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ARTICLE

Freshwater Ecology

Secondary production and biomass in mussel assemblages relate to species richness and stream size but not life history

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Abstract

Increases in species richness with habitat area (species–area relationship, or SAR) and increases in ecosystem function with species richness (biodiversity–ecosystem functioning, or BEF) are widely studied ecological patterns. Incorporating functional trait analysis into assemblage datasets may help clarify interpretations of SAR and BEF relationships in natural ecological systems. For example, life history theory can be used to make predictions about what species are most important in generating ecosystem function given a certain set of environmental conditions. We used quantitative assemblage data for freshwater mussels at nine sites in western Alabama, USA, to test for SAR and BEF relationships. At each site, we calculated species richness, mussel assemblage density, and two fundamental metrics of ecosystem function: biomass and secondary production. We also tested whether the proportional biomass and production contributions from species belonging to each of three life history strategies—*opportunistic strategists* adapted to unstable or frequently disturbed habitats, *periodic strategists* adapted to habitats subject to predictable large-scale disturbances, and *equilibrium strategists* adapted to stable habitats—varied longitudinally with stream drainage area, a proxy for habitat area. Species richness increased with stream size (SAR), and both biomass and production increased with species richness (BEF) and mussel density. There were few longitudinal changes in the proportional contributions of the different life history strategy classifications that we used, but the invasive clam *Corbicula fluminea* contributed proportionally more biomass and production at sites that had smaller drainage areas. This study provides further evidence for a clear longitudinal SAR in stream-dwelling taxa. It also suggests BEF relationships for biomass and secondary production in natural assemblages but underscores the importance of assemblage density in BEF studies that use observational field data. Variation in proportional biomass and production contributions by different life history strategies was likely limited by the size of

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the stream size gradient in our study, as contributions were uniformly high for species with life history traits better adapted to stable and productive habitats such as mid-sized rivers with low or predictable hydrologic disturbance frequencies. This highlights the need to understand how organisms' functional traits govern their relationships to the environment at different scales.

KEYWORDS
biodiversity–ecosystem functioning, bivalve, *Corbicula fluminea*, freshwater mussel, functional trait, invasive species, life history theory, species–area relationship, unionid

INTRODUCTION

The species–area relationship (SAR) and biodiversity–ecosystem functioning (BEF) theory seek to explain how biodiversity is distributed, and how biodiversity contributes to ecological function, respectively. The SAR predicts that species richness increases with habitat area due to increased habitat heterogeneity and population size (Connor & McCoy, 1979; MacArthur & Wilson, 1967; Williams, 1964). BEF relationships indicate that ecosystem functions, such as matter and energy stocks and fluxes, increase with species richness due to positive species interactions (complementarity effects) or the numerical dominance of species that make strong contributions to ecosystem function (selection effects) (Hooper et al., 2005; Loreau et al., 2001). Ecosystem function might therefore be expected to increase proportionally with richness as habitat area increases. However, BEF research originated from field and mesocosm experiments where assemblage composition and environmental conditions are controlled and species richness effects can be isolated (Cardinale et al., 2002; Loreau et al., 2001). In natural, unmanipulated assemblages where only observational data are available, ecosystem function may be more strongly associated with the abundance or density of an assemblage than with species richness (Genung et al., 2020; van der Plas, 2019; Winfree et al., 2015). Therefore, assemblage abundance or density must be accounted for statistically when testing for the presence of BEF relationships using observational data, which can complicate the interpretation of BEF relationships in natural assemblages. Further, the contributions of natural assemblages to ecosystem function are not only determined by density and species richness but also by the functional traits of the constituent species.

The relative contribution of a given species to ecosystem function is determined by a combination of the species' functional effect traits (effects on ecosystem function) and functional response traits (responses to environmental variation) (Suding et al., 2008). Many traits can be considered either response or effect traits—or both simultaneously—depending on the paradigm through which they are viewed. The distinction is made by considering the intent of the study or analysis being conducted. For example, effect traits typically include nutrient cycling and storage, biomass allocation, and production, as these traits are easily conceptualized as altering the flow of matter and energy through ecosystems; on the other hand, response traits are often related to life history, such as fecundity and generation time, because they place clear limitations on when and where organisms occur (Díaz et al., 2013; Suding et al., 2008). This distinction is purely conceptual, as traits that alter the flow of matter and energy also vary with environmental conditions, and life history traits also help determine an organism's impacts on ecosystem function. Here, we use the traditional paradigm that effect traits are related to matter and energy flow, and response traits are related to life history. Regardless of how these traits are conceptualized, the relationship between response and effect traits should dictate how assemblage composition changes with environmental context and how such compositional changes impact ecosystem function (Streit & Bellwood, 2022; Suding et al., 2008).

