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Microhabitat and Landscape Drivers of Richness and Abundance of Freshwater Mussels (Unionida: Unionidae) in a Coastal Plain River

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Abstract: Although rivers support significant unionid mussel (Unionida: Unionidae) diversity, Gulf of Mexico tributary rivers have been subject to changes in water quality and habitat due to altered watershed land use. We quantified mussel species richness and relative abundance and environmental factors in small tributary streams of the Pearl River, Mississippi-Louisiana. Freshwater mussel and habitat surveys were conducted at 27 stream sampling sites over two summers (9 sites revisited), and coverage of seven land use categories and seven geological categories above each reach were calculated. Mussels were patchily distributed (53% of sites sampled yielded mussels) and typically not abundant (only 26% of sites yielded >10 mussels). Surveys revealed nine species, with total abundance ranging from 0–66 mussels and richness ranging from 0–5 species per site. Assemblages were driven by an upper to lower watershed gradient of decreasing CPUE and richness, with microhabitat and water quality, land cover, and geology locally modifying this gradient. Environmental variables did not seem of sufficient magnitude to account for the patchy distributions and low abundances of mussels at most study sites, and we hypothesize that high discharge events related to tropical storm passage may have exerted an overriding influence on mussel assemblages in these streams through direct mortality and/or altered availability of suitable glochidial hosts.

Keywords: coastal plain streams; freshwater mussels; Unionidae; stream habitat; hurricanes

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1. Introduction

North America supports the greatest number of freshwater bivalves in the world, with about 300 species recorded in the order Unionoida [1]. Mussels are ecologically valuable to freshwater ecosystems [2], influencing nutrient cycling and water filtration [3], stimulating production across trophic levels by transferring nutrients and energy from the water column [4], and providing and improving habitat for other organisms [4,5]. Unfortunately, mussels are highly imperiled due to the numerous threats that face freshwater ecosystems [6], with 28% of native North American mussels federally listed as endangered or threatened, 65% considered imperiled [1], and only 70 species considered stable [7].

Many environmental factors operating at different spatial scales have been shown to strongly influence composition and abundance of freshwater mussel assemblages. At the landscape (catchment) level, land cover, e.g., percent wetland (positive) and percent urban cover (negative; [8–11]), percent agricultural land use (negative; [12,13]), percentages of alluvial [14], surficial [15], and aquifer-bearing [16] geologies, watershed slope [14], location within the watershed [17], land use compositional pattern [18], and human density within the watershed (negative; [19]) have all been reported to affect mussel distribution and abundance across the central and mid-central U.S. Although the overall importance of reach-scale variables to mussel density models can be low [18], stream size [20] and riparian habitat characteristics, such as forest versus grass-dominated riparian zones adjacent to mussel beds [21] and riparian wetland forest (positive) and urban development (negative) within buffers located upstream of bed locations [10,11], have also been found to influence mussel abundance and distribution.

At the mussel bed scale, streambed composition, such as predominance of sandy [22] and other fine substrates (positive; [23–27]), as well as low water velocities [27] and absence of shear stress [28,29] have been found to characterize inhabited microhabitats. Additional characteristics, such as the presence of woody debris [26,30] and proximity to the bank [20], have also been reported to promote higher mussel densities. Mussels appear to be very sensitive to contaminants [31,32], with species-specific increases in mortality in response to declining dissolved oxygen (DO) conditions [33,34]. Given the preceding array of explanatory factors that influence freshwater mussel abundance and distribution, development of conservation and restoration strategies faces significant challenges. Moreover, studies have identified substantial uncertainties regarding the influences of substrate composition and stream hydraulics on mussel ecology [35,36]. Nevertheless, the majority of studies indicate freshwater mussel abundance and diversity are negatively associated with excess sedimentation and increased suspended solids [35,37], increased water temperature [38,39], and depleted dissolved oxygen [33,40], factors often linked with agricultural practices and the loss of riparian woodlands [41,42]. Conversely, stable substrates, fine sediments (usually), stable flows and depths [24,43], groundwater inputs [25], and accumulations of woody debris [27,30] appear to favor maintenance of diverse mussel assemblages.

Central North America, including the northern coast of the Gulf of Mexico, is a region with very high diversity of unionid mussels [44]. However, relatively few studies (e.g., [33,36,45–47]) have investigated the ecology of freshwater mussels in streams within the Gulf Coastal Plains ecoregion. These streams are unique relative to those in more temperate regions of the U.S. that have been the focus of most freshwater mussel studies, with Gulf coast streams typically characterized by minimal gradients, fine sediments, hypoxia [40], and extreme periodic increases in discharge from tropical storms and hurricanes (e.g., [48]). The Pearl River basin was selected for this study as representative of a moderately-sized river system along the Gulf coast [49]. The Pearl River is a free-flowing coastal plain stream below Ross Barnett dam in central Mississippi that maintains natural connectivity with the floodplain during high water events. Land use within the Pearl River watershed is predominately agriculture and forestry with increasing urbanization from the New Orleans area along the lower river [50]. Erosion and sedimentation are the prime contributors to Pearl River pollution, and together with historic gravel mining have greatly altered this system [50]. The lower basin has experienced a loss of fish species diversity in recent decades [51,52], and although some losses have been mitigated through regulation of pollutants and disturbance [53], anthropogenic stressors continue to adversely affect the region (e.g., paper mill spills [54]).

Although freshwater mussels in the mainstem Pearl River have been recently surveyed [55], mussel assemblages in smaller tributaries of the lower river have received less attention [56,57]. Consequently, our study sought to document mussel distribution and abundance in tributary reaches of the lower Pearl River watershed. Specifically, we wanted to identify: (1) freshwater mussel species richness and relative abundance and (2) relationships between habitat (micro- and landscape) variables and freshwater mussel assemblages in these tributary streams.

2. Materials and Methods

2.1. Study Area

Coastal plain streams and rivers of the northern Gulf of Mexico are characterized by sand substrates with infrequent patches of embedded gravel, narrow and incised channels, mild elevation gradients, dense riparian hardwood vegetation (e.g., oaks (*Quercus* spp.)), warm water temperatures, and wide ranges of dissolved oxygen, often quite low for aquatic life [49]. Land cover in this region was converted to agriculture post-colonization for indigo (*Indigofera tinctoria*) and later cotton (*Gossypium* spp.). During the 20th century, agricultural lands were converted to timber production, usually loblolly pine (*Pinus taeda*). During the later 20th century and early 21st century, human population expansion urbanized areas along the coast and rivers, and corn (*Zea mays*) agriculture expanded. Generally, agriculture and urban land covers are more common closer to the Gulf of Mexico with more forest land cover at increasing distances from the coast.

