Associations between stream hydrogeomorphology and co-dependent mussel–fish assemblages: evidence from an Ohio, USA river system

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ABSTRACT

1. Understanding linkages among fluvial geomorphology, habitat, and aquatic biota is critical for effective stream ecosystem conservation. However, composite effects of hydrogeomorphic adjustment and condition, which collectively represent channel stability, on freshwater mussel and stream fish assemblages remain unresolved.

2. Associations between stream hydrogeomorphic characteristics (channel geometry, substrate composition, stream flow) and mussel and stream fish assemblages were explored at 20 study reaches characterized by riffle–pool interfaces (RPIs) in Ohio, USA.

3. At a coarse resolution using categorical classifications of equilibrium (i.e. stable) vs. adjusting (i.e. unstable) RPIs, overall fish and darter density was greater at adjusting RPIs ($P = 0.048$ and $P = 0.024$, respectively). Conversely, fish species richness was 1.2× greater at equilibrium than adjusting RPIs ($P = 0.047$).

4. Analysis of quantitative hydrogeomorphic data collected with fine-resolution surveys showed that hydrogeomorphic parameters explained from 20% (darter assemblage evenness) to 55% (density of mussels known to use darters as hosts) of the variation observed in all assemblages. Drainage area was significant in most models with variable influence: $R^2 = 0.10$ for darter species richness to $R^2 = 0.41$ for Simpson's diversity index of mussels with darter hosts. Other important predictor variables included embeddedness, velocity, shear stress, roughness, channel dimensions, and sediment size.

5. Whereas coarse-level fluvial geomorphic classifications may be meaningful for fish, they appear less so for mussels. Fine-resolution quantitative hydrogeomorphic variables provided substantially more information for both assemblages, although hydrogeomorphology–fish and hydrogeomorphology–mussel relationships were not consistent. Some of the strongest relationships related to mussels that use darters as hosts, suggesting that these species are particularly sensitive to hydrogeomorphic conditions.

6. Collectively, these results indicate that fluvial geomorphic condition and characteristics can simultaneously influence co-dependent stream biota. Stream conservation and management plans that include explicit hydrogeomorphic surveys may appreciably benefit cohabitating freshwater fish and mussel assemblages. Copyright © 2014 John Wiley & Sons, Ltd.

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INTRODUCTION

The integration of fluvial geomorphology, habitat, and aquatic biota is increasingly recognized as a powerful framework for stream ecosystem science and conservation (reviewed in Vaughan et al., 2009; Poole, 2010). Many studies have examined links between stream hydrogeomorphology and benthic macroinvertebrate density, diversity, and community composition (Sullivan et al., 2004; Sullivan and Watzin, 2008; Friberg et al., 2009). Multiple fluvial geomorphic features such as channel bedform, flow variability, and embeddedness have also been implicated as important factors governing fish assemblage diversity (Waters, 1995; Cianfrani et al., 2009), composition (Sullivan et al., 2006), and distribution (Baxter and Hauer, 2000; Fukushima, 2001). Furthermore, stream hydrogeomorphic properties including substrate size, shear stress, and channel gradient have emerged as strong predictors of freshwater unionid mussel abundance (Strayer and Ralley, 1993; Hastie et al., 2003; Gangloff and Feminella, 2007), density (Layzer and Madison, 1995; Johnson and Brown, 2000), and species richness (Vaughn and Taylor, 2000).

Whereas understanding of the influence of individual hydrogeomorphic characteristics on stream biotic communities has appreciably increased in recent years, the result of many individual physical processes (i.e. composite effects; sensu Sullivan et al., 2006) related to hydrogeomorphic adjustment and condition remains unresolved. Collectively, adjustment and condition describe channel stability (i.e. dynamic equilibrium). Streams and rivers are formed, maintained, and altered by the water and sediment they carry such that channel equilibrium occurs when sediment discharge, bed sediment particle size, stream flow, and stream slope are in balance (Lane and Richards, 1997). Equilibrium is lost when one of the variables changes, requiring one or more of the other variables to increase or decrease proportionately to maintain equilibrium and leading to adjustment of channel form and structure (Pizzuto et al., 2000). Stream stability may have serious consequences for stream biota that are intimately linked to their physical environment (Sullivan et al., 2004). As a result of shared habitat requirements, trophic relationships, and life-history interdependencies, the influences of fluvial geomorphology on linked biotic assemblages are also likely, although this notion has received little attention to date (but see Wright and Li, 2002; Sullivan and Watzin, 2008), yet may have high conservation payoffs. In particular, further understanding biotic–hydrogeomorphic linkages is highly relevant to current conservation and management efforts as natural resource organizations worldwide are increasingly incorporating hydrogeomorphic surveys as a routine part of stream assessments (Raven et al., 1997; Rowntree and Ziervogel, 1999; Sullivan et al., 2004).

Freshwater mussels – the most endangered group of aquatic animals across North America (Bogan, 2008) and of high conservation concern globally (Strayer, 2008; Haag, 2012) – may be especially susceptible to hydrogeomorphic conditions. As obligate ectoparasites in the larval stage, most freshwater mussels require a host fish (Watters et al., 2009). This reliance on a host fish requires suitable environmental conditions for both mussel and host. Vaughn and Taylor (2000), for instance, found that species richness of cohabitating mussel and fish assemblages were positively correlated in the Red River Drainage of Oklahoma and Texas, USA. For stream-dwelling mussels in the central US, many species of darters serve as critical hosts (e.g. Etheostoma caeruleum (rainbow darter) for Elliptio dilatata (spike)) (Watters et al., 2009).

Both mussels and darters tend to be highly sensitive to habitat alterations and have experienced significant population declines in the US Midwest (Williams, 1993; Lydeard et al., 2004; Osier and Welsh, 2007; Newton et al., 2008; Strayer, 2008). In Ohio, for instance, 54% of native freshwater mussel species are now endangered, extirpated, or extinct (Watters et al., 2009). Stream channelization and loss of riparian vegetation have led to mussel population declines (Strayer et al., 2004) whereas low temperatures downstream of bottom-release impoundments have impeded reproduction (Heinricher and Layzer, 1999). Many darter species, as benthic habitat specialists, are highly vulnerable to sedimentation and substrate embeddedness (Osier and Welsh, 2007).

