Received: 21 February 2025 | Revised: 18 September 2025 | Accepted: 21 October 2025

DOI: 10.1002/ecy.70273

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

# Environmental gradients drive convergence in life history strategies among disparate but coevolved taxonomic groups

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**Funding information**
Fish and Wildlife Service; Oklahoma Department of Wildlife Conservation State Wildlife Grant, Grant/Award Number: FI 3AF01213; Directorate for Biological Sciences, Grant/Award Numbers: DEB1457542, DEB2043012, DEB9306687, DEB9870092; Nature Conservancy; American Electrical Power; Oklahoma Biological Survey; National Science Foundation; U.S. Fish and Wildlife Service; U.S. Forest Service; Alabama Water Institute

**Handling Editor:** Helmut Hillebrand

**Abstract**

Trait-based approaches can improve ecological understanding by linking fitness to the environment. The trilateral life history model is an expansion of r- and K-selection theory that reflects trade-offs between juvenile survival, fecundity, and generation time and describes differential survival of species across environmental gradients. We used this framework to generate and test hypotheses regarding community assembly and the validity of such a model in two disparate taxonomic groups, freshwater mussels and fish. We assessed the distribution of mussel and fish life history strategies across 80 sites spanning aspects of the river continuum concept within the Ouachita Highlands (USA) and asked if their distributions are predicted by a similar life history strategy framework. Because mussel and fish assemblages should both be structured by selective forces in an up- to downstream trajectory, we expected both taxa to converge on more species-rich assemblages with a greater proportion of equilibrium strategists in larger, more stable downstream habitats. We found that both mussel and fish species richness increased with watershed area as well as the proportion of equilibrium strategists in the assemblages. Our study validates the use of the trilateral life history model to test hypotheses about the distribution patterns of two coevolved taxonomic groups.

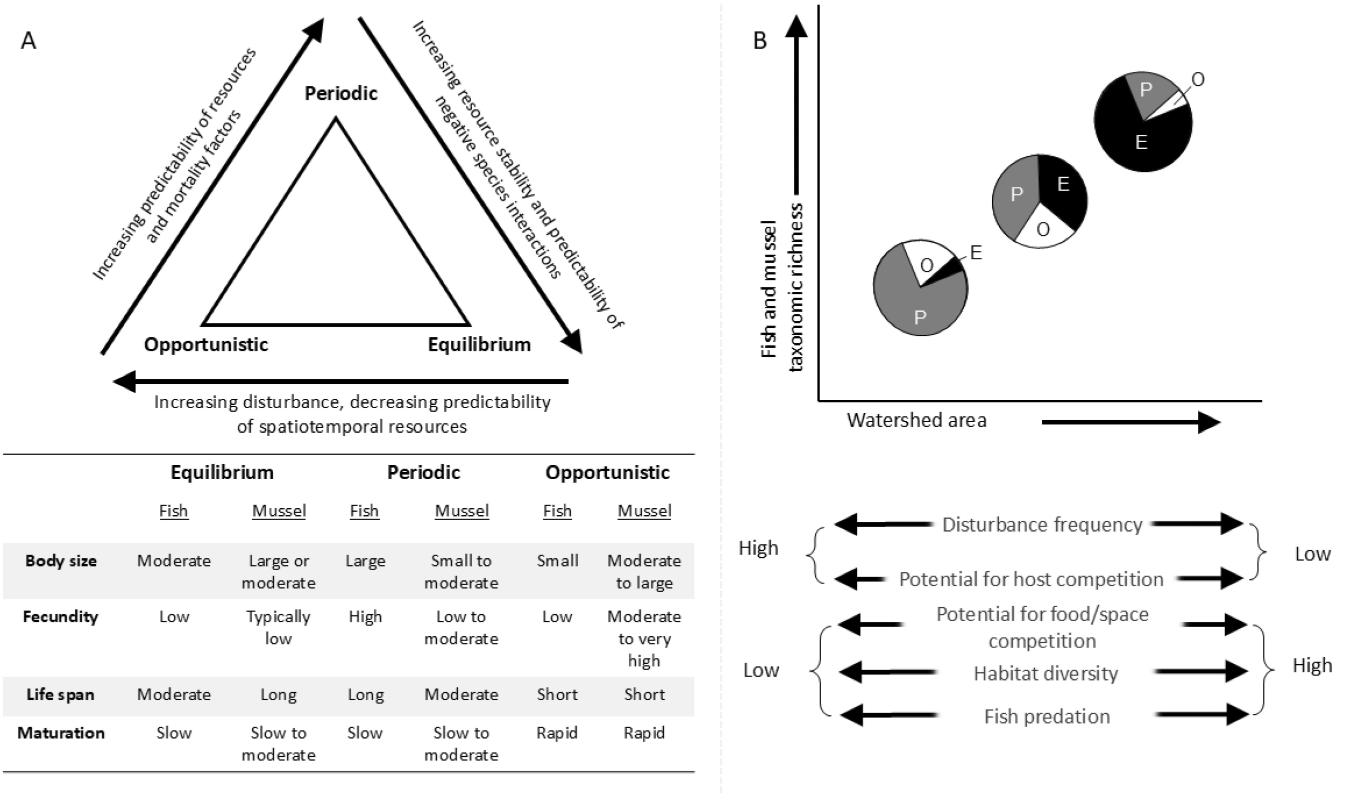
**KEYWORDS**
fish, freshwater, mussels, river continuum, species traits, Unionidae

