

Density-dependent biodiversity effects on physical habitat modification by freshwater bivalves

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Abstract. Several decades of research have shown that biodiversity affects ecosystem processes associated with resource capture and the production of biomass within trophic levels. Although there are good reasons to expect that biodiversity influences non-trophic ecosystem processes, such as the physical creation or modification of habitat, studies investigating the role of biodiversity on physical processes are scarce. Here we report the results of a study using artificial streams to test the influence of freshwater mussel biodiversity on gravel erosion during high flows while manipulating mussel abundance. Mussel species vary in traits that should influence their effects on erosion, such as size, shell morphology, and burrowing behavior. We found that mussel species richness was associated with an increase in erosion at both low and high densities. Planned contrasts showed that the erosion observed in species mixtures was purely additive at low density, indicating that erosion in a species polyculture could routinely be predicted by the performance of monocultures. However, at high density certain combinations of species showed nonadditive effects on erosion, suggesting that organism abundance can fundamentally alter biodiversity effects. Although this may have been a result of altered species interactions at high density, our study design cannot confirm this.

Key words: *biodiversity and ecosystem function (BEF); Bivalvia: Unionidae; ecohydrology; ecosystem engineers; erosion; freshwater mussels; sediment transport; substrate stability.*

INTRODUCTION

The biodiversity of ecological communities can significantly affect the performance of ecosystem processes (Hooper et al. 2005). However, most biodiversity and ecosystem function (BEF) studies have focused on ecosystem processes related to resource capture or production of biomass within trophic levels, or the flow of energy and nutrients between them (Hooper et al. 2005). Biodiversity effects on trophic ecosystem processes such as resource use or prey consumption are expected where niche partitioning has evolved due to competition for common resources. Nevertheless, we might also expect biodiversity effects on non-trophic ecosystem processes, such as creating and modifying habitat due to the diversity of physical structures produced by organisms, but studies investigating this are lacking.

Here we examine how species diversity of an important group of ecosystem engineers can impact the physical transport of sediment in stream ecosystems. Ecosystem engineers are organisms whose physical modifications to habitats have strong effects on other species and ecosystem processes (Jones et al. 1994). In

streams, benthic organisms can physically modify habitats in ways that influence sediment transport during high-flow events. Flood disturbances can regulate the diversity and function of benthic ecosystems across temporal and spatial scales (Resh et al. 1988). Species that stabilize sediments during high flows and prevent sediment entrainment, such as net-spinning caddisflies (Cardinale et al. 2004) and water willow (Fritz et al. 2004), can have significant effects on stream ecosystems. For example, Cardinale et al. (2004) estimated that net-spinning caddisflies could reduce the probability of a riverbed-scouring flood by 17%. Other stream species, such as some benthic fish and crayfish, can destabilize sediments during high flows (Statzner and Sagnes 2008). Species with stabilizing effects tend to bind sediment particles together through biological activity, while species with destabilizing effects tend to be bioturbators (mixers and disruptors of sediment through biological activity such as burrowing). Although some studies have investigated interactive effects of species on substrate stabilization (Statzner and Sagnes 2008), studies investigating the role of community structure and diversity on sediment transport are lacking.

Mollusks function as ecosystem engineers in many habitats (Gutierrez et al. 2003). Freshwater mussels (Bivalvia: Unionidae, hereafter “mussels”) are large, long-lived mollusks that can dominate benthic biomass in streams (Strayer 2008). Mussels are a globally imperiled fauna due to both species extinctions and

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declines in abundance of once common species (Strayer 2008). In streams, mussels typically occur as multispecies assemblages called “mussel beds” (Strayer 2008). Mussel species vary in multiple traits that should influence their ability to affect sediment transport, such as size, shell morphology, and burrowing activity (Allen and Vaughn 2009). Active burrowing species should destabilize sediments through bioturbation, while sedentary species that burrow deeply should stabilize sediments by increasing compaction and cohesion (Allen and Vaughn 2009). Further, mussel size, shape, and shell morphology should modify effects on substrate erosion (Watters 1994). Hydraulic principles suggest that large species with smooth shells exposed to flow will increase near-bed turbulence, destabilizing substrates (Vogel 1994). In contrast, species with textured shells should mitigate the increased turbulence patterns generated by exposed shells that could initiate erosion (Watters 1994). In addition, higher mussel species richness may increase the topographical complexity of the streambed, increasing near-bed turbulence similar to patterns observed with net-spinning caddisfly larvae (Cardinale et al. 2002).

