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On the banks of the Red Cedar: toward socio-ecologically robust riparian management in an iconic Michigan river

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ABSTRACT

Land use is continually evolving in river watersheds and riparian zones, particularly in areas containing dense human populations requiring infrastructure development. Land use planners in south-central Michigan, USA, are challenged to balance infrastructure needs with the ecological integrity of the iconic Red Cedar River, which flows through the Michigan state capital (Lansing) and surrounding suburban and rural areas and supports freshwater diatoms, mussels, fishes, and other organisms. Although land use goals in the Red Cedar River watershed include protecting riverine biodiversity, decision-makers need a systematic method for predicting and mitigating effects of land use change on the river ecosystem. We developed a framework for evaluating habitat associations of diatoms and native unionid mussels in the Red Cedar River using field collections and mixed-effects modeling to facilitate socio-ecologically informed riparian management. Diatoms were significantly more abundant and genus-rich in riffles and pools than runs, whereas mussels were more abundant in riffles than pools, with intermediate run abundance. Diatom relative abundance was most affected by pH (+ effect), depth (+), and water temperature (+), similar to diatom genus richness (pH and depth +). Mussel relative abundance was best explained by depth (−), pH (+), and percent forest cover (+), similar to mussel length (depth +, pH −). Results from this study underscore riparian management strategies for optimizing forest cover, depth, and pH to promote ecologically favorable conditions for diatoms and mussels in the Red Cedar River (e.g. stable, near-neutral pH; diverse tree species with ≥60% forest cover). Advancing understanding of aquatic biota and their habitats, this research provides a foundation for socio-ecologically balanced land use planning in the Red Cedar River and other riverine ecosystems.

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Introduction

Rivers and streams are "arteries" of their surrounding landscapes that transport water from the land to lakes and oceans, supply clean water, control floods, and provide recreational opportunities. However, these ecosystems are vulnerable to land use alteration (Rosso and Cirelli 2013), climate change (Woodward et al. 2010), groundwater withdrawal (Winter 2007), and associated threats to biotic communities and habitats (Hershkovitz et al. 2015; Kanno et al. 2015). Land use has a particularly important bearing on managers' ability to conserve riverine biota and habitats because it can change frequently, across a range of spatiotemporal scales, and with diverse hydrological and ecological effects. For instance, watershed and riparian land use influences river runoff, discharge, evapotranspiration, percolation, groundwater recharge, water temperature, instream habitats, and biotic assemblages (e.g. fishes; Compagnucci et al. 2001; Diana et al. 2006). Clearly, land use conditions and alterations have important hydrological and ecological ramifications in riverine ecosystems, yet these impacts vary among rivers and biota (Bosmans et al. 2017).

Effects of land use change in rivers are particularly strong for biota that are sensitive to physical and chemical habitat alterations. For instance, freshwater diatoms are generally negatively affected (with respect to abundance or community structure) by organic pollution and nutrient enrichment (e.g. nitrates, nitrites, phosphates; Dela-Cruz et al. 2006; Potapova and Charles 2007; Feio et al. 2009), increased substrate embeddedness (Griffith et al. 2002) and suspended solids (Feio et al. 2009), and riparian vegetation disturbance caused by agriculture (Griffith et al. 2002). Diatom community structure is also regulated by river pH (Yangdong et al. 1996; Orendt 1998), water temperature (Richter et al. 2016), and flow regime (i.e. patterns of discharge and current velocity; Potapova 1996), which can change in response to land use alteration (e.g. tree removal adjacent to rivers can decrease pH and increase discharge; Saarinen et al. 2013; Levy et al. 2018). Interactions among multiple environmental gradients (e.g. alkalinity, total phosphorus, riparian habitat type), rather than single gradients alone, are known to regulate diatom community composition (Snell and Irvine 2013). Moreover, effects of local, reach-scale habitat variables on diatom communities are often nested within the context of entire watersheds, suggesting that diatom studies should incorporate several spatial scales and environmental gradients (Snell and Irvine 2013). Overall, the environmental sensitivity of freshwater diatoms – along with their wide geographic distribution, numerical abundance, and well-established autecology (Feio et al. 2009) – makes them excellent indicator organisms and compelling subjects for riverine research, particularly in the context of land use change.

Unionid mussels are also indicators of freshwater biodiversity and ecosystem health (Aldridge et al. 2007) that provide important ecological services. Mussels transfer nutrients from the water column to sediments and recycle them through food webs (Vaughn et al. 2004; Spooner and Vaughn 2006), excrete nutrients and thereby stimulate primary (Vaughn et al. 2007) and secondary (Howard and Cuffey 2006) production, and store nutrients in their body tissues that are eventually used by other organisms (Spooner 2007). Likewise, mussels move energy from the water column to sediments (Vaughn and Hakenkamp 2001; Nichols et al. 2005), enhance resource acquisition by other mussels (DiDonato and Stiven 2001), and convert food into fine particulate organic matter used by other organisms (Raikow and Hamilton 2001; Howard and Cuffey 2006). Moreover, mussels supply habitat for other aquatic organisms via attachment to their shells, or otherwise improve habitat by stabilizing sediments or biodepositing organic matter (Spooner and Vaughn 2006; Vaughn and Spooner 2006; Vaughn et al. 2008).