## INTRODUCTION

A fundamental goal of ecology is understanding how organismal distribution patterns are influenced by environmental factors (MacArthur & Levins, 1967). Trait-based approaches offer a framework for mechanistically linking species traits to major environmental drivers influencing organism fitness. Trait–environment relationships reveal that functional traits exhibit trade-offs, in which certain traits are more favorable for fitness and population persistence under certain environmental conditions (McGill et al., 2006). Life history theory predicts that different habitat templates favor specific suites of traits, resulting in the evolution of life history strategies that enable a species to cope with a range of environmental conditions. Many trait-based studies have focused on single taxonomic groups or guilds, whereas comparisons of trait variation among more distantly related, co-occurring fauna have rarely been assessed simultaneously (but see, Kuczynski et al., 2024).

Streams are spatially heterogeneous, dynamic systems with well-characterized environmental gradients (Townsend & Hildrew, 1994; Vannote et al., 1980). Hydrology fundamentally constrains the availability of habitat, and stream organisms have evolved several general adaptations to such constraints—dispersal capabilities, desiccation resistance, and/or high fecundity to compensate for the loss of adults through drying (Poff, 1997). In addition, streams are dendritic networks that increase in size longitudinally from the headwaters to downstream reaches, impacting basal resource availability and subsequent community composition (i.e., river continuum concept; Vannote et al., 1980). Disturbance regimes also vary along this longitudinal gradient and influence the structure of stream communities (Lake, 2000; Ward, 1998). Upstream assemblages tend to be composed of species with adaptations to frequent disturbances, while downstream reaches with greater habitat size, diversity, and stability harbor assemblages with a broader range of traits that are adapted to more stable conditions (Greig et al., 2022; McHugh et al., 2010). Collectively, the longitudinal nature and consequential disturbance regimes are predicted to constrain trait distribution and stream community composition (Townsend & Hildrew, 1994).

Contrasting adaptations to stream habitat expansion and contraction are exhibited by co-occurring stream fishes and freshwater mussels (family Unionidae). Both taxonomic groups are diverse and imperiled (Dudgeon & Strayer, 2025), but have disparate lifestyles and life histories. Most stream fishes are shorter lived (typically 2–5 years) and highly mobile, allowing for dispersal as stream habitat expands and contracts (Hedden & Gido, 2020). In contrast, long-lived mussels (~10 to >100 years) live burrowed in the sediment, are sedentary as adults, and thus are constrained to perennially wetted habitats (Haag, 2012). Despite these disparities, interspecific variation in life history traits within both groups can be summarized within a similar generalizable trilateral life history model, although the traits defining each group vary (Figure 1A). This model expanded the r- and K-selection life history model (Pianka, 1970) to



| | Equilibrium | | Periodic | | Opportunistic | |
|---|---|---|---|---|---|---|
| | Fish | Mussel | Fish | Mussel | Fish | Mussel |
| **Body size** | Moderate | Large or moderate | Large | Small to moderate | Small | Moderate to large |
| **Fecundity** | Low | Typically low | High | Low to moderate | Low | Moderate to very high |
| **Life span** | Moderate | Long | Long | Moderate | Short | Short |
| **Maturation** | Slow | Slow to moderate | Slow | Slow to moderate | Rapid | Rapid |