Stream ecosystems are excellent models for studying SARs and BEF relationships, as well as for functional trait-based analyses. First, stream assemblages often show clear SARs where species richness increases along a longitudinal gradient in available habitat (Angermeier & Schlosser, 1989; Bronmark et al., 1984; McGarvey & Ward, 2008; Watters, 1992). Habitat area in streams increases longitudinally because ecosystem size increases exponentially with the drainage area contributing to a given point along the length of the river (Sabo et al., 2010). In this way, drainage area can be assumed to be a monotonic proxy for stream habitat area and can be used to test for evidence of SARs. Streams are also useful models for identifying BEF relationships (Lecerf & Richardson, 2010). To test for BEF relationships, it is necessary to define spatially explicit ecosystem boundaries within which both species richness and ecosystem functions can be quantified. It is intuitive to assign boundaries to streams at the landscape scale based on drainage boundaries and at the ecosystem scale based on sequential mesohabitat units and the land–water interface (Minshall, 1988). Finally, stream ecology is rich with tests of trait-based theories and hypotheses because streams have well-characterized environmental gradients (Junk et al., 1989; Townsend & Hildrew, 1994; Vannote et al., 1980). For example, species with traits that confer resilience to disturbance are expected to be dominant in upstream assemblages, while downstream assemblages with greater habitat diversity and stability should contain species with a broader range of traits, or that are specifically adapted to more stable conditions (Heino et al., 2013; Pease et al., 2012; Townsend & Hildrew, 1994). Here, we aim to use data on ecosystem function and assemblage composition in streams to test predictions derived from all three of the fundamental ecological concepts outlined above: SAR and BEF theories, and functional trait analysis.

Secondary production is a fundamental measure of ecosystem function that reflects the flow of energy and matter through consumer assemblages (Benke & Huryn, 2010). At the species level, it is also a functional effect trait that reflects the relative contributions of a given species or group of species to ecosystem energy flow. As such, secondary production can address questions about the nature of BEF relationships and the interplay between response and effect traits (Benke & Huryn, 2010). Many BEF studies document the relationships between species richness and primary production, but few examine how secondary production is related to richness (van der Plas, 2019). BEF relationships for secondary production have been examined in marine ecosystems for fishes, corals, and benthic invertebrate assemblages (Brandl et al., 2019; Clare et al., 2022; Dolbeth et al., 2015). Similar research in freshwater ecosystems has focused primarily on stream-dwelling insect assemblages (Scholl et al., 2023; Statzner & Lévêque, 2007; Statzner & Resh, 1993) because their short life spans are amenable to traditional secondary production methods and published length–mass relationships are available (Benke et al., 1999; Dolbeth et al., 2012).

Freshwater mussels (order Unionida) are globally imperiled (Böhm et al., 2021; Strayer & Dudgeon, 2010), highlighting the need to understand their contributions to ecosystem function and patterns in mussel biodiversity. Mussels are filter-feeding bivalves that often dominate the benthic biomass of streams where they can be important in ecosystem function (Atkinson et al., 2013, 2018; Atkinson & Vaughn, 2015; Strayer et al., 1994). In addition, mussel assemblages often show a strong longitudinal SAR with increasing stream size (Haag, 2012; Haag & Warren, 1998; Ortmann, 1913; Watters, 1992). BEF relationships have also been documented in mussel assemblages at various scales for functions such as aquatic-to-terrestrial resource subsidies, primary production, and nutrient recycling (Allen et al., 2012; Hopper et al., 2023; Vaughn, 2010; Vaughn et al., 2007). A similar relationship may exist between mussel species richness and secondary production due to positive species interactions that promote the filtration or assimilation of suspended particles from the water column. For example, food resource partitioning among mussel species becomes more specialized and the breadth of food resources used by the assemblage as a whole increases with richness (Sánchez González et al., 2023), which may consequently increase secondary production if species take advantage of previously unexploited resources. Species richness is also strongly linked to abundance in mussel assemblages (Bucholz et al., 2023). Dense, species-rich mussel aggregations create skimming near-bed flows that increase larval settlement and potentially filter-feeding efficiency (Irmscher & Vaughn, 2018; Quinn & Ackerman, 2014; Sansom et al., 2020, 2022), which in turn should increase assemblage production. However, BEF relationships for secondary production have rarely been examined for mussels because their long life spans necessitate modified approaches for estimating production (Ollard & Aldridge, 2022), and length–mass equations were unavailable for most species until recently (Atkinson et al., 2020). The availability of methods for estimating mussel biomass and production, coupled with their important ecosystem role and strong SARs, make mussel assemblages ideal systems for evaluating BEF relationships for secondary production in streams.