Despite their ecological importance, freshwater mussels are among the most imperiled animal groups in the world due to habitat loss, pollution, land use change, and invasive species (Vaughn 2010; Cao et al. 2015), making it imperative for conservation scientists and managers to understand how environmental factors influence their distribution and abundance. Mussel communities differ based on flow regime such that species that prefer hydrologically stable sites (e.g. *Elliptio dilatata*; Di Maio and Corkum 1995) tend to be most abundant in flow refugia, areas where riverbed sediments are stable during high-discharge events (e.g. inner and outer banks; Strayer 1999; Zigler et al. 2008; Smit and Kaeser 2016). As such, abundance of these species tends to be negatively associated with stream power (i.e. rate of energy dissipation against stream bed and banks) and bankfull sheer stress, in contrast to species that occupy hydrologically variable habitats such as mid-channels and point bars (e.g. *Fusconaia flava*; Di Maio and Corkum 1995; McRae et al. 2004; Smit and Kaeser 2016). Another important reach-level factor that influences mussel community structure is channel slope, higher values of which promote siltation and destabilization of stream substrates and thereby decrease mussel abundance (Arbuckle and Downing 2002; Gangloff and Feminella 2007; Cao et al. 2015). However, large-scale factors such as geology, land use, catchment size, climate (e.g. temperature, precipitation, growing degree days) also influence mussel community structure and warrant consideration by researchers and managers because they can regulate the effects of smaller-scale factors (e.g. substrate type and stability; Atkinson et al. 2012; Cao et al. 2015; Smit and Kaeser 2016). For instance, land use changes or natural disturbances that degrade water quality or modify flow regimes decrease mussel abundance and diversity (Arbuckle and Downing 2002; Haag and Warren 2008).

In addition to examining how environmental factors influence diatom and mussel communities, it is important to consider how these taxa interact. Richter et al. (2016) discovered that diatom species richness (but not diversity) was lower in German river sites with unionid mussels than those without mussels due to a combination of mussel filtration, grazing activity, and nutrient recycling (Allen et al. 2012; Atkinson et al. 2013). However, in rivers in Oklahoma, USA, sites containing unionid mussels had higher diatom relative abundance than sites without mussels (Atkinson et al. 2013), likely because mussels provided physical habitat for diatom attachment or stimulated diatom production by translocating nutrients and materials. The diversity of diatom-mussel relationships suggests they depend on the particular diatom/mussel species present in rivers or the extent to which mussels modify local environmental conditions experienced by diatoms (Vaughn et al. 2008).

The Red Cedar River arises in south-central Michigan, USA, and flows through the Michigan state capital (Lansing) and Michigan State University (MSU), where the river is an iconic component of the aesthetic appeal and cultural identity of the university and surrounding communities in south-central Michigan. Land use change is frequent in the Red Cedar River watershed due to continual maintenance of and modifications to the infrastructure of MSU and nearby municipalities (e.g. roads, buildings, parking structures). These changes could have ecological consequences in the Red Cedar River and its riparian zone (e.g. decreased vegetation; increased runoff, sedimentation, water temperature, acidity; Diana et al. 2006), but such impacts have not been thoroughly researched, particularly with regard to potential effects on diatom and mussel communities. Although the MSU Campus Master Plan (CMP; Michigan State University 2017) and the basin-wide Watershed Management Plan (WMP; Campbell et al. 2015) specify goals to balance the needs of river-dependent human populations and aquatic biota (e.g. minimize negative water quality impacts, protect biodiversity, enhance environmental stewardship), land

use planners need a systematic method for predicting and mitigating the effects of infra-structural changes on the Red Cedar River ecosystem. Moreover, the recent occurrence of property-damaging floods in the Red Cedar River (e.g. spring 2017 and 2018), and the riparian predominance of green ash (*Fraxinus pennsylvanica*) – which is threatened by the invasive Emerald Ash Borer (*Agrilus planipennis*) – highlight the need to understand ecological relationships to inform Red Cedar River management. For instance, how do water temperature changes affect river biota (e.g. diatoms, native unionid mussels)? How does riparian habitat quality (e.g. forest cover) impact the abundance and distribution of river organisms? How can river managers balance ecological concerns with socioeconomic needs? These and related questions have not been thoroughly addressed in the Red Cedar River, yet they are invaluable for socio-ecologically informed riparian management and land use planning.

Given that land use in the Red Cedar River basin is evolving (Campbell et al. 2015), with potential effects on in-stream and riparian habitats and biota, our goal was to assess relationships between diatom and mussel communities and habitat parameters sensitive to land use change (e.g. forest cover, water temperature; Diana et al. 2006) to inform river management. We emphasized diatoms and mussels because they are indicators of freshwater biodiversity and ecosystem health (Aldridge et al. 2007; Feio et al. 2009) and, in the case of mussels, highly threatened by habitat degradation and invasive species (Vaughn 2010; Cao et al. 2015). Indeed, 19 of Michigan's 45 unionid mussels are listed by the state as endangered, threatened, or of special concern (Badra and Goforth 2003). Our first objective was to compare community characteristics of diatoms (i.e. abundance, genus richness [number of genera]) and native unionid mussels (i.e. abundance, length) among habitat types (i.e. riffle, run, pool) in the Red Cedar River. Our second objective was to measure the effects of land use-sensitive habitat parameters (i.e. depth, forest cover, pH, water temperature, nitrate concentration) on diatom and mussel communities using multiple regression models and associated predictions regarding how future changes in these parameters will impact river biota. Combining results from these objectives, we offer recommendations for socio-ecologically balanced riparian management and land use planning in the Red Cedar River basin. We hypothesized that diatom abundance and genus richness would be greatest in habitats with abundant hard surfaces for biofilm accumulation (generally rocks and root wads in the Red Cedar River; Kelly et al. 2005). Because the Red Cedar River contains abundant diatom attachment surfaces (e.g. cobbles, boulders, root wads) in riffles and fewer surfaces in runs and pools, we expected diatoms to be most abundant and genus-rich in riffles. We also predicted that diatom abundance and genus richness would increase with water temperature and pH (Patrick 1971; Planas 1996), decrease with forest cover and depth (i.e. shading, reduced temperature; Cantonati et al. 2009), and decline with increasing mussel abundance due to mussel grazing activity (Richter et al. 2016). We hypothesized that abundance and length of mussels (i.e. *Elliptio dilatata* in the study area) would peak in runs because they have a balance of moderate velocity and relatively stable sediments that promote flow refugia (Smit and Kaeser 2016), in contrast to pools (mid-channel habitats with unstable sediments in the study area) and riffles (high-velocity habitats with relatively shallow water where predators [e.g. raccoons, *Procyon lotor*] are known to forage in the study area; pers. obs.). We predicted that mussel abundance and length would increase with forest cover, pH, and water temperature (Williams et al. 1993; Hincks and Mackie 1997) and be maximized at intermediate depth (i.e. balance of velocity and sediment stability; Cyr 2008).

