

Scale-dependent longitudinal patterns in mussel communities

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SUMMARY

1. Species richness and assemblage patterns of organisms are dictated by numerous factors, probably operating at multiple scales. Freshwater mussels (Unionidae) are an endangered, speciose faunal group, making them an interesting model system to study the influence of landscape features on organisms. In addition, landscape features that influence species distributions and the scale at which the factors have the greatest impact are important issues that need to be answered to conserve freshwater mussels.

2. In this study, we quantified freshwater mussel communities at 16 sites along three mid-sized rivers in the south-central United States. We addressed the following questions: (i) Are there predictable longitudinal changes in mussel community composition? (ii) What landscape variables best explain shifts in community composition? and (iii) At what scale do landscape variables best predict mussel community composition?

3. After controlling for the influence of longitudinal position along the stream, we compared mussel distributions to a suite of hypothesised explanatory landscape variables across multiple scales – catchment scale (entire drainage area), buffer scale (100-m riparian buffer of the entire catchment) and reach scale (100-m riparian buffer extending 1 km upstream from the sampling site).

4. We found a significant and consistent longitudinal shift in dominant mussel species across all three rivers, with community composition strongly related to distance from the headwaters, which is highly correlated with stream size. After accounting for stream size, variables at the buffer scale were the best predictors of mussel community composition. After accounting for catchment position, mean channel slope was the best explanatory variable of community composition and appeared in all top candidate models at the catchment and buffer scales. Coverage of wetland and urban area were also correlated with community composition at the catchment and buffer scales.

5. Our results suggest that landscape-scale habitat factors influence mussel community composition. Landscape features at the buffer scale performed best at determining community composition after accounting for position in the catchment; thus, further protection of riparian buffers will help to conserve mussel communities.

Keywords: Bray–Curtis ordination, channel slope, community composition, GIS, unionid

Introduction

Species richness and community composition are often dictated by numerous factors operating at multiple spatial scales. In stream ecosystems, both abiotic and biotic attributes are closely related to catchment geology, land

use and climate, especially at the interface between land and water (Hynes, 1975; Burcher, Valett & Benfield, 2007). Recent research has focussed on regional- and landscape-scale factors (e.g. catchment area, land use, geology) that influence stream communities (Allan, 2004; Hopkins, 2009). Stream communities are strongly influenced by

hydrologic factors that shape habitat suitability (Richards, Johnson & Host, 1996; Galbraith, Vaughn & Meier, 2008) and resource availability (Golladay, 1997; Atkinson *et al.*, 2009). Run-off patterns are determined primarily by longitudinal location in a catchment; thus, spatial patterning in streams is primarily linear. However, landscape alterations such as conversion of forests to urban or agricultural areas typically lead to degraded stream conditions and consequently to altered species distributions (Paul & Meyer, 2001; Roy *et al.*, 2003; Riva-Murray *et al.*, 2010). Few studies have examined how the combination of linear location in a catchment and land use structures lotic communities.

Freshwater mussels are a diverse faunal group, particularly in North America (with >300 species), but are also a highly threatened faunal group (Bogan, 2008). They occur in most freshwater habitats with mussel abundance and diversity being greatest in medium to large rivers where they typically occur as dense, multi-species communities called mussel beds (Strayer, 2008). Within mussel beds, biomass can exceed that of other benthic organisms by an order of magnitude and annual production (in dry biomass) can equal that of other macrobenthos (Strayer *et al.*, 1994). Mussels play important roles in aquatic ecosystems by filtering suspended materials, transferring energy and nutrients from the water column to the sediment, biodepositing organic matter, excreting nutrients and providing biogenic habitat for other organisms (Vaughn, Gido & Spooner, 2004; Vaughn, Nichols & Spooner, 2008; Atkinson *et al.*, 2010). Because mussels are both long-lived in comparison with most stream invertebrates (i.e. in comparison with most stream invertebrates; Haag & Rypel, 2011) and relatively immobile as adults, they integrate stressors occurring at multiple temporal and spatial scales – from local to catchment.

The mechanisms that lead to species shifts in aquatic insect communities along longitudinal gradients in rivers have been integrated into conceptual models (e.g. Vannote *et al.*, 1980), but less is known about how mussel communities change along gradients and the formation of a conceptual model to describe shifts in mussel community composition is very recent (Haag, 2012). Previous descriptive studies have discussed succession in mussel community composition because of stream size (Ortmann, 1913; Coker *et al.*, 1921), but only a few studies have quantified this pattern (Strayer, 1983; Haag & Warren, 1998). Distribution patterns of freshwater mussels may be influenced by environmental variables operating at multiple spatial and temporal scales (Strayer *et al.*, 1994; Strayer, 2008), but most quantitative studies of habitat

influences on mussel community composition have been performed at local stream-reach scales (e.g. Strayer & Ralley, 1993; Steuer, Newton & Zigler, 2008). Recent studies have begun to examine broader spatial scales, particularly with regard to the distribution of endangered mussels (Hopkins, 2009; Brown, George & Daniel, 2010), but few have addressed the patterns of community structure. Potential catchment-scale effects on mussel diversity and abundance include physiography (Arbuckle & Downing, 2002) and anthropogenic disturbance in riparian areas (Mcrae, Allan & Burch, 2004; Newton, Woolnough and Strayer, 2008). Overall, the mechanisms underlying how the structure of mussel communities changes along longitudinal gradients in streams are poorly understood.

Here, we address how landscape-scale variables influence shifts in mussel communities along three rivers within the same physiographic province. This region of exceptionally high mussel biodiversity allowed us to examine the composition and distribution patterns of mussel communities, and answer the following questions: (i) Are there predictable longitudinal changes in mussel community composition? (ii) What landscape variables best explain shifts in community composition? and (iii) At what scale do landscape variables best predict mussel community composition?

