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Source: Freshwater Mollusk Biology and Conservation, 24(1) : 1-6

Published By: Freshwater Mollusk Conservation Society

URL: https://doi.org/10.31931/fmbc-d-19-00039

Freshwater Mollusk Biology and Conservation 24:1–6, 2021

DOI:10.31931/fmbc-d-19-00039

REGULAR ARTICLE

FRESHWATER MUSSEL ASSEMBLAGES IN THE BLACK RIVER, MISSOURI AND ARKANSAS

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ABSTRACT

Freshwater mussel assemblages show predictable variation according to large-scale biogeographic factors and stream-size gradients, but smaller-scale assemblage patterns are less well known. The goal of this study was to classify and delineate mussel assemblages of the Black River, Missouri and Arkansas, USA, along an upstream–downstream gradient and with regard to physiography and biogeographical regions. We analyzed mussel assemblages using nonmetric multidimensional scaling and indicator-species analysis. Our results yielded three assemblage groupings distributed along the upstream–downstream gradient and thereby considered aquatic ecological systems (100–1,000 km^2) in a hierarchical spatial classification scheme. These groupings also support previously proposed biogeographical differences for mussels and fishes between the Ozark Highlands and Mississippi Alluvial Plain physiographic regions. Each group was characterized by 2–13 indicator species. Our demonstration of small-scale patterns of mussel assemblage change will be useful for conservation planning and for a better understanding of mussel assemblage dynamics.

KEY WORDS: Black River, Arkansas, Missouri, biogeography, faunal groups, hierarchical spatial classification, conservation planning

INTRODUCTION

Riverine freshwater mussel assemblages in much of North America show predictable variation according to macrohabitat and biogeographical factors (Haag 2012). Stream size is one of the most important macrohabitat factors, with species richness and assemblage composition changing predictably along stream-size gradients (Haag 2012). The North American mussel fauna is presently categorized into four major faunal regions (Mississippian, Eastern Gulf, Atlantic, and Pacific), which are further divided into 17 faunal provinces, and these biogeographical affinities also play a major role in determining assemblage structure in a given stream (Haag 2010, 2012). Although these patterns have been recognized, additional case studies are needed to evaluate their generality, particularly at smaller scales. Furthermore, hierarchical spatial classification can be an effective approach for conservation planning (Higgins et al. 2005). Thus, identifying statistically defined faunal and assemblage groups at a variety of scales will aid in conservation planning and management.

The Black River of Missouri and Arkansas, USA, crosses physiographic and faunal boundaries and supports an important mussel resource (Harris 1999; Neves 1999). The Black River mussel fauna is part of the Mississippian faunal region (Haag 2010). The upstream portion of the watershed lies in the uplands of the Ozark Highlands, and the mussel fauna is categorized within the Interior Highlands faunal province. The downstream portion lies in the lowlands of the Mississippi Alluvial Plain, and the fauna is within the Mississippi Embayment province. A total of 53 mussel species are reported from the Black River, including 47 species from the Missouri portion and 42 species from the Arkansas portion (Hutson and Barnhart 2004; S. E. McMurray, unpublished

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Table 1. Mussel species present in our dataset for the Black River, Missouri and Arkansas. Stream-size associations depict habitats in which a particular species frequently dominates mussel assemblages in the Mississippian faunal region or habitats with which a species is otherwise strongly associated as reported by Haag (2012); species not categorized by Haag (2012) are indicated with a dash (—). Nomenclature follows Williams et al. (2017).

