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Unionid mussels influence macroinvertebrate assemblage structure in streams

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Abstract. Unionid mussels often occur as multispecies aggregates called mussel beds and in dense patches within the mussel beds themselves. Thus, their distributions are patchy at 2 spatial scales. We examined the association between mussel assemblage structure and macroinvertebrate assemblage structure at these 2 spatial scales in rivers of the Ouachita Highlands, Arkansas and Oklahoma, USA. We used multivariate variation partitioning techniques to relate variation in benthic macroinvertebrate distribution and abundance to variation in mussel assemblages, environmental variables, spatial variables, and overlapping or shared variation between these components. At the patch scale, total densities of macroinvertebrates and dominant groups (Oligochaeta, Chironomidae, Ephemeroptera, and Trichoptera) were significantly higher in patches containing mussels than where mussels were absent, and densities of macroinvertebrates were positively correlated with unionid density. In variation partitioning analyses, mussel assemblages explained almost ½ of the variation in macroinvertebrate assemblages at both spatial scales, even after removing effects of similar habitat (environmental variables) and biogeographic history (spatial variables).

Key words: freshwater mussels, patchiness, spatial scale, variation partitioning.

Most organisms, from nematodes on the deep sea floor (Rice and Lambshead 1992) to large migratory mammals (Swihart et al. 2003), exhibit patchy distributions in response to patchily distributed resources (Pickett and White 1985). Different ecological processes create and maintain patchiness at different spatial scales (Downes et al. 1993), but processes occurring at large spatial scales define the limits within which local conditions and local biotic assemblages vary (Poff 1997, Maurer 1999). Regardless of scale, understanding factors underlying patchiness is important because patchiness has consequences for the maintenance of populations and their effects on other ecosystem compartments (Strayer et al. 2004).

Stream invertebrates are notorious for their patchy distributions (Downes et al. 1993) that can occur at a number of spatial scales (Hildrew and Giller 1992). We know a great deal about how the distribution and abundance of benthic macroinvertebrates are influenced by habitat and interactions with other organisms at local scales (Allan 1995); however, macroinvertebrate communities also are influenced by historical constraints that determine regional species pools, physical attributes of the surrounding landscape, disturbance history, and biological attributes of organisms that lead to nonrandom patterns of dispersion (Legendre 1993, Matthaei and Townsend 2000, Vaughn and Taylor 2000). For example, the surrounding terrestrial area has a large influence on stream structure and function and, thus, the distribution of stream organisms (Allan 1995). Watershed area influences both size and composition of macroinvertebrate species pools (Watters 1993, Vaughn 1997). Palmer et al. (1996) predicted that stream invertebrate communities are ultimately under regional control because stream invertebrates typically experience frequent and unpredictable disturbances and have high dispersal capabilities; however, dispersal abilities of some macroinvertebrates, particularly those lacking a winged adult stage, are constrained by the interconnections among streams. Thus, studies examining macroinvertebrate communities should consider not only local environmental factors but also factors that may structure communities at larger spatial scales.

Bivalve mollusks act as ecosystem engineers in many marine and estuarine systems, where they dominate benthic biomass, couple benthic and pelagic materials and energy cycling, and affect the distribution and abundance of other benthic organisms (Dame

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1996). Invasive, epifaunal zebra mussels have similar effects in freshwater systems (Strayer et al. 1999). In both marine and lake systems, organisms colonize bivalve shells and the interstices between shells where organic matter often accumulates (Vaughn and Hakenkamp 2001).

Unionid mussels are infaunal bivalves that can dominate the benthic biomass of lakes and rivers, particularly in eastern North America (Parmalee and Bogan 1998, McMahon and Bogan 2001). Unionids can have strong effects in ecosystems in which they are abundant (Vaughn and Hakenkamp 2001, Spooner 2002, Vaughn et al. 2004). For example, in the River Spree, Germany, filtration by dense assemblages of unionids led to biological oligotrophication by decreasing phytoplankton biomass and total P and increasing water clarity (Welker and Walz 1998). Removal of phytoplankton from the water column by filtering unionids results in biodeposition of nutrient-rich feces and pseudofeces (mucus-bound particles rejected prior to ingestion) to the streambed (Lewandowski and Stanczykowska 1975, Nalepa et al. 1991). Burrowing by unionids increases sediment water content, sediment homogenization, and depth of O_2 penetration (McCall et al. 1979, 1995). Last, the physical presence of unionids in lake and streambed sediments can provide habitat for a variety of benthic plants and animals (Vaughn and Hakenkamp 2001, Spooner 2002).