Methods

Study area

The Ouachita Mountains ecoregion, which covers 46 500 km² in central Arkansas and south-eastern Oklahoma (U.S.), is characterised by a subhumid subtropical climate, mixed forests/woodlands, rugged mountains, broad valleys and several large gravel-bed rivers (Oeat, 2003). This region is a centre of speciation for both terrestrial and aquatic organisms, with a large number of endemic species (Mayden, 1985). Mussel diversity is noteworthy with >60 species, including four federally threatened or endangered species (Vaughn & Taylor, 2000). The three rivers used in this study (Kiamichi, Little and Mountain Fork; Fig. 1) are all tributaries of the Red River and share regional species pools. Furthermore, these rivers support healthy and diverse mussel communities primarily due to relatively low anthropogenic impacts compared to other areas in the United States (Vaughn & Taylor, 1999). Land cover is primarily forest and pasture, but extensive logging does occur (Oeat, 2003). The rivers are very similar hydrologically and geomorphically (Table 1). Mussel beds in the Kiamichi, Little and

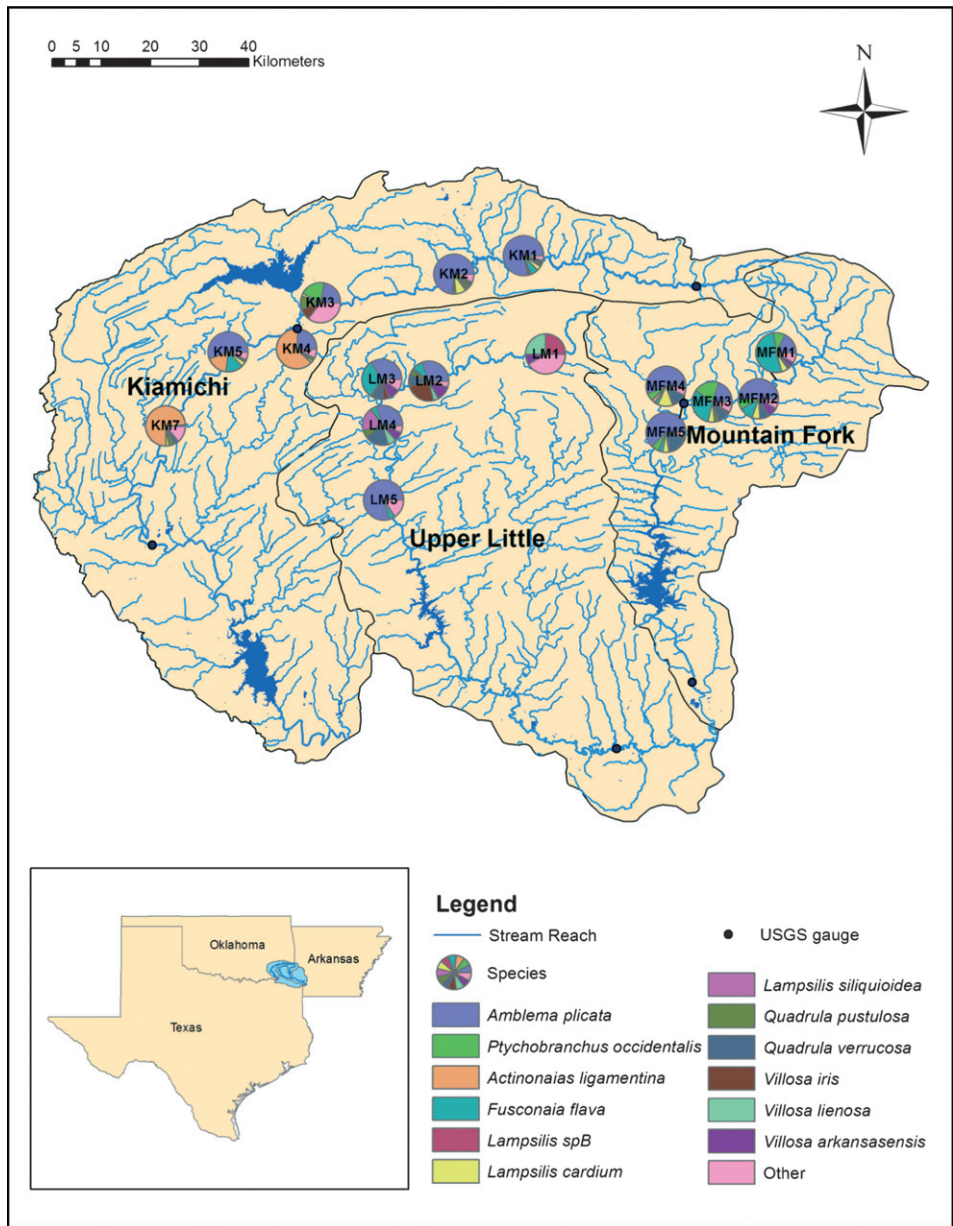


Fig. 1 Sample site locations and relative species compositions for the three study rivers.

Mountain Fork Rivers can contain over 20 mussel species at densities up to 100 m⁻², with biomass exceeding 20 kg m⁻² (Spooner & Vaughn, 2009).