Taxa	Stream Size
Actinonaias ligamentina	Midsized
Alasmidonta marginata	Small
Amblema plicata	Generalist
Arcidens confragosus	Large
Cyclonaias nodulata	Large
Cyclonaias pustulosa	Midsized/large
Cyclonaias tuberculata	Midsized
Cyprogenia aberti	Midsized
Ellipsaria lineolata	Large
Epioblasma triquetra	Midsized
Eurynia dilatata	Small/midsized
Fusconaia flava	Midsized
Lampsilis abrupta	Large
Lampsilis cardium	Midsized
Lampsilis reeveiana	Small/midsized
Lampsilis siliquoidea	Small/midsized
Lampsilis teres	Large
Lasmigona complanata	Midsized
Lasmigona costata	Small/midsized
Leptodea fragilis	Midsized
Ligumia recta	—
Ligumia subrostrata	—
Megalonaias nervosa	Midsized/large
Obliquaria reflexa	Midsized/large
Obovaria olivaria	Large
Plectomerus dombeyanus	Large
Pleurobema sintoxia	Midsized
Potamilus ohiensis	Large
Potamilus purpuratus	Large
Ptychobranchus occidentalis	Small/midsized
Pyganodon grandis	Small
Quadrula quadrula	Midsized/large
Reginaia ebenus	Large
Strophitus undulatus	Small
Theliderma cylindrica	—
Theliderma metanevra	Large
Toxolasma parvum	Small
Tritogonia verrucosa	Midsized
Truncilla donaciformis	—
Truncilla truncata	—
Utterbackia imbecillis	—
Utterbackiana suborbiculata	—
Villosa iris	Small
Villosa lienosa	Small

data; J. L. Harris, unpublished data) and 44 species were present in our dataset (Table 1). The watershed's geographic and faunal heterogeneity and high species richness make the Black River a useful system in which to examine patterns of mussel assemblage composition.

The goal of this study was to classify and delineate mussel assemblages of the Black River along the upstream–downstream gradient and with regard to physiographical and biogeographical regions. We analyzed Black River mussel assemblages using nonmetric multidimensional scaling (NMDS) and indicator species.

METHODS

Study Area

The Black River watershed occupies 22,165 km^2 in southeastern Missouri and northeastern Arkansas, USA (Fig. 1). The Black River originates at the confluence of the East Fork and Middle Fork near Lesterville, Missouri, and flows 480 km through the Ozark Highlands and Mississippi Alluvial Plain ecoregions to its confluence with the White River near Newport, Arkansas. The upstream portion of the Black River in the Ozark Highlands, at about river kilometer 341 and upstream, is characterized by clear water, higher gradient, and shallow stream conditions with substrates dominated by gravel and sand (Chapman et al. 2002). The middle and downstream portions of the Black River on the Mississippi Alluvial Plain have lower water clarity, lower gradient, and deeper stream conditions with substrates dominated by sand and clay (Woods et al. 2004).

Mussel Assemblage Data

We compiled existing mussel sampling data from 63 Black River (BLR) sites from Black River kilometer (BRKM) 81.4 (Site BLR50.6) in Arkansas to BRKM 412.80 (Site BLR256.5) in Missouri (Rust 1993; Hutson and Barnhart 2004). Site numbers (BLR; see Fig. 1) correspond to river mile to allow easier cross-referencing with state agency collection records and U.S. Army Corps of Engineers navigation maps (USACE 1985), both of which are in English units. All sites used in this study were sampled between 1990 and 2003. Sixteen sites were located in Missouri and 47 were in Arkansas. Sampling methods included timed-search sampling in Missouri (mean = 2.2 person-hr/site; Hutson and Barnhart 2004) and 1-m^2 quadrat-based sampling in Arkansas. Quadrat sampling consisted of five haphazardly placed 1-m^2 quadrats in small mussel beds and 10–25 1-m^2 quadrats in large mussel beds (Rust 1993; see also Christian and Harris 2005). There were no small or large mussel beds reported between the mouth of the Black River and BRKM 81.4 (Rust 1993).