Methods

Study area

The Red Cedar River (Figure 1) originates near Cedar Lake in Livingston County, Michigan, before flowing 80 km northwesterly to its confluence with the Grand River (a major tributary of Lake Michigan) in Lansing, Michigan. The river drains 122,000 ha as it flows through rural agricultural lands, suburban communities, and urban areas such as Lansing (Ball et al. 1969). The Red Cedar River watershed is primarily composed of cultivated crops, pasture, and hay (35%) but also encompasses grassland/shrubland (23%), wetland and open water (17%), developed land (15%), and forest (10%; Campbell et al. 2015). Forest cover is generally deciduous (e.g. oak [*Quercus* spp.], maple [*Acer* spp.], hickory [*Carya* spp.]) but includes some conifers (e.g. spruce [*Picea* spp.], cedar [*Thuja* spp.]). The Red Cedar River is fed by 12 major tributaries totaling 1,086 km distributed in 19 subwatersheds on generally flat topography (gradient 0.45 m/km) with gentle rolling plains (Campbell et al. 2015). Geology in the upper 10 km of the Red Cedar River watershed is dominated by end moraines of coarse-textured till, followed by a downstream stretch of approximately 15 km composed of medium-textured glacial till (Campbell et al. 2015). Middle reaches of the Red Cedar River ($n = 25$ km) contain glacial outwash (i.e. sand, gravel) and postglacial alluvium, whereas the lower 30 km of the river is dominated by medium-textured glacial till. The Red Cedar River is recreationally important for canoeing, kayaking, wildlife watching, biking/walking (on adjacent trails), and angling for species such as smallmouth bass (*Micropterus dolomieu*), northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), and bluegill (*Lepomis macrochirus*).

Diatom collection

Diatom samples were collected from the Red Cedar River on the MSU campus in October 2017 in three distinct habitat types: riffles, runs, and pools. Diatoms were collected using a consistent protocol in each habitat type wherein researchers selected collection surfaces (i.e. rocks) with attached biofilms in locations of the river with similar, relatively slow velocities (Kelly et al. 2005). Using stiff, clean toothbrushes initially rinsed in river water, researchers repeatedly scraped rocks for 10 seconds to displace diatoms and biofilm particles for collection in polypropylene centrifuge tubes (50 mL, wide opening) positioned immediately downstream of rocks (Feio et al. 2009; Nagy 2011; Richter et al. 2016). The close proximity of sampling tubes to rocks ensured that samples accurately represented diatom abundance and were not affected by potential influences of surrounding water velocity (unlikely because velocity and diatom collection methods were consistent among sites).

Diatom samples were collected such that habitat types were replicated (riffles [$n = 3$], runs [$n = 3$], and pools [$n = 2$]). Within each individual habitat, diatoms were collected from at least two randomly chosen rocks. All habitats were revisited four times between 3 October, 2017 and 31 October, 2017. For each sampling period, diatoms were collected following the original protocol on the same rocks using surfaces adjacent to but distinct from those used in prior weeks to avoid potential biases associated with previous sampling and accurately represent diatom communities (Richter et al. 2016). In addition, the following environmental data were collected during each sampling period at each sampling location: depth (m), water temperature (°C), pH, percent forest cover (i.e. percent of riparian zone composed of mature canopy trees, averaged across right and left banks), and nitrate concentration (mg/L). Diatom samples were transported to the laboratory

Figure 1. Map of the Red Cedar River watershed in Michigan, USA.

immediately after collection, so a sample preservative was not necessary (Kelly et al. 2005). Diatom samples were affixed to microscope slides and identified using standard methods (Kelly et al. 2005; Feio et al. 2009; Richter et al. 2016) involving Naphrax diatom mountant (Brunel Microscope Ltd., United Kingdom; Sabbe et al. 2003) and a Nikon® upright microscopes (40× objective lens, 100× when necessary).

Mussel collection

Researchers collected native unionid mussels (i.e. *Elliptio dilatata*) in October 2017 at the same habitats where diatoms were sampled (i.e. $n = 3$ riffles, $n = 3$ runs, $n = 2$ pools). Sampling locations were shallow and clear, so reliable sampling representative of the mussel population was achieved using timed searches by hand and sediment excavation with a D-framed net (depth $= 10$ cm; Hornbach and Deneka 1996; Badra and Goforth 2003; Deiner and Altermatt 2014). In each habitat, mussels were collected from at least two randomly selected 1.5-×1.5-m quadrats for a total of 10 minutes per quadrat (Chowdhury et al. 2016). Mussels were enumerated, and shell lengths (cm) were measured using Vernier calipers (Aldridge 1999). Mussels were collected in the same habitats four times between 3 October, 2017 and 31 October, 2017. A consistent collection protocol was used for each sampling period, but quadrats were placed at different locations to avoid potential biases associated with prior collection.