Mussel sampling

We sampled mussels by excavating 10–20 quadrats of 0.25 m² along 100-m study reaches at each site (Fig. 1) and by conducting semi-quantitative timed searches (Vaughn, Taylor & Eberhard, 1997; Strayer & Smith, 2003), which allowed us to assess species composition more fully. Previous work in this system showed that 10 quadrats

provided accurate estimates of the abundance of most mussel species within beds (Vaughn *et al.*, 1997). Mussel sampling was confined to high-density (8.6–86.4 mussels m⁻²) mussel beds. Sampling occurred during the summers of 1994 [Little River (LM) sites 2 and 5, Mountain Fork River (MFM) site 3], 2003–2005 [Kiamichi River (KM) sites 1, 2, 3, 5 and 6] and 2010 (KM site 4; LM sites 1, 3 and 4; MFM sites 1, 2, 4, 5). We repeated timed searches at LM2, LM5 and MFM3 during 2010–2011 to insure there were no major species composition changes between the 1994 quantitative survey and the 2010 semi-quantitative survey.

Table 1 Akaike Information Criterion (AIC) model selection results

| Scale | Parameters in model | <i>K</i> | <i>F</i> -value | <i>R</i> ² | <i>P</i> -value | AIC | Δ_i | <i>w</i> _m |
|-----------|--|----------|-----------------|-----------------------|-----------------|---------|------------|-----------------------|
| Catchment | Slope, % urban, % wetland | 3 | 3 | 0.430 | 0.070 | -74.550 | 0.000 | 0.111 |
| | Slope, % urban, % agriculture, % wetland | 4 | 2.69 | 0.494 | 0.088 | -73.495 | 1.055 | 0.108 |
| | Slope | 1 | 4.35 | 0.237 | <0.05 | -72.910 | 1.640 | 0.080 |
| Buffer | Slope, % wetland | 2 | 5.73 | 0.469 | 0.016 | -76.706 | 0.000 | 0.124 |
| | Slope, % urban, % forest, % wetland | 4 | 3.75 | 0.577 | 0.037 | -76.359 | 0.347 | 0.104 |
| | Slope, % open water, % wetland | 3 | 4.32 | 0.520 | 0.028 | -76.313 | 0.393 | 0.102 |
| Reach | % Forest, % grassland/shrubs, % wetland | 3 | 4.54 | 0.390 | 0.323 | -72.766 | 0.000 | 0.082 |
| | % Forest, % wetland | 2 | 4.42 | 0.318 | 0.308 | -72.710 | 0.056 | 0.078 |
| | % Agriculture | 1 | 3.32 | 0.134 | 0.466 | -72.464 | 0.302 | 0.062 |

The best three models for each scale are shown. Models are shown in order of predictability and in boldface for $P < 0.05$. *K* is the number of variables in the model. The Δ_i is the difference between the AIC of the best fitting model and that of model *i*. The *w*_m is the normalised relative likelihood values known as the model weights. The variable slope refers to mean channel slope.

Landscape analysis

Mussel survey data for each site were compared to geospatial data across multiple spatial scales as suggested by Allan (2004). The spatial scales analysed for each sample point were: (i) catchment scale (entire drainage area); (ii) buffer scale (100-m riparian buffer of the entire catchment); and (iii) reach scale (100-m riparian buffer extending 1 km upstream from the sampling site; Fig. 2). Catchments for each sampling point were derived using the Spatial Analyst Toolkit in ArcMap 9.3.2 (Environmental System Research Institute, Redlands, CA, U.S.A.) with a 30-m digital elevation model (DEM) from the National Elevation Dataset. Mean channel slope was calculated by extracting elevations and distances from the DEM along the National Hydrology Dataset (NHD) flowlines. Mean channel slopes for each spatial scale were: (i) mean of the slope for the entire drainage upstream for the catchment scale; (ii) mean channel slope 10 km upstream of the site for the buffer scale; and (iii) mean channel slope 1 km upstream of the site for the site scale. NHD flowlines were also used to generate a 100-m buffer around the stream channels. Flowlines from the NHD were compared to the National Agricultural Inventory Program (NAIP) 2008 aerial photographs to verify channel locations. We used SSURGO soil data (National Resources Conservation Service, 2006) to assess the connectivity of the river to the floodplain, specifically by quantifying the area that is frequently flooded (water is ponded >50% chance in any year, or >50 times in 100 years). Soils that were classified as being frequently flooded were considered to have high connectivity to the floodplain. Land cover (30-m resolution) was obtained from the 2001 National Land Cover Database (Homer *et al.*, 2004).

Data analyses

Relative abundance (% of total species composition) was used to describe mussel community structure at each site. We used polar ordination with a Sorenson distance measure to describe community structure for each river and then all sites collectively (Bray & Curtis, 1957). The distance between communities indicates the degree to which mutual species similarity factors determine structure (Bray & Curtis, 1957), and allows for community structure to be dissected apart from environmental data. We performed polar ordinations with PC-ORD (version 6.0; Mccune & Melford, 1999) using the variance-regression endpoint selection method. The solution generated by the ordination was one dimensional. Ordinary least-squares linear regression was used to determine whether there was a relationship between distance from the headwaters and the ordination score for the individual rivers and all rivers collectively. To remove the influence of longitudinal position (distance from the headwaters), the residuals from the linear regression performed on all the sites were used as a response variable in the following model building.