Data Analysis

We assessed patterns in mussel assemblage data with nonmetric multidimensional scaling (NMDS) based on Bray-

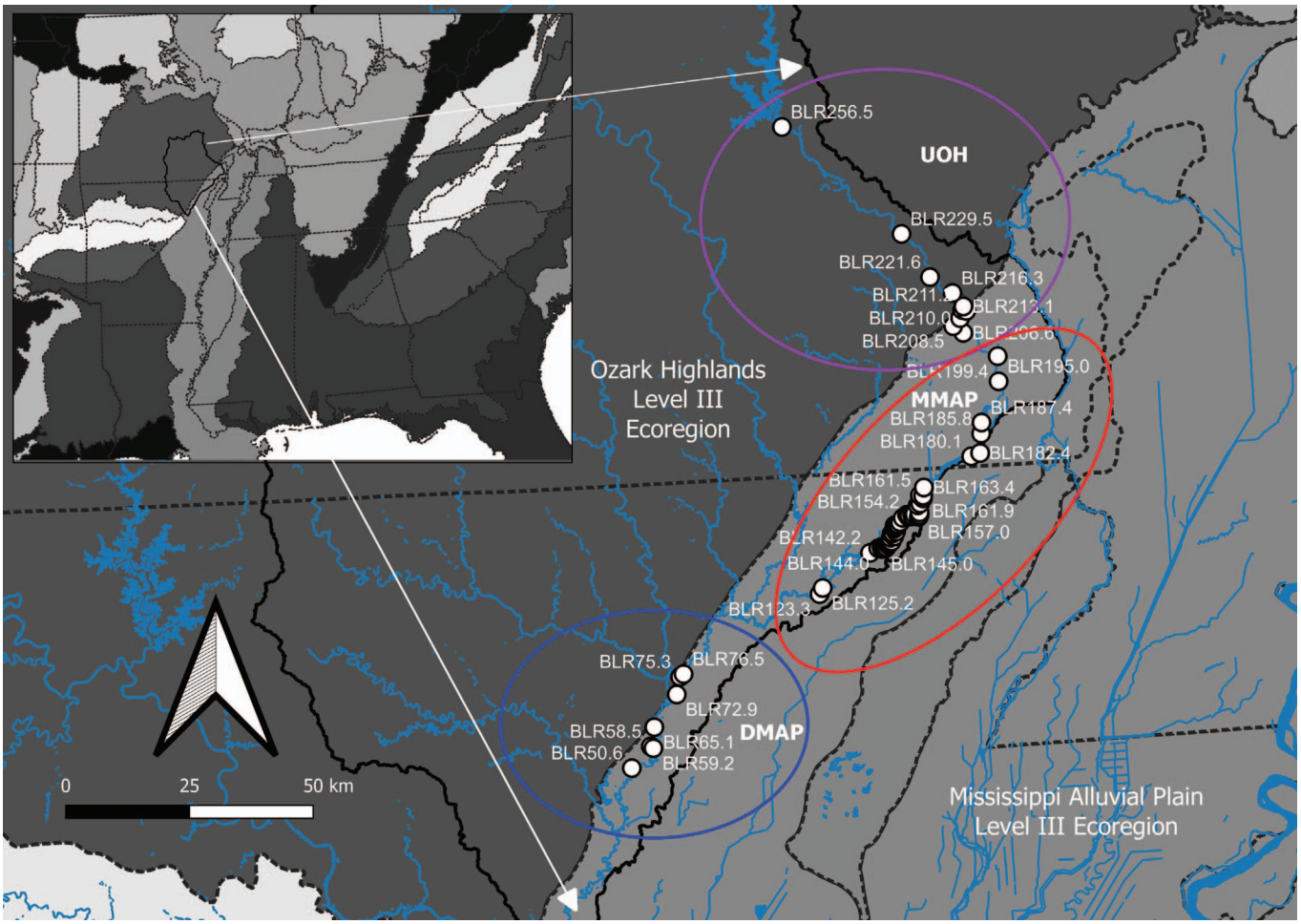

Figure 1. Map of the Black River watershed, Missouri and Arkansas, USA, and sampling sites overlain on the Level III Ozark Highlands (dark gray) and Mississippi Alluvial Plain (lighter gray) ecoregions. The solid black outline shows the watershed boundary and white circles are the Black River mussel sampling sites according to river mile (BLR). Colored ellipses indicate the geographic range of the upstream Ozark Highlands (UOH), midstream Mississippi Alluvial Plain (MMAP), and downstream Mississippi Alluvial Plain (DMAP) mussel assemblage groupings identified by nonmetric multidimensional scaling (NMDS). The inset map shows the location of the study area in the south-central USA.