2.2. Study Sites Selection

The Pearl River and its tributaries support about 40 species of freshwater mussels, including the federally threatened inflated heelsplitter, *Potamilus inflatus* (Unionida: Unionidae), with the mainstem supporting about 29 species [57,58]. Thirty-six sites were sampled (18 in 2015 and 18 in 2016) in 13 perennial tributaries of the lower Pearl River of southeast Louisiana and southwest Mississippi (Figure 1). Nine sites with recorded mussels from 2015 were re-sampled in 2016 to determine the role of interannual variability in estimated relative abundance and richness. Site locations were based on their proximity to the river mainstem and accessibility, which was limited due to the predominance of private land in the study watersheds.

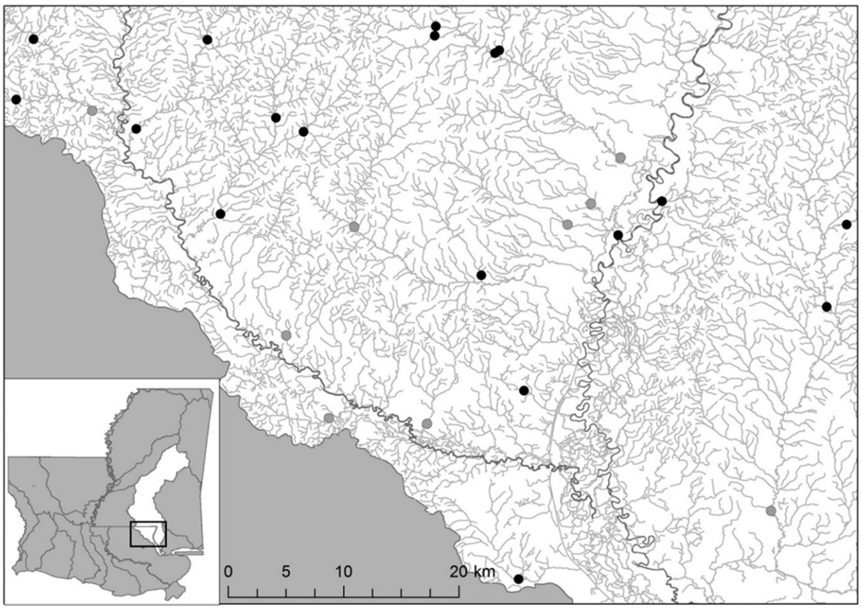

Figure 1. Tributary stream sites sampled during 2015 and 2016 in the Pearl River Basin, shown in white in the inset. Black circles represent sites sampled once. Grey circles on the map indicate sites that were re-sampled during the second sampling period.

2.3. Species Richness and Abundance

As the goal of this survey was to assess overall species composition, a timed visual and tactile mussel survey was carried out at each site [59], which allowed for comparisons with previous studies in the region ([55,56]; but see [60]). Two surveyors snorkeled along each stream bank for 45 min collecting all mussels in the wadeable portions (combined 1.5 h effort), resulting in sampled areas of approximately 45 m^2 (avg 2 min per m^2). Along-bank transects were chosen based on previous reports of greater mussel densities near stream margins [24,41]. All collected mussels were placed in mesh bags until survey completion, at which time identifiable mussels were returned to the stream, and unidentified taxa were placed on ice and returned to the lab for identification [57,61,62]. These data allowed for calculation of catch per unit effort and relative abundance for each species, as well as assemblage richness and evenness at each study site ([63]; but acknowledging concerns in [64]).

2.4. Microhabitat and Landscape Drivers

Cross-stream transects were placed every 10 m along the surveyed reach, and flow velocity (cm/s) and water depth (cm) were measured at 25%, 50%, and 75% of stream width along each transect. We also recorded stream width (m), bank height (m), bank angle, dominant vegetation, and canopy density (%), as well as water quality parameters (dissolved oxygen (DO), specific conductance, turbidity, pH, and temperature) measured with a YSI 650 handheld multi-probe. Three sediment samples were collected across the width of the stream and dry-sieved to obtain percent composition by weight according to a modified Wentworth classification [65]. This variable was expressed as percent less than the maximum sediment size for the class (e.g., % <0.500 mm refers to all sediment less than very coarse sand). Classes included pebble (>16 mm); gravel (2–4 mm; 4–8 mm; 8–16 mm); very coarse (1–2 mm), coarse (0.5–1 mm), medium (0.25–0.5 mm), fine (0.125–0.25 mm), and very fine (0.0625–0.125 mm) sand; and silt (<0.0625 mm [66]). In addition, within-stream distance (km) to the mainstem was estimated with ArcMap 3.2 (Environmental Systems Research Institute, www.esri.com; accessed on 16 October 2016).

All landscape variables were estimated with ArcMap 9.2 and Spatial Analyst (Environmental Systems Research Institute, www.esri.com). Following the methods described in [67,68], based on USGS HUC12 subcatchments, land cover percent area (km^2) was estimated for the drainage area upstream of each sample site with NOAA 2010 C-CAP Regional Land Cover (30 × 30 resolution). Similarly, geological percent area (km^2) was also estimated within the same drainage footprint, based on study site locations within the geology shapefile for model input (United States Geological Survey, Louisiana and Mississippi geology shapefile).

