ARTICLE

Freshwater Ecology

Trait-based and multi-scale approach provides insight on responses of freshwater mussels to environmental heterogeneity

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Abstract

Our understanding of the factors driving the distribution of metacommunities at different scales can be obscured by high variation in species composition between sites and a lack of fine-scale distribution data. Trait-based approaches have long been used to better identify and examine ecological patterns. Most recent studies of riverine metacommunities examining trait-based patterns have focused on shorter lived organisms. Here we focused on a group of longer lived, sedentary riverine organisms, unionid freshwater mussels. The objective of this study was to examine how (1) the distribution of mussels with different life history strategies (trait-based approach) and (2) the relative importance of environmental and spatial factors (as a proxy for dispersal) would differ with spatial scale and position in the river; and to (3) further compare this with patterns derived from a taxonomic approach. Fine-scale distribution data of mussels and environmental factors were collected every 100 m in spatially extensive surveys in an upstream and downstream segment (200 sites/20-km segment) of a semiarid river, making them some of the most spatially intensive surveys documented to date. A combination of redundancy analysis, asymmetric eigenvector mapping, and variation partitioning analyses revealed that more variation was explained by environmental factors where more environmental differences occur between sites. Where environmental heterogeneity was lower, the amount of variation explained by smaller scale spatial factors was higher, likely mostly associated with stochastic rather than dispersal processes. A higher amount of unexplained variation at the taxonomic level suggests that stochasticity may also play an important role in determining species composition. In contrast, different life history groups had a highly predictable distribution pattern driven by environmental heterogeneity, especially between river segments and mesohabitat, which was associated with different flow conditions. The role we predict for environmental heterogeneity and stochasticity in shaping the distribution of mussels in our study river likely also applies to other taxa and ecosystems at a spatial scale at which neither

dispersal limitation nor mass effects occur. Thus, understanding the magnitude and extent of dispersal relative to the amount of environmental heterogeneity may be key for predicting metacommunity structure and dynamics for different organisms.

KEYWORDS

environmental filtering, life history strategy, metacommunity, riverine organisms, space, Unionidae

INTRODUCTION

A primary goal in ecology is to understand the distribution, abundance, and composition of organisms and communities. Metacommunity theory provides a useful framework to evaluate the relative importance of neutral- and niche-based processes (i.e., dispersal, drift, and environmental selection) in structuring ecological communities (Leibold & Chase, 2018; Leibold et al., 2004). The relative importance of these processes in structuring communities predominantly depends upon the spatiotemporal scale of the study and the levels of environmental heterogeneity and connectivity within the study system (Brown et al., 2011; Heino et al., 2015; Leibold & Chase, 2018). Rivers are model ecosystems to test the relative importance of niche- and neutral-based processes in structuring communities because their unique dendritic configurations offer discrete spatial frameworks that could enhance or impede dispersal and because rivers usually exist along substantial environmental gradients (Heino, 2013; Heino et al., 2015).

Ecological theory has long recognized that the distributions of organisms within rivers are usually not random and that communities, subject to various selective forces, usually display various spatial patterns (Humphries et al., 2014; Leibold et al., 2004; Poff et al., 1997; Thorp & Delong, 1994; Thorp et al., 2006; Vannote et al., 1980). Most studies conducted in riverine systems have found that local environmental filtering often plays a more important role in structuring communities than spatial factors (used as a proxy for dispersal); however, this may change depending on the specific taxa being considered and their location within the river network (Brown & Swan, 2010; Grönroos et al., 2013; Heino et al., 2015; Schmera et al., 2018; Tonkin et al., 2018). For example, the network position hypothesis predicts that headwater communities are exclusively controlled by local environmental conditions, whereas mainstem communities are regulated by regional dispersal factors and local environmental processes (Brown & Swan, 2010; Henriques-Silva et al., 2019; Schmera et al., 2018). However, a majority of metacommunity studies analyzing only taxonomic (i.e., species level) data result in a high percentage of unexplained community variation

(e.g., Cottenie, 2005; Leibold & Chase, 2018; Soininen, 2014), which can make it challenging to disentangle specific metacommunity assembly processes for riverine organisms.

Considering functional traits can increase the amount of variation explained by environmental factors and increase our understanding of processes structuring metacommunities, especially when functional traits such as feeding niche can provide insights into the underlying mechanisms of factors driving the distribution patterns (Leibold & Chase, 2018; Tonkin et al., 2016). For example, fishes show predictable changes in functional feeding groups from upstream to downstream in rivers of different continents (Ibanez et al., 2007), although taxonomic composition may vary widely. Thus, examining trait-based patterns can help reveal driving factors that may otherwise be concealed by a high amount of variation in species composition driven more strongly by stochastic processes.

Although ecologists have a long history of grouping organisms based on their traits to better understand biological processes (e.g., Darwin, 1859; Gleason, 1926; Grime, 1974), there has been a resurgence in the past two decades in trait-based approaches to better understand the structure and dynamics of communities in response to environmental change (Funk et al., 2017; Leibold & Chase, 2018; McGill et al., 2006; Petchey & Gaston, 2006). In general, traits can be defined as morpho-physio-phenological feature measurable at the individual level (Violle et al., 2007). Most recent studies examining both taxonomic and trait-based patterns to better understand the role of environmental heterogeneity and dispersal in structuring riverine metacommunities have focused on shorter lived organisms such as macroinvertebrates (e.g., Krynak et al., 2019; Li et al., 2019; Perez Rocha et al., 2018; Wang et al., 2019), plankton (e.g., Huszar et al., 2015), and small-bodied fish communities (e.g., Benone et al., 2020; Peláez & Pavanelli, 2019; Rodrigues-Filho et al., 2020). Much less work has focused on combing taxonomic and trait-based approaches in a multi-scale metacommunity framework for longer lived sedentary riverine organisms, such as freshwater mussels, although several studies have examined ecological processes in relation to traits of freshwater mussels

(e.g., Atkinson et al., 2014; Spooner & Vaughn, 2008; Vaughn, 2012). Freshwater mussels are highly imperiled, have a unique life history that relies on host fish for large-scale dispersal (Downing et al., 2010; Haag & Williams, 2014; Lopes-Lima et al., 2018), and are not as routinely monitored as fish and macroinvertebrates, which may explain to some extent the lack of studies. They are also relatively long-lived (maximum life span: ~8 to >50 years depending upon species and if environmental conditions are favorable), hampering experimental approaches. However, examining the structuring processes of longer lived and sedentary riverine organisms could give valuable insights into the chronic factors impacting species distributions over longer temporal scales.

Unfortunately, there is a lack of quantitative life history trait data for many freshwater mussel species; however, even qualitative trait-based approaches can provide insights into the processes structuring mussel communities. Haag (2012) defined three different life history categories (opportunistic, equilibrium, and periodic), somewhat similar to existing models for plants (Grime, 1974) and fish (Winemiller & Rose, 1992). A recent effort to assign mussel species to life history categories based on the current knowledge of life history traits (life span, age at maturity, maximum length, glochidia length, and fecundity) for mussels found good agreement with previously described categorizations (Moore et al., 2021). In general, opportunistic mussel species can be characterized as fast-growing with short life spans and moderate to high fecundity, whereas equilibrium strategists are long-lived, slow-growing species with relatively low fecundity (Haag, 2012). Periodic species generally exhibit intermediate life history traits compared with opportunistic and equilibrium species (Haag, 2012).

A few recent studies have started to examine the relationship between environmental variables and the distribution of riverine mussels with different life history strategies (e.g., Chambers & Woolnough, 2018; Daniel & Brown, 2014; Hornbach et al., 2019). However, these studies only focused on a single spatial scale and did not provide specific details on the relationship between mussel life history strategies and individual environmental variables. Incorporating a multi-spatial scale approach for studying the distribution of riverine organisms is needed because factors influencing community structure often change with scale and are hierarchically nested (Allen & Starr, 1982; Fausch et al., 2002; Viana & Chase, 2019). Historically, most studies investigating the distribution of mussels were conducted at a single spatial scale. For example, studies at the local (e.g., reach) scale (spatial scale 10^{-1}–10^2 m) found that near-bed hydraulic variables, substrate type, and substrate stability were important in predicting mussel presence (e.g., Allen & Vaughn, 2010; Gangloff & Feminella, 2007; Maio & Corkum, 1995; Strayer, 1999), whereas larger (e.g., regional) scale studies (spatial scale 10^5–10^6 m) found host fish distributions, underlying geology, land use, and stream or catchment size to be more important for differences in mussel presence and community composition (e.g., Arbuckle & Downing, 2002; McRae et al., 2004; Poole & Downing, 2004; Schwalb et al., 2013, 2015; Vaughn, 1997). It is important to notice that fish are both a fundamental resource and a vector for dispersal. The presence of suitable host fish is required for the reproduction of mussels, and dispersal of mussels may be limited by the low mobility of their host fish (Schwalb, Poos, & Ackerman, 2011; Schwalb, Cottenie, Poos, & Ackerman, 2011) or their absence (Douda et al., 2012).

While many studies on mussels or other riverine organisms can be found on a local reach scale and larger regional scale (see above), studies examining the distribution of riverine organisms often lack continuous fine-scale distribution data at intermediate spatial scales (10^3–10^5 m), likely because collecting data at these scales is labor- and cost-intensive (Fausch et al., 2002). Only a few studies have collected extensive fine-scale distribution data of mussels (Inoue et al., 2014; Ries et al., 2016; Terui et al., 2014). Therefore, the objective of this study was to compare a life history strategy classification (hereafter referred to as trait-based approach) and taxonomic-level approach (i.e., species) to examine how the distribution of mussels and the factors driving this distribution would differ with spatial scale (i.e., river vs. segment) and position in the river (upstream vs. downstream). To address our objective, spatially extensive surveys were conducted in upstream and downstream segments (200 sites/segment) of the San Saba River in Texas, USA. We also examined, for a smaller subset of sites, whether any variation in fish existed within our study area. Specifically, we addressed the following questions: How does the relative importance of environmental and spatial factors for the distribution of mussels differ between (1) spatial scales (i.e., river and segment), (2) upstream and downstream segments within the same river, and (3) species (taxonomic-level approach) and life history strategy groups (trait-based approach)?

