PRIMARY RESEARCH PAPER

Species richness of mussel assemblages and trait guilds in relation to environment and fish diversity in streams of Illinois, the USA

Yong Cao · Leon Hinz · Christopher A. Taylor · Brian Metzke · Kevin S. Cummings

Abstract Fish hosts are critical for freshwater mussels. However, correlation between mussel and fish species richness (SR) is variable. Here, we examine how the environment affects this variability. We calculated mussel–fish SR ratios for 459 stream sites to capture the different responses of mussel and fish SR to environmental variables. We used Random-Forests (RF) to model how the SR ratio varied with environmental gradients. We also modeled the percent SR of mussel guilds with different hosting and life-history strategies. The SR ratio was generally low, but highly variable across sites. The ratio variability strongly affected mussel-fish SR correlations and can be explained by environmental factors. Given that environmental gradients also differ among datasets or regions, mussel-fish SR correlation can be expected to vary. The responses of the SR of mussel guilds agree with the expectations. However, land-use and climate co-vary with other environmental variables, and their effects are difficult to assess. We conclude that mussel and fish respond differently to many environmental variables; the importance of fish SR to mussel SR may vary with the environmental settings of streams but often appears to be low. Thus, environmental data may be generally sufficient for mussel-SR modelling and mussel diversity conservation planning.

Keywords Species richness · Mussel diversity · Parasite–host relationship · Habitat preference · Illinois streams

Y. Cao (✉) · C. A. Taylor · K. S. Cummings
Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 1816 S Oak Street, Champaign, IL 61820, USA
e-mail: yongcao@illinois.edu

L. Hinz · B. Metzke
Illinois Department of Natural Resources, 1 Natural Resources Way, Springfield, IL 62702, USA

Introduction

Freshwater mussels are among the most threatened group of species in the US and across the world (Ferreira-Rodríguez et al., 2019; Haag, 2019). A range of human disturbances, such as water-quality pollution, habitat degradation, invasive species, flow alteration, and habitat fragmentation, contribute to their decline (Downing et al., 2010; Galbraith et al., 2010; Haag, 2012, 2019; Modesto et al., 2018). As freshwater mussels are also dependent on fishes as hosts at the larval stage (glochidia) (Haag, 2012; Taeubert et al., 2012), they are also indirectly impacted by human disturbances through the loss of fish hosts (Fritts et al., 2012; Benson et al., 2017; Galbraith et al., 2018).

The importance of the environment and fish hosts to individual mussel species has been well documented and considered in conserving and restoring endangered or threatened species (Haag, 2012; Modesto et al., 2018). As the number of threatened species increases, single-species conservation has been increasingly replaced by multiple-species or community conservation (Regan et al., 2008; Franklin et al., 2011). This shift is particularly relevant for freshwater mussels when a large proportion of mussel species is threatened, and the whole mussel assemblage has declined in most aquatic ecosystems (Haag, 2019; Haag & Williams, 2014; Hornbach et al., 2019). Because almost all freshwater fish species are the hosts of one or more mussel species (Haag, 2012) and individual mussel species declines have been related to a lack of fish hosts (e.g., Fritts et al., 2012), understanding the relationship between mussel and fish species diversity shall help modeling and conservation planning of overall mussel biodiversity. Resource managers would need to know when their conservation efforts should be focused on the physical environment or fish diversity, or both and whether fish-focused monitoring can also capture the status and trends of mussel diversity. Ecologists may need to know whether fish data are essential to model and predict the changes in mussel diversity.

A positive correlation can be expected between mussel and fish SR just as in other parasite-host systems (Wood & Johnson, 2016). However, the reported correlation strength varies greatly among different studies, from nearly perfect (Watters, 1992; Myers-Kinzie et al., 2001; Haag, 2012) to intermediately strong (Vaughn & Taylor, 2000; Krebs et al., 2010; Cao et al., 2013), and weak (Daniel & Brown, 2013; Bey & Sullivan, 2015). One possible reason is that the correlation strength depends on natural environmental setting and human disturbances associated with a given dataset. For example, the stream size and land-use may differ much more among sites in one study than in others. If so, we need to understand how environmental gradients affect the correlation strength. Mussel diversity and abundance were reported to decline substantially in streams while fish assemblages remain stable and healthy (Haag, 2012, 2019). These observations suggest that freshwater mussel and fish assemblages differ in their environmental preferences. However, how mussel and fish SR differently respond to environmental gradients is poorly understood.

One can compare the relationships of mussel and fish SR with the environment and human disturbances by modeling them separately. However, the response curves of SR to an environmental variable can take a variety of forms, e.g., linear, non-linear, step-functions, and multi-modal (Austin & Gaywood, 1994), making it difficult to quantify the differences accurately and precisely. In the present study, we propose to overcome this difficulty by modeling the ratio of mussel and fish SR (referred to as the SR ratio hereafter). If mussel and fish SR values vary along an environmental gradient in the same way, the SR ratio will not change, while if they vary differently along this gradient, the ratio will change. For example, when mussel SR is negatively affected by an environmental factor more than fish SR, the SR ratio will decrease, and vice versa. In the present study, we focus on the relationships between the SR ratio and a wide range of natural environmental variables and measures of human disturbances, such as land-use and spatial connectivity changes.

The responses of mussels to the environment and fish hosts may also vary among different species guilds (Haag, 2012; Randklev et al., 2015; Ries et al., 2015; Hornbach et al., 2018). A species guild can be referred to as a group of species similar in some ecologically relevant way (Wilson, 1999). In the present study, we modeled how different mussel species guilds respond to environmental variables and fish SR. We focused hosting traits and life-history strategies (Haag, 2012; Moore et al., 2021). Host specialists can only use one or a few species for metamorphosis, often in the same family, while generalists use a wide range of species, normally in multiple families (Haag, 2012). The equilibrium species are mainly characterized by a long life span, slow growth rate, and stable habitat requirement; the opportunistic species by short life, fast growth and unstable habitats. The periodic species fall between the two strategists in these characteristics. We ask two questions: (1) is host-specialist SR more strongly affected by fish SR than host-generalist SR? (2) is SR of mussels with equilibrium strategy more sensitive to environmental changes than the SR for the other two types of strategists? The answers to the questions could help us to understand how fish biodiversity changes would affect different mussel guilds or how the SR of a

given mussel guild may indicate the impact of human disturbances.

To accomplish the research goals described above, we compiled mussel and fish datasets for 459 stream sites in Illinois, the USA in this study and used Random-Forests regression, a robust machine learning technique (Breiman, 2001; Cutler et al., 2007) to model the relationships of the SR ratio and mussel guild SR with a range of natural environmental and land-use variables. We also showed how the variability of the mussel-fish SR ratio can be directly related to the strength of mussel-fish SR correlation. The findings of this study shall help to explain why mussel-fish SR correlations can vary among different studies and assist resource managers and researchers to identify where mussel SR is more likely restricted by the physical environment or by fish SR and better understand whether monitoring and conservation planning focused on fish assemblages could protect mussel biodiversity.