2.5. Statistical Analysis

The large number of physical and chemical variables measured and the relatively low mussel frequency of occurrence suggested variable reduction and reorganization was needed [67]. We separated explanatory variables into a set expected to have relatively low correlation among each other and a second set of substrate size variables (substrate size classes) that were expected to have higher correlations among each other, as substrate size variables were expressed as percent less than, which means that large sizes include smaller sizes. The highly interrelated nature of the second set of substrate measures suggested a separate reduction method than the first set. Following [68], we used ordination for temperature, dissolved oxygen, specific conductance, pH, turbidity (NTU), and watershed land cover and geology, expressed in terms of percent composition (e.g., % forested wetland and % high terrace). We explored several ordinations (principal component analysis, detrended correspondence analysis, and nonmetric multidimensional scaling) and selected principal component analysis of the correlation matrix of variables based on criteria described in [68] ((detrended correspondence analysis and non-metric multidimensional scaling; *package vegan*, Program R, vers. 4.1.0 [69,70]; principal component analysis; *PROC FACTOR*, SAS vers. 9.4, SAS Institute, Inc., Cary, NC, USA). Principal components were selected for further analyses by the broken-stick test [71]. For the substrate data, we examined Pearson correlations among size classes [67] to determine less-correlated categories that might be influencing mussels in a different manner than closely correlated size classes (Pearson correlation matrix; *PROC CORR*, SAS vers. 9.4). This process identified three important size classes, % <0.5 mm that was correlated with all larger sizes and was used to represent this correlated group, and % <0.25 mm and % <0.125 mm, both of which were uncorrelated with other sizes.

Mussel catch-per-unit effort (abundance; CPUE) and species richness, based on sample coverage-based richness, sensu [72] and others [73] were analyzed by finite mixture models, which are a useful set of models when multiple processes and probability distributions are needed [74,75]. In this case, mussels were not found in some streams, and when found, mussels CPUE was generally low. Therefore, two processes could be modeled from the data: (1) the process responsible for presence/absence of mussels and (2) the process determining mussel abundance or richness, when present. Although the models herein were applied as zero-inflated models, finite mixture models differ from zero-inflated generalized linear models in how variability is modeled (i.e., within and between mixtures) and often are capable of modeling count data in situations where generalized linear models cannot adequately account for count data variability [76]. Additionally, finite mixture models can quantify the variability accounted for each process of interest. For both CPUE and species richness, we used finite mixture models to fit a zero-inflated negative binomial model with two processes (components), with component one modeling the presence/absence of mussels with a degenerate distribution and component two modeling either CPUE or species richness as the response variable. Explanatory variables included selected substrate size classes (% <0.5 mm, % <0.25 mm, and % <0.125 mm) and principal components (PCs 1–7) in a finite mixture model with a log link and negative binomial distribution (finite mixture model; *PROC FMM*, SAS Vers. 4.3, SAS Institute, Inc., Cary, NC, USA) for CPUE and an identity link and normal distribution finite mixture model for mussel richness. Only the 27 first-time samples of 36 total samples collected were included in the finite mixture model. The nine revisited samples in 2016 were compared to the 2015 samples to examine inter-annual variability as a potential explanation of low relative abundance and richness (i.e., mussels could have been missed during a single site visit and detected in another visit) by generalized linear models with a log link and negative binomial distribution (generalized linear model; *PROC GLIMMIX*, SAS, Vers. 4.3, SAS Institute, Inc., Cary, NC, USA) for CPUE and an identity link and normal distribution for richness. The combination of link and distribution was determined by $X^2/df(\hat{c})$ fit statistic [77].

To determine relationships between microhabitat physical characteristics with land cover and geology, stream substrate size classes associated with either CPUE or species richness were compared to watershed land cover and geology, expressed in terms of percent composition (e.g., % forested wetland and % high terrace) by ordination. Several ordinations were compared for this analysis (e.g., canonical correlation analysis, canonical correspondence analysis, and nonmetric multidimensional scaling), with the final selection based on axis length and STRESS2 criteria (canonical correlation analysis; *PROC CANCORR*, SAS vers. 4.3 and canonical correlation analysis and nonmetric multidimensional scaling; PROGRAM R, vers. 3.3.3, package *vegan*, [69,70].

3. Results

3.1. Mussel Survey

Over the course of the study, a total of 174 mussels belonging to nine different species were collected at 19 of the 36 sites, with 17 sites yielding no mussels. Although none of the nine species were federally listed as threatened or endangered, *Anodontoides radiatus*, *Elliptio crassidens*, *Pleurobema beadleianum*, and *Villosa vibex* are considered species of greatest conservation need in Louisiana [50]. Due to concerns regarding identification of *P. beadleianum*, identification was confirmed based on tissue sequenced (CO1/16S primers) and compared to reference sequences in Geneious software (unpublished data). Total abundance and species richness averaged 4.83 (+1.96 SE) mussels (range 0–66) and 1.22 (+0.26 SE) species (range 0–5) per site, respectively. *Villosa lienosa* was the most abundant and widely distributed species, with six of the species represented by less than 10 individuals (Table 1, Figure 2).

Table 1. Sites where mussels were collected in Pearl River tributary streams during 2015 and 2016. Data include number of each species at each site, relative abundance (percentage of total mussels collected within a site), frequency of occurrence (percentage of sites occupied by each species), and estimated sample coverage based on Chao and Jost [52]. Collections at Ben's Creek, Hays Creek (2 reaches), Lawrence Creek (2 reaches), Peter's Creek (2nd visit), Peter's Cutoff, Pushepatapa Creek (2nd visit), Sal's Branch, Stubb's Creek, Talisheek Creek, Thomas Creek, and West Hobolochitto Creek (2nd reach) yield no mussels and are not included.

Site	*Anodontoides radiatus* (Conrad, 1934)	*Elliptio crassidens* (Lamark, 1819)	*Lampsilis claibornensis* (Lee, 1838)	*Plectomerus dombeyanus* (Valenciennes, 1827)	*Pleurobema beadleianum* (Lea, 1961)
Adams Creek			1		
[1] Adams Creek					
Bogue Lusa Creek					8
[1] Bogue Lusa Creek					2
Crains Creek					1
Deer Lick Creek	1		1		2
House Creek					
Mill Creek					
[1] Mill Creek					
Miller Creek	1		1		6
Peter's Creek					6
Pushepatapa Creek					5
[1] Pushepatapa Creek					1
Silver Creek	3	52			3
Silver Springs Creek			1		
Talley's Creek			3		
[1] Talley's Creek			1		
West Hobolochitto Ck.			1	1	
[1] West Hobolochitto Ck.					
Relative abundance	2.9%	29.9%	4.6%	0.6%	19.5%
Frequency of occurrence	15.8%	5.3%	31.6%	5.3%	47.4%

