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Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams

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Abstract. An increasing number of studies have emphasized the need to bridge the disciplines of ecology and geomorphology. A large number of case studies show that organisms can affect erosion, but a comprehensive understanding of biological impacts on sediment transport conditions is still lacking. We use meta-analysis to synthesize published data to quantify the effects of the abundance, body size, and behavior of organisms on erosion in streams. We also explore the influence of current velocity, discharge, and sediment grain size on the strength of biotic effects on erosion. We found that species that both increase erosion (destabilizers) and decrease erosion (stabilizers) can alter incipient sediment motion, sediment suspension, and sediment deposition above control conditions in which the organisms were not present. When abundance was directly manipulated, these biotic effects were consistently stronger in the higher abundance treatment, increasing effect sizes by 66%. Per capita effect size and per capita biomass were also consistently positively correlated. Fish and crustaceans were the most studied organisms, but aquatic insects increased the effect size by 550× compared to other types of organisms after accounting for biomass. In streams with lower discharge and smaller grain sizes, we consistently found stronger biotic effects. Taken collectively, these findings provide synthetic evidence that biology can affect physical processes in streams, and these effects can be mediated by hydraulic energy. We suggest that future studies focus on understudied organisms, such as biofilms, conducting experiments under realistic field conditions, and developing hypotheses for the effect of biology on erosion and velocity currents in the context of restoration to better understand the forces that mediate physical disturbances in stream ecosystems.

Key words: biophysical interactions; ecogeomorphology; ecohydrology; erosion; meta-analysis; sediment transport.

INTRODUCTION

Research at the intersection of biological and physical processes is needed to fully understand the consequences of global environmental change (Allen et al. 2014). The U.S. National Academy of Sciences recently published a report calling for researchers to investigate how biota influence earth surface processes, in part because purely physical models are often insufficient to predict geophysical processes (National Research Council 2009). Accordingly, interdisciplinary research fields that investigate the coupling of biological communities and geomorphic and hydrologic processes are rapidly evolving. These fields are often referred to as "ecogeomorphology" or "ecohydrology," and have been the focus of a growing body of research in stream systems (Viles et al. 2008, Reinhardt et al. 2010).

Studies that fall under the umbrella of "ecogeomorphology" gained traction in the mid-1990s, when many ecologists began to quantitatively research how organisms can modify their physical environment. Organisms that modify habitats and thereby have substantial effects on ecosystems were often termed "ecosystem engineers" (Jones et al. 1994). Many organisms are now considered as agents of geomorphic change that can affect landscape evolution and ecosystem functions at a variety of spatial and temporal scales (Flecker et al. 2010, Jones 2012). Consequently, results from past ecosystem engineer studies are now being reviewed and reinterpreted in an ecogeomorphological context (Statzner 2012). However, a formal meta-analysis of these studies to investigate which types of organisms have the strongest effects, and under what conditions, is lacking.

Moore (2006) developed a framework for describing the impacts of organisms on their physical environment. Moore (2006) proposed that biotic effects on physical processes are a function of three biological aspects: behavior, body size, and abundance. Moore (2006) also suggested that all three of these biological aspects are mediated by abiotic characteristics of the ecosystem, such as discharge and sediment size. Although this framework clearly outlines the general conditions under which organisms are predicted to have the largest

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impacts on their abiotic environment, these predictions have not yet been rigorously tested.

We evaluate this framework with a meta-analysis using data collected from published literature. Our analyses are focused on the biotic effects on sediment transport conditions in streambeds. For response variables we considered the threshold of sediment motion (often called incipient sediment motion and critical shear stress) or sediment flux (deposition or erosion). Specifically, we test the following hypotheses: (1) greater organism size and abundance (biomass, per capita biomass, and density) increases biotic effects on sediment dynamics; (2) organism types (amphibians, biofilms, crustaceans, fish, insects, macrophytes, and mollusks) differ in their effects due to different physical attributes and/or behaviors (see Plate 1); and (3) hydraulic energy mediates these effects, such that biotic effects are strongest in streams with the lowest velocities, discharges, and sediment grain size.

Methods

Literature search

We searched the literature for appropriate data using the following search terms in the ISI Web of Science: (aquatic OR stream OR river OR freshwater) AND ((sediment OR gravel OR sand OR inorganic OR substrat* OR grain) AND (erosion OR transport OR stability OR accretion OR accumulation OR deposition OR accru* OR mobility OR "coherent strength" OR dynamics OR "critical shear stress" OR retention OR trap*)) AND (ecosystem engineer* OR habitat modif* OR salmon* OR fish* OR tadpole* OR crayfish OR shrimp* OR bivalv* OR insect* OR midge* OR caddisfl* OR stonefl* OR microb* OR macrophyte*). This search yielded 6541 results on 3 May 2013. After discarding nonexperimental and other irrelevant articles, we further refined our search by excluding experiments that were not peer reviewed, did not have a control (nonbiological) treatment, or used organism mimics (e.g., wooden rods mimicking aquatic plants). This search resulted in 48 references from which we extracted data (Table 1). Many references contained data from multiple studies that manipulated different habitat conditions (i.e., pools/riffles or multiple grain sizes). When this was the case, we extracted data from all studies within a single reference, which resulted in a total of 155 different studies. The specific response variables that measured sediment movement varied across studies but were either a measurement of sediment deposition or erosion (sediment depth, mass, volume, velocity, number of particles, or force; see Table 1).