Within this context, relationships between fluvial geomorphology and mussel–fish assemblages were

investigated at 20 stream reaches in Big Darby Creek, Ohio, USA. At a coarse resolution, the primary objective was to quantify differences in mussel and fish density and diversity between geomorphically stable stream reaches (i.e. low channel adjustment, in a state of dynamic equilibrium) and those in a state of adjustment (i.e. unstable). A secondary goal was to explore relationships between fish and mussel assemblages and hydrogeomorphic characteristics at a finer scale of resolution, thereby targeting potential mechanisms behind the coarse-scale patterns. Although largely framed within an exploratory context, it is anticipated that inferences drawn from this research can be used to refine current hydrogeomorphic–ecological associations and their conservation implications.

MATERIAL AND METHODS

Study reaches and categorical stability assessments

Twenty study reaches were selected in Big Darby Creek, a National and State Scenic River that drains 1441 km^2 of central-southern Ohio, USA (Figure 1). Of the ~44 mussel species in Big Darby Creek, 23 have rare or declining populations at the state (vs. federal) level. Many darter species, including the state endangered *Etheostoma maculatum* (spotted darter), and the state threatened *Etheostoma tippecanoe* (Tippecanoe darter) and *Etheostoma camarum* (bluebreast darter) are also endemic to Big Darby Creek. Following a paired-study design, 10 reaches that represented equilibrium (i.e. stable) riffle–pool interfaces (RPIs) and 10 reaches that represented adjusting RPIs were selected. To do this, coarse-resolution field indicators of channel stability were used to determine RPI conditions using signs of channel adjustment: channel degradation (e.g. exposed till or fresh substrate in the stream bed, recently abandoned terraces along the banks), aggradation (e.g. high degree of embeddedness, high width-to-depth ratio), change in planform (e.g. evidence of channel avulsions, newly formed channel bars), and over-widening (e.g. erosion on both sides of the banks in the riffle
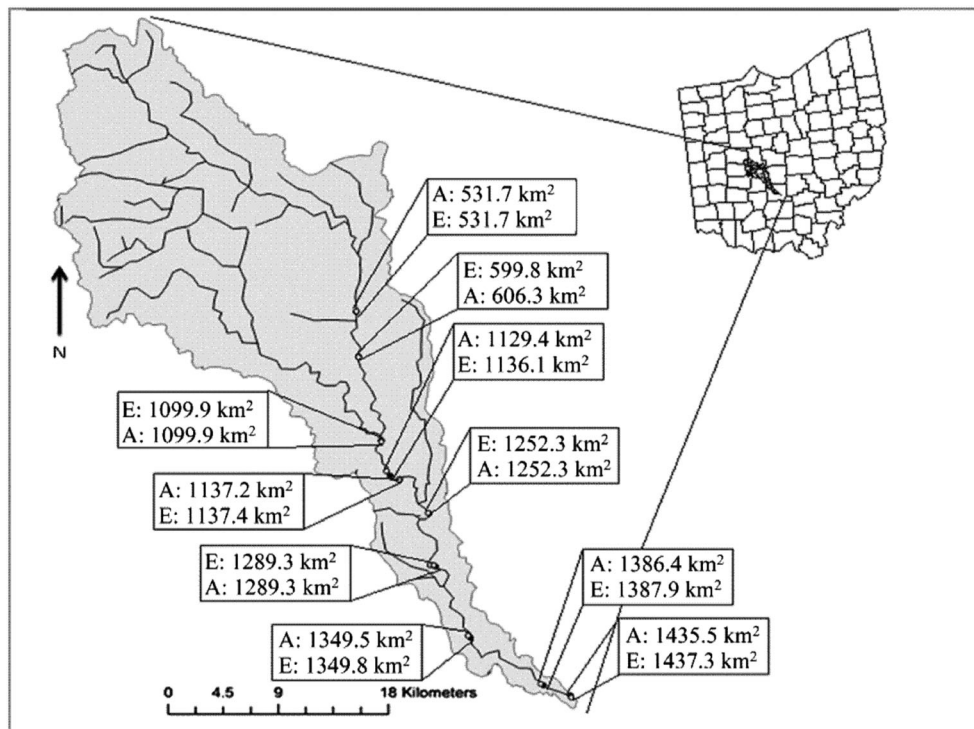

Figure 1. 2011 and 2012 study reaches (*n* = 20) in Big Darby Creek, Ohio, USA. Solid dots indicate equilibrium study reaches and open dots indicate adjusting study reaches. Drainage area for the sub-catchment of each reach is displayed in call-outs.

Aquatic Conserv: Mar. Freshw. Ecosyst. **25**: 555–568 (2015)

section, presence of channelization) conceptually following Sullivan *et al.* (2006). Those stream reaches that exhibited multiple indicators of adjustment were categorized as 'adjusting'. Conversely, reaches that exhibited no or only minor signs of adjustment were designated as 'equilibrium'. Given the paired-study design, surveys focused on highly adjusting and highly stable reaches, thus classifying reaches in the field was relatively straightforward.

Each RPI constituted a study reach and consisted of the flow sequence from the top of the riffle to ~5 m into the downstream pool, and represents critical habitat for both mussels and darters (Matthews, 1985; Strayer, 2008). On average, study reaches spanned ~100 m (from upstream to downstream). Reaches were selected so that each pair was located within the same larger stream segment to minimize differences in the immediate near-shore zone (10–15 m) and water quality to the degree possible (Table 1). Following study-reach selection, coordinated surveys of quantitative hydrogeomorphic measurements, fish, and mussel assemblages were conducted in the summer and early autumn of 2011 and 2012.