Curtis dissimilarity using the vegan package (Oksanen et al. 2018) in R (R Core Team 2018). To correct for differences in sampling methods and effort among sites, we transformed assemblage data to relative abundance at each site by dividing the number of individuals of each species collected at a site by the total number of individuals (all species) collected at each site. Based on visual inspection of initial NMDS analysis, geographic groups were assigned as an *a posteriori* hypothesis of geographic clusters defining assemblage composition. Significance was evaluated by determining if between-group variation, measured as the distance between geographic group centroids, was significantly greater than within-group variation, based on a simulated distribution drawn from resampled data (analysis of similarity, ANOSIM).

We used indicator-species analysis to identify species that were uniquely characteristic of the identified geographic groups (Dufrêne and Legendre 1997). We conducted this analysis using the Indicspecies package in R (Cáceres and Legendre 2009; R Core Team 2018). This analysis assigns an indicator value to each species in each group from 0 to 1, where 0 indicates that a species was not observed at any site in the group, and 1 indicates a species was observed at every site in the group and never outside of the group. Indicator species were identified as those having indicator values that were significant at $P \leq 0.05$ based on a permutation test.

RESULTS

The NMDS analysis revealed a geographic pattern of three clusters representing an upstream Ozark Highland (UOH) assemblage from sites BLR206.6–BLR256.5 (BRKM 332.5–412.8), a midstream Mississippi Alluvial Plain (MMAP) assemblage from sites BLR123.3–BLR195.0 (BRKM 198.4–320.9), and a downstream Mississippi Alluvial Plain (DMAP) assemblage from sites BLR50.6–BLR76.5 (BLKM 81.4–123.1) (Fig. 2). The three assemblages were significantly different based on the standard deviation of sites to their geographic-group centroids (ANOSIM, $R = 0.6809$, $P =$