Meta-analysis design

After literature sources were compiled, we extracted effect size data (means of treatments with organisms present and control treatments with no organisms) from text, tables, or graphs using ImageJ (Rasband 1997). We quantified the log-response ratio (LRR), or the metric of the "biotic effect," as

$$\mathrm{LRR} = \ln\left(\frac{\text{treatment with biology}}{\text{control treatment with no biology}}\right)$$

(Hedges et al. 1999, Gurevitch et al. 2001). Because some species increased the physical process (destabilizers) and some species decreased the physical process (stabilizers) being studied, we used the absolute value of the LRR for subsequent statistical analyses for several reasons: (1) the hypotheses we test predict the magnitude, not the direction of biotic effects; (2) raw LRRs could increase type I errors if two behavior or organism types had the same magnitude, but different signs, of LRR values, leading us to find a significant result of a nonexistent effect size; (3) raw LRRs could also increase type II errors if the predicting variable was unrelated to the sign by increasing the variance of the LRR data, making it more difficult to observe a real effect; and (4) most importantly, we wanted our results to be generalizable to organisms that increase or decrease sediment transport, rather than one or the other. We chose not to weight the calculated LRRs because not all studies reported a measure of variation for their data, and using weighted values would have eliminated close to 30% of our data set (Osenberg et al. 1999, Hillebrand 2008). We primarily relied on a general linear mixed-effect modeling (GLMM) approach to analyze our data as they are highly flexible and allow for a variety of variable and distribution types, as our variables of interest were both categorical (behavior and organism type) and continuous (abundance and hydrologic energy). We used random effect blocking factors, and the fit of some models was improved using Poisson distributions. All analyses described below were conducted in R (R version 2.14.1; R Development Core Team 2012).

Abundance analyses

For all analyses using density and biomass data as explanatory variables, we used a subset of the data set only containing studies that reported density and biomass data. For some papers that reported density but not biomass data, we conducted an additional literature search for biomass data of the focal species ($n = 10$ papers) to use in the analyses. If an experiment manipulated abundance, we took the LRR of the highest and lowest density treatments, and treated these as independent observations from a single experiment ($n = 44$ observations). Density data were square-root($x + 0.5$) transformed, while biomass data were $\log(x + 1)$ transformed. We removed outliers from our data set of transformed densities or biomasses that were greater or less than two standard deviations from the mean.

We conducted four analyses of LRRs with respect to abundance. (1) We used 44 paired observations from the papers that manipulated organism abundance, and used these data to test for the effect of density treatment (high vs. low) on absolute LRRs. Because these data were not

Table 1. Summary of the articles used for the meta-analysis.