Environmental heterogeneity likely increases with spatial scale as rivers usually exist along substantial environmental gradients (e.g., Grönroos et al., 2013; Heino, 2013) and can be substantially higher in more isolated headwater streams compared with mainstem rivers (e.g., Brown & Swan, 2010; Clarke et al., 2008; Datry et al., 2017). Therefore, for questions 1 and 2, we hypothesized that higher environmental heterogeneity at a larger spatial scale (i.e., river vs. segment) and upstream (compared to downstream) would result in more variation of community composition explained by environmental factors at the river scale and in the upstream segment (Figure 1A). We also expected that different environmental factors would be drivers of the
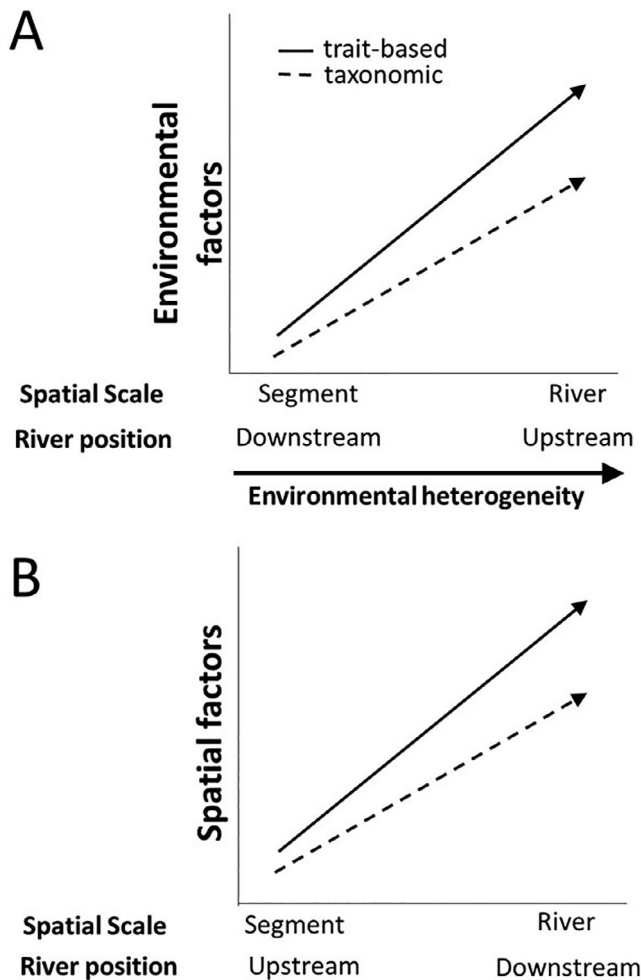
FIGURE 1 Hypothesized change in relative importance of (A) environmental factors along a gradient of environmental heterogeneity, resulting in higher importance of environmental factors at a larger spatial scale (river) and more isolated position in the river (upstream), and (B) spatial factors, being more important downstream and at the river scale.

distribution of mussels at different spatial scales. For example, local-scale environmental factors, such as substrate type, should be more important at the segment scale, whereas regional environmental factors, such as ecoregion, should be more important at the river scale.

In respect to spatial factors, we hypothesized that larger distances between sites at the river scale versus segment scale would more likely cause dispersal limitation, resulting in stronger spatial signals (i.e., more variation explained by spatial factors; Heino et al., 2015; Figure 1B). Additionally, applying the network position hypothesis (Brown & Swan, 2010; Henriques-Silva et al., 2019; Schmera et al., 2018) to segments of the same river (tributary), the relative importance of spatial factors in structuring mussel communities should be higher downstream (compared with upstream) where dispersal

from connected mainstem sources (i.e., Colorado River) is more likely (i.e., mass effects; Figure 1B).

For the third question, we expected that less of the variation in species composition (taxonomic) would be explained by environmental and spatial factors compared with life history strategy groups (trait-based), because of ecological drift causing random differences in species abundances between sites, even in the absence of environmental heterogeneity or similar connectivity and dispersal between sites (Leibold & Chase, 2018).

METHODS

Study area

The San Saba River is a spring-fed river located in central Texas (Figure 2). The San Saba River is located within two ecoregions (level III as defined by the United States Environmental Protection Agency [EPA]). The upstream segment of our study (see below) is located in the Edwards Plateau ecoregion, whereas the downstream segment is in the Cross Timbers ecoregion. The Edwards Plateau region supports grasslands and juniper/oak/mesquite savannas in relatively shallow soils underlain by limestone bedrock (Griffith et al., 2007; tpwd.texas.gov). The Cross Timbers is a mix of savannah and woodlands on fine sandy loam soils with clay subsoils that retain water (Griffith et al., 2007; tpwd.texas.gov). Land use is primarily characterized as semi-arid ranch land in the middle and upper stretches, but is more dominated by pecan orchards and row crop operations in the lower stretch. Mean annual precipitation in the San Saba River averages between 600 and 710 mm, with the upper reaches receiving less precipitation compared with downstream reaches (twdb.texas.gov). Historically, the San Saba River was occupied by approximately 15 species of freshwater mussels (e.g., Howells, 1994, 1995, 1996, 1997, 2005, 2006; Strecker, 1931); however, the San Saba River has experienced recent declines in mussels (e.g., Mitchell et al., 2019).

Field sampling—mussel communities

To examine fine-scale distribution of mussels in the San Saba River, we conducted spatially extensive surveys in two different river segments (upstream and downstream; Figure 2), each 20 km long, during the summer and fall of 2018. Within each segment, two surveyors kayaked downstream and conducted visual and tactile timed searches (0.5-person hours) every 100 m within each 20-km segment, totaling 200 sites per segment (400 sites total). Surveyors searched sediment up to
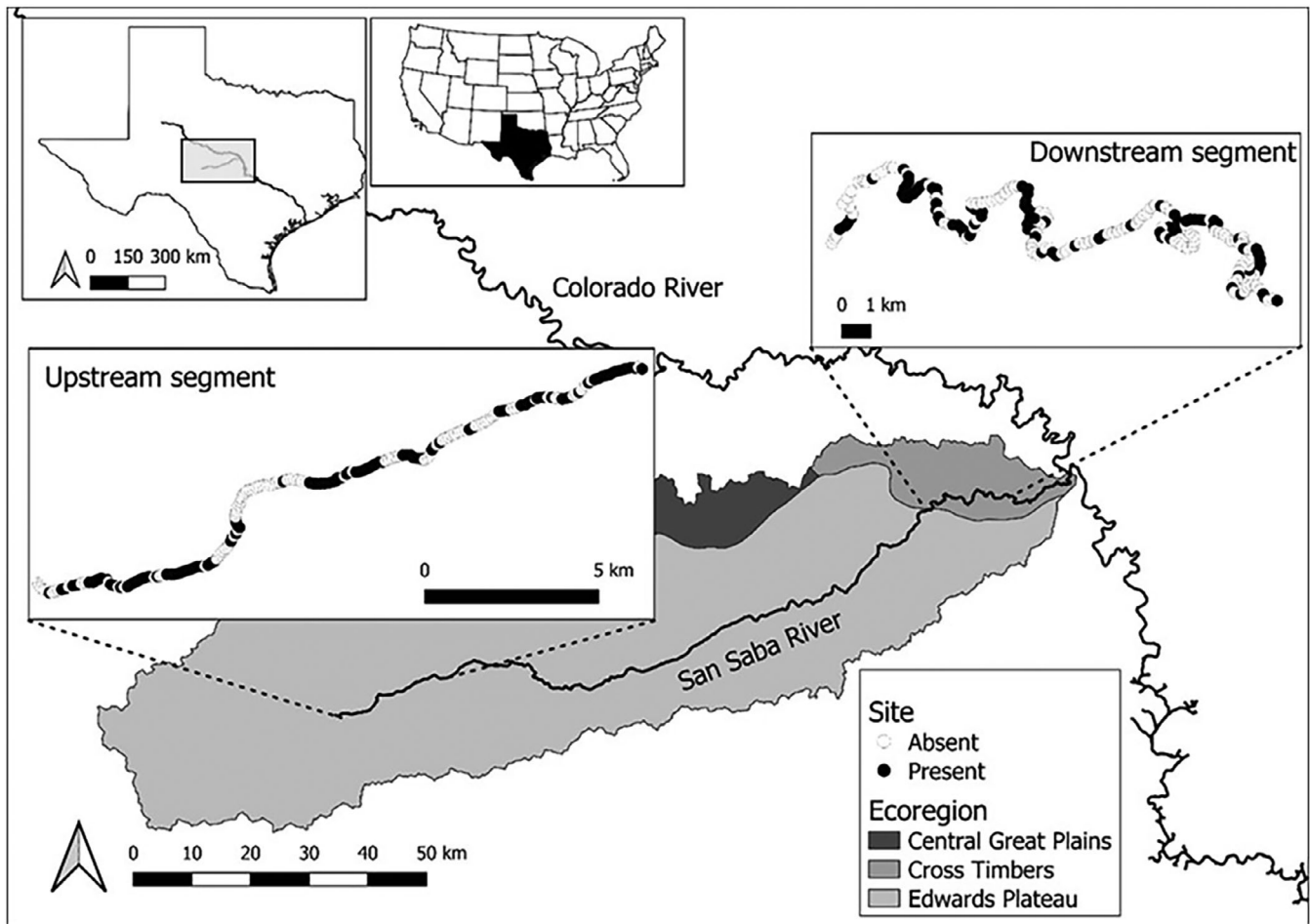
FIGURE 2 Study segment locations within the San Saba River. Dots denote the presence (black dots) and absence (white dots) of mussels at sampling sites within each segment.