Statistical analysis

We expressed diatom and mussel abundance as relative abundance or catch-per-unit-effort (i.e. # diatoms/microscope slide, # mussels/quadrat) to enable reliable comparisons among samples from different locations and thus accurate interpretation of spatial patterns in abundance (Bonar et al. 2009; Rodriguez-Ramos et al. 2015). Because mussels are relatively long-lived and likely respond less to instantaneous environmental measurements than to long-term trends, we used data spanning the year prior to mussel collection (i.e. October 2016–October 2017) to calculate mean annual depth, pH, and water temperature at each sampling site. We then evaluated mussel abundance and length relative to these long-term data. However, instantaneous environmental measurements collected in October 2017 were used to assess diatom relative abundance and genus richness (# genera/microscope slide) as these organisms are short-lived and have fast turnover times. All data related to diatoms (i.e. relative abundance, genus richness), mussels (i.e. relative abundance, length), and environmental factors were normally distributed and homoscedastic as revealed by Shapiro-Wilk and Levene's tests, respectively. Differences in mean diatom relative abundance among riffles, runs, and pools were tested using one-way analysis of variance (ANOVA) with *post hoc* Tukey's Honestly Significant Difference tests ($\alpha = 0.05$). The same procedure was used to evaluate among-habitat differences in mean diatom genus richness, mean mussel relative abundance, and mean mussel length. Linear and polynomial regressions between forest cover and organismal characteristics (i.e. diatom relative abundance and genus richness, mussel relative abundance and length) were performed to assess the potential existence of riparian forest management targets (i.e. levels of forest cover beyond which organismal characteristics increase rapidly). Forest cover was used for these analyses because it is more controllable by managers than other environmental factors (e.g. depth, pH). Linear and polynomial regressions were used to account for potential linear or non-linear relationships between forest cover and organismal characteristics.

Linear mixed-effects models (random intercept) were developed to evaluate the effects of land use-sensitive habitat variables (i.e. depth, forest cover [For], pH, water temperature [Temp], nitrate concentration) on diatom relative abundance and genus richness and mussel relative abundance and length. Model intercepts were allowed to vary by habitat type (i.e. riffle, run, pool). All models followed the structure of global models with associated assumptions:

$$
\begin{aligned}
\text{Response} &= \alpha + \text{Depth} + \text{For} + \text{pH} + \text{Temp} + \text{Nitrate} + (1|\text{Habitat}) + \varepsilon \\
b &= N(0, D_b) \\
\varepsilon &= N(0, D_\varepsilon)
\end{aligned}
$$
b, ε independent

(1)

where "Response" represents an organismal response variable (i.e. diatom relative abundance/genus richness, mussel relative abundance/length), α represents the model intercept, and ε denotes the model error. It was assumed that random effects b and errors ε were normally distributed with mean zero and variance D_b and D_ε, respectively. It was also assumed that b and ε were independent.

For each organismal variable, 10 a priori models were generated to represent multiple working hypotheses (Chamberlain 1965) about the effects of land use-sensitive habitat variables on diatoms and mussels (see Introduction). Models were compared with an information-theoretic approach using bias-corrected Akaike's information criterion (AICc; Burnham and Anderson 2002). Multimodel inference was performed via full-model averaging (Lukacs et al. 2009) for models comprising >90% cumulative Akaike weight (w_i) to make robust inferences from all informative models (i.e. those containing parameters that reduce model deviance; Burnham and Anderson 2002; Arnold 2010). All analyses were performed in program R (RStudio Desktop version 1.1.423; RStudio 2015).

Results

Diatoms

Diatom sampling produced 2,417 individuals representing 18 genera (Table 1). Compared to runs, riffles and pools had greater diatom relative abundance ($F_{2,56}=5.91$; $p< .01$; Figure 2a) and genus richness ($F_{2,56}=4.69$; $p= .01$; Figure 2b). Linear mixed-effects modeling indicated that diatom relative abundance was best explained by a model including pH, depth, and water temperature, but not percent forest cover ($w_i=0.76$; Table 2). An alternative model including only pH and depth also received moderate statistical support (ΔAICc $=3.08$; $w_i=0.16$; Table 2). The individual models and the model-averaged estimator (Table 3) included positive effects of pH, depth, and water temperature on diatom relative abundance.

Diatom genus richness was best explained by a model containing pH, depth, and depth:pH (i.e. interaction of depth and pH; $w_i=0.71$; Table 4). Other models including pH and depth (ΔAICc $=3.56$; $w_i=0.12$) and pH alone (ΔAICc $=4.10$; $w_i=0.09$; Table 4) received moderate statistical support. The individual models and the model-averaged estimator (Table 3) included positive effects of pH and depth and a negative effect of depth:pH on diatom genus richness.

Native unionid mussels

Mussels ($n = 579$ total) were significantly more abundant in riffles than pools ($F_{2,11} = 4.01$; $p = .04$), with runs having intermediate relative abundance (Figure 3). Mussel relative

Table 1. Diatom genera sampled in October 2017 in the Red Cedar River, Michigan.

Genus	October 3	October 10	October 17	October 31	Total
Achnanthes	15	7	25	2	49
Amphora	27	97	112	5	241
Bacillaria	12	3	7	2	24
Caloneis	10	13	32	8	63
Cocconeis	18	18	7	2	45
Cyclotella	19	14	28	2	63
Cymatopleura	9	28	9	3	49
Cymbella	76	23	29	3	131
Diatoma	226	34	31	3	294
Gomphonema	72	20	158	8	258
Gyrosigma	59	5	6	3	73
Melosira	57	38	62	13	170
Navicula	97	105	90	24	316
Nitzschia	105	23	91	10	229
Rhoicosphenia	36	36	31	9	112
Surirella	35	1	50	4	90
Synedra	37	29	56	6	128
Tryblionella	28	22	26	6	82
Total	938	516	850	113	2,417

abundance increased as the riparian zone became more forested, particularly as forest cover increased above 60% ($R^2 = 0.78$; $p < .01$; Figure 4). Mussels were measurably (but not statistically) longer in runs (mean 6.96 cm) than riffles (4.34 cm) and pools (4.19 cm; $F_{2,11} = 1.61$; $p = .24$). Linear mixed-effects modeling indicated that mussel relative abundance was best explained by a model including depth and pH ($w_i = 0.73$; Table 5). An alternative model containing pH and forest cover also received moderate statistical support ($\Delta AICc = 3.66$; $w_i = 0.12$; Table 5). The individual models and the model-averaged estimator (Table 3) included positive effects of depth, pH, and forest cover on mussel relative abundance. Mussel length was best explained by a model including depth and pH ($w_i = 0.91$; Table 6). Other mussel length models were developed but did not receive sufficient AICc support to be considered informative, so model averaging was not performed.