We performed experiments examining the effects of mussel richness and abundance on sediment transport during high flows. We hypothesized that (1) increasing mussel species richness will increase sediment erosion because exposed mussels will increase the topographical complexity of the bed surface and may increase near-bed turbulence, (2) because the density of roughness elements is well known to control turbulence and shear, biodiversity effects are likely to differ at low and high densities, and (3) mussel species with sculptured shell morphologies should stabilize substrates, species that are active burrowers should destabilize substrates, and that these effects should increase with density.

METHODS

Studies investigating the effects of organisms on sediment transport are generally conducted in artificial channels, or “flumes,” where factors influencing sediment transport (such as water velocity, water depth, and sediment composition) can be controlled (Vogel and LaBarbera 1978, Nowell and Jumars 1987, Cardinale et al. 2004). We constructed eight recirculating stream channels modeled after Vogel and LaBarbera (1978) to standardize hydrodynamic and sediment properties across our experimental treatments (Appendix A). Each flume measured $330 \times 38.1 \times 33$ cm, and contained a 33×33 cm working area with a 12.7 cm deep false bottom 264 cm from the flow entrance (eight times the channel width, as recommended by Nowell and Jumars [1987]). Each flume contained a $38.1 \times 33 \times 4.6$ cm collimator constructed of 5.4 mm diameter plastic straws (recommended by S. Vogel, *personal communication*). Current velocity was manipulated with a three-quarter horsepower (~560 W) speed-controlled motor with two propellers separated by a stator on the drive shaft. Some hydraulic aspects of our flumes (as described by

Froude number, Reynolds number, boundary Reynolds number, and shear stress) scale to those observed in natural mussel beds (Allen and Vaughn 2010; Appendix B), and describe hydraulic conditions that are subcritical, turbulent, and hydraulically rough near the bed–water interface.

Prior to each trial, gravel particles (diameter 4.84 ± 1.78 [mean \pm SD], similar to those found in natural mussel beds [Allen and Vaughn 2010]) were homogenized, added to the working area in each stream channel, and gently compacted and leveled. In pilot studies, when mussels burrowed, they displaced gravel above the lip of the working area so that the gravel level was no longer flush with the flume bottom. Further, the amount of gravel displaced was proportional to the number and size of the buried mussels. Gravel displaced above the flume bottom would be exposed to additional forces of drag and lift since it would be more directly exposed to flow, which could introduce a bias in our experiment. To ensure that the gravel level remained constant for all mussel and no-mussel treatments, we standardized substrate volumes among treatments. We estimated the expected volume of gravel that would be displaced by the mussels using data from a previous study of mussel burrowing behavior. We measured the volume of mussels to be added, and then multiplied this value by the mean proportion of mussel body buried in sediment for that species as measured by Allen and Vaughn (2009). This calculation gave us the volume of gravel the mussels would displace from the working area while buried, which was then removed so that each treatment would have a gravel level flush with the bottom of the flume. Gravel particles were then gently compacted and leveled a second time, and the stream channels were filled with water to 33 cm depth. Mussels were added at random points using a grid with 16 equal sections, and were oriented in the gravel with the posterior end facing downstream and siphons facing upstream (a typical natural orientation in streams). Mussels were acclimated at flow velocities of 5 cm/s and allowed to burrow for four days.