Study IDs	Source	Study type	Organism type	Taxa	Behavior	Response	
						Type	Variable
1	1	field	fish	*Oncorhynchus nerka*	B/D	D	sediment erosion (mass)
2–15	2	lab	moll	*Actinonaias ligamentina*, *Amblema plicata*, *Quadrula pustulosa*	B/D	D	sediment erosion (mass)
16–19	3	lab	biofilm	*Spirogyra*, *Mougeotia*	struct	S	sediment deposition (velocity)
20	4	field	macro	*Sparganium erectum*	struct	S	sediment deposition (velocity)
21–24	5	lab	insect	*Hydropsyche depravata*	struct	S	sediment erosion (number of particles)
25	6	field	crust	*Cambarus bartonii*	F	D	sediment deposition (volume)
26	7	field	crust	*Potimirim glabra*	F	D	sediment deposition (mass)
27–28	8	lab	insect	*Chironomus riparius*	struct	S	sediment erosion (number of particles)
29	9	field	fish	*Prochilodus mariae*	F	D	sediment deposition (mass)
30–31	10	field	fish	*Prochilodus mariae*	F	D	sediment deposition (mass)
32–33	11	field	amph	*Rana palmipes*	F	D	sediment deposition (mass)
34	12	field	fish, crust	*Cambarus chasmodactylus*, *Oronectes cristavarious*, *Campostoma anomalum*, *Hypentelium nigrans*, *Catastomus commersoni*	F	D	sediment deposition (volume)
35–39	13	field	macro	*Justica americana*	struct	S	sediment erosion (force)
40–41	14	field	macro	*Justica americana*	struct	S	sediment erosion (force)
42–46	15	field	fish	*Oncorhynchus nerka*	B/D	D	sediment erosion (number of particles)
48–49	16	field	fish	*Oncorhynchus nerka*	B/D	D	sediment erosion (mass)
50–51	17	field	crust	*Cambarus chasmodactylus*, *Orconectes cristavariu*	F	D	Sediment deposition (volume)
52–53	18	lab	crust	*Pacifastacus leniusculus*	F	D	sediment erosion (number of particles)
54–55	19	field	insect	*Hydropsyche contubernalis*	struct	S	sediment erosion (force)
56	20	field	fish, crust	*Orconectes meeki meeki*, *Campostoma anomalum*	F	D	sediment deposition (mass)
57–60	21	field	fish	*Oncorhynchus nerka*	B/D	D	sediment deposition (depth)
61–63	22	field	crust	*Xiphocaris elongata*, *Macrobrachium* spp., *Atya* spp.	F	D	sediment deposition (mass)
64–65	23	field	fish	*Oncorhynchus keta*	B/D	D	sediment erosion (force)
66–67	24	field	fish	*Oncorhynchus nerka*	B/D	D	sediment deposition (mass)
68	25	field	insect	*Stenopsyche marmorata*	struct	S	sediment erosion (force)
69–70	26	lab	crust	*Paranephrops planifrons*	F	D	sediment deposition (mass)
71–72	27	field	fish	*Ancistrus spinosus*	F	D	sediment deposition (mass)
73–75	28	field	fish, crust	*Machobranchum diqueti*, *Machobranchum faustinum*, *Machobranchum heterochirus*, *Astynax fasciatus*, *Cichlasoma septemfasciatum*, *Poecilia gillii*, *Chiclasoma dovii*, *Alfaro cultratus*, *Neetroplus nematopus*, *Cichlasoma nigrofasciatum*	F	D	sediment deposition (mass)
76	29	field	crust	*Xiphocaris* spp., *Macrobrachium* spp., *Atya* spp.	F	D	sediment deposition (mass)
77–78	30	field	crust	*Atya lanipes*, *Xiphocaris elongata*	F	D	sediment deposition (% cover)
79–80	31	field	fish, crust	*Atya* spp., *Xiphocaris* spp., fishes	F	D	sediment deposition (mass)
81	32	field	amph	*Rana warszewitschii*, *Hyla* spp., *Atelopus zeteki*, *Colostethus* spp.	F	D	sediment deposition (mass)
82–83	33	field	fish	*Oncorhynchus keta*	B/D	D	sediment erosion (depth)
84–87	34	field	macro	*Callitriche copocarpa*, *Elodea canadensis*, *Ranunculus peltatus*, *Sparganium emersum*	struct	S, D	sediment deposition (depth)
88–90	35	field	macro	*Sparganium emersum*, *Potmogeton pectinatus*	struct	S	sediment deposition (mass)
91–98	36	lab	fish	*Barbus barbus*, *Gobio gobio*	F	D	sediment erosion (force)
99–106	37	lab	crust	*Orconectes limosus*	F	D	sediment erosion (force, mass)
107	38	lab	insect	*Hydropsyche siltalai*	struct	S	sediment erosion (force)
108–113	39	field	insect	*Dinocras cephalotes*	F	D	sediment erosion (depth)
114	40	lab	crust	*Orconectes limosus*	F	D	sediment erosion (mass)
115–138	41	lab	fish, crust	*Barbus barbus*, *Gobio gobio*, *Oronectes limosus*	F	D	sediment erosion (force, mass)
139–141	42	lab	crust	*Paranephrops zealandicus*	F	D	sediment deposition (mass)
142	43	lab	macro	"Water fern"	struct	S	sediment erosion (force)
143–147	44	field	macro	*Ranunculus* spp.	struct	S	sediment deposition (velocity)
148–149	45	lab	fish	Crucian carp, three-spined stickleback	F	D	sediment erosion (velocity)

TABLE 1. Continued.

Study IDs	Source	Study type	Organism type	Taxa	Behavior	Response Type	Response Variable
150	46	field	insect	*Megarcys signata*	F	D	sediment erosion (volume)
151–153	47	lab	fish, crust	*Pacifastacus leniusculus, Oncorhynchus clarki*	F	D	sediment deposition (% cover)
154–155	48	lab	moll	*Actinonaias ligamentina, Ptychobranchus fasciolaris*	B/D	S,D	sediment erosion (force, mass)

Notes: Multiple studies within a given reference were counted as independent data points if multiple habitat characteristics were manipulated, such as multiple grain sizes. Abbreviations are amph, amphipod; crust, crustacean; macro, macrophyte; moll, mollusk; B/D, burrowing/digging; struct, structure produced; F, foraging; S, stabilize; D, destabilize.

Sources: 1, Albers and Petticrew (2012); 2, Allen and Vaughn (2011); 3, Arnon et al. (2010); 4, Asaeda et al. (2010); 5, Cardinale et al. (2004); 6, Creed and Reed (2004); 7, de Souza and Moulton (2005); 8, Edwards (1962); 9, Flecker (1996); 10, Flecker (1997); 11, Flecker et al. (1999); 12, Fortino (2006); 13, Fritz and Feminella (2003); 14, Fritz et al. (2004); 15, Gottesfeld et al. (2004); 16, Hassan et al. (2008); 17, Helms and Creed (2005); 18, Johnson et al. (2009); 19, Johnson et al. (2011); 20, Ludlam and Magoulick (2009); 21, Macdonald et al. (2010); 22, March et al. (2002); 23, Montgomery et al. (1996); 24, Moore et al. (2004); 25, Nunokawa et al. (2008); 26, Parkyn et al. (1997); 27, Power (1990); 28, Pringle and Blake (1994); 29, Pringle and Hamazaki (1998); 30, Pringle et al. (1993); 31, Pringle et al. (1999); 32, Ravenstel et al. (2004); 33, Rennie and Millar (2000); 34, Sand-Jensen (1998); 35, Schulz et al. (2003); 36, Statzner et al. (2003*a*); 37, Statzner et al. (2003*b*); 38, Statzner et al. (1999); 39, Statzner et al. (1996); 40, Statzner et al. (2000); 41, Statzner and Sagnes (2008); 42, Usio and Townsend (2004); 43, Wang et al. (2010); 44, Wharton et al. (2006); 45, Zambrano et al. (2005); 46, Zanetell and Peckarsky (1996); 47, Zhang et al. (2004); 48, Zimmerman and de Szalay (2007).