10 cm in depth when substrate composition allowed. Each site consisted of a 10-m wide transect that extended from one riverbank to the other. All mussels were identified to species and counted before being placed back into the river at each site. Site coordinates, stream width (ft), stream depth (ft), current velocity (m/s), mesohabitat type (pool, riffle, and run), percentage of substrate type (silt, sand, gravel, pebble, cobble, boulder, and bedrock), water quality parameters (temperature, dissolved oxygen, and conductivity), and percentage of emergent vegetation (0, 0–25, 25–50, and >75) were measured at each sampling site (Appendix S1: Table S1).

Field sampling—fish communities

Differences in mussel distribution have been explained by other studies, at least partly, by differences in fish communities (Dascher et al., 2018; Schwalb et al., 2013; Vaughn, 1997). Although these studies were done at larger spatial scales than this study (comparisons between watersheds) and we did not expect variation in host fish to drive the variation in mussels at the spatial scale of our study (within a river), we wanted to examine whether there was any variation in host fish communities within our study area. The San Saba River can be characterized as having relatively low fish species richness compared with many river drainages in Texas (Dascher et al., 2018). Fish communities were sampled with a multiple gear approach at three sites in each segment. The sites were approximately 5–7 km apart to cover the longitudinal extent of each segment, where mussels were found during the continuous surveys. At each site, three mini-fyke nets and one experimental gill net were set overnight for approximately 12 h. The nets were run the following morning, and the fish that were captured were identified and counted. Fish caught in the nets were not released into the river until electrofishing (see below) was completed. Afterward, fish were sampled using pulsed-DC (60 Hz, 25% duty cycle) backpack electrofishing for 1 h. Fish were stored in a live well until electrofishing was completed, identified to species, counted, and

then released into the river. Effort was made to sample fish from all available mesohabitats (i.e., pool, riffle, and run) within each site.

Remotely sensed data

Land cover data were extracted from the National Land Cover Database (USGS-NLCD, 2019) and overlaid onto sample site locations using QGIS 3.12. Land cover data were summarized for each sampling site at three spatial scales, including (1) a reach scale that included a 100-m buffer on each side of the river that extended 1 km upstream, (2) a segment scale that included a 100-m buffer that extended 20 km upstream, and (3) a catchment scale that included land cover data for the entire watershed upstream of each sampling site. However, preliminary analyses showed that land cover variables were highly correlated between scales, and thus only reach-scale land cover data were used for data analysis. The percentage of land cover data for each sample site was classified into seven categories: open water, developed, forest, shrub, herbaceous, agriculture, and wetlands.

Ecoregions (level III) were downloaded from the EPA and overlaid onto site locations. Mean annual precipitation data (1981–2010) were obtained from the Texas Water Development Board. Historical streamflow data (1999–2018) were collected from USGS stream gages for each river segment and summarized using the Indicators of Hydrologic Alteration software, resulting in 11 ecologically relevant variables to examine the impacts of flow regime on the distribution of mussel communities. Based upon the work of Gao et al. (2009) and Yang et al. (2008), these variables included measures of annual discharge, statistics representing both low and high flow extremes, statistics representing the rate of change and timing of flow events, a monthly flow statistic, and a baseflow index (see Appendix S1: Table S1 for a complete list of variables).

Data analysis

Fusconaia mitchelli and *Truncilla macrodon* were not included in any analyses due to low sample size. Species per unit of effort (SPUE; species/person-hour) and catch per unit of effort (CPUE; mussels/person-hour) were recorded for each site during the survey period. We used a Student's *t*-test to examine differences in SPUE and CPUE between the two river segments. Normality and homogeneity of variance of the data were tested with the Shapiro–Wilk and Levene tests, respectively, and data were $\log_{10}(x + 1)$ transformed to better meet the assumptions of the analyses. We used permutational

multivariate analysis of variance (PERMANOVA) to test for differences in host fish communities within and between both river segments.

To avoid issues of multicollinearity, environmental variables with a variance inflation factor >10 were not included in the analyses. Redundancy analysis (RDA), followed by a forward selection procedure (Blanchet et al., 2008a), was used to determine the relative importance of local and regional environmental variables (listed in Appendix S1: Table S1) in explaining variation in the life history strategy response matrix of mussels within and between river segments. The life history strategy matrix data contained proportion data, which were logit transformed before analyses. Asymmetric eigenvector map (AEM) analysis was used to model the spatial structure of mussels with different life history strategies within the San Saba River. AEM analysis is a spatial modeling technique that was developed for ecosystems such as rivers, in which directional physical processes (e.g., water currents) can asymmetrically affect the distribution of organisms (Blanchet et al., 2008b). This technique considers autocorrelation at different spatial scales. Briefly, AEM analysis examines community data within sites linked by a connection network, which is used to construct a sites-by-edges matrix. For this study, edges represent the physical route between study sites within the river. Edges were weighted using water course distance in kilometers between sites. Spatial eigenvectors can be derived from the site-by-edges matrix in three ways, including principal components analysis, singular value decomposition, or a principal coordinate analysis on a Euclidean distance matrix produced from the sites-by-edges matrix. All three methods produce similar results (Blanchet et al., 2008b). Eigenvectors were calculated using a downstream directional distance matrix accounting for the connectivity between sites. Similarly, to the RDA above, a forward selection process was used for each set of AEM variables to reduce the number of spatial eigenvectors to predict the variation of life history strategy composition of mussels (Blanchet et al., 2008a).

To reiterate, RDA and AEM analyses were computed for both river segments combined (river scale) and then independently for the upstream and downstream segments (segment scale). In total, we completed three RDA and AEM analyses for the trait-based dataset (one of each analysis at the river scale and two of each analysis at the segment scales). Additionally, we performed the same analyses mentioned above using a taxonomic (i.e., species abundance matrix) approach to compare the amount of explained community variation to that of the trait-based approach, for which the mussel species were grouped into the three different life history strategies (see above).

Species abundance data were square root Hellinger transformed to minimize the influence of rare species. River segment was not included in the river-scale analyses as it was completely correlated with ecoregions. Variation partitioning based on RDA was used to determine the relative importance of environmental and spatial variables in explaining variation in community composition of mussels with a traditional taxonomic approach and a trait-based approach at the river and segment spatial scales. Additionally, at the river and segment scale, variation partitioning was used to examine the relative importance of large- versus small-scale spatial patterns in explaining the variation in community composition with a taxonomic and trait-based approach. AEM eigenvectors were categorized as large-scale (river scale: AEM vectors 1–6, segment scale AEM vectors 1–2) or small-scale (river scale: AEM vectors >6, segment scale AEM vectors >2) spatial patterns based on visual assessment (i.e., low-value AEM vectors represent larger scale spatial variation and vice versa). All statistical analyses were conducted in Program R 3.6.1 (R Core Team, 2019). Redundancy analyses, forward selection, and variation partitioning were conducted using the functions "rda," "ordistep," and "varpart" in the "vegan" package (Oksanen et al., 2020). AEM analysis was conducted using the "adespatial" package (Dray et al., 2018).

RESULTS

In total, 1617 live mussels from 11 species were collected from the San Saba River during our spatially extensive surveys (Appendix S1: Table S2). Live mussels were found at 49% ($n = 196$ sites) of all 400 survey sites (Figures 2 and 3). The number of individuals found in the upstream section ($n = 862$) was slightly higher compared with the downstream segment ($n = 755$), and nine species were found in both segments (Appendix S1: Table S2). An average of 0.9 SPUE was found in both segments (range: 0–6 species upstream and 0–5 species downstream).
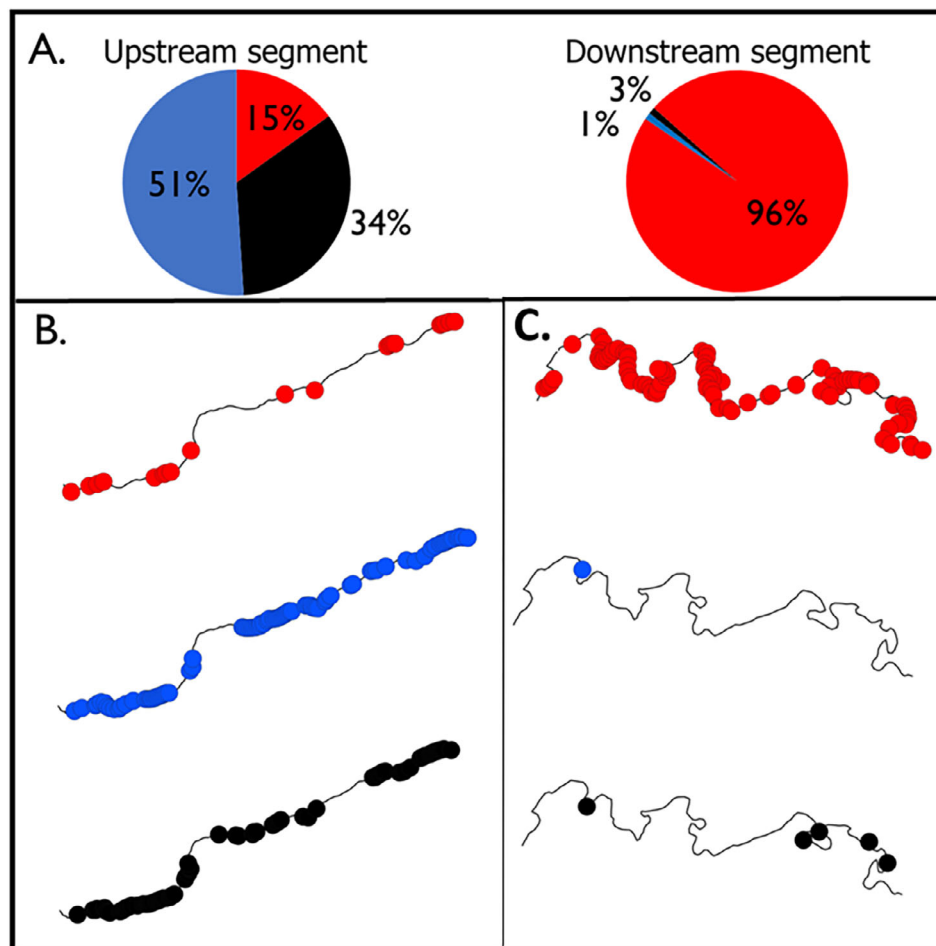

FIGURE 3 Observed percentages of freshwater mussel life history strategists in the upstream and downstream segments of the San Saba River (A). Range maps for mussels with different life history strategies in the upstream (B) and downstream (C) San Saba River. Equilibrium, periodic, and opportunistic species are denoted by red, blue, and black dots, respectively.

