternate in dominance in mussel beds across the Ouachita Uplands region and have different thermal optima and maxima (D. E. Spooner, *unpublished data*). At the summer temperatures experienced in this study, *Actinonaias* filtration rate exceeds that of *Amblema* (Spooner and Vaughn 2005), but this pattern reverses when temperatures reach those experienced in drought conditions. This could translate into very different ecosystem function depending on ambient water temperatures and species composition, which in turn may impact ecosystem processes relevant to benthic invertebrate and fish communities such as water column turnover, nutrient storage, and organic-matter processing rates.

In this study, species assigned a priori to a trait-based functional group (filter-feeding, burrowing bivalves) did not perform identically. In addition, our 16 years of monitoring data indicate that mussel species dominance patterns are shifting in our study river (C. C. Vaughn et al., *unpublished data*). Our data also indicate that overall biomass of all mussel species is declining (Vaughn and Taylor 1999; C. C. Vaughn et al., *unpublished data*), and this trend is also occurring globally (Strayer et al. 2004). Thus, shifts in species dominance are unlikely to compensate for this overall loss of filter-feeding biomass. For example, the differences in processes contributed by *Actinonaias* exceed that due to their higher biomass alone; thus, a very large amount of mussel biomass would be needed to buffer the loss of *Actinonaias* from mussel beds.

This study demonstrates that species within trait-based functional groups do not necessarily have the same effects on ecosystem properties, particularly under different environmental conditions. Thus, biodiversity assessments that assume ecosystem function will be stable as long as the number of functional groups and overall organism biomass are maintained are likely misleading. Further, both individual species performance and overall performance of functional groups will probably change with both species composition and environmental context. Since both species composition and environmental conditions are likely to change over time in most ecosystems, short-term experiments addressing species performance may not appropriately scale up to predict long-term ecosystem consequences (Wohl et al. 2004). Further resolution of the relationships among taxonomic diversity, functional diversity, community structure, and changing environments is critical if we are to apply the emerging concepts from biodiversity–ecosystem function to natural systems and conservation (Srivastava and Vellend 2005).

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