Other features of mussel assemblages make them ideal for evaluating how species' functional traits mediate BEF relationships. In addition to richness, mussel assemblage composition changes predictably from upstream to downstream based on the functional response traits of the constituent species. Mussel life history diversity can be represented by a trilateral continuum between three categorical endpoints, which represent distinct life history strategies: equilibrium, opportunistic, and periodic strategists (Haag, 2012). Equilibrium strategists have long life spans, late maturity and low fecundity, and they dominate stable environments that are typical of mid-sized and large streams. Opportunistic strategists have short life spans, early maturity, and high fecundity, and they dominate unstable or frequently disturbed habitats, such as headwater streams. Periodic strategists have intermediate life span and age at maturity, low fecundity, and small body size, and they dominate habitats with predictable large-scale environmental disturbance events (e.g., drought and flood cycles in small to mid-sized streams). While the variables underlying the life history strategy framework are continuous in nature, species are grouped according to which the three life history strategy endpoints (equilibrium, periodic, opportunistic) they are closest to, based on an ordination of the underlying variables (Haag, 2012). As such, some species do not fall neatly into the prescribed categories. For example, the invasive clam *Corbicula fluminea* (Order Venerida; hereafter *Corbicula*) often cohabits the stream benthic zone alongside native mussels (Crespo et al., 2015; Kelley et al., 2022). *Corbicula* has early maturity and high fecundity that are characteristic of opportunistic strategists, but small body size that is characteristic of periodic strategists (Sousa, Nogueira, et al., 2008). However, spatial patterns in the life history composition of mussel assemblages are evident at large scales. As each life history strategy increases or decreases in relative abundance along an upstream-to-downstream gradient, there may be corresponding changes in each strategy's contributions to assemblage production. These consistent patterns of assemblage succession provide the motivation for hypotheses about how species' traits mediate BEF relationships.

We examined how the magnitude of biomass and secondary production were related to mussel species richness along a gradient of increasing stream size. We also examined how changes in mussel assemblage composition related to life history strategies mediate biomass and production along the stream size gradient. We tested the following predictions: P_1—species richness increases with increasing drainage area due to increases in stream size and available habitat area; P_2—assemblage biomass and secondary production increase with both mussel species richness and density; P_3—opportunistic and periodic life history strategists contribute disproportionately higher biomass and secondary production at upstream sites, with a shift toward higher biomass and production from equilibrium strategists farther downstream.

MATERIALS AND METHODS

Study sites and mussel surveys

We studied mussel assemblages along a stream size gradient in the Sipsey River (drainage area = 2044 km^2) and Lubbub Creek (drainage area = 860 km^2), both tributaries to the Tombigbee River in western Alabama, USA. Both streams are unregulated, except for the lower 9 km of the Sipsey River (beyond our study area), which was impounded in 1976 by Howell Heflin Lock and Dam on the Tennessee–Tombigbee waterway. The watersheds of both streams are largely forested, including extensive floodplain wetlands, and the streams have low background nutrient concentrations (Atkinson et al., 2019). Free-flowing sections of both streams support most of their historical mussel species richness (Haag & Warren, 2010; McCullagh et al., 2002).

We surveyed mussel assemblages at eight sites (40–80 m in length) in the Sipsey River and one site in Lubbub Creek once each from 2016 to 2022 (similar as in Atkinson & Forshay, 2022; see Figure 1). We subdivided each site into 20-m segments along the length of the river. Within each segment, we randomly placed three transects across the width of the river and sampled a 0.25-m^2 quadrat every 2.5 m along each transect. We excavated the substrate within each quadrat to ~15 cm, placed the material in a mesh bag, and sorted the material using a series of three sieves (smallest mesh size = 2.5 mm). We identified, counted, and measured the length (in millimeters) of the longest axis of each mussel, and then returned them to the stream.

Secondary production and biomass

For each individual encountered in surveys, we estimated biomass based on shell length using published length–mass equations (Atkinson et al., 2020). We used these equations to estimate the dry mass (DM) and ash-free dry mass (AFDM) of tissues and DM of shells. We also estimated the AFDM of 5–10 shells per species by drying all shells to a constant weight, and then ashing them at 500°C for at least 4 h. For species without available shells, we estimated AFDM from the mean AFDM:DM ratio across all species with direct measurements. We expressed biomass as tissue AFDM + shell AFDM.

We estimated production first by estimating the age of each individual at the time of collection using a form of the von Bertalanffy growth function (VBGF) to solve for age based on length:

$$\mathrm{Age}_t = \frac{LN\frac{L_\infty - l_t}{L_\infty - t_0}}{-K}, \tag{1}$$

where L_∞ is asymptotic size, l_t is the length at the time of sampling, t_0 is the theoretical age when size is zero, and K is the growth coefficient. This form of the VBGF can yield highly inaccurate estimates of absolute age for older, larger individuals in the upper 50% of the population length range, but it accurately characterizes changes in size over time because variability in year-to-year growth is negligible as individuals approach L_∞ (Haag, 2009). We used published VBGF parameter values for each species, or if no previously published parameters were available ($N = 2$ species), we used values from closely related species (Haag & Rypel, 2011). We then estimated the length of each individual in the previous year using a standard form of the VBGF:

$$L_{t-1} = \left(2.7183^K \times l_t\right) + L_\infty\left(1 - 2.7183^K\right). \tag{2}$$