Explanatory variables for mussel community composition patterns were evaluated using an information-theoretic approach (Akaike Information Criterion, AIC) to determine which landscape variables (mean channel slope, land cover, floodplain connectivity) at each scale (reach, buffer, catchment) were most strongly correlated with mussel community composition. We used the residuals (values that represent community composition after accounting for variation because of stream position) from the linear regression describing the correlation between distance from the headwaters and the Bray–Curtis score for each site as the response variable. Similar ordination

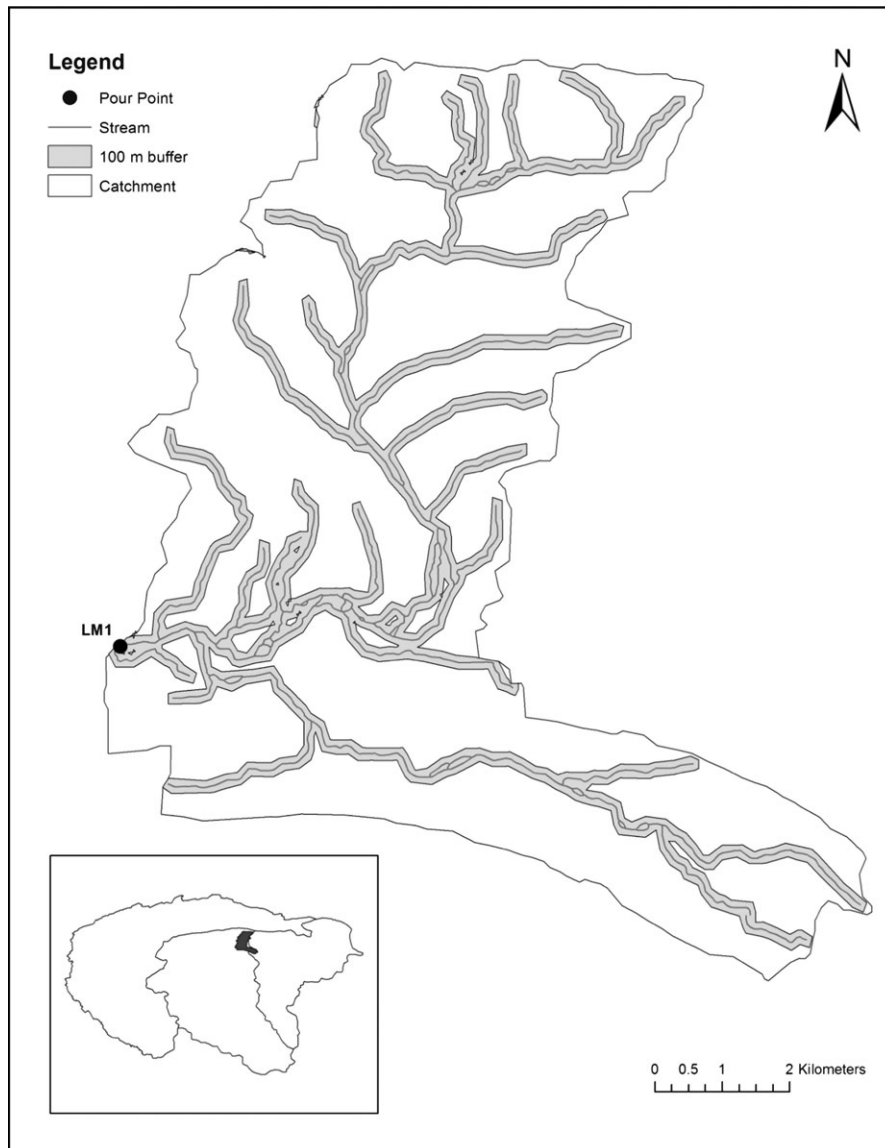


Fig. 2 Scales used for analyses: catchment, buffer and reach. Reach scale is the buffer area 1 km upstream from the sample site. The National Hydrology Dataset stream network is provided for reference. The example given is for the most upstream site in the Little River (LM1).

approaches have been used successfully to examine the relationships between biological assemblage data and environmental factors elsewhere (e.g. Roy *et al.*, 2003; Vaughn *et al.*, 2008; Riva-Murray *et al.*, 2010). We derived several multiple linear regression models and compared them using AIC. Based on maximum-likelihood estimates and the number of model parameters, AIC provides a measure for selecting among competing models of a given data set (Anderson, Burnham & Thompson, 2000). The model having the lowest AIC is selected because it identifies the main explanatory variables while providing the best compromise between predictive power and model complexity (Johnson & Omland, 2004). Models

with $\Delta_i < 2$ are generally considered to have substantial support (Burnham & Anderson, 2002). The Δ_i is the difference between the AIC of the best fitting model and that of model i . We evaluated the relative strengths of models with Akaike weights (w_i), which indicate the strength of evidence that a particular model is the best model, given the data and the set of candidate models being compared. This allowed us to determine which set of landscape variables explain the most variation in composition among mussel communities after controlling for distance from the headwaters. We analysed each spatial scale separately using AIC to determine the variables that best described community composition at

each scale and then compared models from each scale. Multiple linear regressions and the AIC analyses were carried out in SAS v9.2 (SAS Institute, Cary, NC, U.S.A.).

Post hoc substratum test

Substratum (or bed sediment) size is often highly correlated with position within a catchment (Ferguson *et al.*, 1996). Additionally, maximising substratum heterogeneity in ecological communities has been suggested to promote temporally stable and diverse communities (Williams, 1980; Brown, 2003). To test whether substratum characteristics had an effect on mussel community composition at our sites, we conducted pebble counts at all sites (using multiple transects distributed across the mussel bed), with at least 100 pebbles measured at each site (Kondolf *et al.*, 2005). From these pebble counts, we derived texture distribution (D_{10} , D_{50} and D_{90}) and heterogeneity (D_{60}/D_{10} ; Williams, 1980). We performed Spearman rank correlations in SAS v9.2 to test relationships (Spearman $\rho > 0.51$, $\alpha = 0.05$) between mussel community composition (Bray–Curtis score) and substratum metrics, as well as between landscape and substratum metrics. Local substratum metrics were not included in the multivariate models described in the previous section because they are not measured at multiple scales.