Quantitative hydrogeomorphic surveys

Following the initial coarse equilibrium vs. adjusting characterizations of RPIs, quantitative hydrogeomorphic assessments were conducted for each of the 20 stream reaches following procedures outlined in Cianfrani *et al.* (2004) in order to generate a suite of first-order hydrogeomorphic data (Table 2). Using a precision laser (LL300 SPECTRA Self Leveling Laser, Trimble Construction Tools Division, Dayton, Ohio), a longitudinal survey of each RPI was conducted to determine channel slope (m m^{-1}). Two cross-sectional surveys were performed at two

lateral transects running across the stream. Bankfull width (m), cross-sectional area (m^2), maximum depth (m), and mean depth (m) were measured at these transects and the values averaged to generate average values for each reach. Width-to-depth ratio (mean bankfull width ÷ mean bankfull depth) was subsequently calculated for each reach. The pebble count method (Wolman, 1954) was used to estimate bed grain size for each reach with 100 haphazardly selected clasts measured at each of the two transects using a gravelometer (D_{50} and D_{95}; particle size for which 50 and 95% of the particles are finer, respectively). Embeddedness was measured by evaluating the percentage fine sediment surrounding 10 cobbles per reach. Drainage area was calculated using the Hydrology Tool in the Spatial Analyst Toolkit in ArcGIS® 10.1 (Environmental System Research Institute, Redlands, CA, USA) with a 30 m digital elevation model from the USGA Geodata for Ohio (Ohio Geographically Referenced Information Program, 2013). From these field data, second-order hydrogeomorphic variables were generated using the Reference Reach Spreadsheet developed by Mecklenburg (2006) (Table 2).

Mussel and fish surveys

At each study reach, mussel assemblages were sampled using a systematic sampling method with random starts, which gives precise estimates for patchily distributed populations and distributes sampling effort throughout the study reach (Strayer and Smith, 2003). A grid overlay of each RPI was first established, with each grid representing a 0.25–m^2 quadrat. Three random starts were then selected using the Quick Random Number Generator cell phone application (CWE Software LLC, Lincolnshire, Illinois) to generate

Table 1. Summary statistics of water-quality parameters of the 20 riffle–pool interface (RPI) study reaches from Darby Creek, Ohio, USA

	Minimum	Median	Maximum	Mean	SD
Temperature (°C)	15.5	20.1	28.7	20.8	4.19
Conductivity (µS m^{-2})	476.0	830.0	924.0	798.0	105.0
DO (%)	67.1	130.3	293.0	156.8	70.5
pH	8.3	8.6	9.2	8.6	0.2

Table 2. Measured (first-order) and calculated (second-order) hydrogeomorphic characteristics of riffle–pool interface (RPI) study reaches. Second-order variables were generated using the Reference Reach Spreadsheet developed by Mecklenburg (2006)

Hydrogeomorphic characteristics	
First order	Second order
Bankfull width (m)	D'Arcy–Weisbach friction coefficient [a]
Channel slope (m m^{-1})	Discharge rate (m^3 s^{-1}) [b]
Cross-sectional area (m^2)	Froude number [c]
D$_{50}$ (mm)	Relative roughness [d]
D$_{95}$ (mm)	Shear stress (kg m^{-2}) [e]
Drainage area (km^2)	Velocity (m s^{-1}) [f]
Embeddedness (%)	
Maximum depth (m)	
Mean depth (m)	
Width–depth ratio	

[a]D'Arcy–Weisbach friction coefficient (f) calculated as $V = (8gRS/f)^{1/2}$, where V is velocity, g is gravitational acceleration, R is hydraulic radius (=area/wetted perimeter), and S is slope.
[b]Discharge rate (Q) calculated as $Q = VA$, where V is velocity and A is cross-sectional area.
[c]Froude number (F_n) is a dimensionless number expressing the ratio of inertial to gravitational forces: $F_n = V/(gd)^{1/2}$, where V is velocity, g is gravitational acceleration (9.81 m s^{-2}), and d is mean depth.
[d]Relative roughness calculated as $d/D84$, where d is mean depth, and D84 is the measured particle size where 84% of the particles are this size or smaller.
[e]Shear stress calculated as $1000RS$, where specific weight of water is 1000 kg m^{-3}, R is hydraulic radius, and S is slope (%).
[f]Mean channel velocity estimated with Manning's equation: V (velocity) = $1.49R^{2/3} (S/100)^{1/2}/n$, where R is hydraulic radius, S is slope (%), and n is Manning's Roughness Coefficient.

six random numbers for three coordinate pairs, which were measured from the most upstream point on the right bank. Subsequently, an average of 16 quadrats were established at each reach following Strayer and Smith (2003), with the exact number proportional to the area of the riffle. To survey mussels, each quadrat was excavated to a depth of 10–15 cm, or until no more bivalves were found. All unionid mussels collected from each quadrat were kept in an aerated bucket until they were identified and returned to the stream. Mussel density (number m^{-2}) was calculated based on substrate surface area (mean wetted width × reach length (m^2)) of each study reach.

Fish assemblages were surveyed across each study reach using a Smith-Root® LR-24 (Vancouver, Washington) backpack electrofisher under normal flow conditions. Two passes of each site were conducted using dip nets (4.76 mm mesh) and a downstream blocknet with 3.175 mm mesh (given the high flow velocity, an upstream net was not

necessary). After fish were collected, all individuals were held in a shaded, aerated bucket, identified to species, and released. Fish and darter density (number m^{-3}) were calculated based on volume (mean wetted width × reach length × mean depth (m^3)) of each study reach. Diversity for all assemblages was measured using species richness (S), evenness (E), and Simpson's diversity index (D) (see Methods S1, Supplementary material for equations).

Statistical analysis

Based on the paired-reach study design, the primary tool for analysing differences in hydrogeomorphology and characteristics of mussel and fish communities (e.g. density, S, D, E) between equilibrium and adjusting RPIs was the Student's paired t-test. However, because anomalous hydrogeomorphic properties at two reaches – including mid-channel islands (islet or sand bar within a river often with developed vegetation), flood chutes (short cuts taken by a river during high flows), and split channels (whereby one channel separates into two or more smaller channels) – set them apart from their respective pairs, only eight pairs were used in this phase of the analysis. All data were tested at $\alpha = 0.05$.