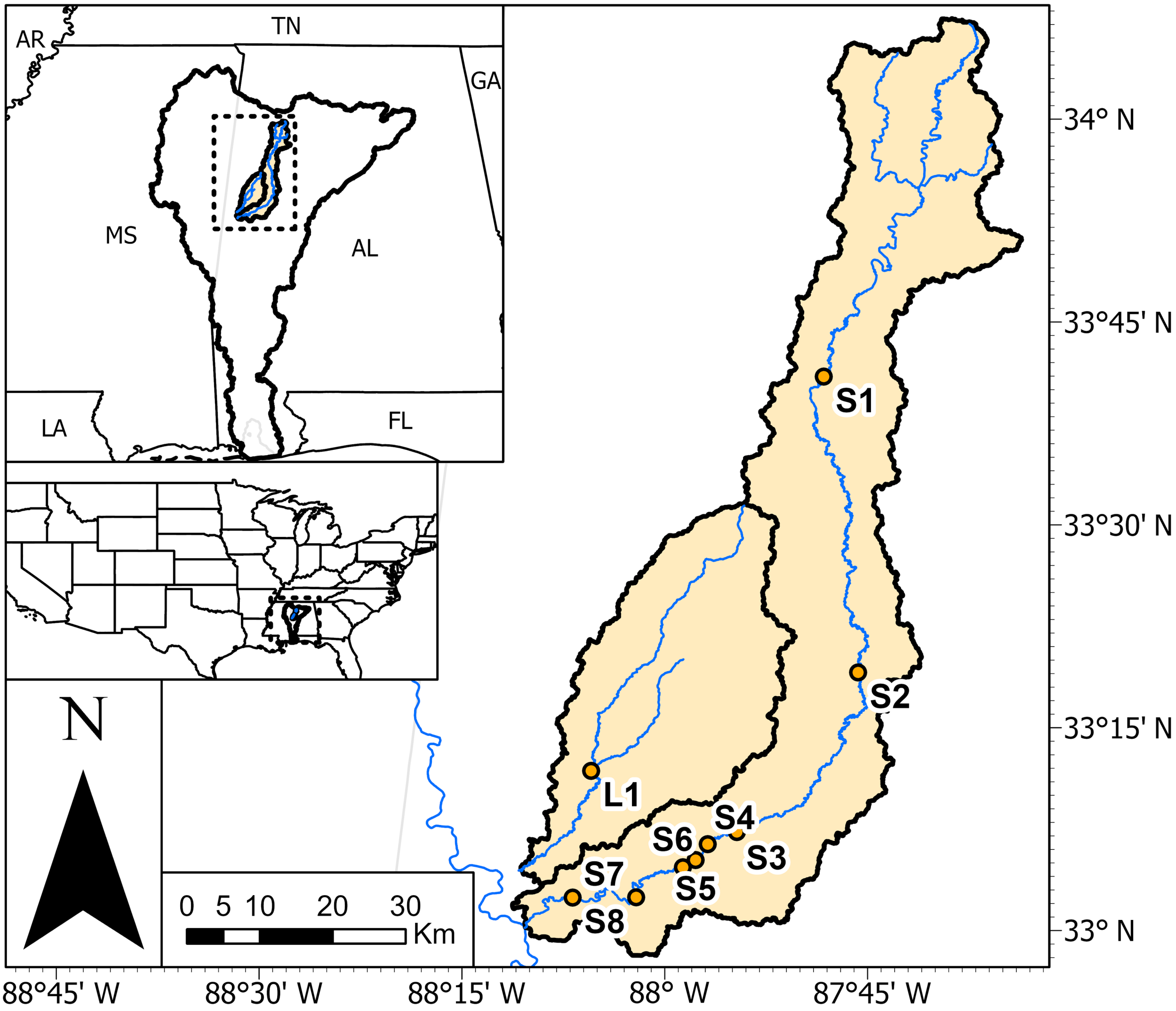

FIGURE 1 Map indicating the study sites in the Sipsey–Lubbub system (beige shaded watershed boundaries) within the Mobile–Tombigbee basin (unshaded watershed boundary). The large inset shows study region (dashed box) within Alabama, USA. The small inset shows the location of the study area (dashed box) within the continental United States.

We estimated biomass based on length at time t and $t-1$, and we estimated individual growth over the year prior to the survey as:

$$\text{Biomass}_t - \text{Biomass}_{t-1}. \tag{3}$$

We define secondary production as the sum of all individual growth accrued across the community over the year preceding sampling (tissue AFDM + shell AFDM, in grams per year). To estimate areal biomass (in grams per square meter) and secondary production (in grams per year per square meter) for each mussel assemblage, we divided the sum of all individual biomass and growth values estimated for all mussels at the site by the area sampled. Hereafter, the terms "biomass" and "production" refer explicitly to these assemblage-level areal calculations. A limitation of this method is that it does not account for production by individuals that died within the year preceding sampling, which could underestimate production in populations with left-skewed age structures. However, healthy mussel populations such as those in the Sipsey River tend to have strongly right-skewed age structures, with many younger individuals (Haag, 2012). Further, the most numerically dominant species in the Sipsey tend to have high adult survival (73%–96%) (Haag, 2012; Haag & Warren, 2010). As such, we treat the percentage of production lost to mortality in our study as negligible. That said, the production estimates we present are likely conservative.