Methods

Mussel and fish sampling data

We used two published data sets from stream mussel and fish surveys (Cao et al., 2015, 2016) to address our research objectives. The mussel samples were collected with 4-person-hour timed searches over a 200-m reach in wadeable streams in the State of Illinois, an agriculturally-dominated region of 143,969 km^2, during 2009–2012, and all individuals, including freshly died ones, were identified to species on site (Cao et al., 2015). The fish samples were collected with electro-seining, a highly efficient method over a reach of 20 times the wetted channel width, no less than 100 m for small streams and not greater than 300 m for large streams and fishes collected were identified to species mostly on site with hybrid individuals removed (IL-DNR, 2010; Cao et al., 2016). Out of the original 937 fish samples collected between 1995 and 2010, we matched 459 with the mussel samples for the location (Fig. 1). Because of the long lifespans of many mussels (most individuals from field surveys were estimated to be > 10 years old), these two datasets were considered well-matched in time. We also compiled the hosting and life-history traits of 39 mussel species recorded in our
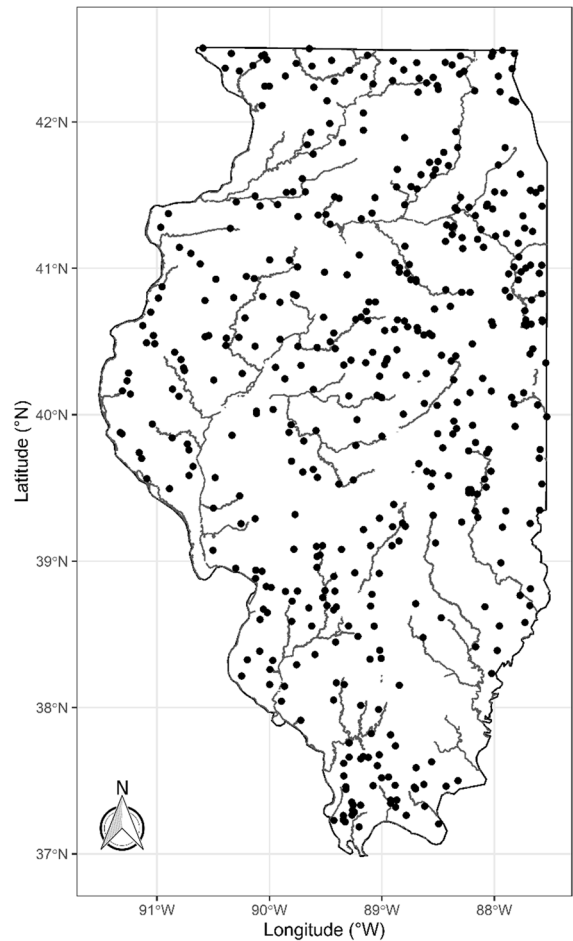

Fig. 1 Study region and the locations of sampling sites for both mussel and fish assemblages in Illinois, USA

dataset based on the literature, mainly Haag (2012) and Moore et al. (2021) (Table 1), and calculated SR for each of the five mussel guilds as well as their percentages out of the total mussel SR at each site.

Landscape environmental data

Aquatic assemblages are often affected by multiple environmental processes operating at different scales (Poff, 1997; Jackson et al., 2001). A wide range of environmental variables summarized at the stream reach and watershed levels were considered in examining the variation of the SR ratio and guild SR among sampling sites in this study.

Table 1 Hosting and life-history (LH) strategies of 39 freshwater mussel species collected from 459 stream sites, Illinois, USA compiled from the literature

Species name	Common name	LH	Host	References
Ortmanniana ligamentina (Lamarck, 1819)	Mucket	E	G	Haag (2012)
Alasmidonta marginata Say, 1818	Elktoe	P	G	Haag (2012)
Alasmidonta viridis Rafinesque, 1820	Slippershell Mussel	P	S	Haag (2012)
Amblema plicata (Say, 1817)	Threeridge	E	G	Haag (2012)
Anodontoides ferussacianus I.Lea, 1834	Cylindrical Papershell	O	G	Haag (2012), NatureServe[a]
Arcidens confragosus (Say, 1829)	Rock Pocketbook	P	G	Animal Diversity Web[a]
Cyclonaias tuberculate Rafinesque, 1820	Purple Wartyback	E	S	Haag (2012)
Eurynia dilatata Rafinesque, 1820	Spike	E	G	Tremblay et al. (2016)
Fusconaia flava (Rafinesque, 1820)	Wabash Pigtoe	E	S	Haag (2012)
Lampsilis cardium Rafinesque, 1820	Plain Pocketbook	P	S	Haag (2012)
Lampsilis fasciola Rafinesque, 1820	Wavyrayed Lampmussel	P	S	Haag (2012)
Lampsilis siliquoidea (Barnes, 1823)	Fatmucket	E	S	Moore et al. (2021)
Lampsilis teres(Rafinesque, 1820)	Yellow Sandshell	O	S	Haag (2012)
Lasmigona complanata (Barnes, 1823)	White Heelsplitter	E	G	Moore et al. (2021)
Lasmigona compressa (I.Lea, 1829)	Creek Heelsplitter	P	G	Marr (2016)***
Lasmigona costata Rafinesque, 1820	Flutedshell	P	G	Haag (2012)
Leptodea fragilis (Rafinesque, 1820)	Fragile Papershell	O	S	Haag (2012)
Ligumia recta (Lamarck, 1819)	Black Sandshell	O	S	Moore et al. (2021)
Ligumia subrostrata (Say, 1831)	Pondmussel	O	G	Haag (2012)
Megalonaias nervosa (Rafinesque, 1820)	Washboard	E	G	Haag (2012)
Obliquaria reflexa Rafinesque, 1820	Threehorn Wartyback	P	S	Vaughn (2012)
Pleurobema sintoxia (Rafinesque, 1820)	Round Pigtoe	E	S	Haag (2012)
Potamilus alatus Say, 1817	Pink Heelsplitter	O	S	Haag (2012)
Potamilus ohiensis (Rafinesque, 1820)	Pink Papershell	O	S	Haag (2012)
Pyganodon grandis (Say, 1829)	Giant Floater	O	G	Haag (2012)
Theliderma metanevra (Rafinesque, 1820)	Monkeyface	E	S	Haag (2012)
Cyclonaias nodulata (Rafinesque, 1820)	Wartyback	E	S	Haag (2012)
Cyclonaias pustulosa (I.Lea, 1831)	Pimpleback	E	S	Haag (2012)
Quadrula quadrula (Rafinesque, 1820)	Mapleleaf	E	S	Haag (2012)
Strophitus undulates Say, 1817	Creeper	P	G	Haag (2012)
Toxolasma parvum (Barnes, 1823)	Lilliput	O	S	Haag (2012)
Toxolasma texasiense I.Lea, 1857	Texas Lilliput	P	S	Hewitt et al. (2019)
Tritogonia verrucosa (Rafinesque, 1820)	Pistolgrip	E	S	Haag (2012)
Truncilla donaciformis (I.Lea, 1827)	Fawnsfoot	O	S	Haag (2012)
Truncilla truncate Rafinesque, 1820	Deertoe	O	S	Vaughn (2012)
Uniomerus tetralasmus Say, 1831	Pondhorn	P	S	NatureServe
Utterbackia imbecillis (Say, 1829)	Paper Pondshell	O	G	Haag (2012)
Venustaconcha ellipsiformis (Conrad, 1836)	Ellipse	P	G	Haag (2012)
Leaunio lienosa (Conrad, 1834)	Little Spectaclecase	O	S	Daniel and Brown (2013)

[a]https://animaldiversity.org

[a]https://explorer.natureserve.org

A stream reach is defined as a stream segment from the headwater to the first tributary or between two tributary confluences (Brenden et al., 2006). Each sampling site was assigned to a stream reach. From the GIS database of Illinois Department of Natural Resources (Holtrop et al., 2005), derived based on the Great Lakes Regional Aquatic Gap Analysis Project of the US Geological Survey (Brenden et al., 2006; McKenna et al., 2013), 69 environmental predictors were selected to model individual fish and mussel species in the study region by Cao et al. (2015, 2016). These predictor variables describe a wide range of stream environments, including stream size, climate, geology, soil, spatial connectivity, land use, and topography at the channel, riparian zone, and watershed scales. Multiple variables also are used to describe complex factors, such as thermal regimes (e.g., Max, Min, and mean temperature) and stream size (Strahler order, link, and watershed size). We used the same set of predictors in the present study, but included the latitude and longitude of a sampling site to detect potential spatial patterns (Online Appendix 1).

Mussel–fish SR ratios vs. mussel–fish SR correlation

The number of fish per mussel species has been noted to vary greatly among different biogeographic regions (Haag, 2012). We used the inverse of this metric (i.e., the mussel-fish SR ratio) to show the difference in environmental preferences between mussel and fish SR, as mentioned earlier. The SR ratio also can be linked to the SR correlation strength directly. When the SR ratio is constant, all data points in a mussel–fish SR plot shall fall on a single line, and the mussel–fish SR correlation will be perfect (Pearson $r = 1.0$), and the ratio becomes the slope of the SR plot. When the variability of the SR ratio increases, i.e., data points spreading more widely, the correlation will become weaker. We demonstrated this relationship by (1) dividing the whole dataset into 4 groups based on the SR ratio (< 0.2, > 0.2–0.4, > 0.4–6, and > 0.6), (2) calculating the coefficient of variation (CV) in the SR ratio and the mussel–fish SR Pearson correlation for each of the four group as well as for the whole dataset, (3) plotting the CV values against the Pearson r. We expected that the correlation coefficient decline with increasing CV.