Site	*Quadrula refulgens* (Lea, 1868)	*Uniomerus declivis* (Say, 1831)	*Villosa lienosa* (Conrad, 1834)	*Villosa vibex* (Conrad, 1834)	Estimated Sample Coverage
Adams Creek			1	1	0.42
[1] Adams Creek			1	1	0.37
Bogue Lusa Creek			7		0.53
[1] Bogue Lusa Creek			1		0.53
Crains Creek					0.17
Deer Lick Creek			2	1	0.64
House Creek			2	2	0.37
Mill Creek			4		0.33
[1] Mill Creek			1		0.33
Miller Creek			1	1	0.64
Peter's Creek			2		0.53
Pushepatapa Creek					0.20
[1] Pushepatapa Creek					0.20
Silver Creek			7	1	0.90
Silver Springs Creek					0.05
Talley's Creek		3	7		0.41
[1] Talley's Creek		3	21		0.41
West Hobolochitto Ck.	2		1		0.06
[1] West Hobolochitto Ck.	1				0.02
Relative abundance	1.7%	3.4%	33.3%	4%	
Frequency of occurrence	10.5%	10.5%	73.7%	31.6%	

[1]. Superscript indicates a revisit in 2016.

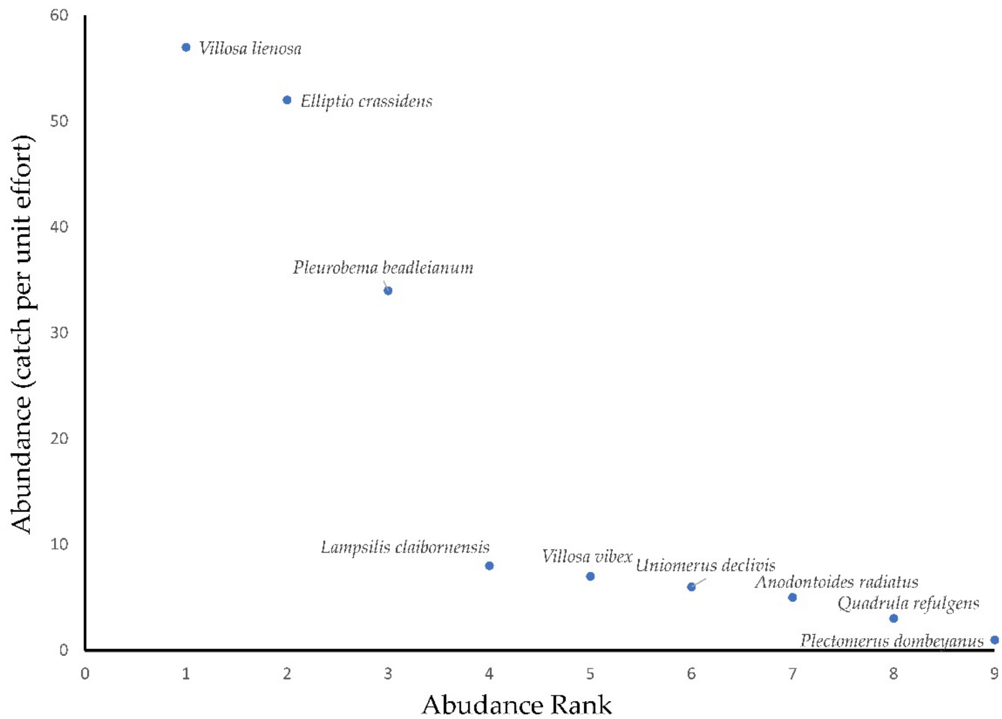

Figure 2. Relationship between species abundance and abundance rank across all sites.

3.2. Microhabitat Characteristics

Riparian vegetation included trees, shrubs, and herbaceous plants, with trees being the most common riparian vegetation at most of the sampling sites. The average canopy cover was 72.6% + 2.4 SE (Table 2). In situ measurements indicated none of the streams were experiencing hypoxia (DO < 2.0 mg/L) at the time of sampling. Although variability among sites in measured habitat metrics was evident, most of the streams were shallow (<0.5 m) with low (<15 cm/s) current velocities. Sediment particles < 0.12 mm made up a small proportion of the substrates at all sites, although overall, >70% of the sediment at 18 of the 27 sites was composed of particles <1.0 mm (Table 3), with only six sites having >10% of the substrate greater than 16 mm.

Table 2. Maximum, minimum, and mean (standard error; SE) values for measured physical and water quality variables in Pearl River tributary streams during 2015 and 2016.

Variable	Mean (SE)	Maximum	Minimum
Temperature (°C)	24.4 (0.4)	29.3	22.1
Dissolved Oxygen (mg/L)	7.2 (0.3)	9.6	3.9
Specific Conductance (µmhos/cm)	0.04 (0.01)	0.1	0.02
pH	7.4 (0.1)	8.3	5.5
Turbidity (NTU)	10.1 (2.7)	59.6	0.3
Depth (cm)	46.3 (1.3)	121.0	
Flow Velocity (cm/s)	14.1 (0.7)	83.8	0
Bank Height (m)	1.5 (0.04)	5.0	0.2
Bank Angle	42.4 (1.4)	90.0	2.7
Stream Width (m)	7.9 (0.3)	21.5	0.4
Distance to mainstem (km)	12.4 (2.2)	44.0	0.1
Canopy Density (%)	72.6 (2.4)	100.0	6.3

Table 3. Percentage of substrate less than each size class in Pearl River tributary streams sampled in 2015 and 2016.