Data analysis

To test for a SAR, we calculated the drainage area upstream of each site as a proxy for stream size, and thus available habitat area for mussels, using the

"Delineate Basin" tool in the USGS StreamStats v4.13.0 web-based GIS application (U.S. Geological Survey, 2019). We then used ordinary least squares (OLS) regression to test whether species richness was related to drainage area across sites. We tested three SAR models: an untransformed linear model, a semi-log exponential function (log-transformed drainage area), and a log–log power function (Connor & McCoy, 1979). We also used OLS regression to test whether drainage area was related to mussel density.

For BEF relationships, we tested whether biomass and secondary production were related to species richness, with each analysis including mussel density as a covariate. Preliminary bivariate regression analyses indicated that the log–log relationships of richness and density with both biomass and production provided the best fit to the data, so we used this form in subsequent analyses (Appendix S1: Tables S1 and S2). We used two separate multiple linear regression models to test the relationships of both biomass and production as functions of richness, density, and their interaction. The richness × density interaction term did not improve model fit for biomass or production, so we dropped the interaction term in our final models. We used variance inflation factors to test whether richness and density violated the multiple regression assumption of collinearity (package *car*). Variance inflation factors for richness and density in both models were low (<2), so we retained both log species richness and log mussel density as explanatory variables in each model.

We used a series of bivariate OLS regressions to test whether the contributions of each mussel life history strategy to total assemblage biomass and secondary production changed with longitudinal position in the river. We also tested whether the relative abundance of each life history strategy changed longitudinally because the life history strategy framework is primarily formulated to predict changes in abundance. We classified all species in our dataset into one of the three life history strategies (opportunistic, periodic, or equilibrium) following Haag (2012; Table 1). We calculated the percentage of total assemblage biomass or production contributed by each species at each site, and we calculated the contributions of each strategy by summing the contributions of individual species within each strategy. Similarly, we calculated relative abundance as the percentage of individuals within the mussel assemblage belonging to each life history strategy. We evaluated separate regression models for each strategy. The explanatory variable for each model was drainage area, and the response variable was either the percentage of biomass, production, or abundance (arcsine transformed) contributed by that strategy. Our assemblage dataset also included large numbers of the invasive clam *Corbicula*. We analyzed the contribution of *Corbicula* to biomass and production separately from the other three life history strategies because *Corbicula* represents an extreme expression of the opportunistic strategy (Haag, 2012). Shapiro–Wilk tests ($p > 0.05$ for all models) and studentized Breusch–Pagan tests ($p > 0.05$ for all models; package *lmtest*) on regression residuals verified that the assumptions of normality and homoscedasticity were met for all models.

TABLE 1 Life history strategy classifications for freshwater mussel species included in the study.

Species	Life history strategy
Amblema plicata	Equilibrium
Corbicula fluminea	N/A
Elliptio arca	Periodic
Elliptio crassidens	Periodic
Ellipsaria lineolata	Periodic
Fusconaia cerina	Equilibrium
Hamiota perovalis	Periodic
Leaunio lienosus	Periodic
Lampsilis ornata	Opportunistic
Lampsilis straminea	Periodic
Lampsilis teres	Opportunistic
Medionidus acutissimus	Periodic
Megalonaias nervosa	Equilibrium
Obovaria arkansasensis	Periodic
Obliquaria reflexa	Periodic
Obovaria unicolor	Periodic
Pleurobema decisum	Equilibrium
Potamilus fragilis	Opportunistic
Potamilus inflatus	Opportunistic
Pustulosa kieneriana	Equilibrium
Pleurobema perovatum	Equilibrium
Potamilus purpuratus	Opportunistic
Quadrula quadrula	Equilibrium
Quadrula verrucosa	Equilibrium
Reginaia ebenus	Equilibrium
Truncilla donaciformes	Opportunistic
Truncilla truncata	Opportunistic
Villosa vibex	Periodic

Post hoc analysis

Our life history analysis suggested that *Corbicula* may strongly influence longitudinal patterns in mussel assemblage biomass and production. To explore the role that the presence of this invasive species may play in mediating the patterns of interest, we conducted a post hoc analysis where we repeated the same analyses that we used to test for the SAR, BEF relationships, and patterns among life history strategies, but we subset the dataset to include only native unionid mussels and exclude *Corbicula*. We used the same combinations of variables and data transformations described above. However, when we included mussel density as a covariate in the models constructed to test whether biomass and secondary production were related to species richness, variance inflation factors were very high (>7), precluding us from including both richness and density in the same model as we did in the full dataset. Thus, we used bivariate OLS regressions to test for biomass–richness, productivity–richness, biomass–density, and productivity–density relationships separately. We performed all calculations and analyses in R v4.2.3 unless otherwise specified (R Core Team, 2023).