The average CPUE was slightly higher upstream (8.6, range: 0–94) compared with downstream (7.3, range: 0–96). However, there were no significant differences in SPUE or CPUE between the upstream and downstream segments ($p > 0.05$ in both cases).

Periodic species (*Lampsilis bracteata* and *Cyrtonaias tampicoensis*) had the highest relative abundance (51%) in the upstream segment followed by an opportunistic species (*Utterbackia imbecillis*; 34%) and equilibrium (15%) species (Appendix S1: Table S2; Figure 3A). Periodic and opportunistic species showed very similar distribution patterns in the upstream segment (Figure 3B). In contrast, equilibrium species were primarily located at sites where periodic and opportunistic species were absent (Figure 3B). The downstream segment was dominated by equilibrium species (e.g., *Cyclonaias petrina*, *C. pustulosa*, and *Tritogonia verrucosa*) and comprised 96% of individuals (Figure 3A; Appendix S1: Table S2). Equilibrium species were found throughout much of the downstream segment (Figure 3C). Conversely, periodic species were located only in the upper section of the downstream segment, and opportunistic species were primarily found in the lower section of the downstream segment (Figure 3C).

A total of 1148 fish from 28 species were sampled within our study segments. All known host fish species (see Ford & Oliver, 2015), which are native to the San Saba River, for mussels that were sampled during the spatially extensive surveys were collected in our study segments. Fish communities were not significantly different within or between river segments (PERMANOVA; $p > 0.05$ in all cases).

Environmental factors

As predicted (Figure 1A), environmental factors (including spatially structured variation) explained considerably more of the variation in life history strategy groups at the river (56%) compared with the segment scale, where 16% of the variation was explained by environmental factors in the upstream segment, but none in the downstream segment (Figure 4). However, many of the environmental factors were spatially structured and the pure effects of environmental factors were small (0%–9% depending upon spatial scale and river position; Figure 4). The larger AEM factors shared much of the variation with environmental factors (up to 62%; Figure 5A) at the river scale, but the smaller AEM factors did not, indicating spatial structuring of environmental factors mostly at a larger spatial scale. Spatial factors (large and small scales) shared low amounts of variation with environmental factors in the upstream (3%–4%) and downstream (0%–5%) segments (Figure 5C,E).
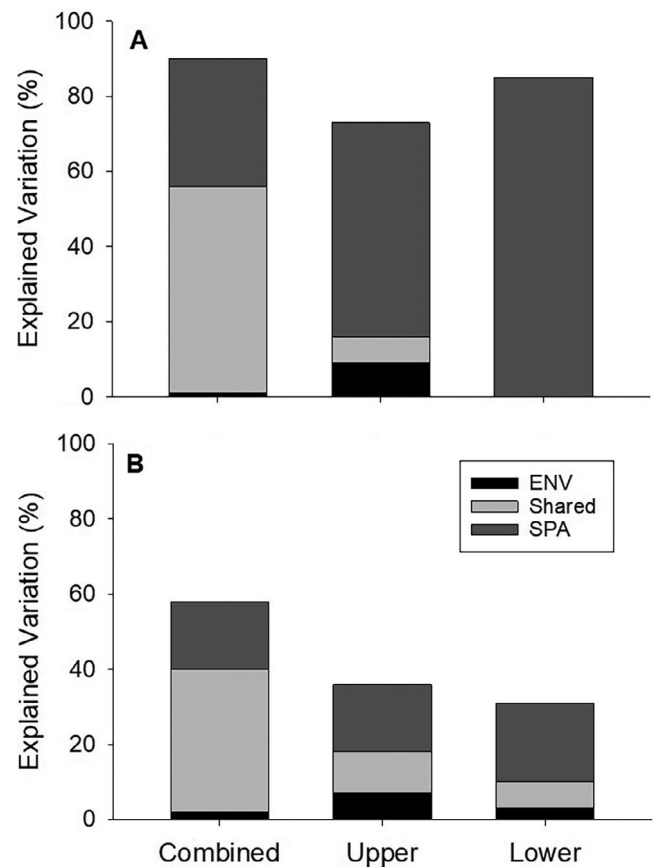

FIGURE 4 (A) Percentage of variation in life history strategy composition explained by pure environmental (ENV) and pure spatial (SPA) effects identified by redundancy analysis and their total shared variation (Shared) within different segments of the San Saba River. (B) Percentage of variation in species community composition explained by pure environmental (ENV) and pure spatial (SPA) effects identified by redundancy analysis and their total shared variation (Shared) within different segments of the San Saba River.

As expected, different environmental factors were significant at different spatial scales. Long-term streamflow metrics were important drivers of the life history strategy composition at the river scale (Table 1; Appendix S1: Table S3 and Figure S1A). For example, equilibrium species were associated with increased summer flows (i.e., increased base flow index and August flow), whereas opportunistic and periodic species were associated with more variable flow rates and more extreme low flow events (Table 1; Appendix S1: Figure S1A). At the segment scale, variables representing differences between mesohabitats (i.e., riffles vs. pools) were important environmental predictors of the life history strategy composition of mussels. Specifically, equilibrium species were primarily associated with shallower and faster flowing sites, whereas periodic and opportunistic species were primarily found in deeper sites (i.e., pools) with lower current velocities (Table 1; Appendix S1: Figure S1C).
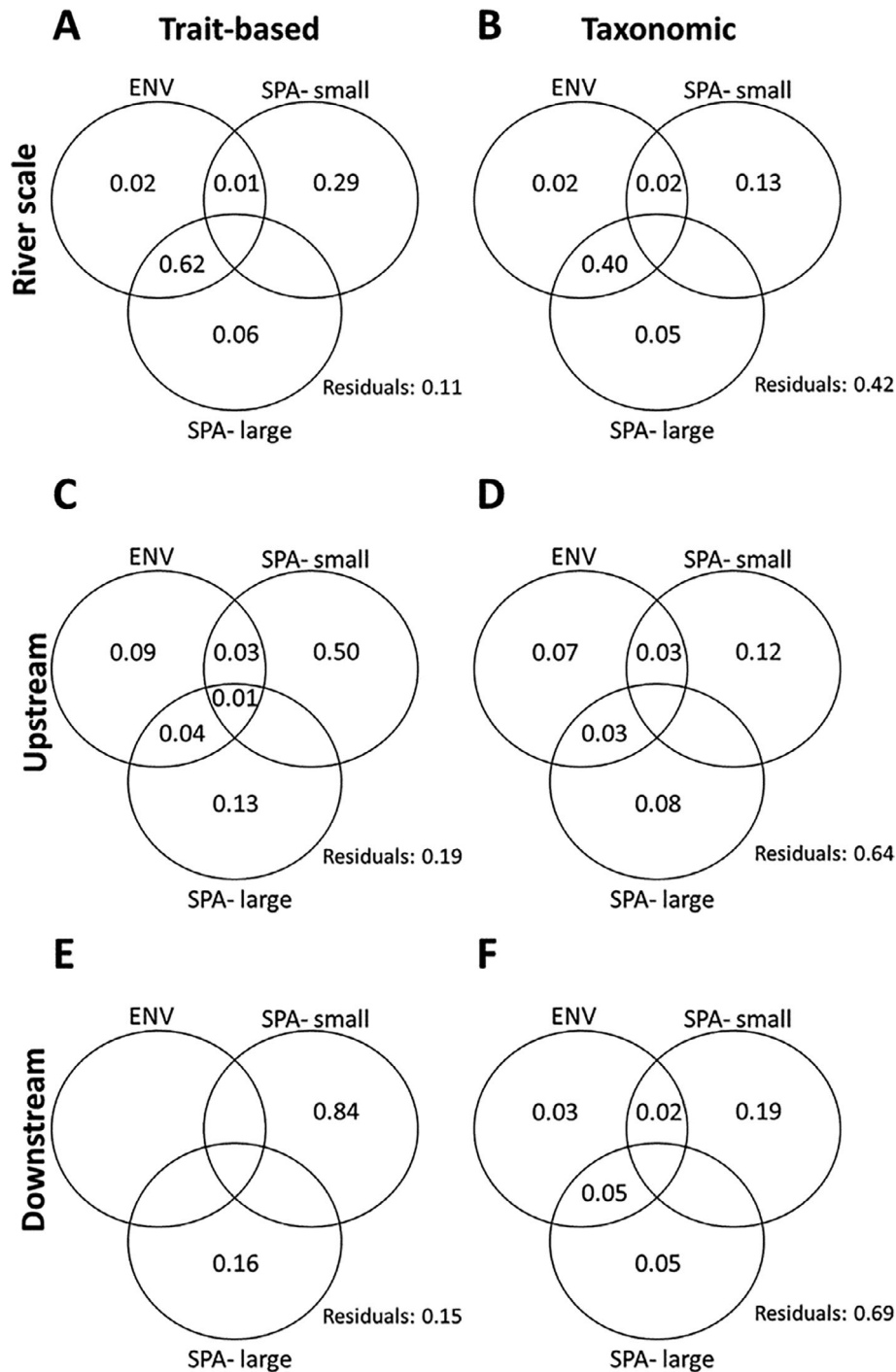
FIGURE 5 Percentage of variation in life history strategies (trait-based; A, C, and E) and taxonomic composition (B, D, and F) explained by environmental (ENV), small spatial scale (SPA-small), and large spatial scale (SPA-large) variables and their shared components at the river scale (A and B, all study segments combined) and segment scale (upstream segment: C and D; downstream segment: E and F). Values < 0 are not shown.