	Sediment Diameter (mm)							
Site	**16**	**8**	**4**	**2**	**1**	**0.5**	**0.25**	**0.12**
Big Trib	99.9	99.9	99.3	98.1	90.4	72.3	14.2	0.6
Adam's Creek	99.2	98.7	97.6	95.6	93.0	62.2	10.7	0.4
Ben's Creek	99.5	99.1	98.1	96.1	92.3	44.9	8.1	0.2
Bogue Lusa Creek	99.8	99.7	99.5	98.7	95.4	35.3	4.9	0.2
Crains Creek	99.2	97.6	96.5	95.1	92.7	32.6	2.9	<0.1
Deer Lick Creek	88.6	74.3	65.9	61.0	56.2	27.4	2.3	0.1
Hays Creek	81.7	57.9	41.7	30.7	25.5	14.7	4.1	0.2
Hays Creek Site 2	91.5	86.3	83.6	81.8	78.1	18.4	1.7	<0.1
House Creek	99.5	99.4	99.2	98.5	97.6	57.4	10.2	0.2
Lawrence Creek	77.0	65.0	55.8	50.0	46.1	14.4	2.4	<0.1
Lawrence Creek Site 2	100.0	99.9	99.9	99.9	99.7	20.4	2.0	<0.1
Mill Creek	82.8	58.3	45.1	38.5	35.0	21.5	2.7	<0.1
Miller Creek	99.2	99.1	98.8	98.3	97.2	29.9	3.1	<0.1
Peter's Creek	99.6	99.1	97.5	96.4	94.7	29.6	7.9	0.4
Peter's Cutoff	98.8	98.1	95.6	91.4	87.4	52.0	18.4	0.7
Pushepatapa Creek	99.8	99.3	98.3	95.9	90.8	41.5	9.2	0.2
Pushepatapa Site 2	90.1	73.7	61.5	54.3	43.9	9.3	1.7	<0.1
Sal's Branch	88.9	59.1	36.6	23.5	17.5	6.2	1.0	<0.1
Silver Creek	72.7	61.8	57.5	52.4	35.6	4.7	1.0	<0.1
Silver Springs Creek	94.6	87.2	83.8	82.1	73.0	41.8	12.8	0.3
Stubbs Creek	95.2	85.9	74.0	60.2	48.1	22.5	2.5	0.1
Talisheek Creek	99.6	99.5	99.4	99.0	96.4	48.9	5.0	0.1
Talley's Creek	91.6	67.1	54.6	47.6	44.7	38.5	5.5	0.1
Thomas Creek	96.3	93.9	90.1	87.1	78.4	49.1	6.5	0.1
West Hobolochitto Creek	100.0	99.9	99.8	99.3	97.6	53.8	5.6	0.1
West Hobolochitto Site 2	99.7	98.5	95.7	92.5	88.5	39.6	3.9	0.1
White Sands Creek	97.76	94.31	91.30	88.6	84.4	46.8	5.7	0.1

3.3. Land Use and Geology

Agriculture was the most abundant land use category, comprising 49% of the total area upstream of sample sites, followed by evergreen forest (22%) and wetlands (22%; Table 4; Figure 3). Deciduous forest was the least abundant land use category, making up only 0.6 percent of the total area upstream of sample sites. Of the geologic types, High Terrace was the most extensive, comprising 67% of the total sample area on the Louisiana side of the river. Deweyville Terrace was the least abundant type, making up 0.2% of the total sample area. Pascagoula Hattiesburg geology was the most extensive geologic type on the Mississippi side of the river, making up 73% of the total area sampled, with coastal deposits being the least extensive at 1.6%.

Table 4. Maximum, minimum, and means (standard error; SE) percent land cover above each mussel sampling site in Pearl River tributary streams sampled in 2015 and 2016.

Variable	**Mean**	**Maximum**	**Minimum**
Land Cover Types			
Developed	1.69% (0.00)	3.44%	0.58%
Agriculture	50.21% (0.02)	63.18%	23.12%
Deciduous Forest	0.64% (0.00)	1.71%	0.14%
Evergreen Forest	20.98% (0.01)	36.79%	9.09%
Mixed Forest	3.90% (0.00)	8.07%	0.79%
Wetland	21.56% (0.02)	53.40%	10.02%
Barren	1.02% (0.00)	8.09%	0.16%

Table 4. *Cont.*

Variable	Mean	Maximum	Minimum
Geology			
% Alluvium	20.55% (0.02)	57.06%	1.39%
% Prairie Terraces	22.84% (0.07)	98.61%	0.00%
% High Terraces	56.48% (0.07)	95.74%	0.00%
% Deweyville Terraces	0.13% (0.00)	2.02%	0.00%
% Pascagoula Hattiesburg	69.82% (0.06)	85.32%	58.61%
% Citronelle Formation	19.83% (0.08)	32.43%	0.00%
% Coastal Deposits	10.35% (0.10)	41.39%	0.00%

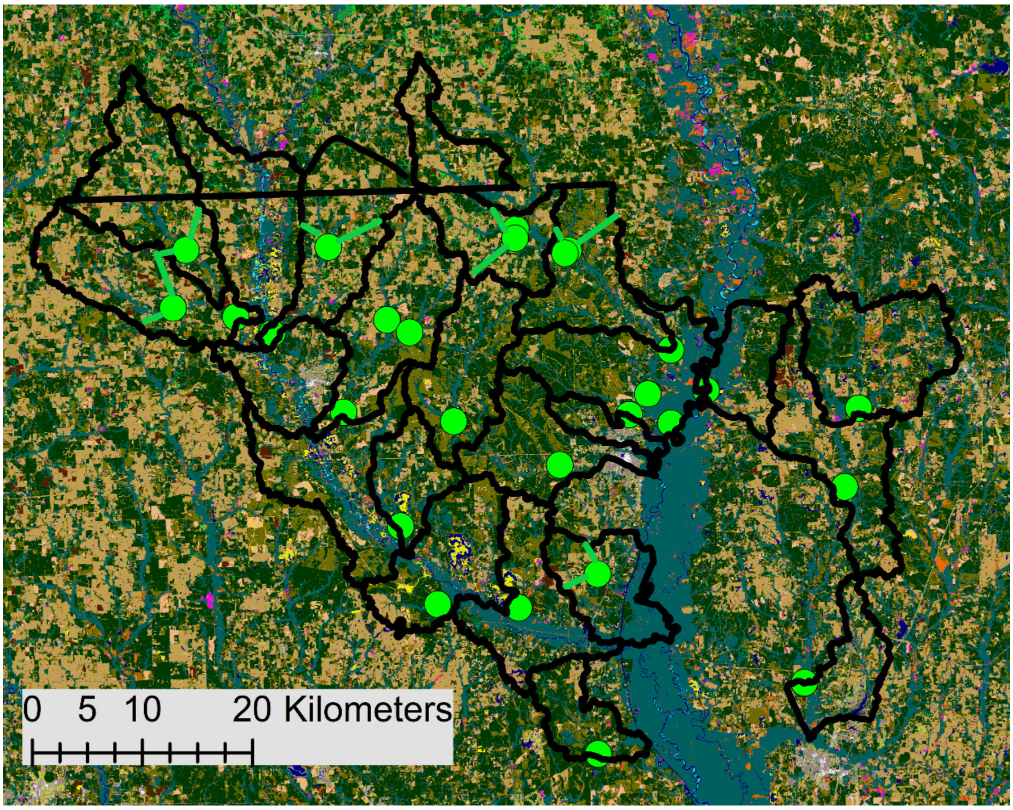

Figure 3. Watershed boundaries used to estimate land cover upstream of sampling sites (green circles). Boundaries (black lines) determined from U.S. Geological Survey hydrological units (12 digits codes). Green lines indicate the portion of the watershed upstream of some sampling sites that was analyzed. Otherwise, the entire upstream contributing watershed area was used. Land cover was obtained from U.S. National Oceanic and Atmospheric Agency 2010 C-CAP Regional Land Cover. Land cover types were developed (orange), water (dark blue), agriculture (tan), deciduous forest (light green), evergreen forest (dark green), mixed forest (olive green), wetland (light blue), and barren (yellow).