We used three mussel species that naturally co-occur in mussel beds in southeast Oklahoma (with any one species being dominant in a given mussel bed), but that vary in traits that should influence their effects on sediment transport (Appendix C). *Actinonaias ligamentina* is large (mean length of individuals used in this experiment was 105.2 mm), is an active epibenthic burrower (burrows above the sediment–water interface [Allen and Vaughn 2009]), and has a smooth shell with no anchoring sculpture (ridges or pustules that help hold a mussel in place in substrates) or anti-scouring sculpture (ridges or pustules that disrupt scouring hydraulic forces [Watters 1994]). *Amblema plicata* is medium sized (mean length 83.9 mm), a sedentary epibenthic burrower (Allen and Vaughn 2009), and has an anchoring sculpture and an anti-scouring sculpture along the posterior slope and dorsal ridge (Watters

1994). *Quadrula pustulosa* is a small (mean length 48.6 mm), sedentary endo-benthic burrower (burrows below the sediment–water interface [Allen and Vaughn 2009; D. C. Allen and C. C. Vaughn, unpublished data]), and has an anchoring sculpture and anti-scouring sculpture along the dorsal ridge (Watters 1994). These traits suggest that *A. ligamentina* should have destabilizing effects on sediments, while *A. plicata* and *Q. pustulosa* should have stabilizing effects. Mussels (*A. ligamentina* [$n = 82$], *A. plicata* [$n = 84$], and *Q. pustulosa* [$n = 80$]) were collected from a single site on the Kiamichi River in southeast Oklahoma. Mussels were held in a Living Stream (Frigid Units, Inc., Toledo, Ohio, USA) for two weeks prior to the experiment and fed 500 mL of cultured algae per stream channel daily.

We manipulated mussel community structure with two density treatments crossed with eight species-composition treatments in a factorial design. The low- and high-density treatments were 6 and 12 mussels per flume (corresponding to densities of 55 and 110 mussels/m²), representing natural densities of mussels observed in rivers in southeast Oklahoma (Allen and Vaughn 2010). The eight species-composition treatments were three “monocultures” (single-species treatments), four “polycultures” (each possible two-species combination and a three-species combination), and a no-mussel control. Each species composition treatment was replicated 12 times at each density. Mussels were randomly assigned to treatments, and treatments were randomly assigned to flumes in each trial. A trial consisted of one density treatment per trial with density treatments randomly assigned to trials, for a total of 24 trials. On day 4 of each trial we measured water temperature, digitally photographed mussel burrowing positions, and measured width, length, and height of exposed shell for each mussel. These measurements and the digital image were used to generate a suite of burrowing variables (see *Burrowing variables*). Flow velocities were then increased to the maximum flow speed (~83 cm/s) for two minutes, which pilot studies showed was enough time for all substrate erosion to occur. Eroded gravel was caught in a 1-mm mesh net downstream of the working section (Appendix A), dried for 48 hours and weighed.

Statistical analyses.—We first analyzed the relationship between mussel species richness and gravel erosion at both density treatments using linear regressions on log-transformed raw masses (grams, g) of eroded gravel, with mussel species richness as the explanatory variable. To analyze the influence of mussel diversity and density treatments on substrate stability, we wanted a metric that was standardized relative to the performance of the no-mussel controls. We subtracted the log-transformed mean value of eroded gravel from no-mussel treatments from each datum of log-transformed eroded gravel from stream channels with mussel treatments. This is essentially a $\log(x + 1) - k$ transformation where x is each datum (raw mass of gravel eroded from a given flume) and k is a constant value (the log-transformed mean

mass of gravel eroded from no-mussel control treatment flume runs). The resulting variable can be defined as increasing erosion relative to controls if the value was positive (or decreasing erosion if negative), which we will refer to as “net change in gravel erosion.” We then ran a mixed-model two-way ANOVA on the net change in gravel erosion with mussel density and species composition treatments as fixed effects, and with trial as a random effect to account for any temporal differences.

Following other BEF experiments (Douglass et al. 2008, Griffin et al. 2008), we conducted 16 a priori planned linear contrasts to test for nonadditive biodiversity effects. The first set of contrasts ($n = 8$) tested the null hypothesis that the observed polyculture mean is the same as the expected mean based on additive monoculture performances (i.e., a two-species polyculture treatment was given a contrast coefficient of 1, while the two monoculture treatments of the species present in that polyculture were given contrast coefficients of -0.5 ; testing the null hypothesis that the mean of the polyculture was equal to the weighted means of its monocultures). The second set of contrasts ($n = 8$) compared the observed polyculture performance against its monoculture with the strongest effect on gravel erosion. These two types of contrasts represent a liberal and a conservative test for nonadditive biodiversity effects, respectively, and we refer to them as such.