Unionids are patchily distributed in stream systems, and this patchiness occurs at multiple spatial scales (Vaughn and Taylor 2000, Strayer et al. 2004). At the reach scale, mussels often occur in aggregates called mussel beds that can range in area from <50 to >5000 m^2. Within such beds, mussel densities are typically 10 to 100× higher than outside of beds. Mussel beds typically occur in areas that are protected during flooding, i.e., in depositional areas with low shear stress and stable sediments (Layzer and Madison 1995, Strayer 1999, Strayer et al. 2004). Mussels also usually have aggregated distributions at the patch scale within mussel beds, occurring in dense clumps separated by areas with few or no mussels (Downing et al. 1993, Strayer 1993).

Given their high biomass in many rivers, ability to contribute nutrients through excretion and biodeposition, bioturbation of sediments, and biogenic structure provided by both live mussels and their spent shells, unionids probably influence the distribution and abundance of co-occurring macroinvertebrates in streams. Given their patchy distributions at multiple spatial scales, the influence of unionids on macroinvertebrates may also be patchy and may vary across spatial scales. We addressed these hypotheses by examining the relationship between unionids and co-occurring benthic macroinvertebrates across 2 spatial scales in rivers of the Ouachita Highlands of the central USA. Our objective was to determine the effects of variation in mussel community structure on macroinvertebrate community structure. We did this by quantifying the distribution and abundance of unionids and macroinvertebrates in stream reaches and within patches nested in reaches. We then used variation partitioning to determine the simultaneous effects of mussel distribution and abundance and environmental and spatial variables on benthic macroinvertebrate community structure at these 2 spatial scales.

Study Area

We selected 30 study sites within 8 streams in the Ouachita Highlands of central and western Arkansas and southeastern Oklahoma, USA. This relatively compact biogeographic area (lat 34°13′52″N, long 95°37′13″W–lat 34°44′47″N, long 92°17′23″W) is a center of speciation for both terrestrial and aquatic organisms (Mayden 1985), contains a rich macroinvertebrate (Allen 1990, Moulton and Stewart 1996) and unionid mussel fauna (Vaughn et al. 1996), and has streams that are relatively unimpacted compared to other areas of North America and Europe (Master et al. 1998, Vaughn and Taylor 1999). Annual precipitation ranging from 100 to 142 cm combined with steep ridge-and-valley topography results in frequent but short-lived spates (Rafferty and Catau 1991, Matthews et al. 2005). Watershed areas of the 8 streams ranged from 816 to 64,454 km^2 and annual mean discharge ranged from 12 to 843 m^3/s during the study (Matthews et al. 2005).

We selected sites known to contain unionids and that also encompassed a broad range of mussel abundance and richness. Sites (mussel beds) ranged in size from 88 to 3300 m^2, mussel species richness at the sites ranged from 1 to 19 species, and mussel mean abundances ranged from 1 to 84 individuals/m^2. We purposely did not sample stream reaches without unionids. Many previous studies have been unsuccessful at predicting which reaches will contain mussels based on traditional macrohabitat characteristics (Strayer 1993, Strayer et al. 2004). We felt a rigorous and workable design was to include sites that spanned the range of mussel-bed richness and abundance because we do not know why mussels do not occur in reaches that seem to contain appropriate habitat and because including such reaches would have greatly increased the amount of environmental variation in our analyses.

Methods

We used a hierarchical sampling strategy of quadrats (patches) nested within sites (mussel beds, reaches) to allow us to compare information across spatial scales. At each site we sampled mussels, macroinvertebrates, and environmental variables from 10 randomly placed 0.25-m^2 quadrats ($n = 300$). We also recorded additional environmental variables at the site scale. Our previous work showed that 10 quadrats provided robust estimates of the abundance of most mussel species within beds (Vaughn et al. 1997). We were not concerned about missing rare mussel species because rare species were not used in analyses. All sampling was conducted in mid- to late summer (June–September 1999–2001), when river water levels and discharge were low, because we wanted to maximize our ability to record abundance of mussels and macroinvertebrates accurately. We also wanted to sample when the effects of mussels were strongest, and laboratory experiments have predicted that mussels filter and add nutrients to a larger proportion of the water column during periods of low discharge (Strayer et al. 1999, Vaughn et al. 2004).