3.4. Analyses of Mussel CPUE and Richness

Principal component analysis followed by the broken stick test resulted in seven interpretable principal components (Table 5). Following [78], we considered |0.50| the threshold for identifying important coefficients, due to our low overall sample size. PC 1 described an upper watershed (i.e., further from the Gulf of Mexico; lower PC scores) to lower watershed (i.e., closer to the Gulf of Mexico; higher PC scores) gradient of water quality, land cover, and geology, specifically temperature (lower upstream), DO (higher upstream), % agriculture (lower upstream), % evergreen forest (higher upstream), % Alluvium (lower upstream), % High Terraces (lower upstream), % Pascagoula Hattiesburg (higher upstream), and % Citronelle Formation (higher upstream). PC 2 described sites higher in the watershed with greater pH, % deciduous forest, % mixed forest, % wetland,

and lower % Coastal Deposits. PC 3 described sites lower in the watershed with lower % agriculture, but higher % alluvium and % Coastal Deposits. PC 4 was negatively associated with % mixed forest. PC 5 was associated with sites with specific geologic conditions (% Deweyville Terraces) and higher pH. PC 6 was negatively associated with % evergreen forest, and PC 7 was positively associated with higher DO.

Table 5. Standardized scoring coefficients between variables with principal components (PCs). Shaded numbers were considered informative in interpretation of each PC.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
Temperature	0.59	0.17	−0.31	0.43	−0.41	0.07	0.22
Dissolved oxygen	−0.55	0.12	0.23	0.28	−0.20	−0.10	0.52
Specific conductance	0.46	0.27	−0.36	0.23	0.44	0.32	0.15
pH	−0.09	0.59	0	0.24	0.50	−0.08	−0.09
Turbidity	0.27	−0.29	0.39	−0.27	0.44	0.23	0.08
% Developed	−0.33	−0.31	−0.38	0.38	0.28	0.27	0.18
% Agriculture	−0.60	−0.24	−0.69	−0.13	0.03	−0.02	0.10
% Deciduous forest	−0.48	0.64	−0.08	−0.37	0.04	0.28	−0.02
% Evergreen forest	0.56	−0.45	0.20	0.06	0.15	−0.56	−0.04
% Mixed forest	−0.36	0.60	−0.08	−0.62	0.18	0.05	0.06
% Wetland	0.24	0.54	0.61	0.21	−0.13	0.36	−0.08
% Barren	0.33	−0.35	0	−0.02	−0.48	0.38	−0.08
% Prairie	0.17	−0.67	−0.08	−0.46	0.02	0.37	0.06
% Alluvium	−0.54	0.01	0.53	0.48	−0.13	0.35	−0.10
% High Terrace	−0.80	0.13	0.01	0.27	0	−0.37	−0.11
% Deweyville	0.08	−0.38	0.17	0.37	0.73	0.11	−0.01
% Pascagoula	0.80	0.48	−0.19	0.02	−0.01	−0.10	0.09
% Citronelle	0.63	0.43	−0.47	0.16	0.01	0.02	−0.17
% Coastal	0.45	0.21	0.54	−0.32	0.10	−0.20	0.31
Variance Explained	23.5%	16.6%	12.3%	10.3%	9.4%	7.2%	5.9%

For mussel CPUE, the zero-inflation component of the finite mixture model was statistically significant (β = 1.16 (±0.58 SE), z = 2.02, p = 0.04) and explained 76.1% of the probability in the model. Water quality, habitat, land cover, and geologic variables only explained 23.9% of Mussel CPUE, which was negatively related to PC 1 (β = −2.69 (±0.56 SE), z = −4.80, $p < 0.01$), PC 2 (β = −2.42 (±0.44 SE), z = −5.86, $p < 0.01$), % less than 0.250 mm (β = −0.050 (±0.0.02 SE), z = −3.28, $p < 0.01$), and % less than 0.125 mm (β = −19.40 (±0.4.70 SE), z = −4.13, $p < 0.01$), and positively related to PC 4 (β = 6.47 (±1.23 SE), z = 5.25, $p < 0.01$), and PC 5 (β = 4.46 (±0.82 SE), z = 5.40, $p < 0.01$). CPUE was higher in upstream sites with higher DO (PCs 1, 7), pH (PCs 2, 5), % evergreen forest (PC 1), % mixed forest (PCs 2, 4), % Pascagoula (PC 1), % Citronelle Formation (PC 1), and % Deweyville Terraces (PC 5). In contrast, CPUE was lower downstream in sites with higher temperatures (PC 1), % less than 0.250 mm, % less than 0.125 mm, % agriculture (PC 1), % wetland (PC 2), % deciduous forest (PC 2), % alluvium (PC 1), % Coastal Deposits (PC 2), and % High Terrace (PC 1).

Mussel estimated richness did not have a statistically significant zero-inflation component in the finite mixture model (β = 0.24 (±0.40 SE), z = 0.60, p = 0.55), which explained 56.0% of the probability in the model. Mussel richness was positively related to higher PC 4 (β = 1.05 (±0.81 SE), z = 4.94, $p < 0.01$), PC 5 (β = 0.81 (±0.15 SE), z = 5.54, $p < 0.01$), PC 7 (β = 0.81 (±0.16 SE), z = 5.11, $p < 0.01$), and negatively associated with higher PC 1 (β = −0.47 (±0.95 SE), z = 5.25, $p < 0.01$), PC 2 (β = −0.51 (±0.06 SE), z = −8.27, $p < 0.01$), % less than 0.250 mm (β = −0.10 (±0.02 SE), z = −4.96, $p < 0.01$), and % less than 0.125 mm (β = −3.56 (±0.66 SE), z = −5.34, $p < 0.01$). Mussel richness was higher in upstream sites with higher DO (PCs 1, 7), % evergreen forest (PC 1), % Deweyville Terraces (PC 5), % Pascagoula Hattiesburg (PC 1), % Citronelle Formation (PC 1), and lower temperature (PC 1), % less than 0.125mm, % mixed forest (PCs 2, 4), % deciduous forest (PC 2), % wetland (PC 2), % Alluvium (PC 1), % High Terraces (PC 1), and % Coastal Deposits (PC 2).