normally distributed, we used a paired sample Wilcoxon test to test for significant differences between high and low density treatments. (2) We used 117 observations to test for the effect of total density on absolute LRRs, using a GLMM with density as the explanatory variable and article as a random blocking factor. (3) We used 101 observations to test for the effect of total biomass on absolute LRRs, using a mixed-effect linear regression model with biomass as the explanatory variable and article as a random effect. (4) We used 87 observations to test for the effect per capita biomass (total biomass/total density, which was then $\log(x+1)$ transformed) on per capita absolute LRRs (absolute LRR/total density), using a GLMM with per capita biomass as the explanatory variable and article as a random blocking factor. For analyses 3 and 4, articles reported biomass data in both dry and wet mass, so we ran initial models including a fixed effect for measurement type (dry or wet mass) as a blocking factor. The dry/wet mass blocking factor was insignificant for both analyses (total biomass, $P = 0.153$; per capita biomass, $P = 0.269$) so it was not included as a factor in final models. If the relationship was not significant for analyses 2–4, we then followed with a 90th-quantile linear regression to test for limiting factor relationships between the variable and the absolute LRR (Cade and Noon 2003).

Behavior analyses

To investigate how organism behavior and identity influenced the effect size, we categorized each species as one that either stabilizes or destabilizes sediments. To quantify whether more species destabilize than stabilize, we also counted the number of unique species that were used across all studies and identified whether they stabilized or destabilized sediments. Each organism that was identified to the species level was counted as unique. We also counted species as unique when only the genus name (and not species) was reported. We compared the absolute impacts of organisms that stabilized (negative effect) and destabilized (positive effect) sediments using the Wilcoxon rank sum test. We further divided organism's behavior into three categories: digging, foraging, and structure-producing. We also categorized species identity into six broad types: amphibians, aquatic macrophytes, biofilm, crustaceans, fish, insects, and mollusks. We tested for the effect of behavior and organism types on LRRs using a GLMM with article as a random blocking factor. For organism type, we first considered the population as a whole by comparing the absolute LRR across organism types. We then investigated a per capita effect (absolute LRR/total density) and a per biomass effect (absolute LRR/total biomass). We did not have density or biomass estimates for the studies investigating biofilms, so this group was dropped from density and biomass analyses. We also did not have biomass estimates from studies that investigated aquatic macrophytes, so this group was not included in LRR/biomass comparisons. Post-hoc tests corrected for multiple comparisons were conducted using the "multcomp" package (version 1.3-2) in R (version 2.14.1; R Development Core Team 2012).

Hydraulic energy analyses

We used the subset of references that reported aspects of the physical conditions in their experiments to test for effects of hydraulic energy on LRR. We selected three variables that commonly represent the physical hydrology of the environment: flow velocity (V); median grain size (D_{50}); and discharge (Q). We used 72 observations for velocity, 99 observations for grain size, and 98 observations for discharge. Discharge was calculated as $Q = V \times A$, where A is the cross-sectional area of the channel that was calculated from channel width and depth estimates when direct estimates of discharge were