FIGURE 1 (A) Conceptual model highlighting the trilateral life history strategy frameworks that have been conceptualized for both mussels and fishes highlighting the similarities and differences among the two taxonomic groups and their response to the environment. (B) We predict that species richness in both mussels and fishes will increase in rivers with larger contributing watershed areas and that assemblages in rivers draining larger watershed areas will be composed of a larger proportion of equilibrium species.

include a third primary strategy (endpoint of a triangular continuum) termed the periodic strategy. The trilateral life history model reflects trade-offs between juvenile survival, fecundity, and generation time (Figure 1A; Haag, 2012; Winemiller & Rose, 1992) and was originally developed from analysis of life history variation in fishes and later applied to other taxa including mussels (Haag, 2012; Moore et al., 2021). Each of the three endpoints represents life history strategies that are favored by certain environmental conditions: opportunistic strategists maximize fitness in more stochastic environments, owing to traits that allow for rapid recolonization; periodic strategists maximize fitness under predictable but cyclical environments due to their delayed maturation and moderate to high fecundity; and equilibrium strategists maximize fitness in stable environments because of their investment in juvenile survival. Although spatial patterns in the life history composition of fish and mussel assemblages are evident at large scales (Haag, 2012; Mims & Olden, 2012), whether the life history strategy composition of fishes and mussels co-occurring across the same environmental conditions responds in similar ways to the environmental gradients associated with stream size and disturbance has yet to be tested.

Mussels have a complex life cycle wherein their larvae are obligate ectoparasites on fish (Haag, 2012). After excysting from the host fish, juvenile mussels drop to the stream bed. Because mussel adults are sedentary, mussels depend on host fish for dispersal and are only abundant and diverse where fish are abundant and diverse (Haag, 2012). Because of this host–parasite relationship, fish assemblage structure can influence mussel assemblage structure and abundance (Schwalb et al., 2013; Vaughn & Taylor, 2000; Watters, 1992). The convergence of both components of the mussel-host system on a similar trilateral life history continuum provides a framework to generate and test hypotheses regarding community assembly dynamics, the validity of such a model, and potential conservation implications that impact both groups.

Here, we assess the distribution of mussels and fish life history strategies along a stream size gradient (i.e., river continuum) within a single biogeographic region. Both taxonomic groups are constrained in their broad-scale distributions and richness by large macroscale processes (i.e., historical contingencies; Haag, 2012; Hocutt & Wiley, 1986), thus asking how watershed size as a proxy for disturbance shapes patterns of richness and trait composition is most appropriate at a regional scale (Matthews & Marsh-Matthews, 2017; Poff, 1997). We asked whether the same life history strategy framework can predict the distribution of these coevolved taxonomic groups. As both mussels and fish assemblages should be structured with a gradient of selective forces in an up- to downstream trajectory, we expected mussels and fish to converge on assemblages composed of greater abundances of species with opportunistic and periodic life history strategies in smaller, more disturbance-prone stream reaches and for assemblages to shift to more species-rich assemblages composed of a greater proportion of equilibrium strategists that are favored in larger, more stable downstream habitats (Figure 1B). Given the relatively sedentary nature of mussels and the mobility of fishes, we further predicted that life history strategies would be distributed more predictably in mussels versus fish.

# METHODS

## Study area

Our study area included the Kiamichi and Little River watersheds in the Ouachita Highlands of southeastern Oklahoma, USA (Appendix S1: Figure S1; Vaughn et al., 2023). This biogeographic area is a center of speciation for both terrestrial and aquatic organisms and contains rich unionid mussel and fish faunas and has streams that are relatively unimpacted compared to other areas of North America and Europe (Vaughn et al., 2023).