Modeling the SR ratios- and guild SR–environment relationships

Random forests (RF) regression (Breiman, 2001) was chosen to model the relationships between the SR ratio and environmental variables for its strong performance in analyzing complex relationships (Cutler et al., 2007). RF is an ensemble algorithm built on the classification-regression tree (Breiman et al., 1984). Through bootstrapping all predictors, a large number of small random subsets of predictors are generated and used to build separate tree models. One-third of all samples by default, were selected at random and set aside for model prediction assessment, and the other 2/3 were used to build a tree model. As model performance may vary with mtry, i.e., the size of predictor subsets used, 5000 trees were built for each RF model at mtry = 1–20, and five replicate RF models were built at each mtry level. The model with the highest R^2 was selected. The importance of a predictor variable was evaluated based on the percent increase of mean standard error (% Inc. MSE) when the order of the targeted predictor was randomized: The higher % Inc. MSE is the more important is a predictor (Breiman, 2001). Partial-dependence plots were used to interpret the response of the mussel–fish SR ratio to a predictor of interest. It is a tool to infer how a response variable (e.g., the SR ratio) changes with a given predictor (e.g., the watershed size) after averaging out the effects of all other predictors (Friedman, 2001).

RF regression is highly resistant to the collinearity of predictors (Breiman, 2001; Cutler et al., 2007), however, a strong collinearity makes the result interpretation difficult. We, therefore, conducted correlation analysis for a subset of key predictors after the models were built to help to identify the likely drivers of the SR ratio and the % guild SR.

We modeled the SR ratio based on all sites, including mussel-absence sites, as it is important to understand why a stream site may support fish species, but not mussels. The guild SRs were strongly correlated with the SR ratio (Online Appendix 2), and their models will unlikely offer much additional information. We thus focused on modeling the percent guild SR (% guild SR) based on 352 sites where mussels were collected.

Results

Across all 459 sites, 39 mussel and 132 fish species were recorded. In both groups, the relative occurrence frequency varied substantially among species, 0.0022–0.4161 for mussel, 0.0022–0.8545. On average, fish species, however, occurred more widely than mussel species by 34% (15% vs. 11% of all sites). Mussel SR varied more substantially among sites than fish SR (i.e., higher CV, Table 2), with no mussels collected at 107 sites. The total number of fish species is three times as high as the number of mussel species. The SR ratio ranged from 0 to 1.1 (mean $=0.21$, standard deviation [SD] $=0.19$) across the 459 sites and strongly skewed to the left (i.e., low at most sites and high at a small number of sites, Fig. 2). The SR ratio is more strongly correlated with mussel SR (Pearson $r=0.89$, $P<0.01$) than with fish

SR (Pearson $r=0.10$, $P>0.05$). Fifteen of 39 mussel species are host generalists, and 24 are specialists. Out of the life history strategies, 14, 13, and 12 species are equilibrium, opportunistic, and periodic, respectively (Table 2). However, at the site level, the host generalists and specialists were almost equally common, and opportunistic species were dominant (Table 2).

The correlations between the SR of the five mussel guilds (two hosting- and three life-history-based) and fish SR are generally low (Online Appendix 2) but slightly stronger for the host specialist guild than for the generalist guild (Pearson $r=0.32$ vs. 0.43, $P<0.01$), something that partly supports our hypothesis. The correlations between the total mussel SR and the SR of different mussel guilds were all strong ($r=0.74$–0.92, $P<0.01$), indicating that the SRs of

**Table 2** Statistical summary of fish and mussel SR metrics for 459 stream sites in Illinois, USA (G = host generalists; S = host specialists; E = equilibrium strategists; P = periodic strategists; O = opportunistic strategists, see Haag (2012) for definitions; PT = proportion, based on 352 mussel-present sites only)

	Fish_SR	Mussel_SR	SR_Ratio	G_PT	S_PT	E_PT	P_PT	O_PT	G_SR	S_SR	E_SR	P_SR	O_SR
Min	6	0	0	0	0	0.00	0.00	0.00	0	0	0	0	0
Max	40	19	1.1	1	1	1.00	1.00	1.00	9	11	12	6	7
Median	19	3	0.17	0.5	0.5	0.33	0.21	0.44	2	1	1	1	1
Mean	19.95	4.31	0.21	0.49	0.51	0.28	0.25	0.46	2.04	2.27	1.58	1.08	1.64
SD	6.86	4.13	0.20	0.28	0.28	0.23	0.23	0.30	2.05	2.51	2.14	1.28	1.60
CV	0.34	0.96	0.93	0.58	0.55	0.82	0.92	0.64	1.01	1.11	1.35	1.18	0.98

SD standard deviation, *CV* coefficient of variation

Fig. 2 Relative frequency distribution of mussel-fish SR ratios across 459 stream sites in Illinois, USA with low values at most sites
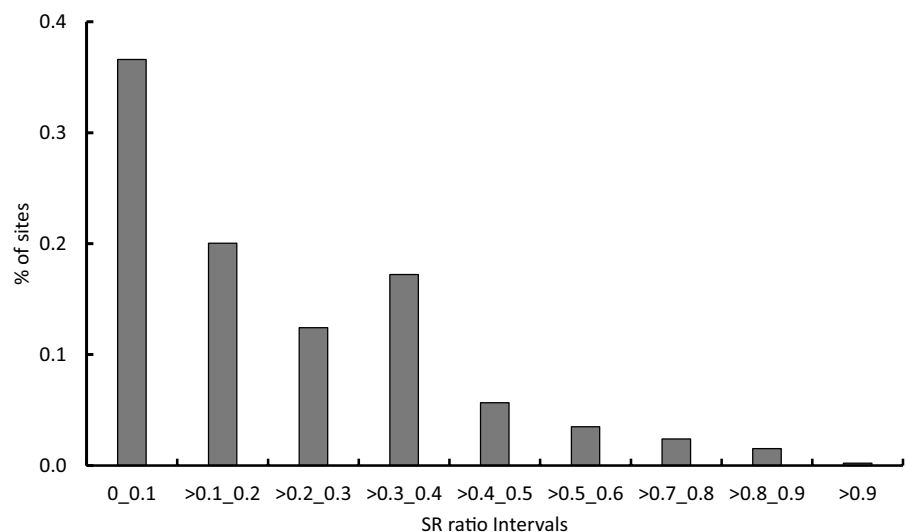
all these guilds strongly co-varied with the total mussel SR across the sampling sites.

Mussel-fish SR ratios vs. mussel-fish SR correlation

The whole dataset and the site group with the SR ratio = 0–0.2 reached the highest CV and weakest mussel-fish SR correlations, while the other three groups showed similarly low CV and strong correlations. As a result, the Pearson r rapidly and linearly declined with increasing CV of the SR ratio (Fig. 3).