Results

Mussel community structure

Species composition and dominance varied across sample sites. Overall, 18 species were detected at our sites in the Kiamichi River, 16 in the Little River and 18 in the Mountain Fork River (Fig. 3). Headwater sites were generally dominated by small-bodied mussels in the Lampsilini tribe (*Lampsilis siliquoidea*, *Villosa iris* and *Villosa lienosa*) that decreased in abundance downstream. *Fusconaia flava* (Pleurobemini tribe) and *Quadrula verrucosa* (Quadrulini tribe) tended to inhabit the mid-reaches. *Amblema plicata* (Amblemini tribe) became increasingly prevalent with increasing distance downstream, excluding the most downstream Kiamichi site. *Actinonaias ligamentina*, *Potamilus purpuratus* and *Obliquaria reflexa* (all larger-bodied mussels in the Lampsilini tribe) only occurred in the furthest downstream sites of the Kiamichi River.

The distributions described above reveal that mussel species composition was structured along a longitudinal gradient, which was also strongly supported by the polar ordination. The polar ordination explained 40% of

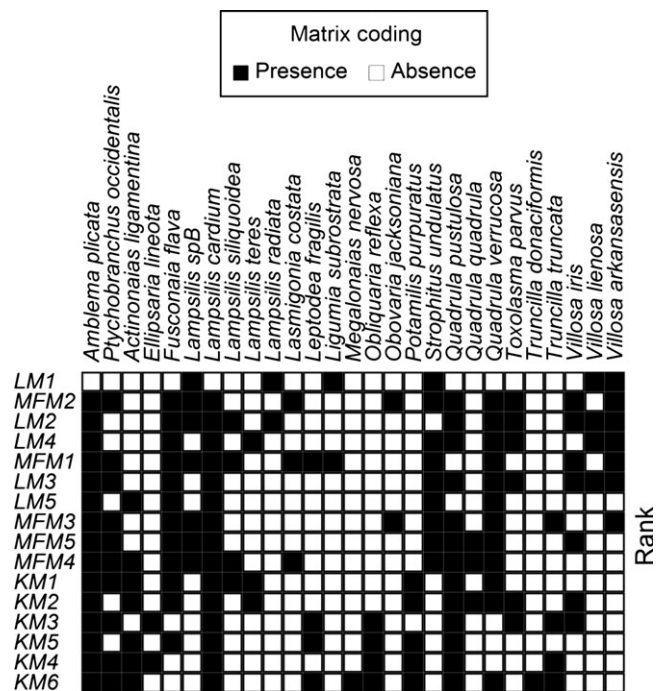


Fig. 3 Ordered matrix illustrating the presence and absence of species at all of the sites. The sites are ranked by the Bray–Curtis ordination score from lowest to highest. The most upstream site in the Little River (LM1) represents one pole in the ordination, while the most downstream site in the Kiamichi River (KM6) represents the other pole.

the variation in mussel communities. Not surprisingly, sites that were geographically closer tended to have more similar communities, and community structure was more similar at sites that were closer in longitudinal position (Fig. 4; Little River, $R^2 = 0.86$, $P = 0.01$; Kiamichi River, $R^2 = 0.66$, $P = 0.05$; Mountain Fork River, $R^2 = 0.53$, $P = 0.16$). Additionally, mussel communities occupying similar longitudinal positions in different catchments were more similar than communities within the same catchment that were far apart in longitudinal distance (all rivers; $R^2 = 0.77$, $P < 0.001$). Drainage area was also a good predictor ($R^2 = 0.73$, $P < 0.001$), but was highly correlated with distance from the headwaters. Across all rivers, mussel community composition changed predictably as the distance from the headwaters increased.

Landscape variables

The three rivers and their respective catchments were similar in physiography and hydrology (Table 1). Catchment area of our sites ranged from 73.5 to 2044 km². Drainage density was similar among the three catchments, ranging from 0.93 to 1.4 km km⁻². Channel slope