Sampling methods

At each sampling site, we recorded water temperature, dissolved O_2, pH, and conductivity at the midpoint of the channel. We placed transects across the stream and recorded depth and current velocity at 1-m intervals. We recorded bankfull width and depth, thalweg depth, channel slope (gradient), bank slope, and width of the riparian area on each bank following procedures in Gordon et al. (1992) and Barbour et al. (1999).

Within each quadrat, we visually estimated the % cover of filamentous green algae, diatoms, cyanobacteria, detritus, and shade at midday. We visually estimated substrate composition as the % cover of 6 Wentworth size classes (bedrock, boulder, cobble, gravel, sand, and silt). The same person made all visual estimates using a mask and snorkel or SCUBA where water depths were $>$0.5 m. We took 4 measurements of substrate resistance in each quadrat and averaged them. We used a penetrometer (Forestry Suppliers #77143, Jackson, Mississippi) to measure substrate resistance (psi) or compaction (Soil and Plant Analysis Council 2000).

We quantitatively sampled macroinvertebrates in each quadrat using a Hess-type sampler modified to vacuum the substrate (Brown et al. 1987). The sampler allowed us to sample areas of varying flow (riffles vs pools) and substrate composition (boulder vs gravel) using the same sampling technique. We disturbed the substrate within the sampling pipe for 5 min, and organisms and debris were sucked from the substrate into the sample bag (423-µm mesh). We preserved macroinvertebrates in 70% ethanol and returned them to the laboratory for identification and counting. We identified all macroinvertebrates except oligochaetes to family; we identified oligochaetes to class.

We sampled mussels in each quadrat last. We excavated each quadrat to a depth of 15 cm, and removed all mussels to shore, identified them to species, and returned them to the stream bed (Vaughn et al. 1997, Vaughn and Spooner 2004).

Data analyses

We examined our data in several ways. At the patch scale, we examined effects of mussel presence/absence and mussel densities in quadrats on macroinvertebrate density. We also examined the effects of mussel presence/absence in quadrats on densities of the most abundant taxonomic groups of macroinvertebrates (Oligochaeta, Ephemeroptera, Trichoptera, and Chironomidae). At both the patch and site scales, we used multivariate variation partitioning techniques (see below) to relate variation in benthic macroinvertebrate assemblages to variation in mussel assemblages, measured environmental variables, spatial variables, and overlapping or shared variation between these components. For all analyses, we square-root transformed densities of mussels and macroinvertebrates to achieve normality (Zar 1999).

We used nested analysis of variance (Zar 1999), with quadrats nested within sites, to test for the effects of mussel presence/absence in quadrats on macroinvertebrate density in quadrats. We used correlation to examine the association between mussel density and macroinvertebrate density within quadrats.

Variation partitioning

At both the patch and site scales, the data we used in the variation partitioning analyses consisted of a response matrix (macroinvertebrate assemblage structure) and 3 predictor matrices (mussel assemblage structure, environmental variables, and spatial variables). At the patch scale, the matrices we used were densities of macroinvertebrate families by quadrat, densities of mussel species by quadrat, environmental variables measured at the patch scale by quadrat, and spatial variables (spatial information was the same for each quadrat within a site; see below). At the site scale, the matrices we used were mean macroinvertebrate family density by site, mean density of each individual mussel species by site, environmental variables measured at the site scale, and spatial variables.