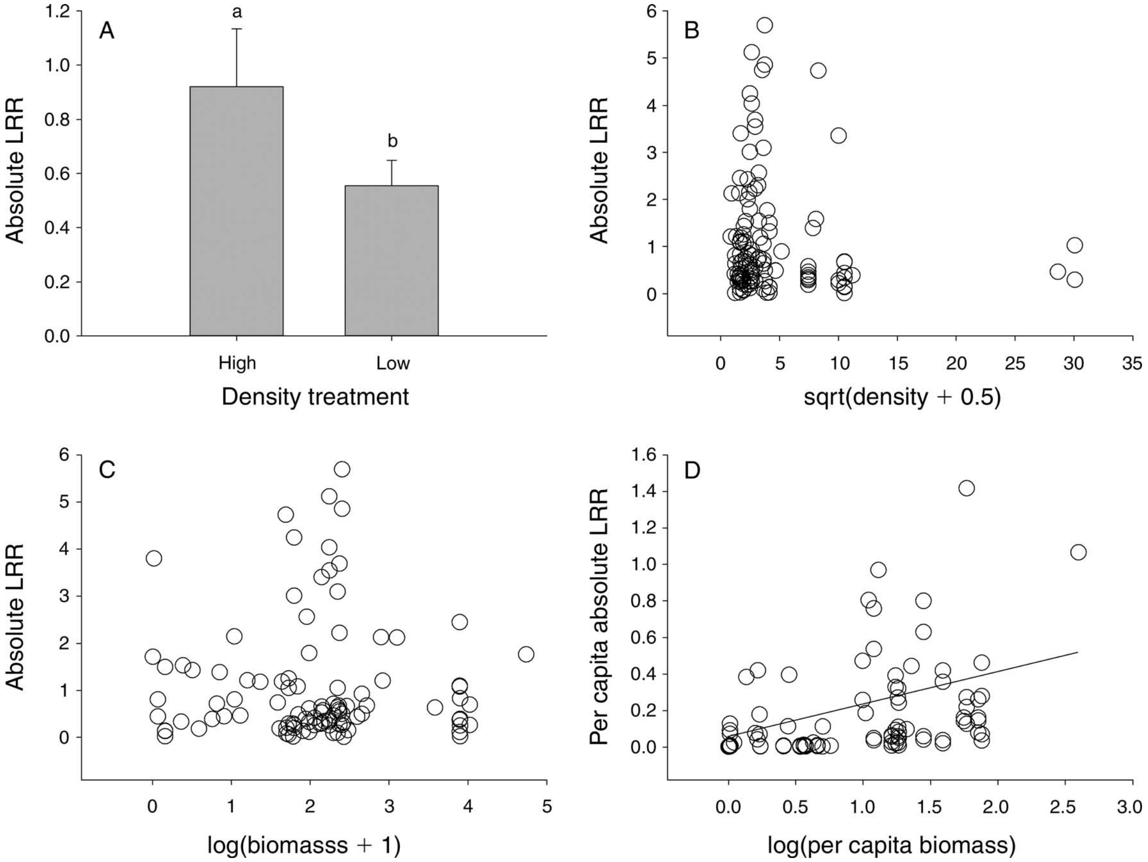

FIG. 1. Results from abundance analyses. (A) Absolute log-response ratios (LRRs) from studies that manipulated organism density. Data from the highest and lowest density treatments were analyzed when studies included more than one density treatment (44 observations). Bars are means, error bars are SE, and different letters denote significant differences ($P \leq 0.05$). (B) Absolute LRRs by square-root-transformed (sqrt) density (measured as number/m^2; 117 observations). (C) Absolute LRRs by log-transformed biomass (measured in grams; 101 observations). (D) Per capita absolute LRRs by log-transformed per capita biomass (measured in grams; 87 observations). GLMM: $y = 0.178x + 0.057$; $P = 0.004$.

not reported in an article (Gordon et al. 2004, Hauer and Lamberti 2007). We tested for the effect of these variables on LRRs using a GLMM with article as a random blocking factor. If no significant relationship was found, then we followed with a 90th-quantile linear regression to test for limiting factor relationships between the variable and the absolute LRR (Cade and Noon 2003). We further categorized this subset of studies by the response variable measured as follows: sediment accrual; erosion; flow conditions; grain size distribution; and incipient sediment motion. We tested for an effect of response variable on the LRRs using GLMM with article as a random blocking factor.

RESULTS

Abundance

We found significant effects of organism density and biomass on the magnitude of the effect size. In studies that manipulated organism density, high-density treatments showed 66% greater effect sizes than low-density treatments (paired-sample Wilcoxon test, $P = 0.011$; Fig. 1A). However, a GLMM testing effect size against total organism density was not statistically significant ($P = 0.697$), nor was the 90th-quantile linear regression ($P = 0.515$; Fig. 1B). Total organism biomass also showed no consistent relationship with respect to effect size (GLMM, $P = 0.939$; 90th-quantile linear regression, $P = 0.594$; Fig. 1C), though per capita biomass showed a statistically significant positive relationship with per capita effect size (GLMM, $P = 0.004$; Fig. 1D).

Behavior

Of the 67 species that were studied (Fig. 2A), 72% destabilized sediment and 28% stabilized sediment (Fig. 2A). The absolute magnitude of the effect size did not differ between destabilizing and stabilizing species (Wilcoxon test, $W = 2034$, $P = 0.53$; Fig. 2B). Species that exhibited foraging behavior (GLMM post-hoc comparison, $P = 0.1$) or structure-producing behavior (GLMM post-hoc comparison, $P = 0.3$) had slightly but not statistically significantly stronger effects compared to species that exhibited digging behavior (Fig. 2C). However, no consistent difference between foraging and