The goal of the second phase of the analysis was to explore the contribution of more detailed, quantitative hydrogeomorphic characteristics to patterns in mussel and fish assemblages. Because this component of the study was not based on a paired design, all 20 reaches were included. For this phase of the analysis, RPIs were considered sufficiently independent from each other given that study reaches were separated by at least one riffle–pool sequence and that fine-scale hydrogeomorphic controls on fish and mussel assemblages have been shown to be expressed at the site level (Sullivan *et al.*, 2006).

Principal component analysis (PCA) was performed on a suite of first- and second-order hydrogeomorphic variables (D$_{50}$, D$_{95}$, channel slope, mean depth, maximum depth, width–depth ratio, embeddedness, cross-section area, velocity, discharge rate, Froude number, D'Arcy-Weisbach friction coefficient, relative roughness, and shear stress) that were identified *a priori* as potentially

important characteristics to fish and mussel assemblages. Those PCA axes with eigenvalues >1 (Rencher, 1995) were retained. Along with drainage area, which was used as a stand-alone variable given the documented associations between fish assemblage characteristics and catchment size (Matthews and Robinson, 1998), the retained PCA axes were used in linear regression models as predictor variables. Mixed stepwise multiple linear regression was used to select optimal predictors for each of the endpoint biological measures (S, E, D, density for fish and mussel assemblages). Variable additions proceeded until the F-statistic for the step change fell below the $P < 0.05$ significance threshold. (See Methods S2 for further statistical considerations.)

Although the focus of this study was to explore the influences of hydrogeomorphic variables on fish and mussels, a correlation analysis was used to describe potential associations between fish and mussel assemblages. All statistical analyses were performed using JMP® Version 10 Statistical Discovery Software (SAS Institute, Cary, North Carolina). Logarithmic ($\log_{10}[x+1]$), square root ($\sqrt{x}$), or square (x^2) transformations were used, where necessary, to normalize data and eliminate heteroscedasticity before analysis (Zar, 1984).

Table 3. Descriptive statistics for mussel assemblages, fish assemblages, and hydrogeomorphic characteristics of riffle–pool interfaces (RPIs) from the 20 study reaches in Big Darby Creek, Ohio, USA. E = evenness, D = Simpson's diversity index, and S = species richness

	Equilibrium RPIs		Adjusting RPIs		All RPIs	
	Mean	SD	Mean	SD	Mean	SD
Biotic variables						
Mussels						
Density (individuals m^{-2})	0.14	0.21	0.12	0.26	0.13	0.23
E	0.44	0.46	0.33	0.44	0.38	0.44
D	0.31	0.37	0.22	0.38	0.27	0.37
S	2.9	3.8	2.4	3.5	2.7	3.6
Mussel$_{darter}$ density (individuals m^{-2})*	0.04	0.05	0.05	0.09	0.04	0.07
Mussel$_{darter}$ E*	0.26	0.42	0.23	0.39	0.24	0.4
Mussel$_{darter}$ D*	0.25	0.36	0.17	0.29	0.21	0.32
Mussel$_{darter}$ S*	0.8	1.1	0.8	0.9	0.8	1
Fish						
Density (individuals m^{-3})	2	0.9	3.1	2.8	2.5	2.1
E	1.12	0.67	1.33	0.91	1.23	0.79
D	0.19	0.04	0.23	0.12	0.21	0.09
S	10.8	2.1	10.3	3.7	10.6	3
Darter density (individuals m^{-3})	1.4	0.9	1.8	1.6	1.6	1.3
Darter E	0.81	0.1	0.75	0.1	0.78	0.1
Darter D	0.3	0.08	0.41	0.13	0.35	0.12
Darter S	5.4	1	4.8	1.5	5.1	1.3
Hydrogeomorphology						
First order						
Bankfull width (m)	35.7	10.5	33.2	11.4	34.5	10.8
Channel slope (m m^{-1})	0.016	0.015	0.009	0.008	0.013	0.012
D$_{50}$ (mm)	45.7	18.5	40.9	23.9	43.3	21
D$_{95}$ (mm)	110.6	68.7	92.8	42.9	101.7	56.5
Drainage area (km^2)	1122.2	314.3	1121.8	312.7	1122	305.2
Embeddedness (%)	36.8	11.6	33.8	20.3	35.3	16.2
Maximum depth (m)	1.4	0.4	1.3	0.6	1.3	0.5
Mean depth (m)	0.9	0.2	0.7	0.3	0.8	0.2
Width–depth ratio	36.8	8.3	44.8	21.4	40.8	16.4
Second order						
D'Arcy–Weisbach friction coefficient	0.1	0.01	0.11	0.02	0.1	0.02
Discharge rate (m^3 s^{-1})	86.3	40.0	61.6	61.9	73.9	52.3
Froude number	0.86	0.37	0.66	0.15	0.76	0.29
Relative roughness	23.9	10.4	22.7	18.7	23.3	14.7
Shear stress (kg m^{-2})	8.74	6.88	4.38	2.29	6.56	5.47
Velocity (m s^{-1})	2.54	0.82	1.82	0.52	2.18	0.76

*Mussel$_{darter}$ refers to mussels that use the species of darters found in study reaches as a host fish.