Discussion

As we hypothesized, diatoms were more abundant and genus-rich in riffles than runs, which likely reflected the prevalence of rocky and woody substrates (i.e. diatom attachment surfaces) in riffles. Comparatively high diatom abundance and genus richness in pools was surprising but likely resulted from the occasional presence of boulders and logs in these habitats. Diatom relative abundance was best explained by pH (+ relationship), depth (+), and water temperature (+), similar to diatom genus richness (pH +, depth +), as in previous research (Yangdong et al. 1996; Orendt 1998; Richter et al. 2016). Percent forest cover had a relatively small effect on diatom abundance and genus richness compared to other habitat variables, in contrast to our hypothesis. pH is known to exert a strong influence on freshwater diatom assemblages (Douglas and Smol 1995; De Nicola 2000), which is consistent with our findings, helping fill a knowledge gap regarding pH preferenda of Red Cedar River diatoms. Many diatom species have preferences for fairly narrow pH ranges (van Dam et al. 1994), with abundances generally decreasing as conditions become more acidic (Planas 1996). However, reported pH levels at which diatom abundance declines precipitously (i.e. between 3.5 and 4.5; Charles 1985; De Nicola 2000) are far more acidic than the pH range documented herein (6.6–7.1). Hence, Red Cedar
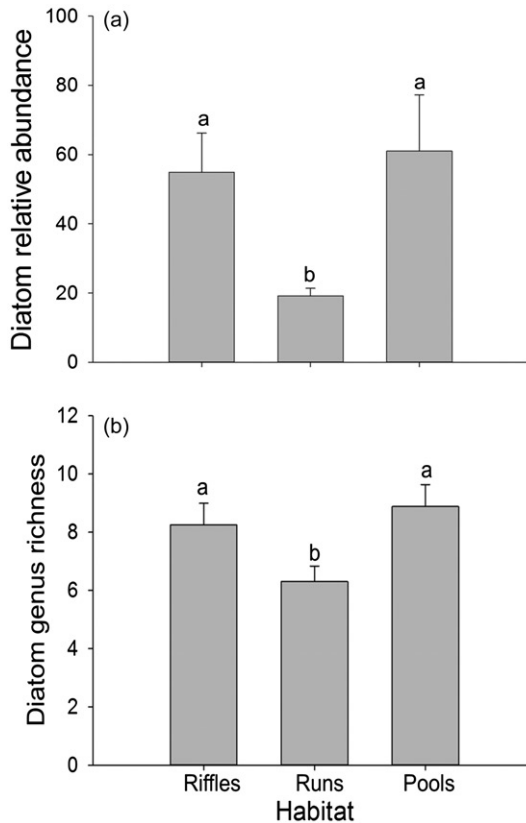
Figure 2. Comparison of (a) mean diatom relative abundance (#/microscope slide) and (b) mean genus richness (# genera/microscope slide) in riffles, runs, and pools in the Red Cedar River. Different letters denote significant differences between habitat types as determined ANOVA by Tukey's Honestly Significant Difference tests ($\alpha = 0.05$). Error bars represent ± 1 SEM.

Table 2. Results of linear mixed-effects modeling to explain variation in diatom relative abundance (RelAb, #/microscope slide) in the Red Cedar River, Michigan as a function of depth (m), forest cover (For, %), pH, water temperature (Temp, °C), and the interaction of depth and water temperature (Depth:Temp).

Model	N	K	AICc	ΔAICc	w_i
RelAb = Depth + pH + Temp+ (1|Habitat)	8	4	595.48	0.00	0.76
RelAb = Depth + pH+ (1|Habitat)	8	3	598.56	3.08	0.16
RelAb = Depth + For + pH+ (1|Habitat)	8	4	600.47	4.99	0.06
RelAb = Depth + Temp+ (1|Habitat)	8	3	605.78	10.29	<0.01
RelAb = Depth + For + Temp+ (1|Habitat)	8	4	608.21	12.72	<0.01
RelAb = For + pH+ (1|Habitat)	8	3	608.62	13.14	<0.01
RelAb = Depth:Temp + Temp+ (1|Habitat)	8	3	609.20	13.71	<0.01
RelAb = Depth:Temp + For + Temp+ (1|Habitat)	8	4	611.62	16.13	<0.01
RelAb = Depth+ (1|Habitat)	8	2	612.04	16.55	<0.01
RelAb = Temp+ (1|Habitat)	8	2	612.50	17.02	<0.01

AICc: bias-corrected Akaike's information criterion; ΔAICc: difference in AICc between each model and the most supported model; K: number of parameters; N: number of habitats sampled; w_i: Akaike weight (relative strength of evidence for each model).

River diatoms were comparatively sensitive to pH during fall sampling, becoming significantly less abundant and genus-rich with even slight acidic deviations from neutral pH.

Diatom abundance and genus richness also increased with water depth. Although depth-distribution profiles have been evaluated for diatoms in Lake Michigan, USA

Table 3. Equations for model-averaged estimators (except mussel length) to explain variation in diatom relative abundance (#/microscope slide), diatom genus richness (# genera/microscope slide), and mussel relative abundance (#/quadrat) as a function of environmental factors (i.e. depth [m], forest cover [%], pH, water temperature [°C]) in the Red Cedar River, Michigan.