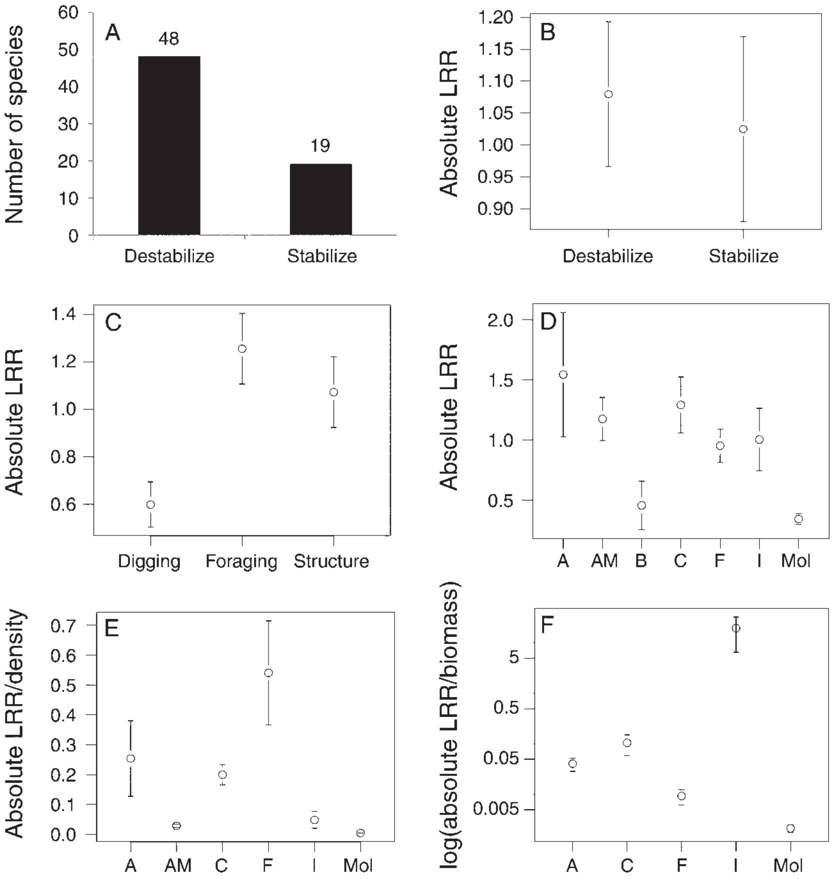

FIG. 2. The effects of organism behavior and species identity type on the effect size. (A) The majority of species studied were species that exhibit destabilizing behavior. Numbers above the bars are the number in each group; only 19 species of the 67 were categorized as stabilizers. (B) The magnitude of the effect size was not significantly different across groups that stabilize vs. destabilize. (C) Organisms that foraged or produced structure had stronger effects on LRR than organisms that exhibited digging behavior. (D) Organism type influenced the LRR, with mollusks having a lower impact than other groups. (E) The per capita effect (LRR/density) indicated slight but nonsignificant differences across species groups. (F) The LRR per unit biomass was significantly greater for insects than other groups. Error bars show SE. Letter abbreviations are A, amphibian; AM, aquatic macrophyte; B, biofilm; C, crustacean; F, fish; I, insect; Mol, mollusk.

structure-producing behavior was detected ($P = 0.9$; Fig. 2C).

Fish were the most studied group, followed by crustaceans, insects, aquatic macrophytes, mollusks and amphibians, and biofilms. Compared to mollusks and bacteria, which showed the smallest effect sizes, the effect size was two times greater on average for all other groups (Fig. 2D). When we divided LRR by density to estimate the per capita effect on erosion, we found no significant differences across organism group (Fig. 2E). However, insects had a 550× stronger biotic effect than any other organism group after accounting for organism biomass (GLMM post-hoc comparison, $P < 0.001$; Fig. 2F).

Hydraulic energy

We did not detect a significant relationship between velocity and LRR (mixed-effects linear regression, $P = 0.151$, $t = 6.62$; Fig. 3A). Although grain size was not significantly related to LRR when all the data were pooled (GLMM, $P = 0.823$, $t = 4.68$), grain size did show a significant negative constraint on LRR (90th quantile regression, $P = 0.002$, $t = -3.25$; Fig. 3B). Discharge showed a significant, negative relationship to LRR (GLMM, $P = 0.037$, $t = -2.13$; Fig. 3C). There were also differences in the LRR across the response variables measured (Fig. 3D). LRR was lowest in studies that monitored changes in incipient motion compared to the average of all other response variables (GLMM, $P = 0.003$). LRR was highest in studies that monitored changes in flow conditions, resulting in a 1.6× increase over the average of other response variables.

DISCUSSION

We found that the abundance, body size, and behavior of organisms were related to their impacts on sediment movement and deposition in streams. Further, these effects were mediated by key physical variables,