Many variables were correlated with multiple PCs and were also usually associated with richness. However, pH was both positively (PC 5) and negatively (PC 2) associated with richness, as was % mixed forest (positively with PC 4, negatively with PC 2.

Although interannual variability was a potential explanation of low relative abundance, richness, and frequency of occurrence, analyses did not support strong evidence of interannual variability in CPUE or richness. Fewer mussels were sampled during the second visit to the nine revisited sites. However, the comparison in the generalized linear model was not statistically significant (β = −0.50 (±0.61 SE), t = −0.82, p = 0.42). Similarly, fewer species were sampled in the second year of sampling revisited sites, yet the difference was also not statistically significant (β = −0.75 (±0.46 SE), t = −1.62, p = 0.13).

Canonical correlation analysis identified one significant canonical variate (CV) correlating land cover and geology with stream characteristics (overall Wilk's Lambda—0.03, $F_{24, 26} = 4.73$, $p < 0.01$, CV 1 approximate $F_{24, 26} = 4.73$, $p < 0.01$, CV 2 approximate $F_{11, 14} = 1.41$, $p = 0.27$). The canonical correlation for the first CV was 0.93, and the CV contrasted both higher % less than 0.250 mm (0.74) and % less than 0.125 mm (0.96) with higher % evergreen forest (0.57), % Deweyville Formation (0.65), % Coastal Deposits (0.51), and lower % agriculture (0.55).

4. Discussion

The overarching goals of this study were to describe relationships between landscape-level and microhabitat environmental variables and the species richness and relative abundance of freshwater mussels in southeastern coastal plain streams. Overall, data analyses suggested two conclusions. First, mussels are generally uncommon in upper tributaries of the Pearl River watershed. Patchy distributions (53% of sites had mussels) and low abundance (26% of sites yielded >10 mussels) characterized mussel assemblages across the study area, despite this region's central location in an overall area of high mussel diversity [7,44,79]. Further, analyses suggested that sampling was more likely to fail to capture mussels than to capture mussels (76%) or a species (56%), i.e., among randomly selected stream sites in this watershed, only approximately one in four sites would yield mussels. Thus, presence/absence of the mussels accounted for considerably more variation in the data than measured microhabitat, land cover, or geology variables.

Second, mussel relative abundance and richness follows a pattern of greater relative abundance and richness in the upper watershed, with both declining in tributaries closer to the Gulf of Mexico, concomitant with changes in water quality, land cover, geology, and substrate. Interestingly, similar influences of longitudinal position in the watershed and landscape variables were reported for mussels in the Kalamazoo River in Michigan [80]. Where mussels were present, decreasing CPUE and richness appeared to be largely driven by an upper to lower watershed gradient. Microhabitat and water quality (dissolved oxygen, pH, temperature, % less than 0.250 mm grain size, and % 0.125 mm), land cover (% agriculture, % wetland, % deciduous forest, % evergreen forest, and % mixed forest), and geology (% Alluvium, % Citronelle, % Deweyville, % Pascagoula, % coastal geology, and % high terrace geology) modified this gradient to locally influence CPUE and richness. This pattern has not been previously reported in the southern coastal plain and is strikingly similar to patterns of higher habitat quality and mussels in the upper watershed of River Raisin, also in Michigan [15]. Taken together, these results suggest opportunities and challenges to mussel conservation and restoration projects in the southeastern coastal plain.

In this study, CPUE and richness were typically much lower compared to earlier studies employing timed-search methods in lower reaches of streams this region [80,81] but were comparable to sites sampled in the Bogue Chitto River watershed by [56] (6.3 individuals per effort; average 1.5 species per site). Importantly, the author of [56] trained this sampling team to ensure comparable methods and effort, and we are confident that surveys accurately reflected mussel assemblages at the study sites. However, sparseness of the assemblages in these streams does not imply unimportance to regional biodiversity. Our collections included *Anodontoides radiatus* and *Uniomerus declivis*, neither of which were found in recent (2012–2014) mainstem Pearl River mussel surveys ([82]; Kayla Kimmel, Baton Rouge U.S. Fish and Wildlife Conservation Office, personal communication), emphasizing the contributions of tributary streams to overall mussel diversity of larger river systems.

Microhabitat data at the study sites were representative of coastal plain systems, i.e., low gradients, extensive woody debris, and silt/sand substrate mix [49,83–85]. Mussels exhibited positive and negative associations with pH, but pH was likely less important than the correlated land cover and habitat variables in the PCA, as pH was below 6.6 in only 3 of the 27 streams and was not found to be an important structuring variable for mussel assemblages in Gulf of Mexico coastal plain streams and rivers [84]. No adverse DO conditions were present at the time of sampling, though hypoxic (<2 mg/L) events and their associated effects on mussels and fishes [40,41] could have occurred nocturnally or seasonally due to stream eutrophication and high BODs [86]. Although relatively high across study sites, DO levels were still positively associated with mussel CPUE and richness, suggesting higher DO or conditions that enhance and maintain higher dissolved oxygen (e.g., reaeration, higher flows, and shading) were important for mussels. The association of higher mussel richness and higher DO was also noted in [84], although they also recognized the association of higher DO with a suite of other characteristics associated with higher mussel abundances, including forested land cover. Low DO is common in Louisiana streams [87], and despite negative associations between low DO levels and mussel abundance (e.g., [41]), other studies also have sampled mussels in coastal streams characterized by very low DO (e.g., [40,88]). In these Pearl River tributaries, it is likely that, similar to pH, associations with DO actually reflect associations with position in the watershed (i.e., upper watershed sites had higher DO and were where most of the mussels were found).