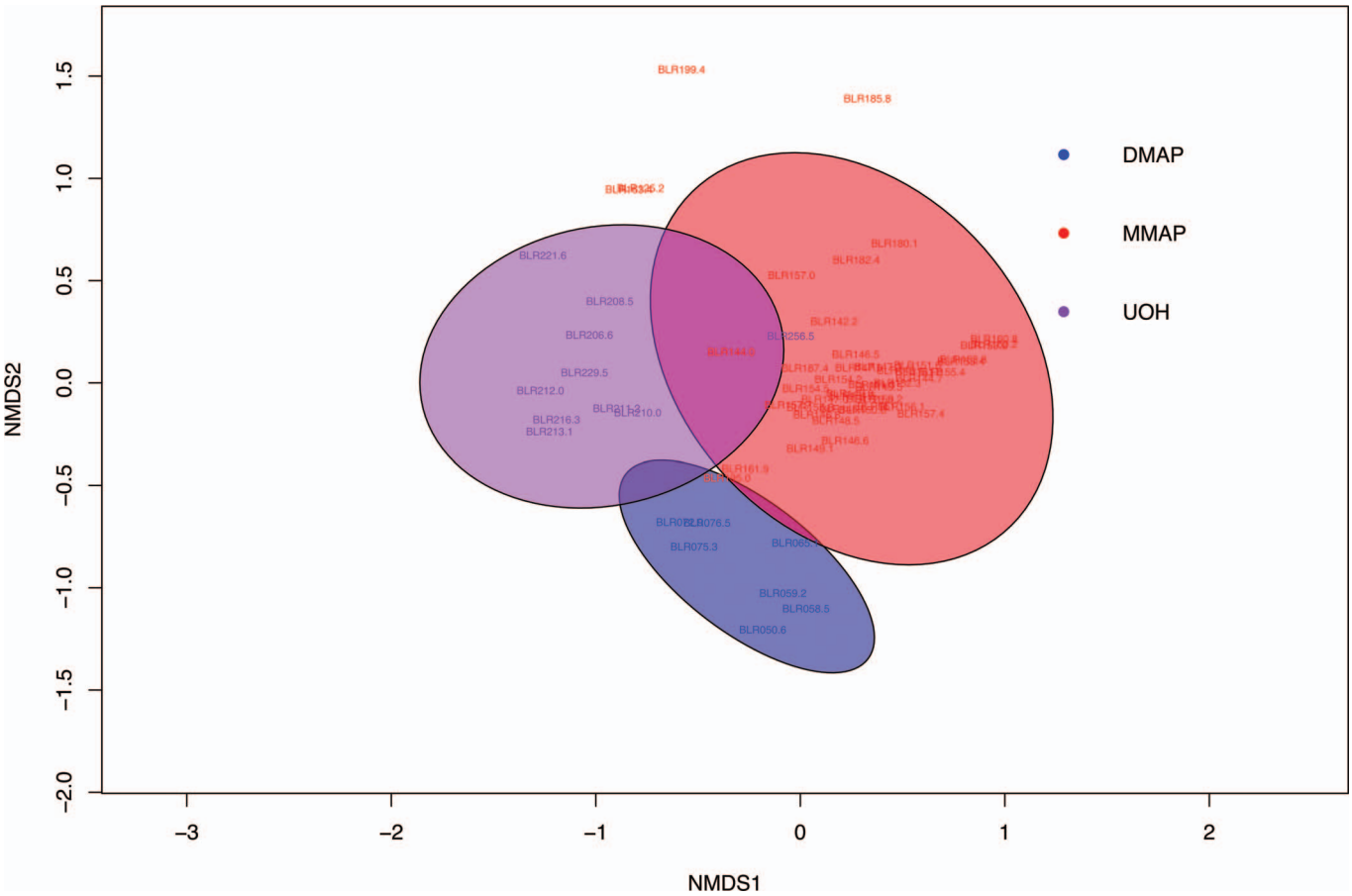

Figure 2. Nonmetric multidimensional scaling (NMDS) plot of mussel assemblages at 63 Black River sampling sites. Ellipses represent 95% confidence intervals around three geographic groupings: upstream Ozark Highlands (UOH), midstream Mississippi Alluvial Plain (MMAP), and downstream Mississippi Alluvial Plain (DMAP). Four sites on the upper part of the graph were not contained in any of the three groupings.

0.001). Four sites did not fall within the 95% confidence interval for any resulting assemblage cluster: BLR 199.4, BLR 185.8, BLR163.4, and BLR125.2, but all four sites were spatially distributed within the range of MMAP sites (Fig. 1).

Indicator-species analysis identified characteristic species for each geographic group (Fig. 3). The upstream UOH group had 13 species that were significant indicators, with the strongest being *Pleurobema sintoxia* (0.987), *Actinonaias ligamentina* (0.936), *Plectomerus dombeyanus* (0.933), *Strophitus undulatus* (0.903), *Lasmigona costata* (0.894), *Cyprogenia aberti* (0.885), and *Fusconaia flava* (0.830). The midstream MMAP group had two significant indicators, *Amblema plicata* (0.937) and *Lasmigona complanata* (0.836). The downstream DMAP group had seven significant indicators, with the strongest being *Obovaria olivaria* (1.000), *Reginaia ebenus* (0.948), *Quadrula quadrula* (0.891), and *Ellipsaria lineolata* (0.844).

DISCUSSION

Our finding of three distinct assemblages dispersed along an upstream–downstream gradient was expected. Mussel assemblages show predictable structure in which dominance is shared by a small group of codominant species and dominance shifts along stream-size gradients (Haag 2012). The UOH assemblage was associated mostly with midsized stream species (*P. sintoxia*, *A. ligamentina*, *L. costata*, *C. aberti*, and *F. flava*), but it also included one small-stream species (*S. undulatus*). The MMAP assemblage was associated with *L. complanata*, a midsize stream species, and *A. plicata*, a stream-size generalist. Finally, the DMAP assemblage was associated with four species, *O. olivaria*, *R. ebenus*, *E. lineolata*, and *Q. quadrula*, all of which are large-stream species.