Spatial factors

As predicted (Figure 1B), a higher proportion of variation in the life history strategy composition was explained by spatial factors in the downstream segment compared with the upstream segment. This applied to both the spatial effects with and without shared variation with environmental variables (i.e., pure spatial effects, 85% vs. 57% downstream and upstream, respectively; Figure 4). Additionally, spatial factors explained a higher amount of variation at the river scale (89%) compared with the upstream segment (64%, including shared variation with

TABLE 1 Significant environmental (local and regional) variables ($p < 0.05$ after forward selection) selected at different spatial scales using the trait-based, taxonomic, and those that were shared by both approaches.

Scale	Selected environmental variables
Trait-based and taxonomic approach	
Local	
River	Depth; percentage water; conductivity
Upstream segment	Depth; current velocity
Regional	
River	Annual flow coefficient of variation (CV); base flow index; date of minimum; rise rate; 3-day max; 7-day min; August flow; extreme low peak; large flood peak; no. reversals
Trait-based approach only	
Local	
River	Riffle
Upstream segment	Percentage water
Taxonomic approach only	
Local	
River	Current velocity; percentage bedrock; pool; percentage cobble
Upstream segment	Percentage sand; percentage bedrock
Downstream segment	Dissolved oxygen; percentage cobble; percentage shrub; riffle

Note: See Appendix S1: Table S1 for a description of all environmental variables.

environmental factors). In contrast to our prediction, spatial factors either explained a similar amount of variation at the river scale (89%) compared with the downstream segment (85%, including shared variation with environmental factors) or less at the river scale (34%) when only considering pure spatial effects compared with both the upstream (57%) and downstream segment (85%; Figure 4).

The spatial structure of the distribution of different life history strategy groups at the river scale was primarily driven by one large-scale spatial variable (V1, adjusted $R^2 = 0.55$; Appendix S1: Table S4 and Figure S2) that separated the downstream segment primarily composed of equilibrium species from the upstream segment, which contained more periodic and opportunistic species (Figure 3; Appendix S1: Figure S2). At the river scale, pure spatial effects (i.e., no shared variation with

environmental factors) were mostly explained by smaller scale spatial variables (AEM values >6) with both the trait-based and taxonomic approaches (Figure 5).

At the segment scale, in the upstream segment, the distribution of opportunistic individuals was explained by larger spatial patterns (V1 and V2) associated with higher abundances in deeper pools throughout much of the upstream segment (Figure 3B; Appendix S1: Figure S3). Periodic species exhibited similar distribution patterns compared with opportunistic individuals in the upstream segment (Figure 3B; Appendix S1: Figure S3). However, periodic species had the highest relative abundance in pools at the upper end of segment (V83) and at the lower quarter of the upstream segment (V33 and V14; Appendix S1: Figure S3). Equilibrium species were found in two primary areas of the upper segment (V21 and V67; Figure 3B; Appendix S1: Figure S3) in shallow riffle and run habitats.

Three prominent spatial patterns of mussels were found in the downstream segment. Equilibrium species were found in consistent numbers throughout the downstream segment, except for two areas that contained higher proportions of pool habitats (V4; Appendix S1: Figure S4) and had higher abundances of periodic or opportunistic species (Figure 3C). Opportunistic species were found primarily in the lower section of the downstream segment (V16 and V70) in riffle habitats, whereas the periodic species were only found in the upper regions (V72, V39, and V47) of the downstream segment where deeper pools were more prominent (Figure 3C; Appendix S1: Figure S4). At the segment scale, pure spatial effects (i.e., no shared variation with environmental factors) were mostly explained by smaller scale spatial variables (AEM values >2) with both the trait-based and taxonomic approaches (Figure 5).

Trait-based versus taxonomic approach

As expected, based on our hypothesis (Figure 1), less of the variation (32%–54% lower depending upon spatial scale) between species (taxonomic approach) was explained by environmental and spatial factors compared with the trait-based approach (Figure 4B). Many patterns revealed by the taxonomic approach were similar to those revealed by the trait-based approach, but there were also some notable differences. While the variation in life history strategies in the downstream segment was exclusively explained by spatial variables, environmental factors (pure effects) explained at least a small amount (3%) of the taxonomic variation (Figure 4). There was also an increase in significant environmental predictors at the taxonomic level compared with the trait-based approach at the river and segment scales (Table 1).

For example, at the river scale, species were associated with changes in long-term flow metrics (similar to the trait-based approach), in addition to differences in ecoregion (Table 1; Appendix S1: Figure S1B). At the segment level, substrate type was an important predictor at the taxonomic level (Table 1; Appendix S1: Figure S1D,E).

There were also two notable differences in respect to spatial variables. First, the percentage explained by pure spatial effects was mostly similar across scales and river positions in the taxonomic approach, whereas more pronounced differences were found with the trait-based approach (downstream segment > upstream segment > river scale, see above; Figure 4). Second, 2–3 times more significant AEM factors were found with the trait-based approach at the river and segment scales compared with the taxonomic approach (Appendix S1: Table S3).

DISCUSSION

Environmental heterogeneity seems to be the main driver for variation in the distribution of riverine mussels, at the life history and taxonomic levels, resulting in a higher amount of variation explained by environmental factors where more environmental differences occur between sites (i.e., higher environmental heterogeneity in the upstream segment and on a river scale). Especially at the river scale, much of the variation in environmental factors was spatially structured with distinct communities, at the life history and taxonomic levels, occurring in the upstream versus the downstream segment, but differences also occurred between the upper and lower parts of a segment. The distribution of mussels was further structured by the presence of pools versus riffles (i.e., differences in water depth, current velocity, and substrate). This environmental structuring was most noticeable with the trait-based approach, showing that different life history groups had a highly predictable distribution pattern, as previously predicted by Haag (2012). In contrast, stochasticity of recruitment (including randomness connected with presence of infested host fish) and demographic events (e.g., Chase, 2007, 2010) are most likely much more important for the specific species community composition at a site, especially between nearby patches with little or no environmental heterogeneity. However, unmeasured environmental variables, such as shear stress at high flow (Lopez & Vaughn, 2021) or high temperatures during past drying events, could also play a role. Studies that have critically evaluated the role of stochastic community assembly and ecological drift are very rare (e.g., Shinen & Navarrete, 2014; Siepielski et al., 2010).

The large-scale differences in ecoregion and underlying geology result in differing flow regimes between the upstream and downstream segments (Appendix S1: Table S4). Differences in hydrologic disturbance within rivers are known to play a key role in structuring communities (Lake, 2000; Poff, 1992; Resh et al., 1988). Thus, it is likely that periodic and opportunistic species dominate in the upstream segment because they are better adapted to the flashier flow regime (i.e., increased disturbance) of the upstream segment. Equilibrium species dominate in the downstream segment because they may be superior competitors (Haag, 2012; Strayer, 2008).

Alternatively, the distribution of life history strategy groups could also be driven by differences in dispersal abilities. In our study, the same equilibrium species were found within the downstream and upstream segments, suggesting that they have efficient or high levels of dispersal to colonize areas throughout the San Saba River. Interestingly, a study on mussel metacommunity structure in Ontario found that the majority of mussels classified as equilibrium and opportunistic species had presumably higher dispersal capabilities via their host fish compared with periodic species (Schwalb et al., 2015). It is likely that equilibrium species have efficient dispersal capabilities due to the high movement ability (lengths >100 km) of their primary host fish group (Ictalurids, e.g., Dames et al., 1989; Fago, 1999; Vokoun & Rabeni, 2005). Conversely, except for *C. tampicoensis*, different opportunistic and periodic species were found in the upstream and downstream segments, suggesting that some species may be either dispersal-limited or habitat specialists adapted to more spring-influenced reaches (upstream) or less flashy flow regimes (downstream). However, our fish survey showed that host fish species of the periodic and opportunistic (primarily Centrarchidae and Sciaenidae) were widespread and abundant throughout the San Saba River, and many species within these families are capable of movements from 15 to 161 km (e.g., Funk, 1957; Gatz Jr & Adams, 1994; Richardson-Heft et al., 2000), suggesting that dispersal limitation is unlikely within the San Saba River and that mussel communities are primarily structured by environmental factors.

Dispersal limitation is more likely to play a role at spatial scales larger than those examined in our study (i.e., between sub-basins and basins). Genetic studies can be useful for examining dispersal limitations in mussels. For example, a population of *L. bracteata* (periodic species) in the San Saba River was found to be genetically different from a population in the Llano River, which is another tributary of the Colorado River (Inoue et al., 2020). Studies examining mussel distribution in relation to host fish distribution found host fish distributions to be an important predictor of mussel distributions between river basins (Daniel et al., 2018; Dascher et al., 2018; Schwalb et al., 2013) or sub-basins (Vaughn & Taylor, 2000; Watters, 1992).

In contrast, studies have often found weak relationships between host fish and mussel distributions at smaller spatial scales within sub-basins (Cao et al., 2013; Krebs et al., 2010; Lyons et al., 2007).

In the downstream segment, mussel distribution patterns were explained mostly (taxonomic approach) or solely (trait-based approach) by spatial factors, suggesting a high importance of dispersal processes, which would be consistent with the network position hypothesis (e.g., Brown & Swan, 2010). Our original hypothesis was that strong spatial effects downstream would be caused by high levels of dispersal from mainstem Colorado River communities (i.e., mass effects). If dispersal rates are high, we might expect an increase in species richness and a higher number of unique species within sites located closer to the mainstem because they are more closely connected to the regional species pool. However, the lower half of the downstream segment (located closest to the mainstem) contained less individuals from fewer species and contained no unique species compared with the upper half of the downstream segment and the upstream segment, potentially suggesting a lack of high dispersal rates within the downstream segment from mainstem communities or indicating that this area contains stressful environmental conditions. The strong response to environmental heterogeneity we observed in the upstream segment and at the river scale suggests that the strong spatial signals may represent the absence of environmental heterogeneity in the downstream segment, especially at the occupied sites, which is causing the apparent lack of environmental effects. Mussels in the downstream section occurred almost exclusively in riffles and runs, which were relatively environmentally homogenous. Pure spatial effects (no correlation with environmental factors) if not caused by dispersal differences may also capture unmeasured environmental differences between sites but may also detect patterns created by stochastic processes (see above).