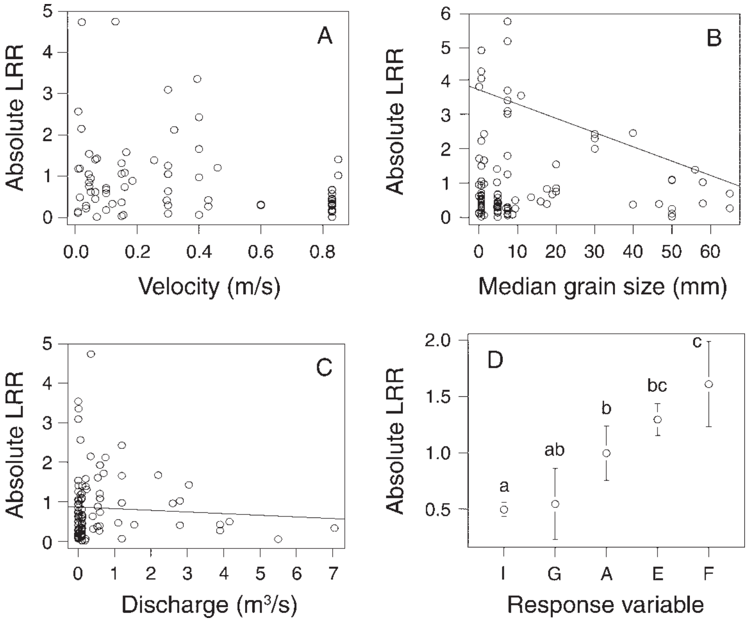

FIG. 3. The effects of physical variables on LRR. (A) Velocity was not significantly related to the LRR. (B) Grain size was negatively correlated with the LRR. Streams with larger grain sizes typically had smaller LRRs. The linear regression fit for grain size is the 90th quantile regression ($y = -0.041x + 3.708$; $P = 0.002$). (C) Discharge showed a significant, negative relationship with LRR ($y = -0.041x + 0.867$; $P = 0.037$). (D) LRR across different physical response variables. Error bars show SE. Axis abbreviations are A, sediment accrual; E, erosion; F, flow; G, grain size distribution; and I, incipient sediment motion. Lowercase letters represent significant differences ($P \leq 0.05$).

such as grain size and discharge. Our findings support the framework that Moore (2006) proposed, and when combined with existing literature, show that a wide range of organisms from microbes to large schools of salmon can have substantial impacts on sediment transport processes related to the formation and structure of riverine systems.

Support for the hypothesis that organism abundance would increase the biotic effect size was mixed. When the abundance of an organism was manipulated directly, we found that the higher density treatment showed larger effect sizes. However, when pooling all studies together, we did not find clear relationships between total abundance (density or biomass) and effect size. This finding likely occurred because different organism types (amphibians, fish, insects, etc.) differ in their biotic effect sizes, which masks an abundance effect when all organism types are pooled together. Organism size increased the biotic effect as evidenced by the positive relationship between per capita effect size and per capita biomass. This relationship likely occurred because larger organisms can manipulate a larger area of habitat, are capable of ingesting and redistributing more fine sediments, and producing a greater bioturbating force to disrupt inherent cohesive forces of sediments. For example, schools of fish like salmon can significantly increase the removal and suspension of fine sediments by 5× during spawning periods (Moore et al. 2004). Future studies should consider the relative effects of biotic and abiotic controls on physical processes in streams across spatial and temporal scales as the density, biomass, and community composition of organisms shifts through the seasons, such as in these temporally explicit spawning events (Hassan et al. 2008).

The magnitude of the biotic effect varied only slightly by taxa group when comparing organism effects at their natural population sizes. Most surprisingly, we found that relatively small animals, like stream insects or crayfish (Pringle et al. 1993, Statzner et al. 1999), have similar or greater effects on sediment transport conditions as less dense but larger species like fish or aquatic macrophytes (Flecker 1996, Fritz and Feminella 2003). Thus, although we did detect a significant relationship between per capita biomass and the biological effect size, these results indicate that at the population level, smaller but more dense populations of insects or crayfish living at natural densities could have similar effects to less dense but larger organisms such as fish. When we considered the biomass of the species studied, again we found that insects had a larger impact than all other species groups when we accounted for their relatively small size. For example, the silk produced by hydropsychid caddisfly larvae that spin catchnets in the benthic substrate to filter feed have been shown to stabilize sediments and increase the recurrence interval of a bed-scouring flood by 44% from 1.67 years to 2.41 years (Cardinale et al. 2004). Through production of silk tubes in benthic mud deposits, chironomid midge larvae can reduce suspended sediments by 4.5× (Edwards 1962). Although only a few studies have identified silk-

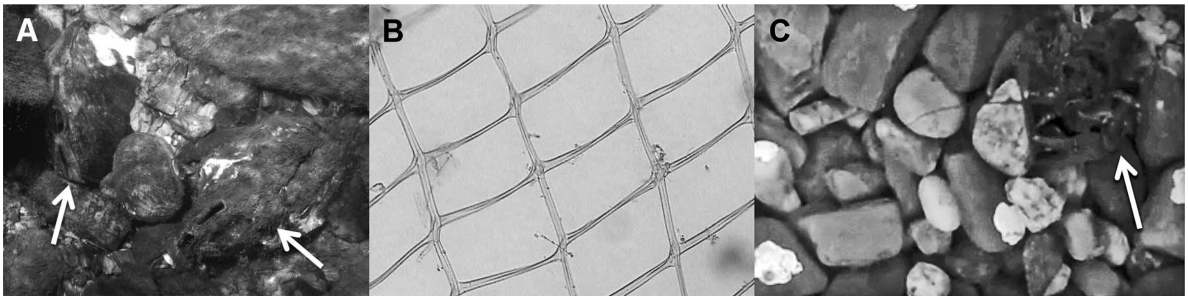

PLATE 1. Examples of biotic engineer activity. (A) Freshwater mussels burrow into sediments. (B) caddisfly silk threads stabilize gravels, and (C) crayfish move sediments using their claws. Photo credits: panel (A), D. C. Allen; panels (B) and (C), L. K. Albertson.

producing insects as ecosystem engineers, our findings suggest that the stabilizing effects of silk could be larger than previously anticipated, potentially because of relatively high densities (thousands per square meter) of silk-producing aquatic insects in some benthic habitats (Edwards 1962, Statzner et al. 1999, Cardinale et al. 2004, Johnson et al. 2009).