Taxa	Response variable	Model
Diatoms	Relative abundance	$Y = -979.93 + 17.67 \times Depth + 137.32 \times pH + 2.13 \times Temp$
	Genus richness	$Y = -43.49 + 3.07 \times Depth - 0.34 \times Depth{:}pH + 7.08 \times pH$
Mussels	Relative abundance	$Y = -225.76 - 73.25 \times Depth + 0.29 \times For + 43.80 \times pH$
	Length (not model averaged)	$Y = 138.87 + 9.54 \times Depth - 20.50 \times pH$

Depth, pH, and water temperature are expressed as weekly measurements across the fall season for diatoms and annual means for mussels.

Table 4. Results of linear mixed-effects modeling to explain variation in diatom genus richness (GRich, # genera/ microscope slide) in the Red Cedar River, Michigan as a function of depth (m), forest cover (For, %), pH, water temperature (Temp, °C), the interaction of depth and pH (Depth:pH), and the interaction of depth and water temperature (Depth:Temp).

Model	N	K	AICc	ΔAICc	w_i
GRich = Depth + Depth:pH + pH + (1|Habitat)	8	4	294.13	0.00	0.71
GRich = Depth + pH + (1|Habitat)	8	3	297.70	3.56	0.12
GRich = pH + (1|Habitat)	8	2	298.24	4.10	0.09
GRich = Depth:Temp + pH + (1|Habitat)	8	3	300.96	6.82	0.02
GRich = Depth + pH + Temp + (1|Habitat)	8	4	301.01	6.87	0.02
GRich = Depth:pH + pH + (1|Habitat)	8	3	301.56	7.43	0.02
GRich = Depth:pH + Depth + Temp + (1|Habitat)	8	4	302.76	8.63	0.01
GRich = Depth:pH + pH + Temp + (1|Habitat)	8	4	304.87	10.74	<0.01
GRich = Depth + For + pH + (1|Habitat)	8	4	306.06	11.93	<0.01
GRich = Depth:pH + For + pH + (1|Habitat)	8	4	309.93	15.80	<0.01

AICc: bias-corrected Akaike's information criterion; ΔAICc: difference in AICc between each model and the most supported model; K: number of parameters; N: number of habitats sampled; w_i: Akaike weight (relative strength of evidence for each model).
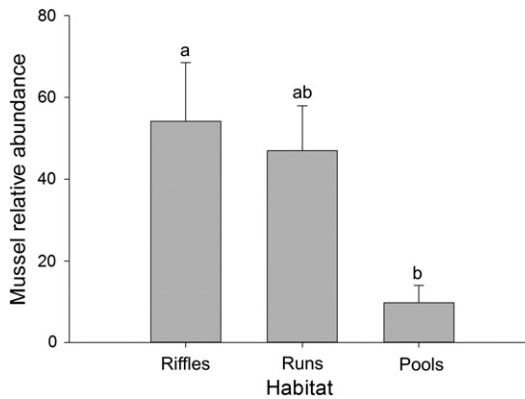
Figure 3. Comparison of mean mussel relative abundance (#/quadrat) in riffles, runs, and pools in the Red Cedar River. Different letters denote significant differences between habitat types as determined ANOVA by Tukey's Honestly Significant Difference tests ($\alpha = 0.05$). Error bars represent ±1 SEM.

(Kingston et al. 1983), these relationships are less understood in Michigan rivers and streams, particularly the Red Cedar River. Freshwater diatoms are influenced to varying degrees by depth gradients (Stevenson and Stoermer 1981; Cantonati and Lowe 2014) because environmental conditions change with depth. For instance, as depth increases, light becomes less available due to reduced sunlight penetration and shading from phytoplankton higher in the water column, conditions that can be expected to reduce diatom abundance and genus richness (Cantonati et al. 2009). However, the portion of the Red
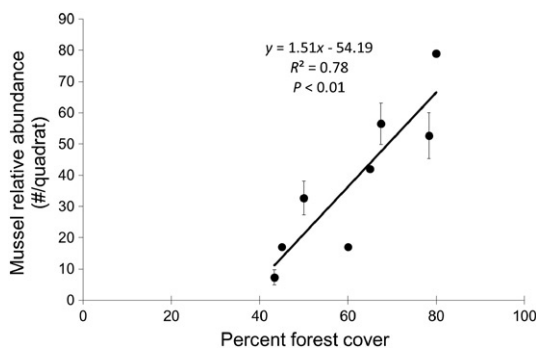
Figure 4. Linear regression between mean mussel relative abundance (#/quadrat) and percent forest cover in the Red Cedar River. Error bars represent ±1 SEM.

Table 5. Results of linear mixed-effects modeling to explain variation in mussel relative abundance (RelAb, #/quadrat) in the Red Cedar River, Michigan as a function of forest cover (For, %), mean annual depth (m), mean annual pH, mean annual water temperature (Temp, °C), mean annual nitrate concentration (mg/L), the interaction of depth and pH (Depth:pH), and the interaction of forest cover and pH (For:pH).