Table-wide adjustments have been recommended to decrease the increased probability of Type I errors when performing multiple-comparison procedures (Rice 1989), but recently others have criticized such methods for obscuring ecologically significant effects and increasing Type II errors (Nakagawa 2004). Therefore, we followed Douglass et al. (2008) and opted not to apply a table-wide adjustment to P values to our contrasts, but rather we report the effect size of each test along with exact P values whenever possible, using both to interpret ecological significance (i.e., if the results of a contrast was statistically significant but had a small effect size, we would view the result with caution). Further, we interpret the results of multiple statistical tests strictly within the context of our broader hypotheses (i.e., whether or not biodiversity effects are present). Effect sizes are reported as the partial omega-squared, ω^2 , which measures the variability of the contrast relative to itself and the error and is not influenced by the main treatment effects,

$$\omega_{(\psi)}^2 = \frac{\sigma_{\psi}^2}{\sigma_{\psi}^2 + \sigma_{\text{error}}^2}$$

which we estimated using the following formula:

$$\omega_{(\psi)}^2 = \frac{F_{\psi} - 1}{F_{\psi} - 1 + 2n}$$

where ψ indicates a contrast, F_{ψ} is the F statistic of the contrast, and n is sample size (Keppel and Wickens 2004).

Burrowing variables.—Burrowing activity of marine bivalves influences erosion (Sgro et al. 2005), and exposed bivalve shells increase near-bed turbulence and promote erosion in marine systems (Widdows et al. 2002). Because freshwater mussel species vary in burrowing activity and depth (Allen and Vaughn 2009), we wanted to see if mussel effects on gravel erosion were partly due to burrowing behavior. We calculated a suite of burrowing variables from measurements of exposed mussel shells (width, depth, and height) and from measurements taken from digital photographs (distance between mussel pairs and mussel orientation relative to flow direction). Using these measurements, we calculated nine burrowing variables that we thought might influence substrate stability: surface area added by mussels (cm^2 ; mean, SD, and sum), mussel orientation relative to flow direction (degrees; mean, SD, and sum), and distance between mussel pairs (cm; mean, SD, and number of pairs <2.5 cm apart). The number of mussel pairs <2.5 cm apart (an arbitrary distance chosen) was measured to estimate the clustering of mussels in an experimental run. We ran a stepwise multiple linear regression analysis on the net change in gravel erosion to see which variables were most important.

RESULTS

Linear regressions showed significant increasing relationships between mussel species richness and gravel erosion at both low ($y = 1.704 + 0.088x$, $P = 0.002$, $R^2 = 0.08$) and high densities ($y = 1.66 + 0.070x$, $P = 0.045$, $R^2 = 0.04$; Fig. 1). The relatively low R^2 values of the linear regressions are partly due to differences between multiple species treatments within a single value of species richness, but also because of variation within treatments. The magnitude of the species richness effect was strong, as the mean gravel erosion in three-species polycultures was 77.1% and 93.8% greater than that of no-mussel controls at low and high density, respectively.

The mixed model two-way ANOVA showed a significant species treatment effect ($F_{6,132} = 2.705$, $P = 0.016$), an insignificant density effect ($F_{1,22} = 1.986$, $P = 0.173$), and an insignificant species-composition \times density interaction ($F_{6,132} = 0.857$, $P = 0.528$) on the net change in gravel erosion (Fig. 2). All planned contrasts testing for nonadditive biodiversity effects were insignificant at low density. At high density, two of four liberal contrasts testing for nonadditive biodiversity effects were significant, and one of four conservative contrasts was significant (Table 1). The observed effect sizes of these contrasts fall within the range of those reported by another BEF study, Douglass et al. (2008). The magnitude of nonadditive biodiversity effects were quite large, as the high-density three-species polyculture observed 51.9% more erosion than expected given additive performances of its monocultures, while the high-density *Amblema plicata* and *Quadrula pustulosa* polyculture observed 49.9% more erosion than additive expectations.