SR ratio–environment relationships

The RF models explained 47% and 40% of the variance in mussel (mtry = 5) and fish SR (mtry = 6), respectively. The directional responses of the two types of SR to the top predictors are similar, positive to measures of stream size (WT_Area and Link, see Online Appendix 1 for definitions), percent agricultural land in the watershed (WT_Agri), and deep bedrock in the watershed (WT_BG100), and negative to the watershed slope (WT_Slope) or channel slope (Channel_Slope) and percent shallow bedrock in the watershed (WT_BR50). However, the response curves of fish and mussel SR differed in disparate and complex ways (see Online Appendix 3 for examples) that were difficult to quantify. Therefore, our use of the SR ratio is well justified. Noticeably, fish SR was ranked 6th for the mussel-SR prediction importance in terms of % Inc. MSE, indicating its moderate effect on mussel SR in the study region.
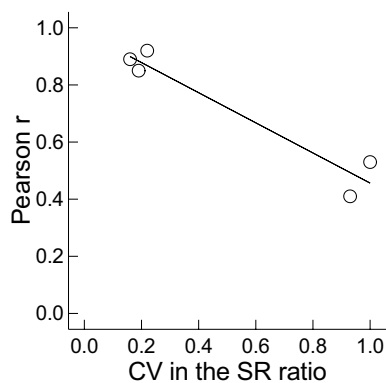

Fig. 3 Effects of the variability measured with coefficient of variation (CV) in the mussel-fish SR ratio on the mussel-fish SR correlation

The RF model explained 30.24% of the total variance in the SR ratio (mtry = 5). Many environmental variables contributed to the explanation of the changes in the SR ratio, with 20 of those reaching ≥ 15% in Inc. MSE (Fig. 4). The top 10 predictors are mostly natural environmental variables, including stream-size measures (WT_Area, Link), slope measures (W_Slope, WT_Slope, or Chan_Grad), and air temperature (WT_JMean, WT_JMin, WT_GDD). Other important predictors include percent agricultural-land and forest in the watershed (WT_Agri and WT_Forest), the percent watershed with bedrock at given depths (WT_BR50, WT_BG100), latitude, and longitude.

Partial-dependence plots showed that the SR ratio strongly increased with the stream size (WT_Area or link), deep bedrock (WT_GB100), and WT_Agri, but decreased with stream or watershed slope (Fig. 5A–C, F). The relationship between the SR ratio and climate variables was more complex; the ratio largely stayed at a high level over the lower range of temperature, followed by a rapid decline (see Fig. 5E for example). The ratio also tended to decrease from the North to the South with a peak in the central Illinois (Fig. 5D) and consistently increased from the West to the East. As a result, the ratio is predicted to be the highest in central-eastern part of the study region.

Most of the key predictors strongly co-varied along latitude and longitude. Stream or watershed slope and shallow bedrock (WT_BR50) increase at a lower latitude, and so do temperature and precipitation (Table 3). In comparison, soil permeability tends to decrease at lower latitudes. WT_Agri is negatively correlated with the slopes and positively with bedrock depth (WT_BG100) and soil permeability (WT_ Perm); WT_Forest showed opposite trends along these three environmental gradients.

Mussel guild SR in relation to the environment and fish SR

The % guild SR is weakly correlated with the SR ratio (Pearson r = 0.20–0.65, $P < 0.01$). The model fitting for the SR of the two hosting guilds are relatively low and equal (R^2 = 0.23). For the three life-history strategies, the model fittings for the SR of the equilibrium and opportunistic guilds are similar to each

Fig. 4 Importance of the top 20 predictors for mussel-fish SR ratios across 459 streams sites in Illinois, USA, measured with percent increase in mean standard error (MSE) when the values of a given predictor is randomized in the Random-Forests regression (see Online Appendix 1 for predictor descriptions)
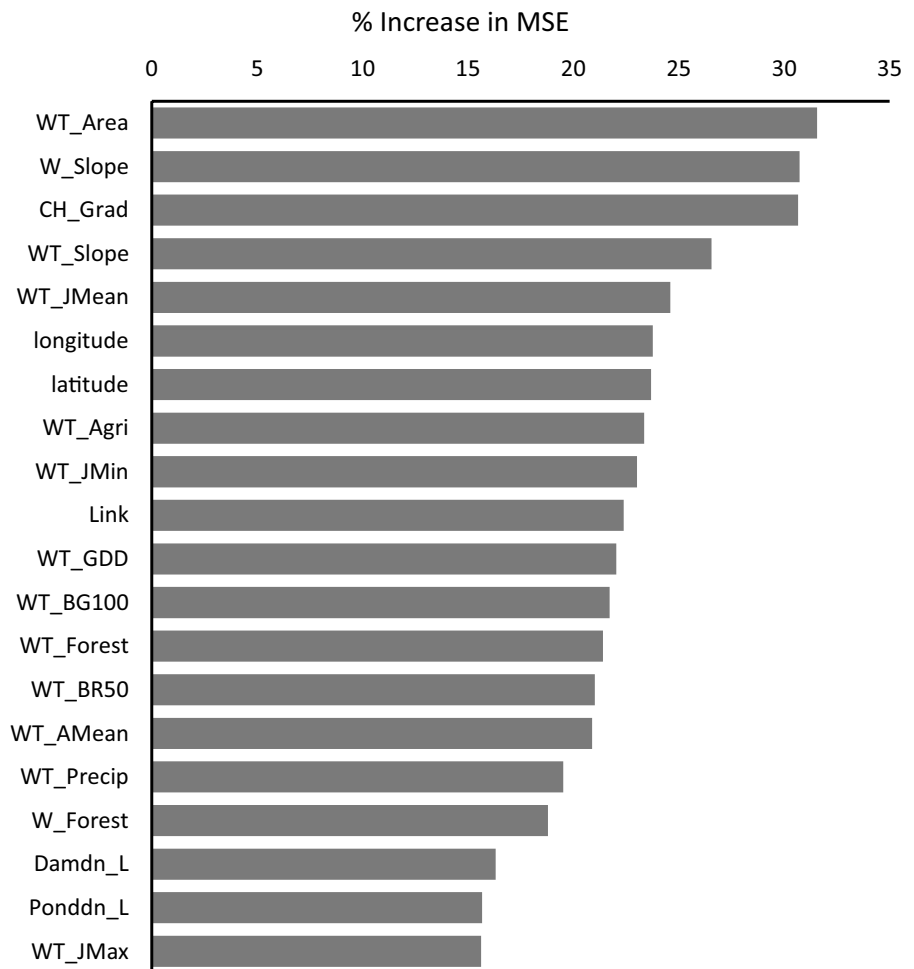
other and better than for the % SR of the periodic guild ($R^2 = 0.30$ vs. 0.16).

The top 15 predictors and the directions of their effects varied among the % guild SR (Table 4), but the natural environmental factors, including stream size, slope, climate, and geology are more important than land-use and spatial connectivity. The responses of the % SR of the equilibrium guild are similar to those of the SR ratio, i.e., positive to stream size, bedrock depth (WT_BG100), Agricultural land (WT_Agri), but negative to stream slope and warm-wet climate. The responses of the opportunist SR are opposite, and those of the periodic SR are mixed. The % SR of host-specialist guilds responded positively to stream size, agricultural land, warm-wet climate, and slope (W_Slope) but

negatively to latitude (Table 4). The responses of the % SR of host-generalist guilds are opposite.