RESULTS

Biotic assemblages

Mussel density across all reaches averaged 0.13 individuals m^{-2} (SD = 0.23 individuals m^{-2}) (Table 3). Mussel S ranged from 0 to 12 ($\overline{x}$ = 3.6). Multiple mussel species were common across all study reaches (*E. dilatata*, *Ptychobranchus fasciolaris* (kidneyshell), *Lampsilis fasciola* (wavy-rayed pocketbook)). Mussels known to use darter species as their fish host (hereafter 'mussel$_{darter}$') ranged from 0 to 3 species ($\overline{x}$ = 1.0) across the study reaches. Fish density ranged from 0.5 to 9.8 individuals m^{-3} ($\overline{x}$ = 1.8 individuals m^{-3}) and fish S ranged from 6 to 13 ($\overline{x}$ = 10.0) (Table 3). Across all reaches, *Etheostoma blennioides* (greenside darter), *Notropis stramineus* (sand shiner), and *Etheostoma zonale* (banded darter) were the most common species, comprising 13.6%, 11.6%, and 11.5% of the assemblage, respectively. Darter species were observed in every study reach, where S ranged from 3 to 7 ($\overline{x}$ = 5.0). The most common darter species included *E. blennioides*, *E. zonale*, and *E. caeruleum*, occurring in 20, 19, and 17 of the 20 reaches, respectively. No significant correlations were found between the diversity or density of mussel and fish assemblages, or between mussel$_{darter}$ and darter diversity or density (P >0.05).

Hydrogeomorphic parameters

Drainage area of study reaches ranged from 531.6 to 1437.3 km^2 ($\overline{x}$ = 1270.9 km^2), although differences in drainage areas between paired adjusting and equilibrium RPIs were minimal (Table 3, Figure 1). Channel slope (m m^{-1}) was generally higher at the equilibrium RPIs (0.004 to 0.051 m m^{-1}, $\overline{x}$ = 0.016 m m^{-1}) than in the adjusting RPIs (0.003 to 0.023 m m^{-1}, $\overline{x}$ = 0.009 m m^{-1}). Average D_{95} (mm) was also larger in the equilibrium RPIs ($\overline{x}$ = 110.6 mm) than in the adjusting RPIs ($\overline{x}$ = 92.8 mm). Conversely, width-to-depth ratio, a measure of channel dimension, was greater and more variable in the adjusting RPIs (19.3 to 91.2, $\overline{x}$ = 44.8) than in equilibrium RPIs (24.1 to 48.2, $\overline{x}$ = 36.8). Average velocity and discharge ranged from 1.3 to 4.5 m s^{-1} and 10.2 to 216.8 m^3 s^{-1} across all study reaches, respectively. On the whole, both average velocity (m s^{-1}) and discharge rate (m^3 s^{-1}) were greater at equilibrium RPIs (Table 3).

Adjusting vs equilibrium RPIs

Mussel density was not significantly different between equilibrium ($\overline{x}$ = 0.18 individuals m^{-3}) and adjusting ($\overline{x}$ = 0.14 individuals m^{-3}) RPIs (P >0.05). Likewise, no difference in mussel$_{darter}$ density was observed between equilibrium ($\overline{x}$ = 0.04 individuals m^{-3}) and adjusting ($\overline{x}$ = 0.04 individuals m^{-3}) reaches (P >0.05). However, for both fish (t = –0.73, df = 14, P = 0.048) and darter assemblages (t = –1.25, df = 14, P = 0.024), density was higher in adjusting RPIs. Fish S was greater at equilibrium than in adjusting RPIs (t = 1.79, df = 14, P = 0.047), although S was not different for any of the other assemblages (P >0.05; Figure 2). Fish E was not significantly different between equilibrium and adjusting RPIs for any of the assemblages considered (P >0.05). D was 1.4 times lower for darter assemblages at equilibrium ($\overline{x}$ = 0.30, SD = 0.09) vs adjusting reaches ($\overline{x}$ = 0.43, SD = 0.13; t = –2.42, df = 14, P = 0.030) indicating significantly greater diversity in equilibrium reaches; for all other assemblages no significant difference in D was observed (P >0.05; Figure 3).
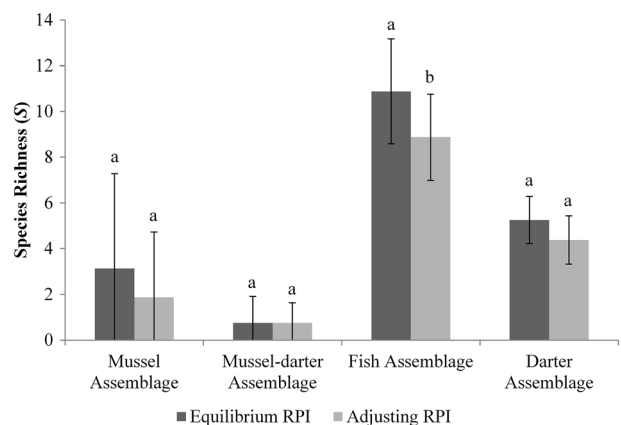

Figure 2. Species richness (S) of mussel assemblages, assemblages of mussels known to use darters as hosts, fish assemblages, and darter assemblages at equilibrium and adjusting riffle–pool interfaces (RPIs) in Big Darby Creek, Ohio, USA (n = 16). Significant differences based on paired t-tests are indicated by different letters a, b (P <0.05). Error bars are ±1 SE from the mean.
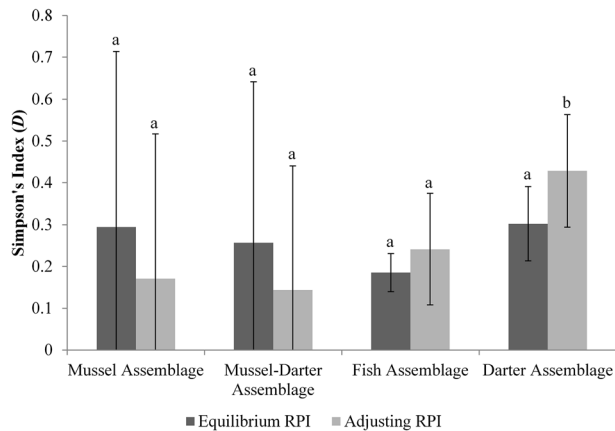
Figure 3. Simpson's diversity index (D) of mussel assemblages, assemblages of mussels known to use darters as hosts, fish assemblages, and darter assemblages at equilibrium and adjusting riffle–pool interfaces (RPIs) in Big Darby Creek, Ohio, USA ($n = 16$). Significant differences based on paired t-tests are indicated by different letters a, b ($P < 0.05$). Error bars are ± 1 SE from the mean.