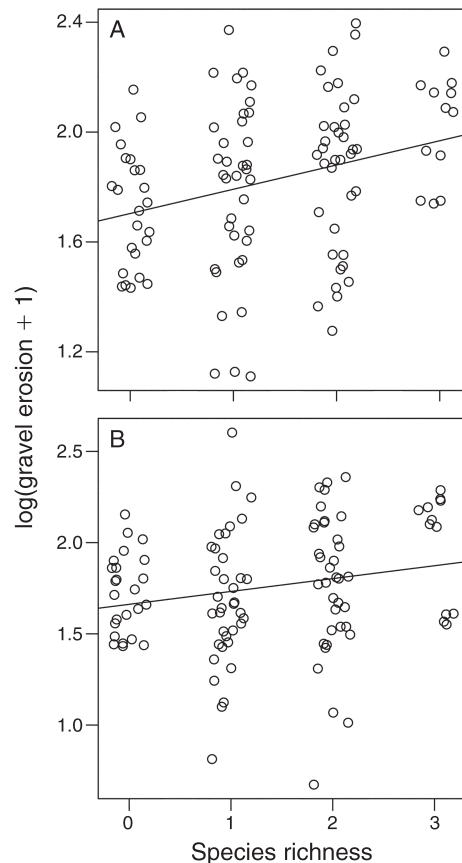


FIG. 1. Log-transformed gravel erosion (measured in grams) as a function of species richness for (A) low-density and (B) high-density treatments. Regression lines are: (A) $y = 1.704 + 0.088x$, $P = 0.002$, $R^2 = 0.08$; (B) $y = 1.66 + 0.070x$, $P = 0.045$, $R^2 = 0.04$. Note the different scales on the y-axes for panels (A) and (B), and that data points are jittered about the x-axis.

Stepwise multiple regression analysis of the net change in gravel erosion using the suite of burrowing variables produced two significant models (Appendix D). The models indicate that the most important burrowing variable was “mussel orientation relative to flow direction,” the only variable in Model 1, which explained approximately 11% of the variation in gravel erosion relative to controls. Model 2 added the burrowing variable SD of topographical surface area added by mussels, which increased the amount of variation explained to approximately 13%. None of the other seven burrowing variables were included in significant multiple regression models.

DISCUSSION

Mussel species richness was associated with an increase in gravel erosion at high flows relative to controls at both low and high density, but the nature of this relationship differed between high- and low-density treatments. At low density, all planned contrasts testing