## Mussel sampling

We surveyed mussels across 92 sites in the Kiamichi and Little River watersheds of southeastern Oklahoma between 1999 and 2021 (Appendix S1: Figure S1). These data result from many discrete and ongoing studies on these rivers (Atkinson et al., 2012; Lopez et al., 2022; Vaughn & Taylor, 2000). All sampling occurred in summer at base or lower flows and was restricted to areas where mussels were aggregated in beds. Following Vaughn et al., (1997), for each site, we first determined the extent of the mussel bed with snorkel surveys, then excavated 15–20 haphazardly placed 0.25-$m^2$ quadrats to a depth of 15 cm. All mussels were identified to species and returned alive to the mussel bed. Mussel species were assigned to the equilibrium, periodic, or opportunistic life history strategy (Appendix S1: Table S1) as in Haag (2012).

## Fish sampling

We sampled 82 sites for fishes in the Kiamichi and Little River watersheds in 2014 and 2015 via seining (Zbinden et al., 2022). Fish were collected by seining all identifiable habitats, as described in detail in Matthews and Marsh-Matthews (2017), within a target of 100 m of wadable stream reach. Specimens were identified and preserved in 10% formalin, identified, and cataloged in the Sam Noble Museum of Natural History at the University of

Oklahoma. Fish species were assigned to the equilibrium, periodic, or opportunistic life history strategy (see Appendix S1: Methods and Table S2) as in Winemiller and Rose (1992) and Mims and Olden (2012).

## Site attribute determination

We generated a dataset of estimated ecological attributes for each site including watershed area, stream slope, and Strahler stream order from the U.S. Geological Survey National Hydrography Dataset Plus Version 2 (McKay et al., 2012) for each site in R (v.4.1.2; R Core Team, 2021). We transformed georeferenced coordinates into spatial objects based on the NAD83 coordinate system with the package *sf*, then used the function discover_nhdplus_id from the package *nhdplusTools* to retrieve the closest associated flowline common identifier (COMID) for each point. The subset_nhdplus function was used to download all attributes associated with each flowline COMID.

## Statistical analyses

We assessed the relationship between watershed area and species richness with linear regression. We calculated the proportion of each life history strategy of mussel and fish assemblages at each site and assessed the relationship between the proportion of the assemblage composition of each of the three life history strategies and watershed area with linear regression. Prior to analysis, proportional data were arcsine-square-root transformed to meet assumptions of normality. Sites sampled for fish were not evenly distributed by watershed area, so we natural log-transformed the area values for fish assemblage analyses. We also assessed assemblage structure across our sites using nonmetric multidimensional scaling (NMDS) ordination based on the Bray–Curtis index with 999 iterations in the package *vegan* to visualize mussels and fish separately in multidimensional space. We color-coded the ordination with Strahler stream order to visually assess assemblage differences across stream sizes. We followed this with a joint plot analysis using watershed area and slope as predictors in the function *envfit* to illustrate associations among these variables and the mussel and fish assemblages.

# RESULTS

## Species richness

We collected a total of 31 mussel species with species richness ranging from 4 to 22 species across sites with watershed areas ranging from 7.3 to 3637 km$^2$. Mussel species richness increased with watershed area (Figure 2A; $R^2 = 0.46$, $F_{1,90} = 77.7$, $p < 0.00001$, $y = 0.003x + 7.8$). We collected a total of 68 fish species with species richness ranging from 1 to 28 species across sites with watershed areas ranging from 6.5 to 5827.3 km$^2$. Generally, fish species richness increased with watershed area (Figure 2B; $R^2 = 0.13$, $F_{1,80} = 13.0$, $p = 0.0005$, $y = 1.0x + 6.76$).