Three (BLR185.5, BLR163.4, and BLR125.2) of the four sites that did not cluster with the UOH, MMAP, or DMAP groups had *A. plicata* and *L. complanata*, indicators for MMAP; however, *A. plicata* and *L. complanata* were absent at the fourth site, BLR199.4. Overall, these four sites mostly had low overall abundances and a mixture of indicator species from a variety of groups. BLR125.2 had representation of UOH indicator species *A. ligamentina* and *F. flava* and the DMAP indicator *Q. quadrula* in addition to MMAP indicators *A. plicata* and *L. complanata*. BLR163.4 had low numbers of the DMAP indicator *Q. quadrula* in addition to low numbers of MMAP indicator species *A. plicata* and *L. complanata*.

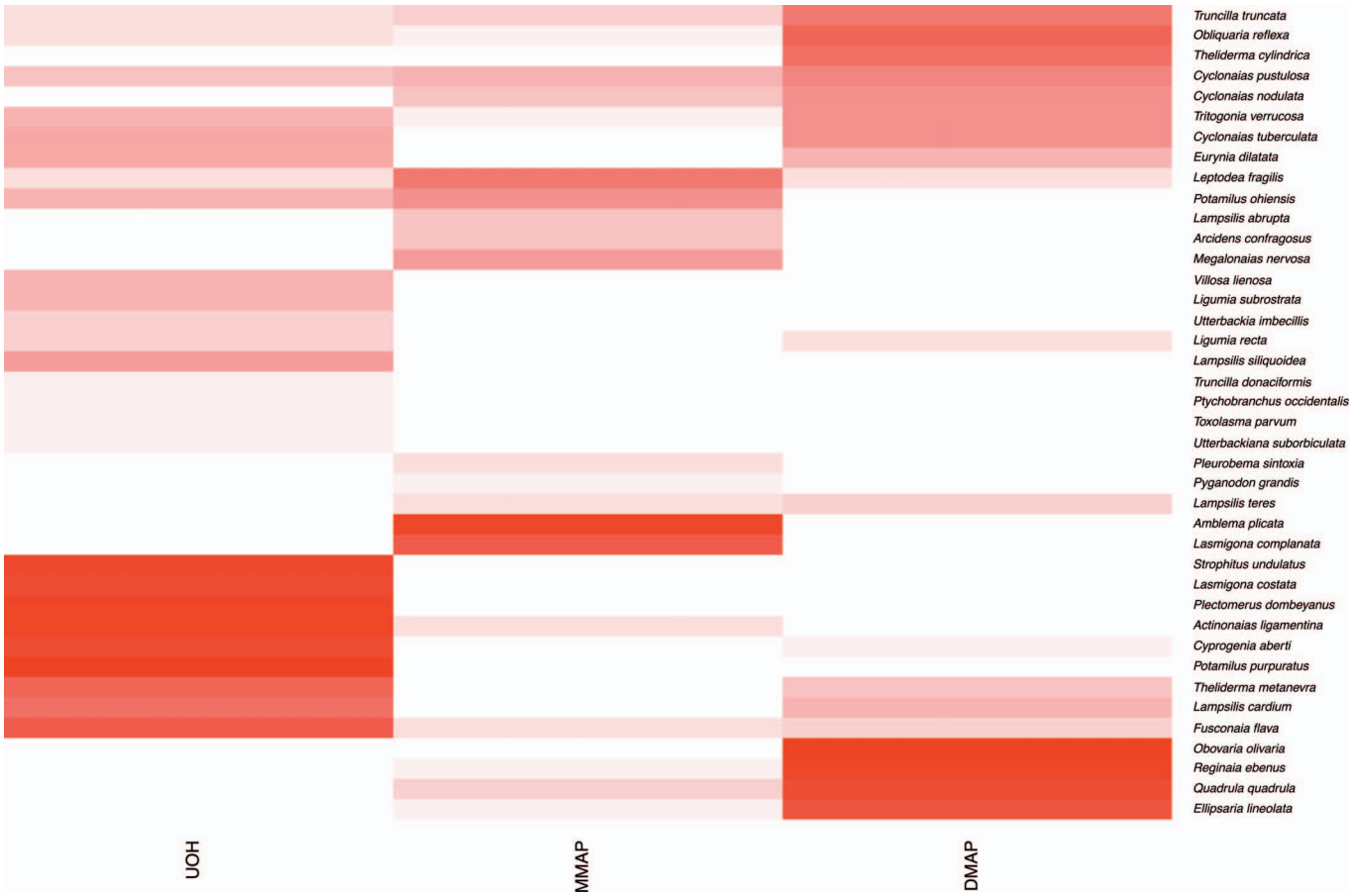

Figure 3. Heat map showing results of indicator-species analysis of mussel assemblages in the Black River within three geographic groups: upstream Ozark Highlands (UOH), midstream Mississippi Alluvial Plain (MMAP), and downstream Mississippi Alluvial Plain (DMAP). Deeper red coloring indicates stronger indicator relationships within each group.

BLR185.5 had low numbers of UOH indicator species *F. flava* and *P. dombeyanus* in addition to low numbers of MMAP indicator species *A. plicata* and *L. complanata*. BLR 199.4 did not have any MMAP indicator species but had low numbers of the UOH indicator species *A. ligamentina*. Therefore, one could argue that BLR125.2, BLR163.4, and BLR185.5 associate with the MMAP group, while BLR199.4 associates with the UOH group.

Our three faunal groupings also were concordant with physiography and biogeographical affinities. The UOH assemblage showed remarkably close association with the Ozark Highlands. Furthermore, one of the indicator species for this assemblage, *Cyprogenia aberti*, is a characteristic member of the Interior Highlands faunal province (Haag 2010). The MMAP assemblage may represent a transitional area between the upland UOH assemblage and the lowland DMAP assemblage. Similar assemblage differences between the Ozark Highlands and the Mississippi Alluvial Plain are seen for fishes in the Black River and adjacent watersheds in southeastern Missouri (Pflieger 1970, 1997; Matthews and Robison 1988).