For both spatial scales, we used canonical correspondence analysis (CCA; ter Braak 1986) calculated with CANOCO (version 4, Microcomputer Power, Ithaca, New York; ter Braak and Smilauer 1998) to determine how well the mussel assemblage and environmental and spatial variables each accounted for variation in the macroinvertebrate assemblage. We subjected eigenvalues to a Monte Carlo procedure to determine if the macroinvertebrate and predictor matrices were associated (ter Braak and Smilauer 1998). We then used partial CCA following Borcard et al. (1992) and Legendre and Legendre (1998) to partition the total variation in macroinvertebrate assemblage structure attributable to mussel assemblage structure, environmental variables, spatial variables, and overlapping or shared variation between these 3 components. CCA performs best when the number of variables in the response matrix is ≥2× the number of variables in the predictor matrices (Legendre and Legendre 1998). We reduced the number of taxonomic variables by restricting our analyses to macroinvertebrate and mussel taxa occurring in ≥10 quadrats (patch scale) or ≥5 sites (site scale) (Table 1). We reduced the number of environmental and spatial variables using the forward-selection procedure in CANOCO. We retained variables if they had *p*-values <0.15 using a Monte Carlo procedure (Table 2). The liberal significance level of 0.15 prevented elimination of variables that might eventually prove biologically relevant in the model (Legendre and Legendre 1998, Vaughn and Taylor 2000).

We used 3 categories of spatial variables in our analyses: geographic location on the landscape, relative position in a stream network, and watershed area upstream of a sampling site. We obtained a matrix of geographic coordinates with a cubic trend surface polynomial that allowed us to estimate the parameters of a trend surface regression equation:

$$\mathrm{Z} = \mathrm{b_1X} + \mathrm{b_2Y} + \mathrm{b_3XY} + \mathrm{b_4X^2} + \mathrm{b_5Y^2} + \mathrm{b_6X^2Y} + \mathrm{b_7XY^2} + \mathrm{b_8X^3} + \mathrm{b_9Y^3}$$

where X and Y are orthogonal coordinates representing latitude and longitude, and Z is macroinvertebrate distribution and abundance information in the form of ordination scores (Borcard et al. 1992, Magnan et al. 1994). We scored the relative position of each site in a stream network by the sequence of nodes taken from the direct path between a given sampling site and the root of the hydrographic tree; we then used this information to construct a locality-by-nodes matrix (Magnan et al. 1994, Vaughn and Taylor 2000). We calculated watershed area upstream from each sampling site using a geographical information system (GIS) and a 1:100,000 digital elevation map with 60 × 60-m cells. We used a spatial matrix in our analyses that consisted of the terms from the cubic trend regression model, the locality-by-nodes information, and watershed area. We used forward selection, as described above, to reduce the number of spatial variables. We used the same spatial data matrix in both the patch- and site-scale analyses because macroinvertebrates at both of these spatial scales should be influenced by similar biogeographic and dispersal constraints (i.e., the biogeographic history of a site and a patch within that site should not be different).

Results

Macroinvertebrate density was significantly higher ($F_{24,271} = 1.56$, $p = 0.05$) in quadrats containing mussels ($n = 170$) than in quadrats without mussels ($n = 130$), and this pattern was consistent across groups of dominant macroinvertebrates (Oligochaeta: $F_{24,269} = 2.81$, $p < 0.001$, Chironomidae: $F_{24,270} = 2.25$, $p < 0.001$, Ephemeroptera $F_{24,270} = 2.07$, $p = 0.002$, Trichoptera: $F_{24,270} = 3.31$, $p < 0.001$; Fig. 1). Mussel density was positively correlated with macroinvertebrate density across the 300 quadrats ($r = 0.35$, $p < 0.001$; Fig. 2), although very little variation was explained by this relationship ($r^2 = 0.12$).

For the patch-scale CCA, each of the explanatory matrices (3 CCAs: mussels, environmental variables, and spatial variables) predicted macroinvertebrate assemblage structure with significant eigenvalues for both the 1st axis and all 4 axes combined (1st-axis eigenvalues, mussels: 0.295, $p = 0.002$; environment: 0.283, $p = 0.002$; space: 0.303, $p = 0.0002$). The predictor matrices explained 42% of the variation in the macroinvertebrate assemblage matrix. Of this explained variation, 43% was explained by either pure or shared mussel effects (Table 3).

For the site-scale CCA, each of the explanatory matrices (3 CCAs: mussels, environmental variables, and spatial variables) predicted macroinvertebrate assemblage structure with significant eigenvalues for both the 1st axis and all 4 axes combined (1st-axis eigenvalues, mussels: 0.192, $p = 0.005$; environment: 0.202, $p = 0.0012$; space = 0.248, $p = 0.0002$). The predictor matrices explained 77% of the variation in the macroinvertebrate assemblage matrix. Of this explained variation, 42% was associated with either pure or shared mussel effects (Table 3).