Although stream temperatures were not highly variable and were lower than critical thermal limits [89,90], analyses indicated mussels were negatively associated with higher temperatures, or the lack of shading in more open downstream channels that would promote increased temperatures. Higher temperatures increase mussel energetic expense, including oxygen consumption and regulation [34]. Although higher temperatures and lower DO could both have negatively impacted mussels, associations with temperature may also have reflected position in the watershed.

Substrate size classes also influenced CPUE and richness, with CPUE and richness decreasing with increasing % less than 0.250 mm and % less than 0.125 mm. Although juvenile mussels have been positively associated with larger substrate particle sizes [15,22,43], adults are often associated with finer sediments, based on the idea that reduced habitat disturbance (e.g., velocity and turbulence) favors mostly fine substrates, which in turn is positively associated with mussel presence, species richness, and abundance [24,35]. However, in this study, adult mussels were more abundant with higher richness in sites with relatively coarser substrate sizes. Generally, sites with higher fine sediment were associated with coastal deposits and geology lower in the watershed. However, a few sites with fine sediment (Adam's Creek, Silver Springs Creek, and Big Creek Tributary) were associated with more evergreen forest cover further from the Gulf of Mexico. These finer sediment sizes have been reported to reduce aquatic insect richness as well [86,91,92], and these results further support efforts to control excess fine sediment inputs in these coastal streams. Although not assessed in this study, it is likely the fine sediment in these sites was the result of past timber harvesting activities in these pine forests, which has been shown to contribute significant amounts of fine materials to coastal plain streams, particularly in the absence of best management practices [93].

Geology and land cover are intrinsically tied with position in the watershed [83] and may be affecting substrate composition and indirectly playing a role in mussel abundance and distribution. High areal coverages of developed land, primary agriculture, and low land cover percentages of evergreen forest suggested increased runoff may be limiting habitat suitability in some of these streams. High Terrace watersheds are often characterized by elevated soil erosion, bank failures, channel instability, flashy stream flow, and high rates of sediment displacement [86]. Increased urban/disturbed land area is associated with increased runoff and more erratic hydrology in small streams [94]. Increasingly flashy hydrographs resulting from greater water yield in developed (agriculture, urbanization, deforestation) lands may be reducing mussel habitat quality in adjacent streams from benthic scouring and shear stress (e.g., [28,29]), and increased mortality from displacement [14,22]. Negative associations with deciduous forest, mixed forest, and wetlands were surprising, given that the native cover type in lower elevations in this region is bottomland hardwoods [95], which was positively associated with mussels in Texas [19]. Historical collections of many mussel species in bottomland hardwood streams and rivers, including ones sampled in this study, have been reported [56,57]. However, bottomland hardwoods have been reduced and altered over time, and changes to these forests have been associated with declines and localized extirpations in native fish species [50,51]. As a consequence, the negative land cover associations detected in this study may reflect past changes in the landscape resulting in instream habitats that are no longer suitable for freshwater mussels.

Between the collection efforts of [56] during the summers of 2004 and 2005 and this study, Hurricanes Katrina (August 2005), Rita (September 2005), and Gustav (August 2008) impacted this region, potentially affecting mussel abundance, richness, and habitat. Disturbances associated with the passage of Hurricane Katrina were implicated in the decline of some mussel species in the Pearl River mainstem [55], although overall impacts on the river's mussel assemblage were not substantial. In the same region, significant declines in fish abundances and localized extirpations were reported following passage of Hurricanes Katrina and Rita [52,96]. Similarly, post-hurricane shifts in fish species assemblages were found in the Atchafalaya River and Pascagoula River [97,98]. Although pre- and post-hurricane mussel surveys have not been conducted in these coastal plain tributaries, these data together with those of [56] suggest (in the absence of widespread watershed land-use changes in this area) hurricane effects on mussel richness and abundance may be spatially and temporally extensive in the smaller upstream tributaries of these coastal plain river systems. Given slow growth and low reproductive rates, freshwater mussels may be particularly susceptible to long-term assemblage changes related to periodic large disturbances, such as flash flooding events associated with hurricanes and other high-precipitation tropical storms characteristic of the southeastern U.S. coastal plain. Further, storm-event related loss of mussel richness could be exacerbated by a reduction in multi-species facilitation [4,99] and altered distribution and abundance of appropriate glochidial fish hosts [41]. Similar responses to precipitation events have been observed to influence plant richness [100–102], and due to the sessile nature of freshwater mussels, the response of mussels to these disturbances may be more like plants than fish. Although sampling before and after hurricanes can be logistically difficult, development of long-term mussel and fish monitoring sites in selected streams would be invaluable for assessing the relative roles of anthropogenic and weather-related factors in structuring mussel assemblages in coastal streams along the Gulf of Mexico. We are aware of no system-wide changes in land use that could account for this pattern of scarcity across several watersheds on both sides of the lower Pearl River, which was un-expected given the documented high diversity of this region. Although we have no long-term data to support our hypothesis, we believe high velocity scouring events associated with increases in rainfall and stream discharge during the passage of three hurricanes and other major rain events within the last 13 years may have impacted mussel assemblages in these smaller tributary systems to a greater extent than that found in the river mainstem. Importantly, our results suggest conservation of mussel biodiversity of coastal plain systems should emphasize reducing catchment water yield during extreme precipitation events and enhancing resilience of tributary systems through amelioration of habitat scouring (e.g., increasing woody debris recruitment to streams), as well as minimization of stream alterations (e.g., perched culverts) that could fragment streams or otherwise restrict movements of glochidial fish host species.

5. Conclusions

In summary, although unionid mussel assemblages exhibited positive associations with more forested land cover, coarser substrates, higher dissolved oxygen concentrations, and lower temperature, these relationships do not explain the paucity and sporadic distribution of mussels in these coastal plain streams. Potentially, other unmeasured factors prevent mussels from occurring, or as suggested herein, climatic impacts may be reducing mussel densities periodically, with long-term recovery that is not apparent in snapshot mussel surveys. Where mussels occur, mussel abundance and richness both decline rapidly with higher levels of fine sediment sizes and less dramatically with more agricultural use in the upstream watershed, lower dissolved oxygen, and warmer stream temperatures. Forested land cover was associated with coarser substrate, higher dissolved oxygen, and cooler temperatures. Therefore, protection and regeneration of forested land cover would likely promote freshwater mussel abundance and richness in these coastal plain stream systems.

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