Model	N	K	AICc	ΔAICc	w_i
RelAb = Depth + pH + (1|Habitat)	8	3	81.80	0	0.73
RelAb = For + pH + (1|Habitat)	8	3	85.46	3.66	0.12
RelAb = Depth + For + (1|Habitat)	8	3	85.61	3.81	0.11
RelAb = Depth + For:pH + (1|Habitat)	8	3	89.26	7.46	0.02
RelAb = Depth:pH + For + (1|Habitat)	8	3	89.53	7.73	0.02
RelAb = Depth:pH + Temp + (1|Habitat)	8	3	90.93	9.13	0.01
RelAb = Depth:pH + Nitrate + (1|Habitat)	8	3	92.18	10.38	<0.01
RelAb = For:pH + Temp + (1|Habitat)	8	3	94.41	12.61	<0.01
RelAb = For:pH + Nitrate + (1|Habitat)	8	3	96.87	15.07	<0.01
RelAb = Depth + For + pH + (1|Habitat)	8	4	131.33	49.53	<0.01

AICc: bias-corrected Akaike's information criterion; ΔAICc: difference in AICc between each model and the most supported model; K: number of parameters; N: number of habitats sampled; w_i: Akaike weight (relative strength of evidence for each model).

Table 6. Results of linear mixed-effects modeling to explain variation in mussel length (cm) in the Red Cedar River, Michigan as a function of forest cover (For, %), mean annual depth (m), mean annual pH, mean annual water temperature (Temp, °C), mean annual nitrate concentration (mg/L), the interaction of depth and pH (Depth:pH), and the interaction of forest cover and pH (For:pH).

Model	N	K	AICc	ΔAICc	w_i
Length = Depth + pH + (1|Habitat)	8	3	60.25	0	0.91
Length = Depth + Temp + (1|Habitat)	8	3	65.50	5.25	0.07
Length = Depth + Nitrate + (1|Habitat)	8	3	68.99	8.74	0.01
Length = Depth:pH + Temp + (1|Habitat)	8	3	69.39	9.14	0.01
Length = For + pH + (1|Habitat)	8	3	71.05	10.8	0.00
Length = Depth + For + (1|Habitat)	8	3	72.55	12.3	0.00
Length = Depth:pH + Nitrate + (1|Habitat)	8	3	72.89	12.64	0.00
Length = Depth + For:pH + (1|Habitat)	8	3	76.41	16.16	0.00
Length = Depth:pH + For + (1|Habitat)	8	3	76.52	16.27	0.00
Length = Depth + For + pH + (1|Habitat)	8	4	119.85	59.6	0.00

AICc: bias-corrected Akaike's information criterion; ΔAICc: difference in AICc between each model and the most supported model; K: number of parameters; N: number of habitats sampled; w_i: Akaike weight (relative strength of evidence for each model).

Cedar River studied herein was relatively shallow (generally <1 m) and clear, meaning light limitation with increasing depth was unlikely to appreciably influence diatom abundance and genus richness. This was contingent on high water clarity, as excess sedimentation due to factors such as riparian habitat degradation could reduce water clarity and

light penetration and thereby influence diatom abundance and genus richness. However, the study area had abundant forest cover provided by riparian trees and shrubs, which helped maintain high water clarity and prevented a potential reduction in diatom abundance with riparian shading (Michels et al. 2006). Our results indicate that the most important factors regulating fall diatom abundance and genus richness in the Red Cedar River (e.g. depth, pH) operate independent of riparian shading, as documented in other streams (Hlúbiková et al. 2014). Hence, it is important to continue monitoring relationships between depth, pH, and diatom communities in the Red Cedar River given the potential for fluctuations in discharge, sediment, and acidity due to anthropogenic influences at MSU (e.g. infrastructure development) and throughout the watershed (e.g. water withdrawal, climate change; Vörösmarty et al. 2000; Sophocleous 2004). After all, Peters (1959) documented seven genera of Red Cedar River diatoms (i.e. *Cocconeis, Cyclotella, Cymbella, Diatoma, Gomphonema, Navicula, Synedra*), whereas 18 genera were observed in the present study. This suggests a temporal change in genus richness, reflecting potential alterations in depth, pH, water temperature, or combinations of these factors and further supporting the importance of long-term diatom monitoring across multiple environmental gradients in the Red Cedar River (Snell and Irvine 2013).

Water temperature had a positive effect on diatom abundance (but not genus richness) in the Red Cedar River. Diatom metabolism is regulated by water temperature such that growth and reproduction (and hence abundance) generally increase in warmer environments, as documented herein. Diatoms have been classified into cold water ($<15\,°C$), temperate ($15–25\,°C$), and warm water ($>25\,°C$) forms based on optimum temperature ranges for growth (Patrick 1971). Water temperatures in the present study ranged from 5.9 to $20\,°C$, suggesting the occurrence of cold-water and temperate diatoms. Temperate genera evidently predominated, as the overall positive temperature-abundance relationship suggests that increased abundances of temperate species between 15 and $20\,°C$ (and declines between 5.9 and $15\,°C$) numerically outweighed the opposite trends exhibited by cold-water genera. Although water temperature has measurable effects on diatom communities (Richter et al. 2016), it was a less important predictor than depth and pH in the present study. Red Cedar River managers can control the latter factors by protecting and rehabilitating riparian buffer zones to mitigate fluctuations in depth (e.g. erosion, sedimentation) and pH (e.g. increased acidity due to runoff) and thereby benefit diatom communities.

Native unionid mussels were abundant in riffles and relatively scarce in pools, indicating that riffles had suitable water velocity and stable sediments preferred by *Elliptio dilatata* (Di Maio and Corkum 1995). Mussels were also relatively abundant in runs, which likely offered favorable water velocity and sediment stability. However, contrary to our hypothesis, these factors evidently did not cause greater mussel abundance in runs than riffles, similar to Hegeman et al. (2014). Low mussel abundance in pools supported our hypothesis and suggests unstable sediments and lack of flow refugia during high-discharge events (Di Maio and Corkum 1995; Smit and Kaeser 2016).