Discussion

Mussel and macroinvertebrate distributions

Mussel assemblages explained almost ½ of the variation in macroinvertebrate assemblages at both

TABLE 1. Macroinvertebrate and mussel taxa used in the variation partitioning analyses. We reduced the number of taxa in the analysis by including only those macroinvertebrate and mussel taxa that occurred in ≥10 quadrats (patch scale) or ≥5 sites (site scale). X = taxon used in analysis.

Macroinvertebrate taxon	Patch scale	Site scale	Mussel species	Patch scale	Site scale
Athericidae	X		*Alasmidonta marginata*	X	X
Baetidae	X	X	*Actinonaias ligamentina*	X	X
Baetiscidae	X		*Amblema plicata*	X	X
Brachycentridae	X		*Cyprogenia aberti*	X	X
Caenidae	X	X	*Elliptio dilatata*	X	
Ceratopogonidae	X	X	*Ellipsaria lineolata*	X	
Chironomidae	X	X	*Fusconaia flava*	X	X
Coenagrionidae	X	X	*Lampsilis cardium*	X	
Corduliidae	X	X	*Lasmigona costata*	X	X
Corydalidae	X	X	*Megalonaias nervosa*	X	
Elmidae	X	X	*Obliquaria reflexa*	X	X
Empididae	X	X	*Plectomerus dombeyanus*	X	
Ephemeridae	X	X	*Pleurobema sintoxia*		X
Glossiphoniidae	X	X	*Ptychobranchus occidentalis*	X	X
Gomphidae	X	X	*Quadrula pustulosa*	X	X
Gyrinidae	X	X	*Quadrula quadrula*	X	
Heptageniidae	X	X	*Strophitus undulatus*	X	
Hydrophilidae	X		*Tritogonia verrucosa*	X	X
Hydropsychidae	X	X	*Truncilla truncata*	X	
Hydroptilidae	X	X	*Villosa arkansasensis*	X	X
Isonychiidae	X	X			
Lebertiidae	X	X			
Leptoceridae	X	X			
Leptophlebiidae	X	X			
Oligochaeta	X	X			
Perlidae	X	X			
Philopotamidae	X	X			
Planariidae	X				
Pleuroceridae	X				
Polycentropodidae	X	X			
Polymitarcyidae	X	X			
Potamanthidae	X	X			
Psephenidae	X	X			
Pyralidae	X	X			
Simuliidae	X	X			
Talitridae	X				
Tipulidae	X	X			
Tricorythidae	X	X			

patch and site scales, even after removing effects of similar habitat (environmental variables) and biogeographic history (spatial variables). This pattern was particularly robust within mussel beds at the patch scale where macroinvertebrate densities were positively related to mussel densities. We did not sample sites without mussels, but we did sample sites with mussel densities that ranged from very low ($1/m^2$) to high ($84/m^2$).

Patchy distributions of organisms are usually a response to resources that have patchy distributions. At the patch scale, mussels probably facilitate co-occurring macroinvertebrates by enriching resources by creating biogenic structure, stabilizing and oxygenating stream sediments, and providing food resources directly or indirectly by enhancing other food resources (Vaughn and Hakenkamp 2001). At the site scale, denser mussel beds may contain more patches of mussels and, therefore, may provide more resources to macroinvertebrates than sites with less-dense mussel beds. Thus, denser mussel beds may be colonized preferentially over less-dense beds. At both scales, mussels increase overall spatial habitat diversity by creating biogenic structure and associated processes.

Bivalves and their empty shells provide habitat for macroinvertebrates in both marine and lake systems, where organisms colonize shells and the interstices between shells where organic matter often accumulates (Beckett et al. 1996, Gutierrez et al. 2003). For example, reef-dwelling oysters occupy a small propor-

Table 2. Environmental variables used in the variation partitioning analyses. We reduced the number of environmental and spatial variables using the forward-selection procedure in CANOCO. Variables were retained if they had p-values <0.15 using a Monte Carlo procedure. X = variable used in analysis. CV = coefficient of variation.