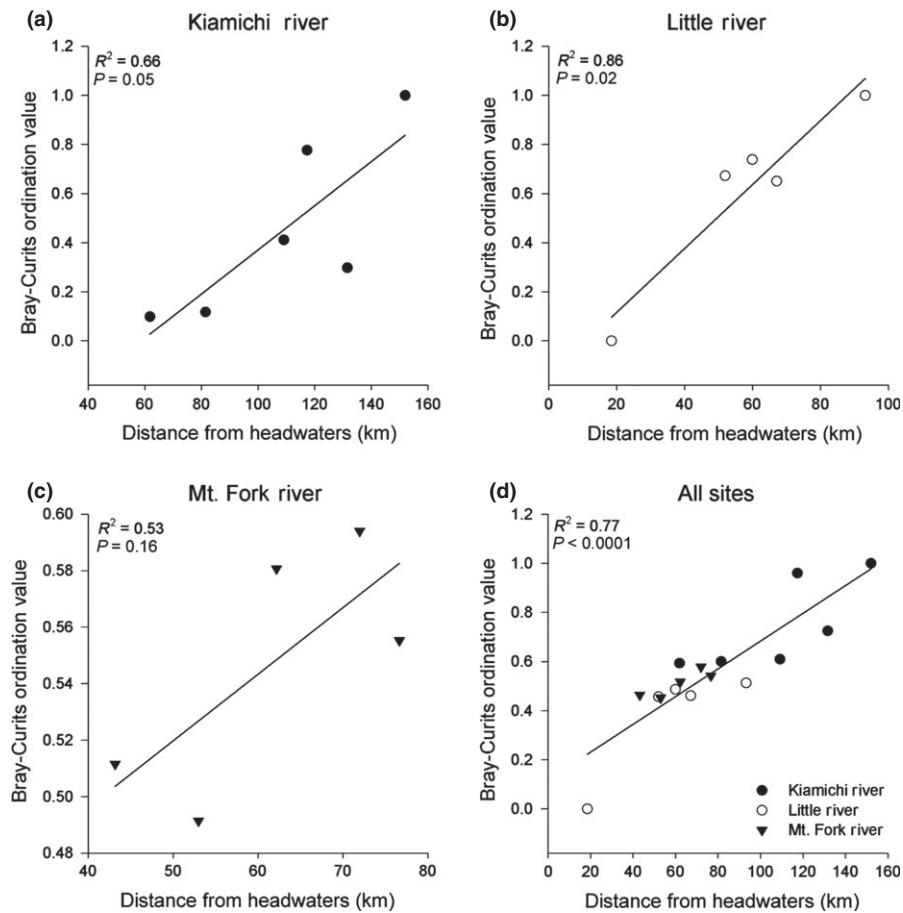


Fig. 4 Relationships between distance from the headwaters and the Bray–Curtis ordination value for the three rivers (a–c) and all sites combined (d). The Bray–Curtis ordination value is indicative of community structure; values that are more similar are sites that have more species in common and are similar in which species are dominant. Overall, sites that were closer together within a catchment had more similar species compositions, while sites across all catchments that were approximately the same distance from the headwaters had more similar species compositions.

was variable with headwater locations being the steepest (maximum 15.1 m km^{-1}). However, mean channel slope across the catchments was not highly variable (range of the most downstream sites: $2.3\text{--}4.3 \text{ m km}^{-1}$). Land cover varied across sites with among-site variation increasing with decreasing spatial scale (see Supporting Information). Forest was the dominant land cover at all three scales; however, its relative percentage decreased from catchment (70.9–87.1%) to reach scale (15.3–78.3%). Forest coverage was the only variable that was strongly correlated with distance from headwaters ($|r| = -0.75$). Water coverage varied little among the catchments, but was more variable at the reach and buffer scales. Wetland coverage was more variable at the reach and buffer scales and was highest in the Kiamichi River. Water (0–26.1%) and wetland (0–56.8%) percentages were particularly high at the reach scale. There were also differences in land cover among the catchments, including greater agricultural and urban cover in the Kiamichi (8–15.4%

and 2.6–3.1%, respectively) and Mountain Fork (8.8–15.3% and 3.8–4.1%, respectively) catchments compared to the Little River (1.2–3.2% and 1.6–3.3%, respectively) catchment. The rivers varied with respect to the area that was flooded frequently (5.1–11.4%), with the Mountain Fork River (5.1–5.9%) having the least area frequently flooded at the catchment scale.

The variables retained for the AIC models were mean channel slope, % water, % urban, % agriculture, % grassland/shrub, % forest, % wetland and % area frequently flooded. Correlation matrices indicated that multicollinearity was low among this subset of independent variables ($|r| < 0.60$).

Mussel community composition versus landscape variables

After accounting for distance from the headwaters, the residual variation in freshwater mussel community composition (23% remaining variation) was best described by

catchment- and buffer-scale predictors (Table 1). At the catchment scale, a model including channel slope, % wetland and % urban best predicted mussel community composition ($w_m = 0.111$, $R^2 = 0.43$), but this was not significant at $\alpha < 0.05$ ($P = 0.07$). Overall, channel slope accounted for over 23% of the residual variation in species composition at the catchment scale. The remainder of the variability was explained by % wetland and % urban land use, with both variables in the top three models; however, those models had a $P > 0.05$. At the buffer scale, channel slope and % wetland were in the top model ($w_m = 0.124$, $R^2 = 0.47$). Channel slope was also the primary explanatory variable at the buffer scale, accounting for over 26% of the residual variation in community composition. Per cent wetland was included in the top three models and explained 9% of the residual variation in species composition, while other land cover variables (% forest, % urban and % open water) had lower explanatory power in the models. Reach scale did the poorest job of describing mussel community composition with no single variable being in the top models (Table 1). Per cent wetland coverage was also influential at the reach scale and was included in the top 2 models. *Post hoc* substratum analyses revealed that community composition was not significantly correlated (Table 2) with minimum (D_{10} ; $\rho = 0.09$, $P = 0.73$), median (D_{50} ; $\rho = -0.18$, $P = 0.30$) or maximum (D_{90} ; $\rho = 0.22$, $P = 0.41$) substratum size or heterogeneity (D_{60}/D_{10} ; $\rho = -0.27$, $P = 0.34$). The only landscape and substratum metrics that were

significantly correlated with one another (among all scales) were D_{90} and channel slope at the site scale ($\rho = 0.57$, $P = 0.02$). Overall, land cover variables at the catchment and buffer scales better described mussel community composition after accounting for longitudinal position within the catchments.

Discussion

Longitudinal gradients and landscape drivers

We found that mussel community composition was influenced primarily by longitudinal position in the catchment or stream size, and by landscape factors after accounting for stream size. In addition, there was a predictable downstream shift in mussel community composition that was influenced by a few variables at the buffer scale. Sites in different catchments that were comparable distances from headwaters were more similar in mussel community composition than sites within the same catchment that were farther apart (Fig. 4), showing that species turnover is attributable to longitudinal position and suggesting that similar factors are regulating species compositions in these rivers. Higher species turnover with increasing longitudinal distance between sites can reflect dispersal patterns, increasing habitat heterogeneity over broader spatial scales, or both (Balvenera *et al.*, 2002; Brown, 2003; Maloney & Munguia, 2011). Overall, headwater communities were more variable and were composed of smaller, shorter-lived species, which may indicate that these communities experience greater environmental variability than more downstream sites, as shown by Haag (2012).