## Life history strategies and assemblage structure

For mussel life history strategies, the proportion of the assemblage comprised of equilibrium species increased with watershed area (Figure 2C; $R^2 = 0.10$, $F_{1,90} = 10.84$, $p = 0.0014$, $y = 0.000092x + 1.00$). Similarly, the proportion of the fish assemblage composed of equilibrium species increased with watershed area (Figure 2D; $R^2 = 0.10$, $F_{1,80} = 10.47$, $p = 0.0013$, $y = 0.052x + 0.\ 37$). In both mussels (Figure 2E; $R^2 = 0.15$, $F_{1,90} = 14.11$, $p = 0.0003$, $y = -0.00009x + 0.47$) and fish (Figure 2F; $R^2 = 0.042$, $F_{1,80} = 4.54$, $p = 0.036$, $y = -0.041x + 0.47$), the proportion of the assemblage comprised of periodic species declined with watershed area. Neither the proportion of the mussel assemblage comprised of opportunistic species (Figure 2G; $R^2 = -0.01$, $F_{1,90} = 0.132$, $p = 0.717$) nor the proportion of fish species making up the opportunistic life history strategy was related to watershed area (Figure 2H; $R^2 = 0.0006$, $F_{1,80} = 1.05$, $p = 0.308$). Our NMDS analysis revealed some structuring of mussel (Appendix S1: Figure S2A) and fish (Appendix S1: Figure S2B) assemblages by Strahler stream order. Our joint plot analysis indicated that watershed area was an important contributing factor for both mussel and fish assemblages ($r^2 = 0.49$, $p < 0.001$, $r^2 = 0.16$, $p = 0.004$) and stream slope was also an important factor impacting mussel assemblage composition ($r^2 = 0.23$, $p = 0.001$).

# DISCUSSION

Predicting species richness and the composition of biological communities is a major challenge for ecologists. Our study revealed associations among richness, life history strategies, and stream size across two divergent, coevolved taxonomic groups, mussels and fish, consistent with constraints and adaptive responses to environmental conditions. As predicted, we document higher species richness and a higher proportion of species belonging to the equilibrium life history strategy in both mussel and fish assemblages in a downstream trajectory. Larger rivers have more predictable flow regimes and greater habitat heterogeneity (Ward, 1998) promoting a larger number of species with different traits and species with