RESULTS

Species richness ranged from 6 to 23 across sites in the Sipsey–Lubbub system, and total mussel density ranged from 5 to 40 individuals m^{-2}. Species richness was the lowest in Lubbub Creek (L1; $S = 10$) and the most upstream Sipsey site (S1; $S = 6$), and the highest at the most downstream Sipsey site (S8; $S = 23$). The linear relationship of species richness with drainage area explained more variation than the semi-log and log–log relationships ($F_{1,7} = 25.7$, $p = 0.001$, $R^2 = 0.79$; Appendix S1: Table S3; Figure 2a). Mussel density was not related to drainage area ($F_{1,7} = 3.44$, $p = 0.106$; Figure 2b). When we excluded *Corbicula*, native mussel richness ($F_{1,7} = 25.7$, $p = 0.001$, $R^2 = 0.79$; Appendix S1: Figure S1) and density increased with drainage area ($F_{1,7} = 6.2$, $p = 0.041$, $R^2 = 0.47$; Figure 2c).

Biomass ranged from 3.0 to 38.5 g m^{-2} across sites. Biomass was related to species richness ($t_6 = 3.9$, $p = 0.008$) but was not related to mussel density ($t_6 = 0.8$, $p = 0.458$), and the model explained much of the variation in biomass across sites ($F_{2,6} = 15.6$, $p = 0.004$, $R^2_{\text{adj}} = 0.79$; Figure 3a). When we excluded *Corbicula*, native mussel biomass was positively related to both species richness ($F_{1,7} = 33.8$, $p = 0.001$, $R^2 = 0.83$; Figure 3b) and density ($F_{1,7} = 34.3$, $p = 0.001$, $R^2 = 0.83$; Appendix S1: Figure S2a).

Secondary production ranged from 0.2 to 4.7 g m^{-2} year^{-1} across sites. Production was positively related to both species richness ($t_6 = 5.9$, $p = 0.001$) and mussel density ($t_6 = 5.7$, $p = 0.001$), and the model explained a high percentage of the variation in production across sites ($F_{2,6} = 85.5$, $p < 0.001$, $R^2_{\text{adj}} = 0.95$; Figure 3c). When we excluded *Corbicula*, native mussel production was also positively related to both species richness ($F_{1,7} = 34.6$, $p = 0.001$, $R^2 = 0.83$; Figure 3d) and density ($F_{1,7} = 534.2$, $p < 0.001$, $R^2 = 0.99$; Appendix S1: Figure S2b).

Equilibrium strategists contributed a high percentage of biomass and secondary production at all sites (biomass, 70%–87%; production, 59%–91%), but neither was related to drainage area (biomass, $F_{1,7} = 1.3$, $p = 0.287$; production, $F_{1,7} = 1.9$, $p = 0.207$; Figure 4a,b). However, the relative abundance of equilibrium strategists was more variable (9%–61%) and did increase with drainage area ($F_{1,7} = 16.4$, $p = 0.005$, $R^2 = 0.70$; Figure 4c). Periodic and opportunistic strategists each contributed a lower percentage of biomass and production (periodic: biomass, 0%–16%, production, 0%–16%; opportunistic: biomass, 3%–26%, production, 0%–12%), and had lower relative abundances (periodic: 0%–19%, opportunistic: 0%–7%). The proportional contributions of both biomass and production by periodic strategists were positively related to drainage area (biomass: $F_{1,7} = 8.22$, $p = 0.024$, $R^2 = 0.54$; production: $F_{1,7} = 6.1$, $p = 0.043$, $R^2 = 0.47$; Figure 4d,e), as was relative the abundance of periodic strategists ($F_{1,7} = 9.0$, $p = 0.020$, $R^2 = 0.56$; Figure 4f). There was no relationship between proportional biomass or production and drainage area for opportunistic species, (biomass: $F_{1,7} = 0.0$, $p = 0.828$; production: $F_{1,7} = 2.3$, $p = 0.174$; Figure 4g,h), but the relative abundance of opportunistic species did increase slightly from upstream to downstream ($F_{1,7} = 9.1$, $p = 0.020$, $R^2 = 0.56$; Figure 4i). *Corbicula* contributed a low percentage of biomass at all sites (0%–5%), but proportional biomass was negatively related to drainage area ($F_{1,7} = 19.1$, $p = 0.003$, $R^2 = 0.73$; Figure 4j). The proportional contribution of *Corbicula* to production varied widely across sites (1%–41%), and proportional production declined sharply with increasing drainage area ($F_{1,7} = 10.5$, $p = 0.014$, $R^2 = 0.60$; Figure 4k). *Corbicula* relative abundance ranged from 17% to 90%, and showed a similar decline with increasing drainage area ($F_{1,7} = 18.3$, $p = 0.004$, $R^2 = 0.72$; Figure 4l). When we excluded *Corbicula*, proportional biomass increased with drainage area for periodic strategists ($F_{1,7} = 7.8$, $p = 0.027$, $R^2 = 0.53$), but otherwise there were no significant changes in proportional biomass, production, or relative abundance with increasing drainage area for any of the three life history strategies ($p > 0.05$ for all models; Appendix S1: Figure S3). Species-level density, biomass, and production values for all study sites can be found in Appendix S1: Table S4.