Mussel relative abundance was best explained by depth (−), pH (+), and forest cover (+). Similarly, mussel length was best explained by depth (+) and pH (−). Mussel depth distributions are limited by physical forces (e.g. exposure to winds, wave action) and thermocline depth in inland lakes, such that maximum densities occur at intermediate depths that have relatively low turbulence, stable sediments, and abundant food (Cyr 2008). The negative relationship between depth and mussel abundance observed herein suggests that deeper habitats (e.g. pools) in the Red Cedar River were generally unfavorable for mussels, likely due to smaller, less stable sediments than shallower, nearshore

areas with larger, more stable substrates that provide flow refugia during high-discharge events (Strayer 1999; Smit and Kaeser 2016). Indeed, sediment particle size is known to be positively correlated with mussel abundance in Michigan rivers (Badra and Goforth 2003). This relationship is reflected in Figure 3, as mussel abundance increased from pools (generally sand and silt) to riffles (cobbles and boulders), reflecting an increase in sediment size, stability, and flow refugia for mussels (Di Maio and Corkum 1995; Smit and Kaeser 2016). Like diatoms, freshwater mussels are sensitive to changes in pH (Rooke and Mackie 1984; Hincks and Mackie 1997) and depth (Cyr 2008). Strongly acidic conditions and declines in pH can impede ion exchange and cause mussels to lose calcium to the external environment (Hunter 1990), both of which impair metabolism, reduce growth (e.g. length), and increase mortality. Mussels are particularly responsive to pH changes in certain Michigan rivers, including Hannah Creek (eastern Upper Peninsula), where a pH decline of only 0.06 (from 8.23 to 8.17) removed mussels from population surveys (Harriger et al. 2009). Similarly, mussels in the Red Cedar River responded positively to pH via increased relative abundance over a relatively small pH range (6.6–7.1).

The positive relationship between native unionid mussel abundance and forest cover likely reflects the importance of riparian trees in minimizing erosion and siltation, which are major threats to native unionid mussel populations, along with channel modification, habitat destruction, and invasive species (Williams et al. 1993; Hanlon et al. 2009). Siltation, often caused by sediment erosion resulting from riparian deforestation and agricultural practices that degrade stream banks, is an especially important threat in the Red Cedar River basin due to relatively high agricultural land use (35%; Campbell et al. 2015). Hence, Red Cedar River managers should partner with the agricultural stakeholders to maintain and expand riparian tree coverage as a way to sustain mussel abundance and diversity (Morris and Corkum 1996; Cosgrove et al. 2017) and promote the aesthetic benefits of forested landscapes at MSU and in surrounding river communities (Michigan State University 2017). Riparian conservation is critical amid range expansion of Emerald Ash Borer (EAB), which has invaded southeast Michigan and threatens hundreds of millions of ash trees throughout the state (Herms and McCullough 2014). Because green ash is predominant on the banks of the Red Cedar River, the ability of river managers and citizens to mitigate the spread of EAB (via restricted wood movement, insecticide treatment, active monitoring and research, etc.) has implications for the health of aquatic biota in the river. This is especially true for native unionid mussels, the abundance of which increased rapidly above 60% forest cover. It is important for Red Cedar River managers to implement a riparian conservation program that simultaneously protects green ash trees and enhances tree diversity to buffer against potential forest and mussel community changes resulting from EAB invasion. Restoration plantings of silver maple (*Acer saccharinum*), red maple (*A. rubra*), willow (*Salix* spp.), eastern cottonwood (*Populus deltoides*), and other floodplain species to meet or exceed 60% forest cover would be an effective way to promote tree diversity and achieve goals of the CMP, offering opportunities for the MSU and surrounding communities help sustain floodplain forests and mussel populations. Such plantings would also reduce runoff, erosion, and sedimentation, which would help stabilize pH, mitigate declines in depth, and thereby maintain or enhance diatom abundance and genus richness, as documented herein.

Although our study was not designed to comprehensively evaluate interactions between diatom and mussel communities in the Red Cedar River, our data suggest that such interactions exist. Diatoms were most abundant and genus-rich (Figure 3) in pools, where mussels were least abundant (Figure 4). Likewise, diatoms were least abundant and genus-rich in runs, where mussels were abundant. Relative to riffles and pools, runs had

environmental conditions that were more conducive for diatom growth and abundance (i.e. greater pH and water temperature). Thus, relatively low diatom abundance in runs suggests mussel grazing pressure (Richter et al. 2016). Both diatoms and mussels were abundant in riffles (Figures 3 and 4), likely due to the preponderance of rocky and woody substrates, which simultaneously provide diatom attachment surfaces and flow refugia (e.g. non-turbulent areas adjacent to submerged rocks and logs) that are preferred by certain mussel species (Smit and Kaeser 2016), including *Elliptio dilatata* (Di Maio and Corkum 1995). In addition, water velocity in riffles of the Red Cedar River is likely slower, on average, than the threshold velocities that mussels can tolerate, allowing mussels to persist despite documented predation by raccoons (pers. obs.), which is evidently not severe enough to appreciably influence mussel abundance. Overall, we recommend that diatom-mussel interactions, particularly spatiotemporal patterns in the occurrence of commensalism versus diatom grazing by mussels, are focal points for future Red Cedar River research.

In conclusion, our research advances scientific understanding of the habitat associations of Red Cedar River biota that are ecologically important and, in the case of native unionid mussels, threatened by habitat alterations resulting from land use changes. In so doing, this study informs land use planning in the Red Cedar River watershed, offering decision-makers important ecological data for river management and infrastructure development (e.g. road, sidewalk, and bridge construction/refurbishment). In particular, riparian management strategies should be designed to optimize forest cover, depth, and pH to promote ecologically favorable conditions for diatoms and native unionid mussels (e.g. stable, near-neutral pH; diverse tree species with $\geq$60% forest cover) and infrastructure development to support vibrant human communities. Overall, our research furnishes a framework for studying habitat associations of aquatic biota in ways that facilitate socio-ecologically robust riparian management in an iconic Michigan river.

Disclosure statement

No potential conflict of interest was reported by the authors.

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