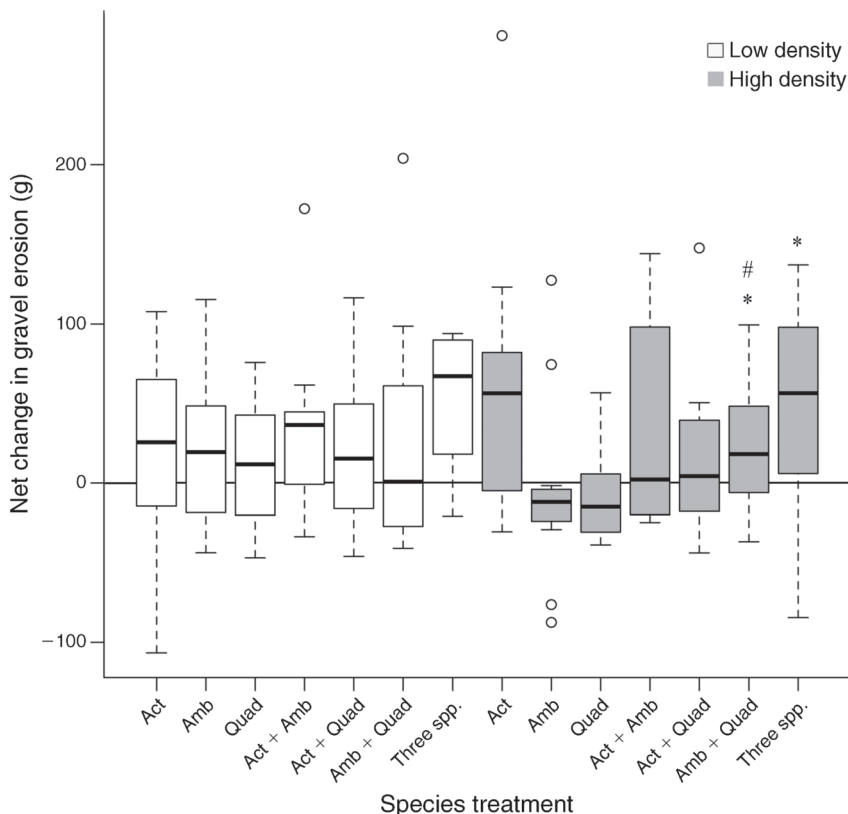


FIG. 2. Boxplots showing the net change in gravel erosion relative to controls for mussel diversity treatments. White and gray boxplots designate low and high densities, respectively, and the solid horizontal line represents the control mean value. “Act” refers to *Actinonaias ligamentina*, “Amb” refers to *Amblema plicata*, “Quad” refers to *Quadrula pustulosa*, and “Three spp.” refers to the three-species polyculture. Asterisks (*) above a boxplot designate a significant ($P < 0.05$) liberal nonadditive biodiversity contrast for that treatment, and a “#” symbol denotes a significant conservative nonadditive biodiversity contrast for that treatment. The heavy horizontal line in the center of each box is the median, the light horizontal line at lower and upper bounds of the rectangular box are the upper and lower quartiles. The ends of dashed “whiskers” represent minimum and maximum values up to 1.5 times the interquartile range; if data points exist beyond the whiskers, they are displayed as circles.

TABLE 1. Summarized results from contrasts testing for biodiversity effects.

Contrast	Liberal			Conservative		
	$F_{1,132}$	ω^2	P	$F_{1,132}$	ω^2	P
Act + Amb, Low	0.532	†	0.463	0.177	†	0.674
Act + Quad, Low	0.001	†	0.973	0.067	†	0.797
Amb + Quad, Low	0.169	†	0.682	0.117	†	0.732
Three spp., Low	2.555	0.061	0.112	1.017	0.001	0.315
Act + Amb, High	0.002	†	0.962	1.857	0.033	0.175
Act + Quad, High	0.112	†	0.739	3.146	0.082	0.078
Amb + Quad, High	6.393	0.183	0.012	4.451	0.126	0.034
Three spp., High	5.150	0.147	0.025	0.005	†	0.942

Notes: Liberal contrasts test the null hypothesis that polyculture performance can be predicted additively from performance of its monocultures. Conservative contrasts test the null hypothesis that polyculture performance is the same as its monoculture with the strongest effect on gravel erosion (see *Methods*). Partial omega-squared (ω^2) estimates effect size (see *Methods*), P values in boldface type highlight $P < 0.05$. “High” and “Low” refer to density treatments, “Act” refers to *Actinonaias ligamentina*, “Amb” refers to *Amblema plicata*, “Quad” refers to *Quadrula pustulosa*, and “Three spp.” refers to the three-species polyculture.

† The formula we used to estimate the omega-squared used the F statistic of the contrast, and if $F < 1$, the formula gives a negative effect size (see *Methods*). A negative effect size is illogical since effect size, by definition, can only be a value between 0 and 1. Thus, in those cases where F was less than 1, we do not report the effect size.

for nonadditive biodiversity effects were insignificant. This suggests that the performance of species polycultures on erosion could be routinely additively predicted from the performance of species monocultures. However, at high density certain species polycultures had significant nonadditive biodiversity effects on gravel erosion. This suggests that mussel abundance fundamentally altered the nature of biodiversity effects on gravel erosion. Mussel species traits that influence substrate erosion may be interacting at high densities and not at low densities, although our study design is unable to confirm this. Nevertheless, the results of our study support others that have found that organism abundance can modify the BEF relationship (Douglass et al. 2008, Griffin et al. 2008).