Variable	Patch scale	Site scale
% boulder	X	X
% cobble	X	
% gravel	X	
% sand	X	
% silt	X	
Substrate heterogeneity	X	X
Mean substrate compaction	X	
CV substrate compaction	X	
% filamentous green algae	X	
% diatoms	X	
% detritus	X	
% shade at midday	X	
Minimum flow		X
CV depth		X
Conductivity		X
Gradient		X

tion of the space in coral reefs, but they provide niches for a disproportionately high variety of taxa (Barnes 2001). In lakes, epifaunal zebra mussels elevate densities of aquatic invertebrates at local scales by providing structural refugia and biodeposited food (Mayer et al. 2002). Unionid shells in streams probably act in a similar way, providing habitat on shell surfaces and in the interstices between shells.

Mussels may improve streambed habitat suitability for macroinvertebrates by stabilizing the sediment and through bioturbation. Mussel beds typically occur in areas of streams that remain stable during floods (flow refugia) (Strayer 1999). Strayer et al. (2004) speculated that firmly buried mussels could stabilize sediments in mussel beds, and we have observed this process qualitatively in our study rivers (CCV, unpublished data). If mussels stabilize sediments, they may provide refugia for macroinvertebrates and their food resources during spates (Resh et al. 1988). Marine and lentic bivalves increase O_2 penetration and stimulate microbial metabolism as they burrow through the sediment (biuoturbation) (McCall et al. 1979, 1995, Levinton 1995, Dame 1996). Stream unionids also bioturbate sediments (Spooner 2002, Vaughn et al. 2004), and it is likely that this process improves habitat suitability for many macroinvertebrates.

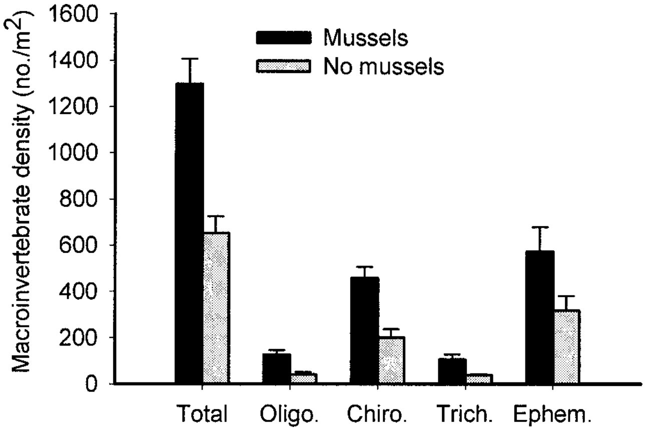

Fig. 1. Mean (+1 SE) densities of total macroinvertebrates and dominant macroinvertebrate groups in quadrats with and without mussels. All differences were significant at $p \leq 0.05$. Oligo. = Oligochaeta, Chiro. = Chironomidae, Trich. = Trichoptera, Ephem. = Ephemeroptera.

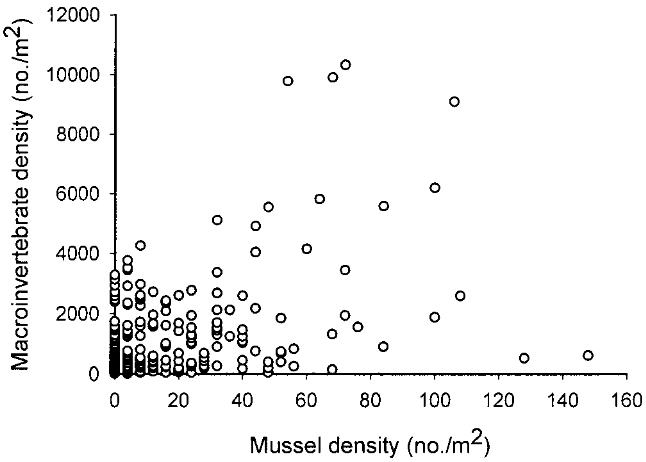

Fig. 2. Scatterplot for the relationship between mussel density and macroinvertebrate density for the 300 quadrats.

Mussels and their biological processes probably

Table 3. Partitioning of explained variation at patch and site scales.