Given our results, we predict that mussel communities within the San Saba River are primarily structured by environmental heterogeneity, which is presumably higher upstream and at the river scale, and stochasticity (Figure 6), which becomes more important where environmental heterogeneity is lower (Figure 6). Additionally, environmental factors are predicted to have a stronger influence on the composition of mussels at the life history level, whereas stochasticity will play a larger role in determining mussel composition at the taxonomic level (Figure 6).

Our results suggest that the absence of certain species may not be necessarily associated with differences in environmental conditions, but may be driven by stochastic assembly processes, which need to be considered in
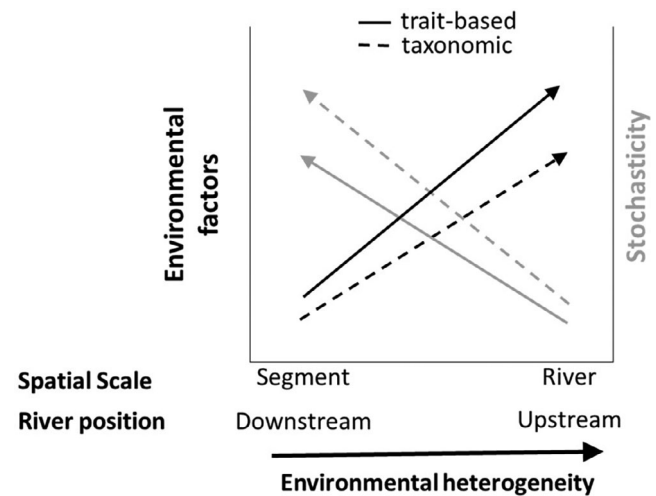

FIGURE 6 Predicted importance of environmental factors and stochasticity in structuring the life history strategy (trait-based) and taxonomic composition of mussels along a gradient of environmental heterogeneity at different spatial scales and river network positions.

conservation and management decisions. Effective conservation strategies should therefore also pay attention to species with similar traits and their distribution when defining potential critical habitat. Species with similar traits could also be used as surrogate species for ecological studies, especially if those species are more abundant (Pracheil et al., 2016).

While our multi-scale trait-based approach led to a better understanding of the structuring processes of mussel communities, we acknowledge its limitations. To gather our extensive dataset, we traded off a larger number of sites with shorter search times at each site. However, the species richness and abundances found at our survey sites were comparable with recent studies in the San Saba River (Mitchell et al., 2019; Randklev et al., 2018), which used considerably longer search times. Since mussels are long-lived, environmental conditions that occurred several years ago, for example, shear stress during extreme high flow (Lopez & Vaughn, 2021) or high temperatures during past extreme low flow conditions, are likely even more relevant for the distribution of mussels than the local environmental variables we were able to measure and use in our analyses. However, measurements of relevant environmental conditions (e.g., shear stress at high flows) can be dangerous to obtain during extreme flow events and difficult to extrapolate if only measurements at base flows are possible. Environmental conditions during extreme flow events (not measured in this study) may likely be more relevant for determining presence and absence at a particular site than changes in mussel community composition, but this would require further research. Further, the limited availability of quantitative life history traits limited our analysis to Haag's (2012) broad genus-level classification,

which aggregates the variety of life history strategies into three distinct life history groups. A more complete list of quantified traits (e.g., life span, fecundity, growth rates) for freshwater mussel species would allow for better understanding of the relationship between community structuring and specific traits. This, in turn, could enable researchers to adopt a more quantitative and continuous approach.

Based on our unique and detailed extensive survey data in combination with a trait-based and taxonomic-level approach, we gained additional insights into relevant environmental and spatial drivers at different spatial scales, which likely would have remained undetected in conventional survey designs and taxonomic analyses. It also facilitated the development of a predictive model for our study system (Figure 6). We encourage researchers to implement similar high-resolution sampling designs over larger spatial scales and along a gradient of environmental heterogeneity and to test whether our predictions outlined in Figure 6 also apply for a wider variety of taxa across a broad range of ecosystems. The role we predict for environmental heterogeneity and stochasticity in shaping the distribution of mussels in our study river likely also applies to other taxa and ecosystems (e.g., terrestrial woody and perennial plants, corals) at a spatial scale at which neither dispersal limitation nor mass effects occur. Thus, understanding the magnitude and extent of dispersal relative to the amount of environmental heterogeneity may be key for predicting metacommunity structure and dynamics for different organisms.

In addition, researchers should focus on more manipulative and controlled experiments (e.g., translocation studies) to better tease apart the relative importance of environmental filtering, dispersal, and other neutral processes (i.e., ecological drift) in structuring metacommunities. Future studies should also examine how trait-based and taxonomic patterns of organisms change at various temporal scales, as temporal dynamics and trajectories are emerging as an important component of metacommunity dynamics.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Mitchell et al., 2023) are available from Dryad: https://doi.org/10.5061/dryad.msbcc2g3d.

REFERENCES

Allen, D. C., and C. C. Vaughn. 2010. "Complex Hydraulic and Substrate Variables Limit Freshwater Mussel Species Richness and Abundance." *Journal of the North American Benthological Society* 29: 383–94.

Allen, T. F., and T. B. Starr. 1982. *Hierarchy: Perspectives for Ecological Complexity*. Chicago, IL: University of Chicago Press.

Arbuckle, K. E., and 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: 310–6.

Atkinson, C. L., J. P. Julian, and C. C. Vaughn. 2014. "Species and Function Lost: Role of Drought in Structuring Stream Communities." *Biological Conservation* 176: 30–8.

Benone, N. L., C. G. Leal, L. L. dos Santos, T. P. Mendes, J. Heino, and L. F. de Assis Montag. 2020. "Unravelling Patterns of Taxonomic and Functional Diversity of Amazon Stream Fish." *Aquatic Sciences* 82: 1–11. https://doi.org/10.1007/s00027-020-00749-5.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008a. "Forward Selection of Explanatory Variables." *Ecology* 89: 2623–32. https://doi.org/10.1890/07-0986.1.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008b. "Modelling directional spatial processes in ecological data." *Ecological Modelling* 215: 325–36.

Brown, B. L., and C. M. Swan. 2010. "Dendritic Network Structure Constrains Metacommunity Properties in Riverine Ecosystems." *Journal of Animal Ecology* 79: 571–80. https://doi.org/10.1111/j.1365-2656.2010.01668.x.

Brown, B. L., C. M. Swan, D. A. Auerbach, E. H. Campbell Grant, N. P. Hitt, K. O. Maloney, and C. Patrick. 2011. "Metacommunity Theory as a Multispecies, Multiscale Framework for Studying the Influence of River Network Structure on Riverine Communities and Ecosystems." *Journal of the North American Benthological Society* 30: 310–27.

Cao, Y., J. Huang, K. S. Cummings, and A. Holtrop. 2013. "Modeling Changes in Freshwater Mussel Diversity in an Agriculturally Dominated Landscape." *Freshwater Science* 32: 1205–18.

Chambers, A. J., and D. A. Woolnough. 2018. "Discrete Longitudinal Variation in Freshwater Mussel Assemblages within Two Rivers of Central Michigan, USA." *Hydrobiologia* 810: 351–66. https://doi.org/10.1007/s10750-016-3055-5.

Chase, J. M. 2007. "Drought Mediates the Importance of Stochastic Community Assembly." *Proceedings of the National Academy of Sciences of the United States of America* 104: 17430–4. https://doi.org/10.1073/pnas.0704350104.

Chase, J. M. 2010. "Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments." *Science* 328: 1388–91. https://doi.org/10.1126/science.1187820.

Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2008. "Macroinvertebrate Diversity in Headwater Streams: A Review." *Freshwater Biology* 53: 1707–21.

Cottenie, K. 2005. "Integrating Environmental and Spatial Processes in Ecological Community Dynamics." *Ecology Letters* 8: 1175–82. https://doi.org/10.1111/j.1461-0248.2005.00820.x.

Dames, H. R., T. G. Coon, and J. W. Robinson. 1989. "Movements of Channel and Flathead Catfish between the Missouri River

and a Tributary, Perche Creek." *Transactions of the American Fisheries Society* 118: 670–9.

Daniel, W. M., and K. M. Brown. 2014. "The Role of Life History and Behavior in Explaining Unionid Mussel Distributions." *Hydrobiologia* 734: 57–68. https://doi.org/10.1007/s10750-014-1868-7.

Daniel, W. M., A. R. Cooper, P. J. Badra, and D. M. Infante. 2018. "Predicting Habitat Suitability for Eleven Imperiled Fluvial Freshwater Mussels." *Hydrobiologia* 809: 265–83.

Darwin, C. 1859. *On the Origin of Species*. London: John Murray.

Dascher, E. D., L. E. Burlakova, A. Y. Karatayev, D. F. Ford, and A. N. Schwalb. 2018. "Distribution of Unionid Freshwater Mussels and Host Fishes in Texas. A Study of Broad-Scale Spatial Patterns across Basins and a Strong Climate Gradient." *Hydrobiologia* 810: 315–31. https://doi.org/10.1007/s10750-017-3168-5.

Datry, T., G. Singer, E. Sauquet, D. J. Capdevilla, D. Von Schiller, R. Subbington, C. Magand, et al. 2017. "Science and Management of Intermittent Rivers and Ephemeral Streams (SMIRES)." *Research Ideas and Outcomes* 3: 23.