Species behavior also influenced the biotic effect. When categorized by behavior type, we found that species with foraging or structure-producing behaviors had larger effect sizes than those with digging behaviors. For example, detritivorous fish in South American rivers can ingest large quantities of fine sediments, preventing fine sediment accrual in the benthos and altering algal and invertebrate community abundance and structure (Flecker 1996). Nevertheless, we found that there was no difference in the magnitude of the response ratio across species that destabilize vs. stabilize. Thus, species that modify habitats in ways that reduce erosion, such as silk-producing insects, biofilms, or aquatic macrophytes, have as large of an impact as those that increase movement of sediments, such as fish, tadpoles, or crayfish.

We also found that the majority of studies that investigate biophysical interactions studied organisms that exhibit destabilizing behaviors. This tendency could represent either the interests of the authors or, alternatively, the propensity for more species to exhibit dominant behaviors that destabilize sediments in streams. It has been suggested that feedbacks might be important in systems that are dominated by ecosystem engineers (Fisher et al. 2007, Murray et al. 2008, Reinhardt et al. 2010). Our findings further support this idea since both destabilizers and stabilizers appear to have important effects on physical conditions for sediment transport. Because ecosystem engineers alter physical conditions, such as flow velocities and grain size distributions, which in turn regulate the composition and abundances of biological assemblages, engineers could have large, indirect effects on entire stream ecosystems (Poff and Allan 1995, Lake 2000). The relative influence of destabilizers and stabilizers, especially in diverse systems where species that stabilize and destabilize might be living together in the same stream, remains to be verified under field conditions.

As predicted, stream physical conditions also modified the magnitude of biotic effects (Moore 2006). We detected a significant negative relationship between the biotic effect and discharge, which may occur because discharge represents a comprehensive measurement that includes both stream cross-sectional area and velocity (Gordon et al. 2004). Our results also showed that the largest biotic effects (90th quantile) decreased with increasing grain size, suggesting that maximum biotic effects were constrained by sediment size. However, we found no evidence of a significant relationship between velocity and LRR. Overall these findings suggest that streams with higher discharges and larger grain sizes are dominated by physical and not biological forces.

Our findings are inherently limited by sampling bias, a common feature of meta-analyses. It is typical for researchers to study organisms that they believe, a priori, could influence the physical process of interest. As a result, our findings should be limited to the suite of organism types that have been studied in this data set. Given the mixed support we found for the hypothesis that organismal abundance would increase the biotic effect size, we also reiterate that organism type appears to be just as important of a factor for determining biological effect size as abundance and that these biological effects can be mediated by the physical conditions of a stream. Thus, the relationships detected with this data set may not hold for all species, especially those that have not yet been studied, and may be contingent upon physical variables such as grain size and discharge.

Future considerations

Most studies that we found in the literature focused on fish and crustacean species, and only a few investigated the biotic effects of aquatic macrophytes, amphibians, mollusks, or biofilms. This bias suggests that a focus on additional species in future studies could broaden the generality of our results. For example, biofilms are known to produce extracellular substances that can bind particles together but their role as ecosystem engineers has not been well-studied (Grabowski et al. 2011, Vignaga et al. 2013). In addition, most studies we surveyed focused on single, usually dominant, species. Only a few studies investigated interactions among species, which previous work has shown to be significant (Statzner and Sagnes 2008, Allen and Vaughn 2011, Albertson et al. 2014). Given increasing concerns about global biodiversity loss, future studies could focus on how diversity and species traits can affect physical processes (Solan et al. 2004, Allen et al. 2014). Most studies also used organisms within a single trophic level, and did not consider predator–prey interactions, which are known to regulate ecosystem functions (Bruno and Cardinale 2008, Sanders et al. 2014). Finally, the scale of most studies has been short term, spatially limited, and site specific, indicating a need for creative approaches for studying biotic effects at larger spatial and temporal scales. The spatial and temporal extent of biological effects is relatively understudied (Hassan et al. 2008, Johnson et al. 2011, Rice et al. 2012), but rivers could provide an excellent testing ground because they exhibit natural gradients in physical conditions and ecological community structure across space and through time as different cohorts of aquatic insects, crustaceans, and fish mature (Vannote et al. 1980, Merritt et al. 2008). For example, Hassan et al. 2008 investigated the relative roles of abiotic and biotic controls and found that while fish spawning was a dominant regulator of river bed morphology during the fall, winter, and spring seasons, flooding was dominant in the summer.

Although the influence of biology on the physical processes that shape Earth's landscape is debated (Dietrich and Perron 2006), we found evidence that a variety of organisms have substantial effects on sediment erosion and deposition in streams. There is now an opportunity to bring together disciplines that have largely evolved independently but that have been moving toward a more comprehensive understanding of interactions between biological and physical forces (Allen et al. 2014). It has also been suggested that a more quantitative understanding of biotic effects in streams might improve and guide restoration designs and help evaluate the success of restoration projects, including restoration of riparian habitats in urban settings where vegetation has been reduced, plant community structure has shifted, and channel morphology has been altered as a result (Palmer and Bernhardt 2006). The findings reported here add to a number of recent reviews that have concluded that organisms have critical effects on physical processes in streams and biological forces are important to include in models that predict erosion in stream ecosystems.

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