Discussion

A great amount of effort has been focused on the relationships between individual mussel species and their fish hosts (Modesto et al., 2018). In comparison, less attention has been paid to the mussel–fish SR relationship, which varies greatly among studies (Watters, 1992; Vaughn & Taylor, 2000; Bey & Sullivan, 2015). Our analysis examined how the SR ratios are affected by environmental gradients and how different mussel species guilds are related to the environment and fish SR. We found that mussel and fish SR
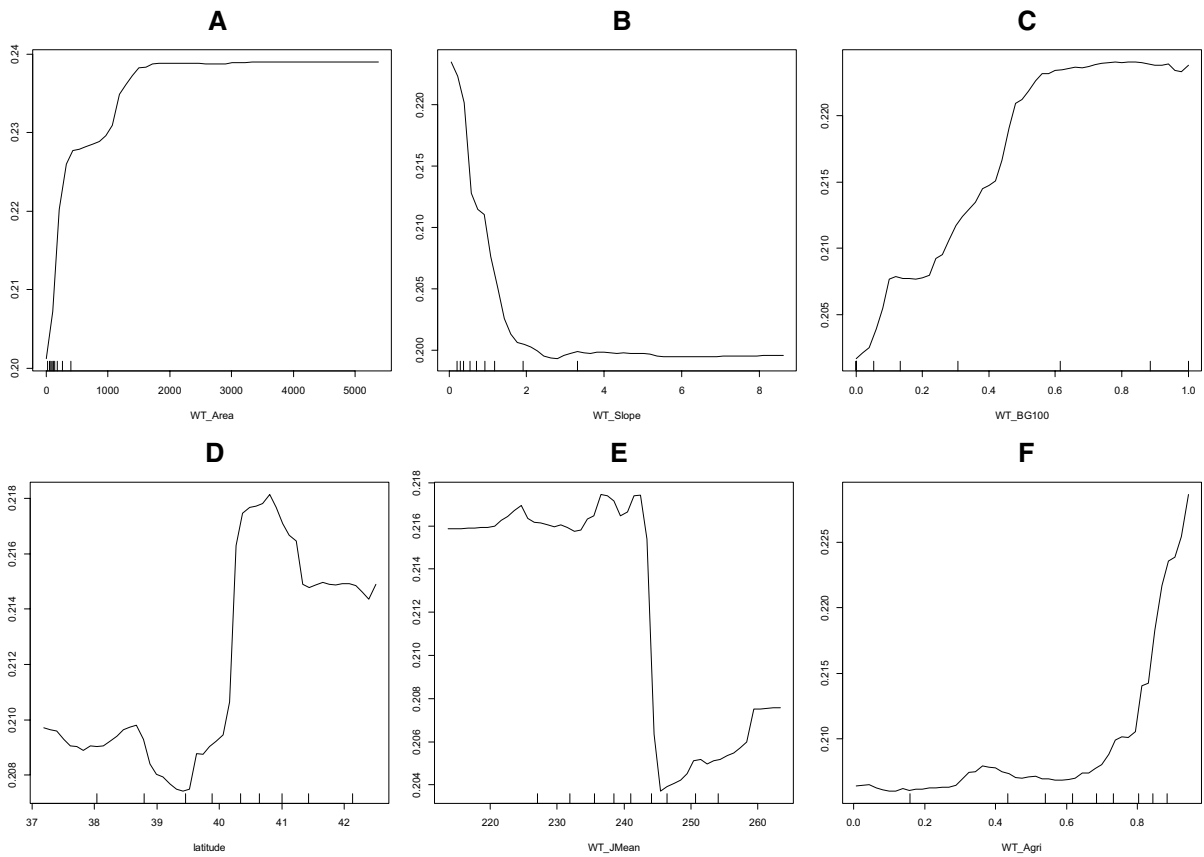
Fig. 5 Partial-dependence plots of Random-Forests regression suggesting the responses of mussel-fish SR ratios to key environmental predictors in streams of Illinois, USA

Table 3 Pearson correlations among key natural environmental, climate, and land-use variables for 459 stream sites at the watershed scale in the State of Illinois, USA, all significant at the $P = 0.05$ level except those labelled with * (see Wasserstein & Nicole, 2016 for the interpretation of P value)

	Latitude	Longitude	WT_Slope	WT_Agri	WT_Forest	WT_BG100	WT_BR50	WT_AMean	WT_Precip
Longitude	0.09*								
WT_Slope	− 0.43	− 0.33							
WT_Agri	0.34	*0.06*	− 0.73						
WT_Forest	− 0.61	− 0.13	0.87	− 0.83					
WT_BG100	0.42	0.37	− 0.44	0.36	− 0.43				
WT_BR50	− 0.48	− 0.36	0.59	− 0.50	0.57	− 0.83			
WT_AMean	− 0.99	− 0.08	0.39	− 0.30	0.57	− 0.40	0.44		
WT_Precip	− 0.90	0.08*	0.57	− 0.52	0.74	− 0.40	0.50	0.87	
WT_Perm	0.28	0.16	− 0.09*	0.05*	− 0.11	0.17	− 0.20	− 0.28	− 0.16

Table 4 Response types and importance ranking of the top 15 predictors to percent SR of five mussel guilds based on the partial-dependence plots of Random-Forests regression applied to 459 stream sites in Illinois, USA (%IncMSE = percent increase in mean standard error, a measure of importance; see Online Appendix 1 for descriptions of the predictors); responses are categorized as increase (↑), decrease (↓), peaking (^), U- or V-shaped (V)

Predictors	Category	Rank	%IncMSE	Response
% Host-generalist SR ($R^2 = 0.23$)				
WT_GDD	Climate	2	18.59	↓
WT_JMean	Climate	3	18.41	↓
WT_JMax	Climate	4	16.84	↓
WT_AMean	Climate	5	15.98	↓
WT_JMin	Climate	6	13.15	↓
WT_Precip	Climate	15	10.28	↓
WT_Carb	Geology	8	12.34	↑
WT_Shale	Geology	9	12.30	↓
WT_Forest	Geology	12	10.87	V
WT_BR50	Land-use	14	10.57	↓
WT_Agri	Land-use	10	12.24	↓
Latitude	Location	1	18.83	↑
WT_Perm	Soil	13	10.76	↑
Link	Stream Size	7	12.52	↓
WT_Area	Stream Size	11	11.97	↓
% Host-specialist SR ($R^2 = 0.23$)				
WT_JMax	Climate	2	18.72	↑
WT_GDD	Climate	3	17.76	↑
WT_JMean	Climate	4	17.43	↑
WT_AMean	Climate	5	17.03	↑
WT_JMin	Climate	7	13.42	↑
WT_Precip	Climate	12	11.63	↑
WT_Carb	Geology	6	13.48	↓
WT_Shale	Geology	10	11.99	↑
WT_Forest	Land-use	15	10.33	^
WT_Agri	Land-use	11	11.98	↑
Latitude	Location	1	19.47	↓
WT_Perm	Soil	9	12.09	^
WT_Area	Stream Size	8	12.37	↑
Link	Stream Size	13	11.44	↑
W_Slope	Topography	14	10.53	↑
% Equilibrium-strategist SR ($R^2 = 0.30$)				
WT_JMin	Climate	2	19.84	↓
WT_JMean	Climate	4	18.09	↓
WT_AMean	Climate	5	17.41	↓
WT_JMax	Climate	8	15.44	↓
WT_GDD	Climate	9	15.26	↓
WT_Precip	Climate	15	10.54	↓

Table 4 (continued)

Predictors	Category	Rank	%IncMSE	Response
% Equilibrium-strategist SR ($R^2 = 0.30$)				
WT_BG100	Geology	3	19.60	↓
WT_BR50	Geology	7	16.80	↑
WT_Forest	Geology	14	10.90	↓
Latitude	Location	6	16.98	↑
Longitude	Location	12	12.17	↑
WT_Area	Stream Size	1	20.41	↑
Link	Stream Size	10	13.74	↑
WT_Slope	Topography	11	12.69	↓
W_Slope	Topography	13	11.45	↓
% Opportunistic-strategist SR ($R^2 = 0.31$)				
WT_JMean	Climate	1	20.25	↑
WT_JMin	Climate	2	19.06	↑
WT_GDD	Climate	3	19.00	↑
WT_AMean	Climate	4	18.47	↑
WT_JMax	Climate	6	17.00	↑
WT_Precip	Climate	8	14.32	↑
WT_BG100	Geology	11	13.68	↓
WT_BR50	Geology	14	12.57	↑
WT_Forest	Land-use	7	14.67	↑
WT_Agri	Land-use	10	14.01	↓
Latitude	Location	5	17.89	↓
Longitude	Location	9	14.28	↓
WT_Area	Stream Size	12	12.81	↓
Link	Stream Size	15	12.51	↓
WT_Slope	Topography	13	12.68	↑
% Periodic-strategist SR ($R^2 = 0.16$)				
WT_JMean	Climate	3	12.74	V
WT_JMax	Climate	4	12.40	V
WT_GDD	Climate	6	11.72	V
WT_AMean	Climate	7	11.68	V
WT_JMin	Climate	10	10.23	V
WT_Precip	Climate	12	9.95	↑
WT_Shale	Geology	11	10.13	↑
WT_Forest	Land-use	8	11.25	V
WT_Agri	Land-use	2	12.92	↑
W_Agri	Land-use	13	9.61	↑
R_Water	Land-use	14	9.39	V
Latitude	Location	1	13.05	↓
WT_Perm	Soil	5	12.40	↑
WT_Area	Stream Size	9	11.02	↓
WT_Slope	Topography	15	9.19	↑

differed in their responses to certain environmental gradients, and some mussel species guilds are more closely associated with the environment or fish SR. These results can help us to reconcile the inconsistencies in mussel–fish SR relationships previously reported, provide new insights into the relative importance of fish and physical environment, and may inform effective mussel biodiversity conservation.