Douda, K., P. Horký, and M. Bílý. 2012. "Host Limitation of the Thick-Shelled River Mussel: Identifying the Threats to Declining Affiliate Species." *Animal Conservation* 15: 536–44.

Downing, J. A., P. Van Meter, and D. A. Woolnough. 2010. "Suspects and Evidence: A Review of the Causes of Extirpation and Decline in Freshwater Mussels." *Animal Biodiversity and Conservation* 33: 151–85.

Dray, S., G. Blanchet, D. Borcard, G. Guenard, T. Jombart, G. Larocque, and M. S. Dray. 2018. "Package 'adespatial'." R Package, 2018, 3–8.

Fago, D. 1999. "Movement of Channel Catfish in the Lower Wisconsin River and Pools Numbers 10 and 11 of the Mississippi River Using Radiotelemetry." In Catfish 2000: Proceedings of the International Ictalurid Symposium. American Fisheries Society, Symposium 24:177–185.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. "Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes: A Continuous View of the River Is Needed to Understand how Processes Interacting among Scales Set the Context for Stream Fishes and Their Habitat." *Bioscience* 52: 483–98. https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2.

Ford, D. F., and A. M. Oliver. 2015. "The Known and Potential Hosts of Texas Mussels: Implications for Future Research and Conservation Efforts." *Freshwater Mollusk Biology and Conservation* 18: 1–14. https://doi.org/10.31931/fmbc.v18i1.2015.1-14.

Funk, J. L. 1957. "Movement of Stream Fishes in Missouri." *Transactions of the American Fisheries Society* 85: 39–57.

Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C. Laughlin, et al. 2017. "Revisiting the Holy Grail: Using Plant Functional Traits to Understand Ecological Processes." *Biological Reviews* 92: 1156–73.

Gangloff, M. M., and J. W. Feminella. 2007. "Stream Channel Geomorphology Influences Mussel Abundance in Southern Appalachian Streams, USA." *Freshwater Biology* 52: 64–74.

Gao, Y., R. M. Vogel, C. N. Kroll, N. L. Poff, and J. D. Olden. 2009. "Development of Representative Indicators of Hydrologic Alteration." *Journal of Hydrology* 374: 136–47.

Gatz, A. J., Jr., and S. M. Adams. 1994. "Patterns of Movement of Centrarchids in Two Warmwater Streams in Eastern Tennessee." *Ecology of Freshwater Fish* 3: 35–48.

Gleason, H. A. 1926. "The Individualistic Concept of the Plant Association." *Bulletin of the Torrey Botanical Club* 1: 7–26.

Griffith, G., S. Bryce, J. Omernik, and A. Rogers. 2007. *Ecoregions of Texas*. Austin, TX: Texas Commission of Environmental Quality.

Grime, J. P. 1974. "Plant Strategies and Vegetation Processes."

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, and L. M. Bini. 2013. "Metacommunity Structuring in Stream Networks: Roles of Dispersal Mode, Distance Type, and Regional Environmental Context." *Ecology and Evolution* 3: 4473–87.

Haag, W. R. 2012. *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. New York: Cambridge University Press.

Haag, W. R., and J. D. Williams. 2014. "Biodiversity on the Brink: An Assessment of Conservation Strategies for North American Freshwater Mussels." *Hydrobiologia* 735: 45–60. https://doi.org/10.1007/s10750-013-1524-7.

Heino, J. 2013. "The Importance of Metacommunity Ecology for Environmental Assessment Research in the Freshwater Realm." *Biological Reviews* 88: 166–78.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. "Metacommunity Organisation, Spatial Extent and Dispersal in Aquatic Systems: Patterns, Processes and Prospects." *Freshwater Biology* 60: 845–69.

Henriques-Silva, R., M. Logez, N. Reynaud, P. A. Tedesco, S. Brosse, S. R. Januchowski-Hartley, T. Oberdorff, and C. Argillier. 2019. "A Comprehensive Examination of the Network Position Hypothesis across Multiple River Metacommunities." *Ecography* 42: 284–94. https://doi.org/10.1111/ecog.03908.

Hornbach, D. J., M. C. Hove, K. R. MacGregor, J. L. Kozarek, B. E. Sietman, and M. Davis. 2019. "A Comparison of Freshwater Mussel Assemblages along a Land-Use Gradient in Minnesota." *Aquatic Conservation: Marine and Freshwater Ecosystems* 29: 1826–38. https://doi.org/10.1002/aqc.3167.

Howells, R. G. 1994. "Preliminary Distributional Surveys of Freshwater Bivalves in Texas." In: Progress Report for 1992. Management Data Series 105. Austin, TX. https://tpwd.texas.gov/site/openrecords.

Howells, R. G. 1995. "Preliminary Distributional Surveys of Freshwater Bivalves in Texas." In: Progress Report for 1993. Management Data Series 119. Austin, TX. https://tpwd.texas.gov/site/openrecords.

Howells, R. G. 1996. "Preliminary Distributional Surveys of Freshwater Bivalves in Texas." In: Progress Report for 1994. Management Data Series 120. Austin, TX. https://tpwd.texas.gov/site/openrecords.

Howells, R. G. 1997. "Preliminary Distributional Surveys of Freshwater Bivalves in Texas." In: Progress Report for 1996. Management Data Series 144. Austin, TX. https://tpwd.texas.gov/site/openrecords.

Howells, R. G. 2005. "Preliminary Distributional Surveys of Freshwater Bivalves in Texas." In: Progress Report for 2004. Management Data Series 233. Austin, TX. https://tpwd.texas.gov/site/openrecords.

Howells, R. G. 2006. "Statewide Freshwater Mussel Survey." Final Report Submitted to Texas Parks and Wildlife, Austin, TX.

Humphries, P., H. Keckeis, and B. Finlayson. 2014. "The River Wave Concept: Integrating River Ecosystem Models." *Bioscience* 64: 870–82. https://doi.org/10.1093/biosci/biu130.

Huszar, V. L., J. C. Nabout, M. O. Appel, J. B. Santos, D. S. Abe, and L. H. Silva. 2015. "Environmental and Not Spatial Processes (Directional and Non-Directional) Shape the Phytoplankton Composition and Functional Groups in a Large Subtropical River Basin." *Journal of Plankton Research* 37: 1190–200. https://doi.org/10.1093/plankt/fbv084.

Ibanez, C., T. Oberdorff, G. Teugels, V. Mamononenekene, S. Lavoué, Y. Fermon, A. K. Paugy, and A. K. Toham. 2007. "Fish Assemblages Structure and Function along Environmental Gradients in Rivers of Gabon (Africa)." *Ecology of Freshwater Fish* 16: 315–34.

Inoue, K., J. L. Harris, C. R. Robertson, N. A. Johnson, and C. R. Randklev. 2020. "A Comprehensive Approach Uncovers Hidden Diversity in Freshwater Mussels (Bivalvia: Unionidae) with the Description of a Novel Species." *Cladistics* 36: 88–113.

Inoue, K., T. D. Levine, B. K. Lang, and D. J. Berg. 2014. "Long-Term Mark-and-Recapture Study of a Freshwater Mussel Reveals Patterns of Habitat Use and an Association between Survival and River Discharge." *Freshwater Biology* 59: 1872–83.

Krebs, R. A., W. C. Borden, E. R. Steiner, M. S. Lyons, W. Zawiski, and B. M. Walton. 2010. "Determinants of Mussel Diversity in Lake Erie Tributaries." *Journal of the North American Benthological Society* 29: 506–20.

Krynak, E. M., Z. Lindo, and A. G. Yates. 2019. "Patterns and Drivers of Stream Benthic Macroinvertebrate Beta Diversity in an Agricultural Landscape." *Hydrobiologia* 837: 61–75.

Lake, P. S. 2000. "Disturbance, Patchiness, and Diversity in Streams." *Journal of the North American Benthological Society* 19: 573–92.

Leibold, M. A., and J. M. Chase. 2018. *Metacommunity Ecology*, Vol 59. Princeton, NJ: Princeton University Press.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7: 601–13. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Li, Z., J. Wang, Z. Liu, X. Meng, J. Heino, X. Jiang, X. Xiong, X. Jiang, and Z. Xie. 2019. "Different Responses of Taxonomic and Functional Structures of Stream Macroinvertebrate Communities to Local Stressors and Regional Factors in a Subtropical Biodiversity Hotspot." *Science of the Total Environment* 655: 1288–300. https://doi.org/10.1016/j.scitotenv.2018.11.222.

Lopes-Lima, M., L. E. Burlakova, A. Y. Karatayev, K. Mehler, M. Seddon, and R. Sousa. 2018. "Conservation of Freshwater Bivalves at the Global Scale: Diversity, Threats and Research Needs." *Hydrobiologia* 810: 1–14.

Lopez, J. W., and C. C. Vaughn. 2021. "A Review and Evaluation of the Effects of Hydrodynamic Variables on Freshwater Mussel Communities." *Freshwater Biology* 66: 1665–79.

Lyons, M. S., R. A. Krebs, J. P. Holt, L. J. Rundo, and W. Zawiski. 2007. "Assessing Causes of Change in the Freshwater Mussels (Bivalvia: Unionidae) in the Black River, Ohio." *The American Midland Naturalist* 158: 1–15.

Maio, J. D., and L. D. Corkum. 1995. "Relationship between the Spatial Distribution of Freshwater Mussels (Bivalvia: Unionidae) and the Hydrological Variability of Rivers." *Canadian Journal of Zoology* 73: 663–71.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. "Rebuilding Community Ecology from Functional Traits." *Trends in Ecology and Evolution* 21: 178–85. https://doi.org/10.1016/j.tree.2006.02.002hei.

McRae, S. E., J. D. Allan, and J. B. Burch. 2004. "Reach- and Catchment-Scale Determinants of the Distribution of Freshwater Mussels (Bivalvia: Unionidae) in South-Eastern Michigan, USA." *Freshwater Biology* 49: 127–42.