	% of explained variation	
	Patch scale	Site scale
Variation attributed to a single explanatory matrix		
Mussel assemblage structure	30	21
Environmental variables	24	20
Spatial variables	22	24
Variation shared among explanatory matrices		
Mussels + environmental variables	3	3
Mussels + spatial variables	8	15
Spatial variables + environmental variables	11	14
Mussels + spatial variables + environmental variables	2	3

enhance food resources for macroinvertebrates. Mussel shells provide a substratum for periphyton, an important macroinvertebrate food source (Vaughn and Hakenkamp 2001), and nutrients excreted by living mussels (Davis et al. 2000, Vaughn et al. 2004) increase the growth of periphyton on their shells (Spooner 2002). Organic matter biodeposited by mussels probably provides food for detritivorus invertebrates, such as deposit-feeding chironomids and oligochaetes, both of which were denser in quadrats with mussels.

Variation partitioning

Similar amounts of variation in macroinvertebrate assemblage structure were partitioned among mussels, environmental variables, and spatial variables at both spatial scales. We expected environmental variables to account for a large proportion of variation in macroinvertebrate assemblages. Many streams are highly disturbed systems that tend to be governed by physical processes such as floods and drought (Palmer et al. 1996, Poff 1997). Flood frequency and current velocity influence colonization patterns at a regional scale and determine substrate size and deposition patterns at a local scale and, thus, ultimately govern the availability of habitat for both mussels and macroinvertebrates (Allan 1995).

We also expected spatial factors to be important to macroinvertebrate assemblages. Interconnections among watersheds represent dispersal pathways for mussels (as larvae attached to host fish) (Vaughn 1997, Vaughn and Taylor 2000) and for many larval macroinvertebrates. Thus, interconnections among watersheds have strong effects on macroinvertebrate colonization. Watershed area is important because it affects macroinvertebrate (Allan 1995), mussel (Watters 1993, Vaughn 1997), and fish-host species pools and influences physical events such as flood frequency. The surrounding terrestrial area has a large influence on stream structure and function and, thus, the distribution of stream organisms (Allan 1995). In addition, the straight-line distance across one section of a landscape, such as a floodplain, may represent different environmental conditions and dispersal barriers to adult insects than another section of a landscape, such as a mountain (Vaughn and Taylor 2000).

The amount of variation that was shared or overlapping between the 3 predictor matrices was approximately equal at both spatial scales. The largest overlaps were between mussels and spatial variables and between environmental and spatial variables. Difficulty in separating the effects of mussels, environmental variables, and spatial variables on macroinvertebrate assemblages is expected. Macroinvertebrates and mussels undoubtedly respond to some of the same environmental and spatial factors. In addition, long-lived mussels and short-lived macroinvertebrates probably respond to the environment at different temporal scales. The key result from our study is that mussels had a strong influence on macroinvertebrates after statistically accounting for the influences of environmental and spatial variables.

Unexplained variation is often high in variation partitioning analyses for a number of reasons. These reasons include noisy (i.e., measured with some error) environmental variables, variables that are indirectly correlated (Okland and Eilertsen 1994, McCune 1997), and unmeasured factors. More of the total variation was explained at the site scale than at the patch scale, but the amount of variation explained at the 2 scales was expected to differ because the analyses included different numbers of response variables. Some environmental variables known to be important to macroinvertebrates at small spatial scales, such as microscale variations in flow and depth characteristics (Lancaster 2000, Kilbane and Holomuzki 2004), were not measured. Had these variables been included, the amount of explained variation at the patch scale probably would have been greater. Nevertheless, the utility of variation partitioning techniques lies in allowing decomposition of the variation that *is* explained (Okland and Eilertsen 1994), and a large proportion of the explained variation at the patch scale was associated with mussels.

Our study demonstrated that riverine mussels influence the distribution and abundance of co-occurring benthic macroinvertebrates. Freshwater mussels are threatened and decreasing globally (Bogan 1993), and even populations of common species are undergoing catastrophic declines (Neves et al. 1997, Vaughn and Taylor 1999). Our results and results of other studies of ecosystem services provided by riverine bivalves (Strayer et al. 1999, Spooner 2002, Vaughn et al. 2004) indicate that this catastrophic loss of mussel biomass may lead to changes in the macroinvertebrate fauna of streams.

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