Influences of quantitative hydrogeomorphic characteristics

The PCA of hydrogeomorphic and instream habitat characteristics identified four axes with eigenvalues >1, explaining 87% of the total variance (Table 4, Data S1, Supplementary material). Eleven regression models using PCA axes and drainage area as predictors and fish and mussel descriptors as responses were significant, illustrating that hydrogeomorphic characteristics were influential for a suite of linked mussel–fish characteristics

(Table 5). Across all models, the strength of the models ranged from R^2 of 0.20 (Darter E) to 0.55 (Mussel$_{darter}$ density). Drainage area was significant in 10 of the 11 models, explaining from 10% of the observed variation in darter S to 39% and 41% in fish D and mussel$_{darter}$ D, respectively. However, drainage area exerted a positive influence in some models (e.g. Fish and Darter S) and negative in others (Mussel$_{darter}$ S and D). Embeddedness Axis was also a common predictor variable (seven models), with R^2 values ranging from 0.08 (Mussel$_{darter}$ density) to 0.31 (Mussel$_{darter}$ E). The Velocity and Shear Stress and the Channel Dimensions and Roughness Axes contributed to significant Mussel$_{darter}$ density and D models; the Velocity and Shear Stress Axis contributed to the Mussel$_{darter}$ S model. For darter E and D, the Sediment Size Axis was a key explanatory variable (Table 5).

DISCUSSION

In this study, coarse-level classifications (i.e. geomorphic 'stability' of riffle–pool interfaces) discriminated between select measures of abundance and diversity of fish assemblages, but not mussels. Finer resolution quantitative hydrogeomorphic variables provided substantially more information

Table 4. Eigenvalues (>1.0) and the percentage variance captured by the principal components, along with each principal component's loadings and the proportion of the variance (r^2 = loading^2 × eigenvalue) shared with the PCA axes

Eigenvectors	PC1 - Channel Dimensions and Roughness		PC2 - Velocity and Stress		PC3 - Sediment Size		PC4 - Embeddedness	
	Loading	r^2	Loading	r^2	Loading	r^2	Loading	r^2
Bankfull width (m)	0.29	0.50	-0.17	0.12	-0.08	0.01	0.28	0.08
Channel slope (m m^{-1})	-0.21	0.27	0.37	0.56	-0.20	0.08	0.08	0.01
Cross-sectional area (m^2)	0.36	0.76	-0.05	0.01	-0.02	0.00	-0.09	0.01
D$_{50}$ (mm)	-0.10	0.05	0.02	0.00	0.64	0.87	0.00	0.00
D$_{95}$ (mm)	-0.04	0.01	0.04	0.01	0.65	0.89	0.03	0.00
D'Arcy–Weisbach friction coefficient	-0.30	0.54	-0.16	0.10	-0.09	0.02	-0.26	0.07
Discharge rate (m^3 s^{-1})	0.35	0.71	0.19	0.14	0.05	0.00	-0.08	0.01
Embeddedness (%)	0.18	0.19	0.04	0.01	-0.02	0.00	0.84	0.72
Froude number	-0.21	0.27	0.40	0.65	-0.11	0.02	0.05	0.00
Maximum depth (m)	0.38	0.84	0.12	0.06	0.00	0.00	-0.17	0.03
Mean depth (m)	0.37	0.82	0.16	0.10	0.10	0.02	-0.12	0.02
Relative roughness	0.35	0.72	0.13	0.07	-0.18	0.07	-0.28	0.08
Shear stress (kg m^{-2})	-0.13	0.09	0.45	0.84	-0.07	0.01	0.04	0.00
Velocity (m s^{-1})	-0.03	0.01	0.48	0.95	0.00	0.00	0.03	0.00
Width–depth ratio	-0.12	0.09	-0.35	0.50	-0.24	0.12	0.09	0.01
Eigenvalue	5.87		4.11		2.13		1.03	
Variance (%)	39.14		27.39		14.18		6.85	

Table 5. Explanatory variables and their coefficients in the significant multiple regression models for characteristics of mussel assemblages, assemblages of mussels known to use darters as hosts ($mussel_{darter}$), fish assemblages, and darter assemblages. E = evenness, D = Simpson's diversity index, and S = species richness

Model	Variable	Coefficient	R^2	F-statistic
Mussel density (ind. m^{-2}; $P = 0.015$)	Intercept	0.7966		
	Drainage area	-0.0005	0.29	0.015
$Mussel_{darter}$ density (ind. m^{-2}; $P = 0.013$)	Intercept	0.6305		
	Drainage area	-0.0004	0.36	0.001
	Embeddedness Axis	0.0510	0.08	0.098
	Velocity and Stress Axis	-0.0256	0.07	0.108
	Channel Dimensions and Roughness Axis	0.0159	0.04	0.249
$Mussel_{darter}$ S ($P = 0.035$)	Intercept	2.7010		
	Drainage area	-0.0017	0.14	0.022
	Embeddedness Axis	0.4308	0.18	0.040
	Velocity and Stress Axis	-0.1610	0.10	0.124
$Mussel_{darter}$ E ($P = 0.006$)	Intercept	0.7859		
	Embeddedness Axis	0.2378	0.31	0.004
	Drainage area	-0.0005	0.14	0.056
$Mussel_{darter}$ D ($P = 0.006$)	Intercept	1.1985		
	Drainage area	-0.0009	0.41	0.001
	Velocity and Stress Axis	-0.0455	0.06	0.126
	Channel Dimensions and Roughness Axis	0.0397	0.07	0.131
Fish S ($P = 0.018$)	Intercept	6.1654		
	Embeddedness Axis	1.2126	0.22	0.046
	Drainage area	0.0039	0.16	0.053
Fish E ($P = 0.013$)	Intercept	2.4721		
	Drainage area	0.0007	0.26	0.027
	Embeddedness Axis	0.1683	0.15	0.058
Fish D ($P = 0.004$)	Intercept	-0.3974		
	Drainage area	-0.0003	0.39	0.004
	Embeddedness Axis	-0.0436	0.09	0.103
Darter S ($P = 0.022$)	Intercept	3.6254		
	Embeddedness Axis	0.5801	0.26	0.028
	Drainage area	0.0013	0.10	0.119
Darter E ($P = 0.043$)	Intercept	0.7585		
	Sediment Size Axis	-0.0337	0.20	0.043
Darter D ($P = 0.045$)	Intercept	-0.2909		
	Sediment Size Axis	0.0326	0.18	0.115
	Drainage area	-0.0001	0.13	0.113
	Embeddedness Axis	-0.0370	0.08	0.180