Mitchell, Z., A. Schwalb, and K. Cottenie. 2023. "Trait-Based and Multi-Scale Approach Provides Insight on Responses of Freshwater Mussels to Environmental Heterogeneity." Dryad. Dataset. https://doi.org/10.5061/dryad.msbcc2g3d.

Mitchell, Z. A., L. E. Burlakova, A. Y. Karatayev, and A. N. Schwalb. 2019. "Changes in Community Composition of Riverine Mussels after a Severe Drought Depend on Local Conditions: A Comparative Study in Four Tributaries of a Subtropical River." *Hydrobiologia* 848: 3015–29. https://doi.org/10.1007/s10750-019-04058-3.

Moore, A. P., N. Galic, R. A. Brain, D. J. Hornbach, and 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: 3386–402.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, and H. Wagner. 2020. "vegan: Community Ecology Package." R Package Version 2.5-6.

Peláez, O., and C. S. Pavanelli. 2019. "Environmental Heterogeneity and Dispersal Limitation Explain Different Aspects of β-Diversity in Neotropical Fish Assemblages." *Freshwater Biology* 64: 497–505. https://doi.org/10.1111/fwb.13237.

Perez Rocha, M., L. M. Bini, S. Domisch, K. T. Tolonen, J. Jyrkänkallio-Mikkola, J. Soininen, J. Hjort, and J. Heino. 2018. "Local Environment and Space Drive Multiple Facets of Stream Macroinvertebrate Beta Diversity." *Journal of Biogeography* 45: 2744–54.

Petchey, O. L., and K. J. Gaston. 2006. "Functional Diversity: Back to Basics and Looking Forward." *Ecology Letters* 9: 741–58. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Poff, N. L. 1992. "Why Disturbances Can Be Predictable: A Perspective on the Definition of Disturbance in Streams." *Journal of the North American Benthological Society* 11: 86–92.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. "The Natural Flow Regime." *Bioscience* 47: 769–84. https://doi.org/10.2307/1313099.

Poole, K. E., and J. 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: 114–25.

Pracheil, B. M., R. A. McManamay, M. S. Bevelhimer, C. R. DeRolph, and G. F. Čada. 2016. "A Traits-Based Approach for Prioritizing Species for Monitoring and Surrogacy Selection." *Endangered Species Research* 31: 243–58.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Randklev, C. R., E. T. Tsakris, M. S. Johnson, T. Popejoy, M. A. Hart, J. Khan, D. Geeslin, and C. R. Robertson. 2018. "The Effect of Dewatering on Freshwater Mussel (Unionidae) Community Structure and the Implications for Conservation and Water Policy: A Case Study from a Spring-Fed Stream in the Southwestern United States." *Global Ecology and Conservation* 16: 00456.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. "The Role of Disturbance in Stream Ecology." *Journal of the North American Benthological Society* 7: 433–55.

Richardson-Heft, C. A., A. A. Heft, L. Fewlass, and S. B. Brandt. 2000. "Movement of Largemouth Bass in Northern Chesapeake Bay: Relevance to Sportfishing Tournaments." *North American Journal of Fisheries Management* 20: 493–501.

Ries, P., N. R. De Jager, S. J. Zigler, and T. J. Newton. 2016. "Spatial Patterns of Native Freshwater Mussels in the Upper Mississippi River." *Freshwater Science* 35: 934–47.

Rodrigues-Filho, C. A., R. C. Gurgel-Lourenço, E. A. Ramos, J. L. Novaes, D. S. Garcez, R. S. Costa, and J. I. Sánchez-Botero. 2020. "Metacommunity Organization in an Intermittent River in Brazil: The Importance of Riverine Networks for Regional Biodiversity." *Aquatic Ecology* 54: 145–61. https://doi.org/10.1007/s10452-019-09732-1.

Schmera, D., D. Árva, P. Boda, E. Bódis, Á. Bolgovics, G. Borics, A. Csercsa, et al. 2018. "Does Isolation Influence the Relative Role of Environmental and Dispersal-Related Processes in Stream Networks? An Empirical Test of the Network Position Hypothesis Using Multiple Taxa." *Freshwater Biology* 63: 74–85. https://doi.org/10.1111/fwb.12973.

Schwalb, A. N., K. Cottenie, M. S. Poos, and J. D. Ackerman. 2011. "Dispersal Limitation of Unionid Mussels and Implications for Their Conservation." *Freshwater Biology* 56: 1509–18.

Schwalb, A. N., T. J. Morris, and K. Cottenie. 2015. "Dispersal Abilities of Riverine Freshwater Mussels Influence Metacommunity Structure." *Freshwater Biology* 60: 911–21. https://doi.org/10.1111/fwb.12544.

Schwalb, A. N., T. J. Morris, N. E. Mandrak, and K. Cottenie. 2013. "Distribution of Unionid Freshwater Mussels Depends on the Distribution of Host Fishes on a Regional Scale." *Diversity and Distributions* 19: 446–54. https://doi.org/10.1111/j.1472-4642.2012.00940.x.

Schwalb, A. N., M. S. Poos, and J. D. Ackerman. 2011. "Movement of Logperch: Implications for Dispersal of Endangered Snuffbox Mussels Via Its Obligate Host Fish." *Aquatic Sciences* 73: 23–231.

Shinen, J. L., and S. A. Navarrete. 2014. "Lottery Coexistence on Rocky Shores: Weak Niche Differentiation or Equal Competitors Engaged in Neutral Dynamics?" *The American Naturalist* 183: 342–62. https://doi.org/10.1086/674898.

Siepielski, A. M., K. L. Hung, E. E. Bein, and M. A. McPeek. 2010. "Experimental Evidence for Neutral Community Dynamics Governing an Insect Assemblage." *Ecology* 91: 847–57. https://doi.org/10.1890/09-0609.1.

Soininen, J. 2014. "A Quantitative Analysis of Species Sorting across Organisms and Ecosystems." *Ecology* 95: 3284–92.

Spooner, D. E., and C. C. Vaughn. 2008. "A Trait-Based Approach to Species' Roles in Stream Ecosystems: Climate Change, Community Structure, and Material Cycling." *Oecologia* 158: 307–17.

Strayer, D. L. 1999. "Use of Flow Refuges by Unionid Mussels in Rivers." *Journal of the North American Benthological Society* 18: 468–76.

Strayer, D. L. 2008. *Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance*, Vol 1. Berkeley, CA: University of California Press.

Strecker, J. K. 1931. "The Distribution of the Naiades or Pearly Fresh-Water Mussels of Texas."

Terui, A., Y. Miyazaki, A. Yoshioka, K. Kaifu, S. I. S. Matsuzaki, and I. Washitani. 2014. "Asymmetric Dispersal Structures a Riverine Metapopulation of the Freshwater Pearl Mussel *Margaritifera laevis*." *Ecology and Evolution* 4: 3004–14.

Thorp, J. H., and M. D. Delong. 1994. "The Riverine Productivity Model: An Heuristic View of Carbon Sources and Organic Processing in Large River Ecosystems." *Oikos* 70: 305–8. https://doi.org/10.2307/3545642.

Thorp, J. H., M. C. Thoms, and M. D. Delong. 2006. "The Riverine Ecosystem Synthesis: Biocomplexity in River Networks across Space and Time." *River Research and Applications* 22: 123–47. https://doi.org/10.1002/rra.901.

Tonkin, J. D., J. Heino, and F. Altermatt. 2018. "Metacommunities in River Networks: The Importance of Network Structure and Connectivity on Patterns and Processes." *Freshwater Biology* 63: 1–5. https://doi.org/10.1111/fwb.13045.

Tonkin, J. D., S. Stoll, S. C. Jähnig, and P. Haase. 2016. "Elements of Metacommunity Structure of River and Riparian Assemblages: Communities, Taxonomic Groups and Deconstructed Trait Groups." *Ecological Complexity* 25: 35–43.

USGS-NLCD. 2019. "National Land Cover Database 2016: United States Geological Survey National Map Viewer."

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. "The River Continuum Concept." *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–7. https://doi.org/10.1139/f80-017.

Vaughn, C. C. 1997. "Regional Patterns of Mussel Species Distributions in North American Rivers." *Ecography* 20: 107–15.

Vaughn, C. C. 2012. "Life History Traits and Abundance Can Predict Local Colonisation and Extinction Rates of Freshwater Mussels." *Freshwater Biology* 57: 982–92.

Vaughn, C. C., and C. M. Taylor. 2000. "Macroecology of a Host–Parasite Relationship." *Ecography* 23: 11–20. https://doi.org/10.1111/j.1600-0587.2000.tb00256.x.

Viana, D. S., and J. M. Chase. 2019. "Spatial Scale Modulates the Inference of Metacommunity Assembly Processes." *Ecology* 100: e02576.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. "Let the Concept of Trait Be Functional!" *Oikos* 116: 882–92. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Vokoun, J. C., and C. F. Rabeni. 2005. "Variation in an Annual Movement Cycle of Flathead Catfish within and between Two Missouri Watersheds." *North American Journal of Fisheries Management* 25: 563–72.

Wang, L., Y. Gao, B. P. Han, H. Fan, and H. Yang. 2019. "The Impacts of Agriculture on Macroinvertebrate Communities:

From Structural Changes to Functional Changes in Asia's Cold Region Streams." *Science of the Total Environment* 676: 155–64. https://doi.org/10.1016/j.scitotenv.2019.04.272.

Watters, G. T. 1992. "Unionids, Fishes, and the Species-Area Curve." *Journal of Biogeography* 19: 481–90.

Winemiller, K. O., and K. A. Rose. 1992. "Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation." *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196–218. https://doi.org/10.1139/f92-242.

Yang, Y. C. E., X. Cai, and E. E. Herricks. 2008. "Identification of Hydrologic Indicators Related to Fish Diversity and Abundance: A Data Mining Approach for Fish Community Analysis." *Water Resources Research* 44: 1–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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