Mussel species treatments significantly differed in their effect on gravel erosion relative to no-mussel controls. Because freshwater mussels vary in burrowing behavior (Allen and Vaughn 2009), and because burrowing activity by bivalves in marine systems promotes erosion (Sgro et al. 2005), we hypothesized that burrowing behavior by mussels might be a plausible mechanism to explain mussel effects on gravel erosion. Although our multiple regression models using burrowing variables only explained 13% of the variation in gravel erosion, our analysis lends some support to this hypothesis. The burrowing variable “mussel orientation relative to flow direction” was the single best variable in our multiple regression models (explaining 11% of variation on its own). There are two possible explanations for increases in substrate erosion when mussels are oriented in ways that deviate from the flow direction (when the mussel’s anterior-posterior axis is not parallel to the flow direction). First, mussel species that are more active burrowers are more likely to move and deviate from their original position and disrupt cohesive properties of sediment in the process. Alternatively, when the orientation of a mussel deviates from the flow, it is less hydrodynamic and generates larger wake patterns whose ascending vortices can promote erosion (Vogel 1994). Ultimately, the relatively low explanatory power of our burrowing models suggests that there are additional mechanisms underlying mussel effects on sediment transport that we did not measure.

The National Research Council recently addressed the need to develop a better mechanistic understanding of how biota influence physical transport processes (National Research Council 2010), and our results suggest hypotheses for future study. First, organisms that are active burrowers are likely to disrupt cohesive forces of the streambed itself, decreasing the critical shear stress required to initiate sediment entrainment. Second, organisms that produce exposed physical structures, such as shells or nets, should increase near-bed turbulence that could promote erosion. In our experiment, the *Actinonaias ligamentina* treatment was the monoculture with most gravel erosion at both densities (Fig. 2), and this species was also the most active

burrower in the experiment (Allen and Vaughn 2009). Furthermore, as a smooth-shelled species, *A. ligamentina* lacks any shell sculpture that could reduce turbulence generated by its exposed shell (Watters 1994). Third, the structural complexity of the physical structures produced by biota, such as the presence of anchoring or anti-scouring sculptures on mussel shells, could further modify the effect of organisms on near-bed hydraulics. In this study, *Amblema plicata* and *Quadrula pustulosa* monocultures had the lowest amount of gravel erosion. Neither species are active burrowers, and both have anti-scouring and anchoring shell morphologies (Watters 1994). Fourth, these traits have the potential to interact in nonadditive ways when multiple species are present. In our study, two high-density polycultures had significant nonadditive increases in erosion when compared to their respective monocultures (Fig. 2). Because these mussel species differ in size, shell shape (smooth vs. ridges vs. pustules), and burrowing depth, these traits may interact to generate a more topographically complex surface that can increase turbulence similar to what has been observed with caddisflies (Cardinale et al. 2002). Additional studies are necessary to test these hypotheses.

Finally, it is important to consider the design and scale of our experiment when interpreting and extrapolating our results. While the hydraulic conditions in our artificial streams appear to scale to some aspects of at least one natural stream (Appendix B), there are other aspects of our flumes that are by necessity unrealistic: our flumes are much smaller than a natural mussel bed that can be several thousand square meters in area, our experiment was conducted at a relatively short time frame, and we only manipulated flows at two different velocities. Because of these limitations, we are unsure if we would observe the same results at the larger scale of a natural river with a wider range of flows. In addition, because mussel habitat in rivers is patchily distributed and limited to areas of low scour during high-flow events, mussel effects on sediment transport are likely localized and are also likely to be small relative to sediment transport dynamics within an entire watershed. An in-depth field study is necessary to understand how mussels influence erosion at larger spatial and temporal scales.

BEF studies often focus on the effects of species richness because of the worldwide extinction crisis, but biodiversity losses also include declines in abundance of common species, and shifts in species dominance patterns (Hooper et al. 2005). Because common species are typically drivers of ecosystem processes (Moore 2006), such declines have profound implications for ecosystem function. Our results show that declines in abundance can also modify how biodiversity affects ecosystem processes. Further, our study shows that the structure of biological communities can influence physical transport processes, which is central to improv-

ing our understanding of how ecosystems and landscape processes are linked.

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APPENDIX A

Diagram of the flumes used in this experiment (*Ecological Archives* E092-084-A1).

APPENDIX B

Comparison of the estimated hydraulic variables describing flow conditions in our flumes vs. the range of those measured in mussel beds in the Little River, Oklahoma (*Ecological Archives* E092-084-A2).

APPENDIX C

Photographs of mussel species used in the experiment (*Ecological Archives* E092-084-A3).

APPENDIX D

Summary of stepwise multiple regression analysis of net change in substrate erosion using a suite of burrowing variables (*Ecological Archives* E092-084-A4).