for both mussel and fish assemblages, but hydrogeomorphology–fish and hydrogeomorphology–mussel relationships were not consistent either in direction or magnitude. Some of the strongest relationships related to the component of the mussel community that uses darter species as hosts, suggesting that these mussel species are particularly sensitive to hydrogeomorphic conditions. In addition, given that the current list of potential host fishes may be incomplete for the region, other mussel species may use darters as hosts and may also be highly sensitive to hydrogeomorphic change. Taken as a whole, the results illustrate that fluvial geomorphic condition and characteristics can simultaneously influence interdependent stream biota and suggest that an ecohydrogeomorphic approach

(*sensu* Vaughan *et al.*, 2009; Sullivan, 2012) may be a valuable tool in co-dependent fish–mussel conservation strategies.

Categorical hydrogeomorphic condition – adjusting vs equilibrium RPIs

Significant differences between adjusting and equilibrium RPIs were observed for fish (Figure 3), but not mussels, which may relate to the difference in mobility between mussels and fish. Fish, being more mobile and thereby integrating a broader area of the stream (e.g. through their daily foraging activities) may reflect the composite, reach-level effects of stream hydrogeomorphology. Fish have been shown also to be associated with coarse-level, categorical measurements of channel change in previous studies. Gorman and Karr

(1978), for example, observed that fish species diversity was lower in modified streams as opposed to natural streams. Sullivan *et al.* (2006) found that fish community diversity, density, and condition (i.e. as measured by a regional index of biotic integrity) were related to composite geomorphic adjustment in Vermont, USA streams. Although Sullivan *et al.* (2006) observed that fish density was greater in more stable reaches, the opposite pattern was found in the current study wherein both fish and darter density was lower in more stable reaches. In the study by Sullivan *et al.* (2006) the reach lengths were orders of magnitude larger (250–3000 km) than the reaches in this study (~100 m on average), and therefore fish responses were not limited to only a subset of the fish assemblage as in this study. Focused sampling on RPIs may have led to lower fish densities than if the full complement of stream habitats (i.e. runs, full pools, lateral habitats) had been surveyed (Langeani *et al.*, 2005).

Equilibrium RPIs, which supported greater fish S (Figure 2), were characterized by multiple physical habitat features thought to promote fish diversity including unembedded cobbles, a mixture of velocity–depth regimes (e.g. deep–fast, shallow–fast, etc.), and heterogeneous cover (large wood, overhanging vegetation, etc.) (Waite and Carpenter, 2000; Sullivan *et al.*, 2006; Casatti *et al.*, 2009). Similarly, greater darter diversity (as measured by D, Figure 3), was found in well-developed riffles in equilibrium RPIs with adequate microhabitats (e.g. velocity shelters, substrate, etc. (Chipps *et al.*, 1994; Harding *et al.*, 1998)). Dominant species within these assemblages included *E. blennioides*, *E. caeruleum*, and *E. zonale*, which are relatively abundant darter species in Ohio and are often found cohabiting in riffles of medium-sized streams (Trautman, 1981).

The lack of any relationship between mussels and RPI condition may indicate that composite hydrogeomorphic evaluations that synthesize reach-level adjustment are not of sufficient resolution. Because mussels are restricted in movement, they may experience the environment at the microhabitat scale. However, this does not preclude the potential for mussels to respond to changes in overall channel stability. For example,

Johnson and Brown (2000) found that mussel beds were more common in sections of their study stream where the substrate was more stable through time. Likewise, Cooksley *et al.* (2012) demonstrated that *Margaritifera margaritifera* (freshwater pearl mussel) were absent in unstable areas of high sediment deposition in the River Dee, Scotland. Greater understanding of the potential effects of channel adjustment on mussel assemblages will require further investigation.

Quantitative hydrogeomorphic variables influencing fish and mussel assemblages

Multiple investigations have shown that the distribution and abundance of host fishes can be strong determinants of mussel assemblage structure (Watters, 1992; Haag and Warren, 1998; Vaughn and Taylor, 2000). Although the primary focus in this study was the influences of hydrogeomorphic variables on fish and mussels, the lack of any significant correlations between both density and diversity of darter and mussel$_{darter}$ assemblages indicated that this may not be the case in the system studied. Indeed, both darter and mussel$_{darter}$ assemblages were influenced by hydrogeomorphic PC axes, indicating similar environmental determinants of the two taxa.

Drainage area, a common predictor in the models (Table 5), has been shown to be positively related to fish assemblage diversity and density in many studies (Newall and Magnuson, 1999; Park *et al.*, 2006). Mussel assemblage descriptors have been linked both to species richness of fish and drainage area. For instance, Watters (1992) found that the number of unionid and fish species was positively related to drainage area across Ohio, USA river systems ranging from 10 to 530 140 km^2, implicating both increased habitat heterogeneity (Atkinson *et al.*, 2012) as well as a greater likelihood of higher mussel diversity with increased host choices and/or life histories (Negishi *et al.*, 2013).