Mean channel slope at both the catchment and buffer scale influenced mussel community composition. Changes in slope may lead to a more variable stream-reach habitat and may be a driver of longitudinal shifts in community composition. Our results corroborate the findings of Arbuckle & Downing (2002) who showed that channel slope was important in determining density and species richness of mussel beds in an agriculturally influenced drainage. Channel slope has been shown to influence species compositions of other aquatic organisms, including shrimp and fish (Covich *et al.*, 1996; Mcgarvey & Hughes, 2008). Sites located closer to the headwaters tend to be more variable because they undergo more frequent high shear stress events during high flows and more drying down conditions during low flows. While headwater streams often are in high elevations with greater slopes, they are also smaller which influences pool size and permanence. Depths and vol-

Table 2 Substratum size and heterogeneity from pebble counts

| River | Site | D_{10} (mm) | D_{50} (mm) | D_{90} (mm) | Substratum heterogeneity (D_{60}/D_{10}) |
|----------|------|---------------|---------------|---------------|--|
| Kiamichi | KM1 | 2 | 25 | 100 | 22.5 |
| | KM2 | 2 | 15 | 115 | 12.5 |
| | KM3 | 2 | 15 | 50 | 10.0 |
| | KM4 | 2 | 30 | 145 | 17.5 |
| | KM5 | 10 | 50 | 172 | 7.0 |
| | KM6 | 9 | 29 | 95 | 4.0 |
| Little | LM1 | 4 | 30 | 85 | 10.0 |
| | LM2 | 2 | 40 | 255 | 32.5 |
| | LM3 | 10 | 35 | 80 | 4.0 |
| | LM4 | 0.5 | 45 | >256 | 80.0 |
| | LM5 | 10 | 40 | >256 | 5.5 |
| Mt. Fork | MFM1 | 5 | 28 | >256 | 8.0 |
| | MFM2 | 2 | 22 | >256 | 20.5 |
| | MFM3 | 11 | 52 | 114 | 5.5 |
| | MFM4 | 3 | 31 | 82 | 13.0 |
| | MFM5 | 1 | 22 | 77 | 28.0 |

None of these variables had significant Spearman rank correlations ($\rho > 0.51$) with the Bray–Curtis score.

umes of pool habitats generally decrease with increasing elevation, making headwater habitats less stable during drought (Sabo *et al.*, 2010). High water temperature is associated with drought in these rivers, and some species have been found to be more sensitive to high temperatures (e.g. *A. ligamentina*) than others (e.g. *Amblema plicata*) (Spooner & Vaughn, 2008). Larger volumes of water lead to habitats that are better buffered against thermal extremes, probably contributing to the community composition we observed. Additionally, high shear stress, which is often associated with headwater streams, has been shown to be associated with lower abundances of mussels (Gangloff & Feminella, 2007; Allen & Vaughn, 2010). Highly variable habitats are often considered to be suboptimal for aquatic organisms, whereas more stable habitats probably allow higher survivorship and reproductive success (e.g. Hutchinson, 1957; Brown, 1984). Life history of these organisms may be closely tied to the habitats in which certain species are successful (Haag, 2012). Thus, communities located closer to the headwaters may be better adapted than downstream communities to deal with stress, both dewatering associated with drought (Galbraith, Spooner & Vaughn, 2010) and high shear stress associated with spates.

Wetland coverage also seemed to influence mussel community composition at the catchment and buffer scales. Wetland coverage was positively correlated with distance from the headwaters and was still an influential explanatory factor for community composition after accounting for longitudinal position in the catchment. Inundation of wetlands provides water storage allowing attenuation of floods that mitigates the influence of high-flow pulse events on downstream sites (Mitsch & Gosselink, 2000; Zedler, 2003). The shift in community composition because of % wetland coverage is probably due to some species being more tolerant of high-flow events. Smaller, shorter-lived species (e.g. *V. lienosa*) that occupied the headwater sites may have greater turnover making them better suited to high stress environments. Rypel, Haag & Findlay (2009) found that mussel growth was negatively correlated with the annual flood pulse count. In our study, the Kiamichi River had higher percentages of wetland coverage, while the Mountain Fork had the least. The Mountain Fork sites had higher abundances of *Ptychobranchnus occidentalis*, *Strophitus undulatus* and *Fusconaia flava*, indicating that these species are not associated with wetland coverage. Species that were associated with the lower Kiamichi sites, such as *A. ligamentina*, probably need more stable flows that are associated with higher wetland coverage. Wetlands help reduce the frequency and magnitude of flooding which

contributes to greater habitat stability. Our results suggest that the protection of riparian wetlands may contribute to maintaining freshwater mussel communities.

Although we found a minor influence of urban land coverage at the buffer scale on mussel species composition, all sites had <4.2% urban coverage. Further research is necessary to understand the influence of urbanisation on mussel communities (see Brown *et al.*, 2010). Previous studies have shown shifts in aquatic insect assemblages in catchments with >10% impervious surface cover (Paul & Meyer, 2001; Roy *et al.*, 2003; Utz, Hilderbrand & Boward, 2009), which suggests that changes in hydrology, increased nutrient loads and increased sediment loads from urbanisation could also alter mussel community composition (Gangloff *et al.*, 2009). Because the rivers in this study are threatened by planned municipal water extractions (Oklahoma Water Resources Board, 2011) and further dam construction (Vaughn & Taylor, 1999; Galbraith *et al.*, 2010), an understanding of factors influencing mussel community composition is critical to future river management plans.