First, our analysis provided an explanation of the reported variable correlations between mussel and fish SR at the site scale. We demonstrated the clear and negative relationship between the variability in the SR ratio and the mussel-fish SR correlation (Fig. 3). Statistically, the inconsistent mussel-fish SR correlation is driven by different levels of variability in the SR ratio among studies. The ecological question is why the SR ratio varies among sites, regions or studies. Our RF model for the SR ratio showed that the different responses of mussel and fish assemblages to environmental gradients at least partly explained the variation of the SR ratio among sites. Given that the types and lengths of key environmental gradients for mussel and fish assemblages are essentially region- or dataset-specific, the mussel-fish SR correlations can be expected to vary among datasets.

Second, we showed what specific natural environmental gradients mussel and fish SR appeared to respond differently. Both fish and mussel SR increased with stream size (Online Appendix 3), as observed by others (Osborne & Wiley, 1992; Watters, 1992; Krebs et al., 2010). However, the increase in the SR ratio with the watershed size (Fig. 4A) indicates that mussel SR is more constrained by small stream size than fish SR. In fact, there are no or few mussel species in many small streams (Watters, 1992; Myers-Kinzie et al., 2001; Krebs et al., 2010). These observations are not surprising because many fish species can quickly colonize and recolonize small streams with seasonal or unstable flow (Datry et al., 2017), but mussels cannot. A stable flow in larger streams is preferred by both mussel and fish species (Haag & Warren, 1998, 2008; Troia & Gido, 2014), but it appears to benefit mussel even more. Both mussel and fish SR also decreased with increasing slope in our study (Online Appendix 3), but again the decrease in their ratio (Fig. 4B) suggests mussel SR is more sensitive to slope than fish species. A higher slope often implies less stable substrates and higher erosion (Arbuckle & Downing, 2002), which should

affect mussel species as benthos and filters more than fishes. Hewitt et al. (2019) also noted that the number of fish species per mussel species that prefer low-slope streams was low, or the SR ratio is high. The SR ratio further decreased with the increasing % of shallow bedrock in the watershed (Fig. 5C). Watershed geology is known to be important for mussel assemblages, probably by affecting stream substrates, slope, flow, and water chemistry (Arbuckle & Downing, 2002; Newton et al., 2008). Future studies should examine how bedrock depth and other geological characteristics affect stream habitats and flow regimes in the study region. In Illinois, the spatial patterns of the watershed topography, soil, and surficial geology are known to be strongly affected by the Illinois and Wisconsin glaciations (Forbes, 1908; Grimley et al., 2017). The glacial history may also have affected the dispersal processes of both fishes and mussels and then the mussel SR and SR ratio. However, both metrics increased significantly from Northeastern to Central-Eastern Illinois, although both areas were glaciated, and decreased in Southern Illinois, which was not glaciated (Grimley et al., 2017). This pattern implies little direct effect of glaciations on these two metrics. Overall, our results suggest that the responses of mussel and fish species to main environmental gradients often are the same in direction but different in magnitude.

Climate often constrains the abundance and distributions of aquatic species through thermal and flow regimes (Olden & Naiman, 2010). In our study, both the SR ratio and the % SR of the five mussel guilds are strongly associated with temperature and precipitation (Fig. 4, Table 4), often decreasing with increases in both variables. This result seems to suggest that climate is limiting mussel SR in Illinois. However, the climate in the region strongly co-varied with stream slope, surficial geology, and soil permeability (Table 3). Several southern states in the US support higher freshwater mussel diversity in spite of their hotter and wetter climate, such as Tennessee and Arkansas in the US (Haag, 2012). The climate effect observed here is likely to be an artifact, and the real drivers are the co-variables above. Co-variation among environmental variables can present a challenge in modeling and predicting the impacts of climate changes, and modeling based on climate variables alone may be not reliable. However, the climate gradient is global and largely directional, while other

environmental gradients, such as those mentioned above, are typically regional or local. Therefore, modeling the effect of climate at the level of continental or a large geographic region, such as the whole Midwestern US (Schartel et al., 2021), may overcome the difficulty associated with the co-variation.

Land-use is a major threat to freshwater biodiversity (Dudgeon et al., 2006; Blann et al., 2009). The negative impact of agricultural land-use on freshwater mussels has been widely reported (Arbuckle & Downing, 2002; Poole & Downing, 2004; Hornbach et al., 2019). However, our analysis contradicted these previous studies, i.e., the SR ratio appeared to increase with the percent agricultural land in the watershed (WT_Agri) and decreased with the increasing percent forested land in the watershed (WT_Forest). This result also disagrees with one previous study in the central-eastern part of the region (Cao et al., 2013). We think that this inconsistency is caused at least partly by the strong co-variation of land use with the stream slope, soil permeability, and depth of bedrock in the watershed in our study region (Table 3). This reasoning should also be applicable to the % SR of the mussel guilds. As a result, we could not effectively assess the effects of land use on the SR ratio and the different mussel guild SR in this study. As with climate impact, researchers need to carefully examine whether or how land use may co-vary with natural environmental gradients when assessing its ecological impacts and strive to overcome the challenge.

How important fish hosts are to mussel species relatively to the physical environment appears debatable. Inoue et al. (2017) hypothesized that mussel distributions are nested within fish-host distribution, and mussel species distribution is largely controlled by abiotic factors (Inoue et al., 2017). We showed that fish species are distributed more widely on average than mussel species, and mussel-fish SR correlation is weak at the site scale. These results support the hypothesis above. The average SR ratio is also low (0.21), which is equal to approximately 5 fish species per mussel species, compared with 1.9–13.7 fish species per mussel species previously reported (Haag, 2012). The low SR ratio suggests generally high fish host availability to mussel species, which agrees with the low importance of fish SR to mussel SR compared with environmental variables in our RF model. Physical environmental data thus may be generally

sufficient for mussel-SR modeling and conservation planning, although fish hosts are known to be critical for specific mussel species (Fritts et al., 2012; Benson et al., 2017; Galbraith et al., 2018). We also noted that in some small, but significant number of streams the SR ratios were high (Fig. 1). Fish SR may be more important in those streams because mussel species could compete for fish hosts (Rashleigh & DeAngelis, 2007; Hewitt et al., 2019) and needs to be carefully weighed in conservation planning for those streams.

The wide range of the SR ratios observed in the present study also implies that fish SR is a poor index of mussel SR in the study region. This result agrees with the observations that mussel SR and abundances can change substantially while a fish-based biological index of integrity (IBI) remained stable (Cao et al., 2017; Haag, 2019). To effectively protect mussel biodiversity, mussel assemblages need to be routinely monitored by environmental or natural resources agencies rather than relying on fish SR and IBI.

The relationships between the % SR of the five mussel guilds and the environment and fish SR largely agree with the general expectations (Haag, 2012; Randklev et al., 2016). The positive response of the % SR for the equilibrium guild to stream size and the negative response to stream slope (Table 4) agree with the preference of the guild for generally stable flow in large streams. Daniel & Brown (2013) also reported this species guild was limited to high-order streams. The positive responses of the % SR of the opportunistic mussel guild to slope and negative response to stream size agree with the general observation that the species of this guild often occupy hydrologically unstable or disturbed habitats (Haag, 2012; Randklev et al., 2016). The correlations of fish SR with the SR of host-specialists is only moderately stronger than with the SR of host generalists. We wonder whether the difference in correlation would be greater if phylogenetic diversity instead of SR is used to measure fish diversity. If fish phylogenetic diversity is indeed more closely related to the % SR of host specialists, the higher % SR of host-specialists at low latitude (Table 4) may be explained because fish phylogenetic diversity increases in the South-East in the US (Qian et al., 2020).