In our study area, stream size and physiography/biogeography are confounded because the Black River becomes larger as it flows off the Ozark Highlands and onto the Mississippi Alluvial Plain. Consequently, we cannot assess the relative importance of these two factors in influencing mussel assemblage composition. Other unmeasured factors also likely affect these assemblages. For example, local environmental variables can be correlated with mussel assemblages (Arbuckle and Downing 2002; Poole and Downing 2004), and distribution and abundance of fish hosts also can be a strong predictor of mussel assemblage structure (Vaughn and Taylor 2000; Schwalb et al. 2013).

When our study is considered in a spatial classification framework (Higgins et al. 2005), individual mussel beds are equivalent to macrohabitats (1 to 100 km^2), our three assemblage groupings (UOH, MMAP, DMAP) are equivalent to aquatic ecological systems (100 to 1,000 km^2), the Black River represents an ecological drainage unit (1,000 to 10,000 km^2), and the Mississippian faunal region (Haag 2010) represents an aquatic zoogeographic unit (10,000 to 100,000 km^2). Our identification of distinct UOH, MMAP, and DMAP mussel assemblages provides the basis for conservation planning aimed at maximizing biodiversity within a hierarchical spatial and biogeographic context (National Native Mussel

Conservation Committee 1998; Freshwater Mollusk Conservation Society 2016).

ACKNOWLEDGMENTS

Funding for this project was provided by the Arkansas Game and Fish Commission, Arkansas Natural Heritage Commission, Arkansas State University, Missouri Department of Conservation, U.S. Army Corps of Engineers, and the U.S. Fish and Wildlife Service. We thank M. C. Barnhart and C. Hutson for their field work in Missouri and S. W. A. Chordas, G. L. Harp, and P. Rust for their field work in Arkansas. J. McLean provided information on Corps of Engineers Black River maps. This paper benefited from edits and comments from three anonymous peer reviewers and the editor.

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