Scale dependency of mussel community composition

We found a predictable longitudinal shift in mussel community composition across the broad catchment scale (as influenced by position in the catchment), but the influence of land cover variables was best explained at the buffer scale. Previous studies have found correlations between riparian buffer condition and mussel communities (Mcrae *et al.*, 2004; Poole & Downing, 2004; Brown *et al.*, 2010). The effect of buffer condition on mussel communities is not definitive, but our results and others suggest that natural buffers maintain healthy mussel populations better than modified buffers (Poole & Downing, 2004), probably due to their mitigation of catchment disturbances (Jones *et al.*, 2010).

Stream organisms are influenced by factors at various temporal and spatial scales, including impacts at the catchment scale (Mcrae *et al.*, 2004; Andrew & Wulder, 2011). The temporal scale at which an organism experiences environmental factors can have a large influence on which spatial scale is most explanatory. For example, the presence and community structure of short-lived aquatic insects has been successfully predicted from local-scale variables, while the composition of longer-lived aquatic insects and fishes is better explained by catchment-scale variables (Morley & Karr, 2002; Yates & Bailey, 2011). Because mussels are long-lived and sedentary, their community structure should be reflective of factors that may change temporally at small spatial scales, but that are

integrated over time at larger spatial scales. For example, reach-scale land use measured recently may not reflect reach-scale conditions 20 or 30 years ago when a mussel bed was colonised, but such patchiness in land use should be apparent over time at the catchment scale. Variability measured at broad spatial scales may serve as a coarse filter on community composition because it influences aspects of local habitat suitability (Poff, 1997). This suggests that impacts at the catchment scale influence reach-scale processes, which can have a consequential effect on biotic communities.

Reach-scale factors were not predictive of mussel community composition in this study. While several reach-scale studies have found that shear stress influences the location and structure of mussel beds (Gangloff & Feminella, 2007; Allen & Vaughn, 2010), most studies focussing solely on local factors, such as substratum size, substratum heterogeneity and water chemistry, have not shown these to be good predictors of mussel community composition (Strayer, 2008). This is most likely because mussel community compositions should be governed by a hierarchy of factors including spatial variability (biogeographic history, biological attributes of species), dispersal (fish hosts dispersing mussels among patches, see below) and habitat (including both biotic and abiotic factors) (Vaughn & Taylor, 2000; Daraio, Weber & Newton, 2010). Thus, local factors are probably important, but are influenced by factors at a broader spatial scale (Burcher *et al.*, 2007). The catchment and buffer scales are probably better predictors because they encompass this hierarchy.

Our study provides empirical evidence of factors associated with mussel community composition, but did not investigate the mechanisms behind these patterns. There are broader scale mechanistic variables that may influence mussel community composition that we were unable to include in our study, such as the distribution and assemblage structure of fishes. Adult mussels are sedentary and movement of mussels between habitat patches is through dispersal of larval mussels (glochidia) attached to the gills and fins of fishes (Vaughn & Taylor, 2000). Mussel species vary in the type and number of suitable fish hosts, mechanisms employed in infecting the host(s), and timing of glochidial development and release (Barnhart *et al.* 2008). This variation has consequences for mussel dispersal abilities and population dynamics; thus, mussel distribution and abundance can be strongly influenced by the composition of the co-occurring fish assemblages (Haag & Warren, 1998; Vaughn & Taylor, 2000; Schwalb, Garvie & Ackerman, 2010; Schwalb *et al.*, 2011). Fish of the Ouachita Highlands are distinct and

speciose, and the rivers we studied contain similar fish faunas (Mayden, 1985). Fish assemblages can also be influenced by factors operating at the buffer and catchment scale (Andrew & Wulder, 2011; Yates & Bailey, 2011), and species turnover of fish, as was found in our study with mussels, occurs as a function of longitudinal stream distance (Maloney & Munguia, 2011). Thus, the occurrence of mussels and fishes may be influenced by the same set of catchment characteristics (Vaughn & Taylor, 2000; Rashleigh, 2008).

Mussels are sedentary and relatively long-lived (typically 10–25 years, but up to 190 years; Haag & Rypel, 2011) and thus likely respond slowly to landscape changes. In our study region, long-term habitat stability has aided the persistence of mussel communities, but new stressors may be causing shifts in species composition because land use alters catchments and riparian areas (Spooner & Vaughn, 2008; Jones *et al.*, 2010). Although their life history traits, such as immobility and dependence on fish hosts for dispersal, render them poorly adapted to deal with landscape change (Strayer *et al.* 2004), this is not always evident because relict, non-reproducing populations of adults can survive for many decades in degraded areas (Haag, 2009). Thus, freshwater mussels are probably subject to a large extinction debt (Haag, 2012) whereby there may be a long time lag between landscape alteration and final species extinctions (Spooner *et al.*, 2011; Vaughn, 2012). Therefore, effects of landscape disturbances, such as increased sedimentation, introduced species or high nutrient loads, may be slow and in some cases irreversible (Allan, 2004; Newton *et al.*, 2008). Our study indicates that mussel community composition is structured by a hierarchy of factors governed at the catchment and riparian buffer scale, but owing to their long life spans, the full effects of landscape change on mussels may not be fully realised for a long time. However, because catchment- and riparian-scale factors are important, protecting riparian buffers and associated wetland habitats should support healthier mussel populations and help lessen the potential extinction debt.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Watershed scale (entire drainage area upstream from sampling site) characteristics.

Table S2. Buffer scale (100 m wide, extending entire stream network upstream from sampling site) characteristics.

Table S3. Reach scale (100 m buffer 1 km upstream from sampling site) characteristics.

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