Our model explained a significant proportion of the variance in most response variables (e.g., the SR ratio), but a large proportion remained unexplained. Aquatic biodiversity is affected by many processes

operating at different spatial and temporal scales (Poff, 1997; Jackson et al., 2001). We focused on the GIS-based landscape-level variables in this study. Local habitat characteristics, water quality, and flow regimes are among other potential drivers of the SR ratio not considered. However, it is challenging to effectively characterize these factors. Water quality is often driven by weather events and flow (Sherson et al., 2015), and continuous monitoring over the long term is needed to assess its impacts on aquatic biodiversity, but unavailable in the study region. Flow data also generally fall short for wadeable streams. With continuous monitoring loggers for water quality and flow increasingly applied to stream surveys (Chapin et al., 2014; Parker et al., 2020), these difficulties could be overcome over time. For the modeling of mussel guild SR, the uncertainty associated with the categorization of biological traits in some species (Moore et al., 2021), may also contribute to the unexplained variance. Finally, biological pathogens could be a key diver of mussel diversity, but are poorly understood (Brian & Aldridge, 2019; Waller & Cope, 2019; Richard et al., 2020). The need for their inclusion in mussel surveys and SR modeling is warranted.

In conclusion, the mussel-fish SR ratios were generally low but highly variable among sampling sites. The high variability appeared caused by the different responses of mussel and fish SR to multiple environmental gradients, including stream size, stream slope, and watershed geology. The type and lengths of key environmental gradients likely vary among datasets, and so are the mussel-fish SR correlation. Overall, the physical environment appeared to be more important to mussel SR than fish SR in the study region. Land-use and climate could strongly co-vary with other environmental factors, and great caution is needed to model and predict their effects on mussel assemblages.

Author contributions YC—developed the main idea, analysed the data, and drafted the manuscript. LH—contributed to idea development and manuscript writing. CT—contributed to data compiling and manuscript writing. BM—contributed to data compiling and manuscript writing. KC—contributed to idea development and manuscript writing.

Data availability Data will be uploaded on publically-accessible site after the manuscript is accepted.

Code availability NA.

Declarations

Conflict of interest The authors declared that they have no conflict of interest.

Ethical approval This study has not been published or submitted for publishing anywhere else. No animal use is involved in this study, which is based on published data sets. All researchers who made significant contributions are included.

Consent to participate All co-authors are actively participated this study.

Consent for publication All authors agreed on the submission.

References

Arbuckle, K. E. & J. A. Downing, 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Canadian Journal of Fisheries and Aquatic Sciences 59: 310–316.

Austin, M. O. & M. J. Gaywood, 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. Journal of Vegetation Science 5: 473–482.

Benson, J. A., P. G. Close, B. A. Stewart & A. Lymbery, 2017. Upstream recolonization by freshwater mussels (Unionoida: Hyriidae) following installation of a fishway. Aquatic Conservation: Marine and Freshwater Ecosystems 28: 512–517.

Bey, C. R. & S. M. P. Sullivan, 2015. Associations between stream hydrogeomorphology and co-dependent mussel–fish assemblages: evidence from an Ohio, USA river system. Aquatic Conservation: Marine and Freshwater Ecosystems 25: 555–569.

Blann, K. L., J. L. Anderson, G. R. Sands & B. Vondracek, 2009. Effects of agricultural drainage on aquatic ecosystems: a review. Critical Reviews in Environmental Science and Technology 39: 909–1001.

Breiman, L., 2001. Random forests. Machine Learning 45: 5–32.

Breiman, L., J. H. Friedman, R. A. Olshen & C. G. Stone, 1984. Classification and Regression Trees, Chapman and Hall, New York.

Brenden, T. O., L. Wang, P. W. Seelbach, R. D. Clark, M. J. Wiley & B. L. Sparks-Jackson, 2006. A spatially constrained clustering program for river valley segment

delineation from GIS digital river networks. Environmental Modelling Software 23: 638–649.

Brian, J. I. & D. C. Aldridge, 2019. Endosymbionts: an overlooked threat in the conservation of freshwater mussels? Biological Conservation 237: 155–165.

Cao, Y., J. Huang, K. S. Cummings & A. Holtrop, 2013. Modeling changes in freshwater mussel diversity in an agriculturally dominated landscape freshwater. Science 32: 1205–1218.

Cao, Y., A. Stodola, S. Douglass, D. Shasteen, K. S. Cummings & A. Holtrop, 2015. Modelling and mapping the distribution, diversity and abundance of freshwater mussels (Family Unionidae) in wadeable streams of Illinois, USA. Freshwater Biology 60: 1379–1397.

Cao, Y., L. Hinz, B. Metzke, J. A. Stein & A. M. Holtrop, 2016. Modeling and mapping fish abundance across wadeable streams of Illinois, USA based on landscape-level environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 73: 1031–1046.

Chapin, T. P., A. S. Todd & M. P. Zeigler, 2014. Robust, low-cost data loggers for stream temperature, flow intermittency, and relative conductivity monitoring. Water Resource Research 50: 6542–6548.

Cutler, D. R., T. C. Edwards Jr., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson & J. J. Lawler, 2007. Random forests for classification in ecology. Ecology 88: 2783–2792.

Daniel, W. M. & K. M. Brown, 2013. Multifactorial model of habitat, host fish, and landscape effects on Louisiana freshwater mussels. Freshwater Science 32: 193–203.

Datry, T., N. Bonada & A. J. Boulton, 2017. Intermittent Rivers and Ephemeral Streams: Ecology and Management, Academic Press, London.

Downing, J. A., P. Van Meter & D. A. Woolnough, 2010. Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels. Animal Biodiversity and Conservation 33: 151–185.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévéque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Review 81: 163–182.

Ferreira-Rodríguez, N., Y. B. Akiyama, O. V. Aksenova, R. Araujo, M. C. Barnhart, Y. V. Bespalaya, A. E. Bogan, I. N. Bolotov, P. B. Budha, C. Clavijo, S. J. Clearwater, G. Darrigran, V. T. Do, K. Douda, E. Froufe, C. Gumpinger, L. Henrikson, C. L. Humphrey, N. A. Johnson, O. Klishko, M. W. Klunzinger, S. Kovitvadhi, U. Kovitvadhi, J. Lajtner, M. Lopes-Lima, E. A. Moorkens, S. Nagayama, K.-O. Nagel, M. Nakano, J. N. Negishi, P. Ondina, P. Oulasvirta, V. Prié, N. Riccardi, M. Rudzīte, F. Sheldon, R. Sousa, D. L. Strayer, M. Takeuchi, J. Taskinen, A. Teixeira, J. S. Tiemann, M. Urbańska, S. Varandas, M. V. Vinarski, B. J. Wicklow, T. Zając & C. C. Vaughn, 2019. Research priorities for freshwater mussel conservation assessment. Biological Conservation 231: 77–87.

Forbes, S. A., 1908. The fishes of Illinois. Illinois State Laboratory of Natural History 1: 19–70.

Franklin, J., H. M. Regan, L. A. Hierl, D. H. Deutschman, B. S. Johnson & C. S. Winchell, 2011. Planning, implementing, and monitoring multiple-species habitat conservation plans. American Journal of Botany 98: 559–571.

Friedman, J. H., 2001. Greedy function approximation: a gradient boosting machine. Annals of Statistics. 29: 1189–1232.

Fritts, A. K., M. W. Fritts II, D. L. Peterson, D. A. Fox & R. B. Bringolf, 2012. Critical linkage of imperiled species: Gulf Sturgeon as host for Purple Bankclimber mussels. Freshwater Science 31: 1223–1232.

Galbraith, H. S., D. E. Spooner & C. C. Vaughn, 2010. Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. Biological Conservation 143: 1175–1183.

Galbraith, H. S., J. L. Devers, C. J. Blakeslee & J. C. Cole, 2018. Reestablishing a host–affiliate relationship: migratory fish reintroduction increases native mussel recruitment. Ecological Applications 28: 1841–1852.