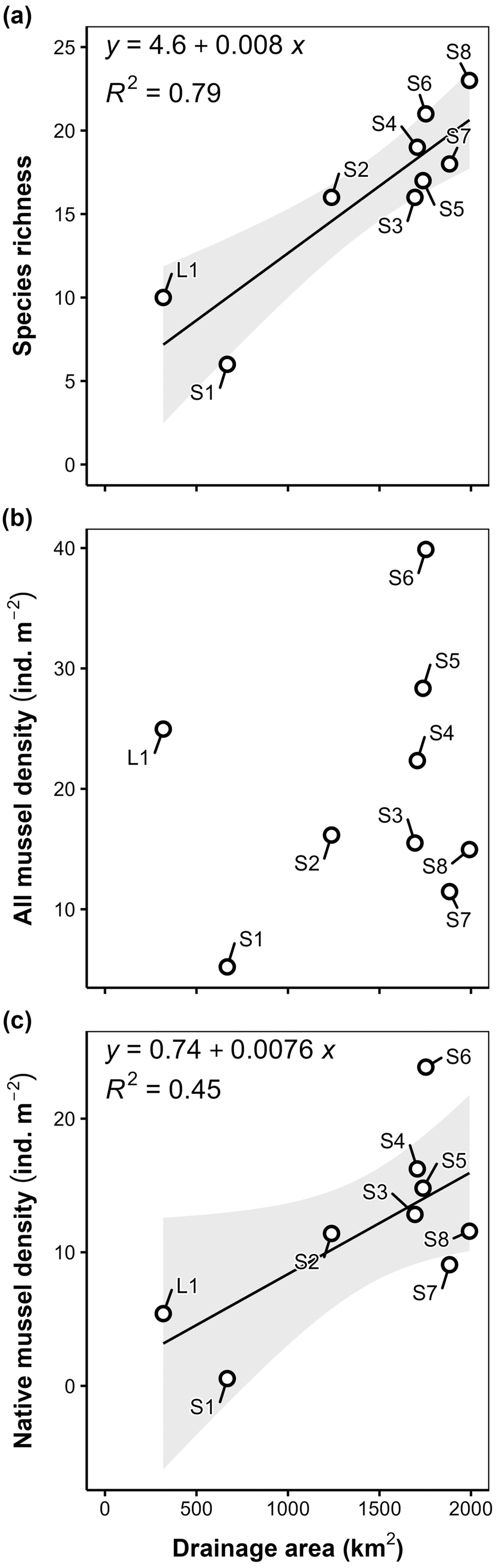

FIGURE 2 (a) Species richness of mussel assemblages in the Sipsey–Lubbub system increased approximately linearly with increasing drainage area. (b) Variation in mussel assemblage density did not vary in association with drainage area when all mussels were considered. (c) When only native unionid mussels were considered, assemblage density increased with drainage area. ind, individuals.

DISCUSSION

The species richness of mussel assemblages in the Sipsey–Lubbub system increased with drainage area as predicted (P_1). This is consistent with prior findings showing that mussels and other stream animal assemblages display SARs across a range of spatial scales (Angermeier & Schlosser, 1989; Bronmark et al., 1984; Haag, 2012; Haag & Warren, 1998; McGarvey & Ward, 2008; Ortmann, 1913; Sepkoski & Rex, 1974; Watters, 1992). Determining the specific mechanisms underlying the positive SAR that we observed across our study sites was beyond the scope of this study, but the SAR could stem from variation in either habitat diversity or local immigration and extinction processes (Connor & McCoy, 1979). Sampling effects, which occur when species richness increases solely due to the amount of habitat that is sampled, should be negligible in our study because sampling was scaled to the size of each site. Sepkoski and Rex (1974) attributed a regional SAR for mussel assemblages in the eastern United States to a decreasing probability of local species extinctions with increasing stream size. This explanation is also plausible for our findings, as the sites where species richness was lowest (L1, S1) are also the most isolated from potential source populations with higher densities and species richness from which immigrants might arrive (Connor & McCoy, 1979). For other freshwater assemblages, habitat diversity has been invoked as a probable driver of the SAR (Angermeier & Schlosser, 1989; Bronmark et al., 1984). Habitat diversity may play a role in generating SARs in mussel assemblages, but it is difficult to speculate on this role because the knowledge of mussels' habitat needs remains limited (Haag, 2012; Newton et al., 2008; Sansom et al., 2022). Ultimately, these mechanisms are not mutually exclusive and both habitat and population dynamics likely constrain SARs.