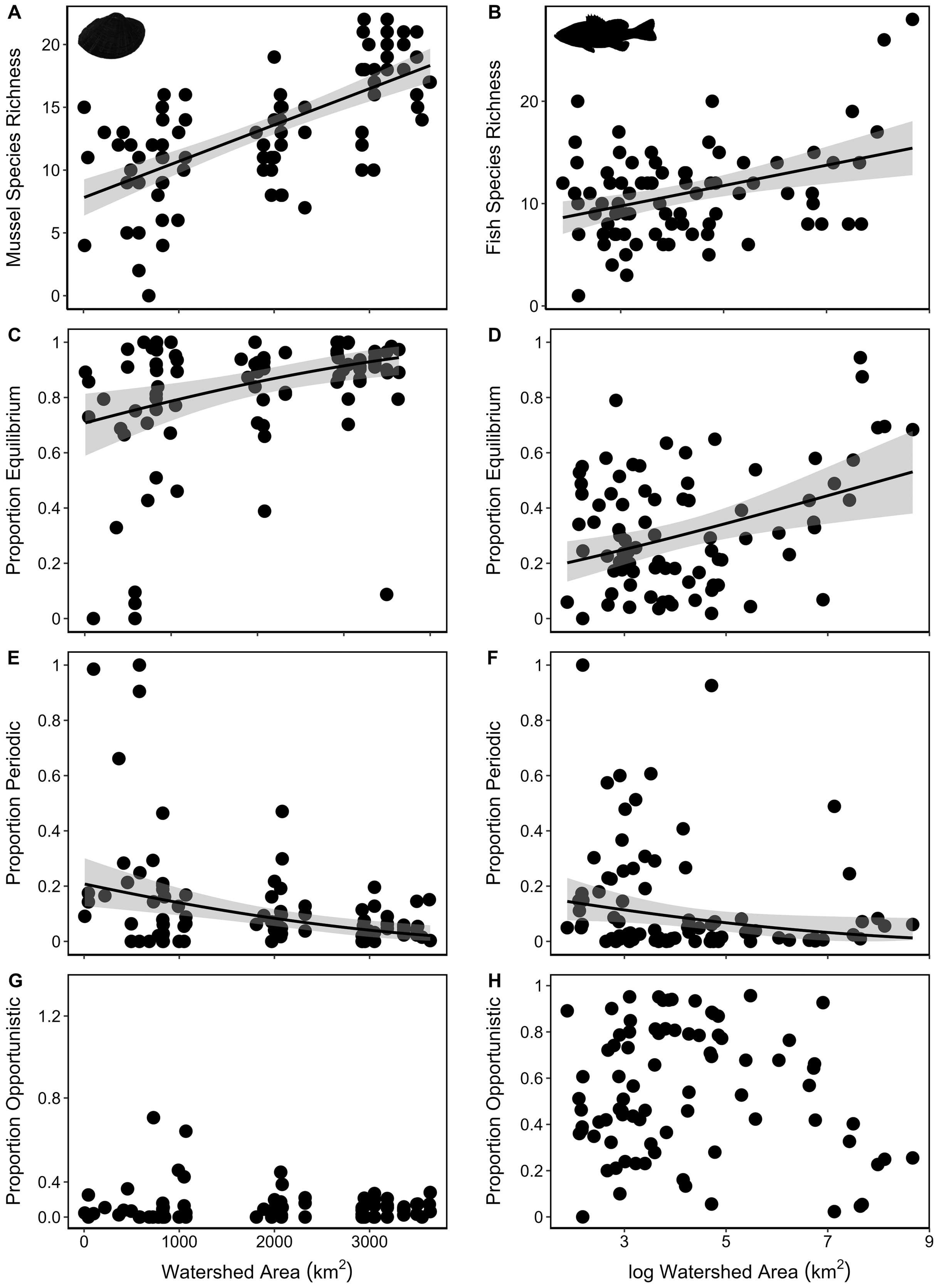


**FIGURE 2** Legend on next page.

traits that are adaptive for those conditions (e.g., longer lived). However, at large, continental scales, stream size–species richness patterns may vary dramatically due to different assemblage structures associated with biogeographic regions and disturbance histories (Haag, 2012). Linking species' life history traits with large-scale landscape patterns allows for both more predictive biology and better conservation knowledge given the host–parasite relationship of these two groups.

As river ecosystem structure and function shift predictably in a downstream direction (Vannote et al., 1980), species richness and assemblage structure are also expected to change, with higher richness anticipated in downstream reaches with greater habitat area and heterogeneity. Previous work has shown increases in aquatic insect (Minshall et al., 1985), freshwater mussel (Atkinson et al., 2012; Chambers & Woolnough, 2018; Strayer, 1983; Watters, 1992), and fish species (Matthews, 1998; Matthews & Robison, 1998) in a downstream trajectory up to midsized reaches. The positive relationship between mussel and fish species richness and watershed area could be due to both greater habitat availability and more stable environments typically associated with larger streams (McHugh et al., 2010). In addition to greater overall species richness, sites in the larger streams likely harbor greater functional diversity (Petchey & Gaston, 2002), which may promote ecosystem stability. Previous work on mussels indicates that sites with higher mussel species richness (and watershed area) have greater rates of biomass production and nutrient cycling relative to lower diversity sites (Hopper, González, et al., 2023; Lopez et al., 2024). Research further linking patterns of species richness, and functional trait and functional effect trait diversity, with watershed size could better elucidate how these patterns translate into ecosystem-level effects (e.g., Gonzalez et al., 2020).

As predicted, our study indicated that assemblages had a greater proportional abundance of equilibrium species (generally K-selected) in larger streams in both mussels (e.g., *Amblema plicata*) and fish (e.g., *Lepomis megalotis*). That corroborates with a study on freshwater mussels in a different region (i.e., upper Mississippi River basin; Hornbach et al., 2024) as equilibrium species are longer lived and have late maturity and are better adapted to larger rivers. Further, we observed a lower proportional abundance of periodic species in downstream reaches in both taxonomic groups. Smaller streams are generally temporally more unstable than downstream reaches as they experience frequent disturbance from drought, floods, and oxygen stress; thus, periodic species are more apt to make up a larger proportion of the community in areas that tend to have higher disturbance. Proportional abundance of opportunistic species was not predicted by watershed size in either group, which may be expected as their populations may be more sporadic and respond more to temporal changes in the environment. For mussels, this may be because our study design primarily focused on mussel assemblages, which are associated with mussel beds that are typically found in hydrologically stable stream habitats where opportunistic species are rarely found (Haag, 2012). While all three life history strategies occurred across reaches, their relative frequencies align with theoretical predictions (Mims & Olden, 2012) as they reflect species-specific responses to environmental variation shaped by their broader ecological niches such as habitat requirements and reproductive constraints (Pianka, 1970). These niche-based factors interact with environmental variance to allow coexistence of multiple strategies while still producing shifts in proportional dominance of strategies. Despite some differences in the life history strategy framework for mussels and fish (e.g., periodic fishes have high fecundity and late maturation while periodic mussels have early age at maturation and low fecundity), it was useful in understanding the distribution of trait strategies for both groups.