Grimley, D. A., A. C. Philips, A. D. McKay III & A. M. Andewrs. 2017. Geomorphic expression of the Illinois Episode glaciation (marine isotope stage 6) in Illinois: Moraines, sublobes, subglacial lineations, and possible ice streaming. In Kehew, A. E. & B. B. Curry (eds), Quaternary Glaciation of the Great Lakes Region: Process, Landforms, Sediments, and Chronology: Geological Society of America Special Paper 530: 1–25.

Haag, W. R., 2012. North American Freshwater Mussels, Cambridge University Press, New York.

Haag, W. R., 2019. Reassessing enigmatic mussel decline in the United States. Freshwater Molluscs Biology and Conservation 22: 43–60.

Haag, W. R. & M. L. Warren, 1998. Role of ecological factors and reproductive strategies in freshwater mussel communities. Canadian Journal of Fisheries and Aquatic Sciences 55: 297–306.

Haag, W. R. & M. L. Warren, 2008. Effects of severe drought on freshwater mussel assemblages. Transactions of American Fisheries Society 137: 1165–1178.

Haag, W. & J. D. Williams, 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735: 45–60.

Hewitt, T. L., C. L. Wood & D. Ó. Foighil, 2019. Ecological correlates and phylogenetic signal of host use in North American unionid mussels. International Journal for Parasitology 49: 71–81.

Holtrop, A.M., D. Day, C. Dolan, & J. Epifanio. 2005. Ecological classification of rivers for environmental assessment and management: stream attribution and model preparation. Illinois Natural History Survey Technical Report 2005/04. Illinois Natural History Survey, Champaign, IL.

Hornbach, D. J., D. C. Allen, M. C. Hove & K. R. MacGregor, 2018. Long-term decline of native freshwater mussel assemblages in a federally protected river. Freshwater Biology 63: 243–263.

Hornbach, D. J., M. C. Hove, K. R. MacGregor, J. L. Kozarek, B. E. Sietman & M. Davis, 2019. A comparison of freshwater mussel assemblages along a land-use gradient in Minnesota. Aquatic Conservation: Marine and Freshwater Ecosystem 29: 1826–1838.

IL-DNR, 2010. Fisheries Manual of Operation: Filed Sampling Protocols for Rivers and Streams. IL Department of

Natural Resources, Division of Fisheries/Illinois Natural History Survey, Champaign, IL.

Inoue, K., K. Stoeckl & J. Geist, 2017. Joint species models reveal the effects of environment on community assemblage of freshwater mussels and fishes in European rivers. Diversity and Distributions 23: 284–296.

Jackson, D. A., P. R. Peres-Neto & D. J. Olden, 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58: 157–170.

Krebs, R. A., W. C. Borden, E. R. Streiner, M. S. Lyons, W. Zawiski & B. M. Walton, 2010. Determinants of mussel diversity in Lake Erie tributaries. Journal of the North American Benthological Society 29: 506–520.

McKenna, J. E., D. M. Carlson & M. I. Payne-Wynne, 2013. Predicting locations of rare aquatic species' habitat with a combination of species-specific and assemblage-based models. Diversity and Distributions 19: 503–517.

Modesto, V., M. Ilarri, A. T. Souza, M. Lopes-Lima, K. Douda, M. Clavero & R. Sousa, 2018. Fish and mussels: Importance of fish for freshwater mussel conservation. Fish and Fisheries 19: 244–259.

Moore, A. P., N. Galic, R. A. Brain, D. J. Hornbach & V. E. Forbes, 2021. Validation of freshwater mussel life-history strategies: a database and multivariate analysis of freshwater mussel life-history traits. Aquatic Conservation: Marine and Freshwater Ecosystems 31: 3386–3402.

Myers-Kinzie, M. L., S. P. Wente & A. Spacie, 2001. Occurrence and distribution of freshwater mussels in small streams of Tippecanoe County, Indiana. Proceedings of the Indiana Academy of Science 110: 141–150.

Newton, T. J., D. A. Woolnough & D. J. Strayer, 2008. Using landscape ecology to understand and manage freshwater mussel populations. Journal of North American Benthological Society 27: 424–439.

Olden, J. D. & R. J. Naiman, 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55: 86–107.

Osborne, L. L. & M. J. Wiley, 1992. lnfluence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries & Aquatic Sciences. 49: 671–681.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391–409.

Poole, K. E. & A. Downing, 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. Journal of the North American Benthological Society 23: 114–125.

Qian, H., Y. Cao, D. J. Li, C. Chu, B. Sandel & X. L. Wang, 2020. Geographic patterns and environmental correlates of phylogenetic relatedness and diversity for freshwater fish assemblages in North America. Ecography 43: 1814–1824.

Randklev, C. R., H. H. Wang, W. E. Grant, J. E. Grove, S. Robertson & R. N. Wilkins, 2015. Land use relationships for a rare freshwater mussel species endemic to Central Texas. Journal of Fish and Wildlife Management 6: 327–337.

Randklev, C. R., N. Ford, S. Wolverton, J. H. Kennedy, C. Robertson, K. Mayes & D. Ford, 2016. The influence of stream discontinuity and life history strategy on mussel community structure: a case study from the Sabine River, Texas. Hydrobiologia 770: 173–191.

Rashleigh, B. & D. L. DeAngelis, 2007. Conditions for co-existence of freshwater mussel species via portioning of fish host resources. Ecological Modelling 201: 171–178.

Regan, H. M., L. A. Hierl, J. Franklin, D. H. Deutschman, H. L. Schmalbach, C. S. Winchell & B. S. Johnson, 2008. Species prioritization for monitoring and management in regional multiple species conservation plans. Diversity and Distributions 14: 462–471.

Richard, J. C., E. Leis, C. D. Dunn, R. Agbalog, D. Waller, S. Knowles, J. Putnam & T. L. Goldberg, 2020. Mass mortality in freshwater mussels (*Actinonaias pectorosa*) in the Clinch River, USA, linked to a novel densovirus. Scientific Reports 10: 14498.

Ries, P. A., T. J. Newton, R. J. Haro, S. J. Zigler & M. Davies, 2015. Annual variation in recruitment of freshwater mussels and its relationship with river discharge. Aquatic Conservation: Marine and Freshwater Ecosystems 26: 703–714.

Schartel, T. E., Y. Cao, B. Henning, M.-L. Feng & L. C. Hinz Jr., 2021. Modelling and predicting freshwater mussel distributions in the Midwestern USA. Aquatic Conservation: Marine and Freshwater Ecosystems. https://doi.org/10.1002/aqc.3720.

Sherson, L. R., D. J. Van Horn, J. D. Gomez-Velez, L. J. Crossey & C. N. Dahm, 2015. Nutrient dynamics in an alpine headwater stream: use of continuous water quality sensors to examine responses to wildfire and precipitation events. Hydrological Processes 29: 3193–3207.

Taeubert, J. E., A. M. P. Martinez, B. Gum & J. Geist, 2012. The relationship between endangered thick-shelled river mussel (Unio crassus) and its host fishes. Biological Conservation 155: 94–103.

Tremblay, M. E. M., T. J. Morris & J. D. Ackerman, 2016. Loss of reproductive output caused by an invasive species. Royal Society Open Science 3: 150481.

Troia, M. J. & K. B. Gido, 2014. Towards a mechanistic understanding of fish species niche divergence along a river continuum. Ecosphere 5: art41.

Vaughn, C. C., 2012. Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels. Freshwater Biology 57: 982–992.

Vaughn, C. C. & C. M. Taylor, 2000. Macroecology of a host-parasite relationship. Ecography 23: 11–20.

Waller, D. L. & W. G. Cope, 2019. The Status of Mussel Health Assessment and a Path Forward. Freshwater Mollusk Biology and Conservation 22: 26–42.

Wasserstein, R. L. & A. L. Nicole, 2016. The ASA statement on p-values: context, process, and purpose. American Statistician 70: 129–133.

Watters, G. T., 1992. Unionids, fishes, and the species-area curve. Journal of Biogeography 19: 481–490.

Wilson, J. B., 1999. Guilds, functional types and ecological groups. Oikos 86: 507–522.

Wood, C. L. & P. T. J. Johnson, 2016. How does space influence the relationship between host and parasite diversity? Journal of Parasitology 102: 485–494.