Embeddedness has often been shown to be negatively related to fish via a range of mechanisms (Nerbonne and Vondracek, 2001; Walters *et al.*, 2009). For example, embeddedness can depress benthic insect populations (Nerbonne

and Vondracek, 2001; Kochersberger *et al.*, 2012) and limit food availability for benthic insectivores such as darters (Osmundson *et al.*, 2002; Walters *et al.*, 2009; McGinley *et al.*, 2013). Although the results of this study were largely inconsistent with these findings (Table 5), relatively low levels of embeddedness across the study reaches ($\overline{x} = 35\%$) was probably insufficiently high to be prohibitive to fish (Drennen, 2003).

For mussels, the results indicate that a limited degree of embeddedness may be important for providing a sufficiently stable substrate, which is probably particularly important during high flow periods (Allen and Vaughn, 2010). However, extreme levels of embeddedness may be detrimental to mussels (Strayer, 2008). The observation that only mussel$_{darters}$ were influenced by embeddedness suggests that host–embeddedness relationships are also at play. For example, in the study system the mussel$_{darter}$ assemblage was dominated by *E. dilatata*, which relies primarily on *E. caeruleum* as a host (Watters *et al.*, 2009). Weston *et al.* (2010) found a positive correlation between embeddedness and the density of *E. caeruleum,* which commonly forages on the surface of the substrate rather than in the interstitial spaces. Thus, in spite of moderately elevated embeddedness*, E. caeruleum* may persist in sufficiently high densities to provide hosts for *E. dilatata* and facilitate its presence.

High shear stress was associated with lower abundance of mussels in the study system, a result consistent with Gangloff and Feminella (2007) and Allen and Vaughn (2010). Many species of adult mussels are thought to require intermediate current velocities that are sufficiently high to supply adequate food resources while not being so turbulent as to interfere with feeding or dislodge mussels downstream (Strayer, 2008). For example, Hastie *et al.* (2000) found an optimal current velocity of 0.25–0.75 m s^{-1} for populations of *M. margaritifera*. In this study, velocity was appreciably higher, ranging from 1.25 to 4.51 m s^{-1} ($\overline{x} = 2.18$ m s^{-1}). As with the Embeddedness Axis, the Velocity and Shear Stress Axis did not predict characteristics of the overall mussel assemblage, indicating that mussel$_{darter}$ species may have characteristics that make them more susceptible to

higher velocities and greater shear stress, such as little (e.g. *Lasmigona costata* (fluted shell)) to no shell sculpture (e.g. *E. dilatata* and *P. fasciolaris*), which has been shown experimentally to be beneficial for anchoring and anti-scouring (Watters, 1994).

Substrate size has been shown to be of considerable importance to stream fish through a variety of mechanisms (e.g. limiting food sources, reproduction and growth rates; Osmundson *et al.*, 2002; Shields *et al.*, 1994). In some cases, bed composition has been shown to be the dominant factor explaining fish assemblage characteristics (Walters *et al.*, 2003). In general, an increase in substrate size from fines to gravel and cobble is positively correlated with measures of fish diversity (Berkman and Rabeni, 1987; Waters, 1995; Jones *et al.*, 1999). The negative relationships observed in this study between sediment size and darter diversity probably indicates that levels of fine sediment were not sufficiently excessive to obscure biologically important habitat components such as spawning gravels, microhabitat refuges, and macroinvertebrate habitat (Chapman and McLeod, 1987; Harding *et al.*, 1998; Larsen *et al.*, 2009). These relationships may also be attributable to the fact that fine substrates (e.g. silt–sand) were typically found lower in the catchment where fish diversity tended to increase.

In spite of many strong relationships, there remains substantial unexplained variation in the models. Greater consideration of water quality (including contaminant, nutrient, and suspended sediment loads) is likely to be important, particularly for systems exhibiting high variability in water-quality parameters (Vaughn and Taylor, 2000; Cooksley *et al.*, 2012; Miller and Mackin, 2013). Linking the results with broader-scale factors, such as influences of land use and land cover and spatial variability, would strengthen mechanistic understandings of the impacts of hydrogeomorphic factors on fish and mussel assemblages. For example, Esselman and Allen (2010) and Kautza and Sullivan (2012) illustrated that local (i.e. reach level instream and riparian habitat), landscape (i.e. land cover, canopy cover, drainage area), and spatial factors (i.e. underlying spatial structure of sample sites across the study area) contributed to patterns seen in fish

assemblages. Further understanding the impacts of fluvial geomorphic conditions on linked mussel–fish assemblages will also require investigations that target hydrogeomorphic influences on the various life stages of both mussels and fish. Identifying threshold stream hydrogeomorphic conditions of particular concern to mussels and their fish hosts will also be important (Österling *et al.*, 2010).

Nonetheless, these results provide evidence that fluvial geomorphic condition and characteristics can simultaneously influence co-dependent stream fish and mussel assemblages. As stream channels are increasingly altered, critical mussel–fish interactions may be disrupted, leading to reduced survival of both taxa. Findings from contemporary studies such as this may only be capturing initial responses. Owing to relict, non-reproducing populations of adults that may survive for many decades in impaired rivers (Haag, 2009), mussel responses are likely to become evident only long after environmental alteration, leading to a significant extinction debt (Haag, 2012). The development of hydrogeomorphic-based management goals may facilitate dual-taxonomic management and conservation strategies and represent an important step in moving from single-species management to preserving functional species interactions. Thus, using fluvial geomorphology to underpin the monitoring of stream physical conditions can promote proactive planning and management of interacting and co-dependent species, and aid in addressing some of the challenges of single-species conservation approaches (Lindenmayer *et al.*, 2002; Dudgeon *et al.*, 2006; Ozaki *et al.*, 2006). Fluvial geomorphic surveys could also be used to target suitable areas for mussel or fish reintroductions and to prioritize restoration sites. Thus, we conclude that conservation and management strategies that include a hydrogeomorphic component may have substantial short- and long-term benefits for co-dependent stream fish and mussel assemblages.

ACKNOWLEDGEMENTS

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