We expected that the distribution of life history strategies would be more predictable in mussels than fish due to their sedentary nature in comparison to mobile fish. However, the distribution of strategies was similar in both groups despite the greater mobility of fish. This concordance may be because fish are hosts for the larval stage of mussels (Haag, 2012). Thus, fish assemblage structure plays a substantial role in determining mussel assemblage composition. Indeed, previous work has found that the number of fish species in a watershed or at the site scale predicts mussel species richness (Dascher et al., 2018; Schwalb et al., 2013; Vaughn & Taylor, 2000; Watters, 1992). More research studying the co-distribution of mussels and fish could help discern the relative strength of biotic (host fish) and abiotic factors underlying mussel assembly structure.

The trilateral life history model provides a predictive framework for comparing population and species

**FIGURE 2** Both mussel (A) and fish (B) species richness increase with watershed area. Proportion of mussels and fish that fit within the equilibrium (C and D, respectively), periodic (E and F, respectively) and opportunistic (G and H, respectively) life history strategies across sites that vary in watershed area in the Ouachita Highland region. Proportional data ($y$-axes in panels C–H) are arc-sine square-root-transformed and the $x$-axes for the sites in which fish were collected are natural log-transformed. Mussel silhouette created by Carla Atkinson. Fish silhouette by Carlos Cano-Barbacil via a public domain CCO 1.0 license on Phylopic.

assemblage responses to environmental gradients. Mussels and fish are diverse, imperiled, and codependent taxa, and both broadly impact ecosystem function (Atkinson et al., 2013, 2023; McIntyre et al., 2007). We demonstrated that the life history composition of fish and mussel assemblages is generally related to watershed area, which may assist in predicting assemblage responses to natural and anthropogenic disturbances. Improved understanding of how different life history strategies respond to stream flow regimes and other habitat features will provide valuable insights to guide freshwater biodiversity conservation. Expansion of species trait databases (Frimpong & Angermeier, 2009; Hopper, Bucholz, et al., 2023) will improve predictive power to address the mechanisms underlying the distributional patterns observed here. Enhancing our understanding of functional trait distribution and co-occurrence will be fundamental to the recovery of these imperiled and coevolved taxa and the long-term success of river conservation. By quantifying functional trait distribution in natural assemblages, we gain an additional understanding of the spatial and temporal distribution of biodiversity, which can inform conservation prioritization (Petchey & Gaston, 2002).

## ACKNOWLEDGMENTS

We thank the many students, postdoctoral researchers, and other colleagues who assisted with mussel surveys over the decades and numerous landowners for allowing access to sampling sites from their property. Funding for mussel surveys was provided by American Electrical Power, the Oklahoma Biological Survey, the Oklahoma Department of Wildlife Conservation, the National Science Foundation (DEB9306687, DEB9870092, DEB1457542), the Nature Conservancy, the U.S. Fish and Wildlife Service, and the U.S. Forest Service. Funding to compile and analyze the long-term data was provided by NSF DEB2043012. Funding for fish surveys was provided by the Oklahoma Department of Wildlife Conservation State Wildlife Grant FI 3AF01213 (T-74-1) and the University of Oklahoma. The Alabama Water institute provided support for page charges associated with this publication.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Atkinson, 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.26955985.v1.

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## SUPPORTING INFORMATION

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

**How to cite this article:** Atkinson, Carla L., Alex J. Franzen, Garrett W. Hopper, Jonathan W. Lopez, Zachery D. Zbinden, and Caryn C. Vaughn. 2025. "Environmental Gradients Drive Convergence in Life History Strategies among Disparate but Coevolved Taxonomic Groups." *Ecology* 106(12): e70273. https://doi.org/10.1002/ecy.70273