We also found that biomass and secondary production increased with species richness as predicted by BEF theory (P_2). While experimental studies allow the isolation of richness effects from those of assemblage density or environmental conditions, observational studies such as this one must rely on statistical models to attempt to disentangle these co-occurring effects. Both production

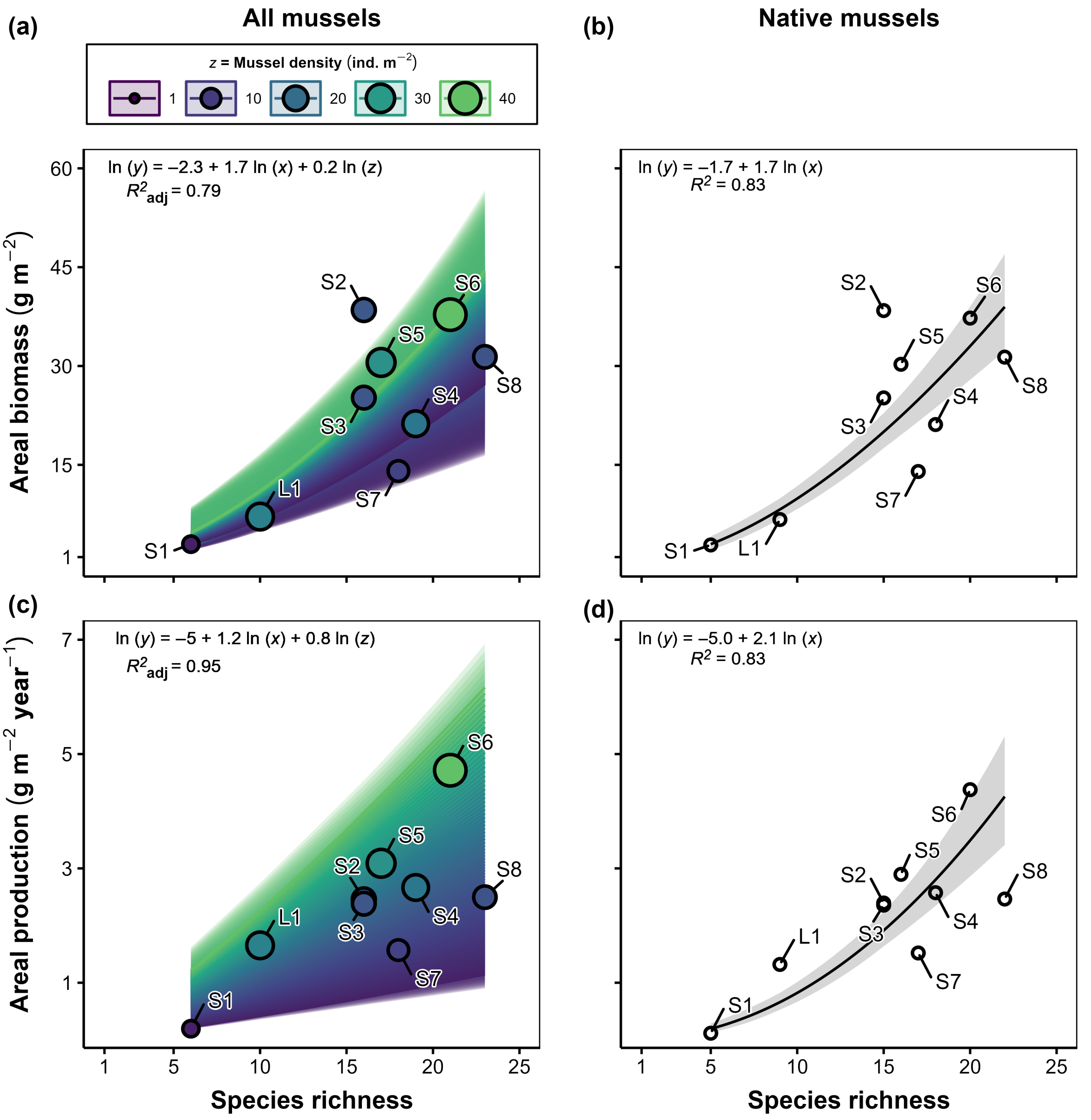

FIGURE 3 (a, b) Biomass and (c, d) secondary production estimated for mussel assemblages in the Sipsey–Lubbub system show positive log–log responses to species richness after accounting for covariation in mussel density. Panels (a) and (c) show the multiple regression relationships in which all mussels are considered. The fill color of the points in the foreground of panels (a) and (c) represent the *observed* mussel densities at each site. The color in the shaded portion of the background in panels (a) and (c) shows a dense field of regression lines modeled over a gradient of *potential* mussel densities (range = 0–40). Panels (b) and (d) show the bivariate regression relationships in which only native unionid mussels are considered and *Corbicula fluminea* is excluded. All axes and equations are back-transformed.

and biomass showed wedge-shaped positive relationships to species richness as mussel density increased, suggesting that production and biomass may not be uniformly high when species richness is high. Rather, species richness may increase the potential biomass and production of an assemblage, while other factors such as assemblage density may help to determine realized biomass and production. Our regression models indicated that both species richness and mussel density were positively related to production. However, only species richness was positively related to biomass—mussel density was not. This initially seems paradoxical but can

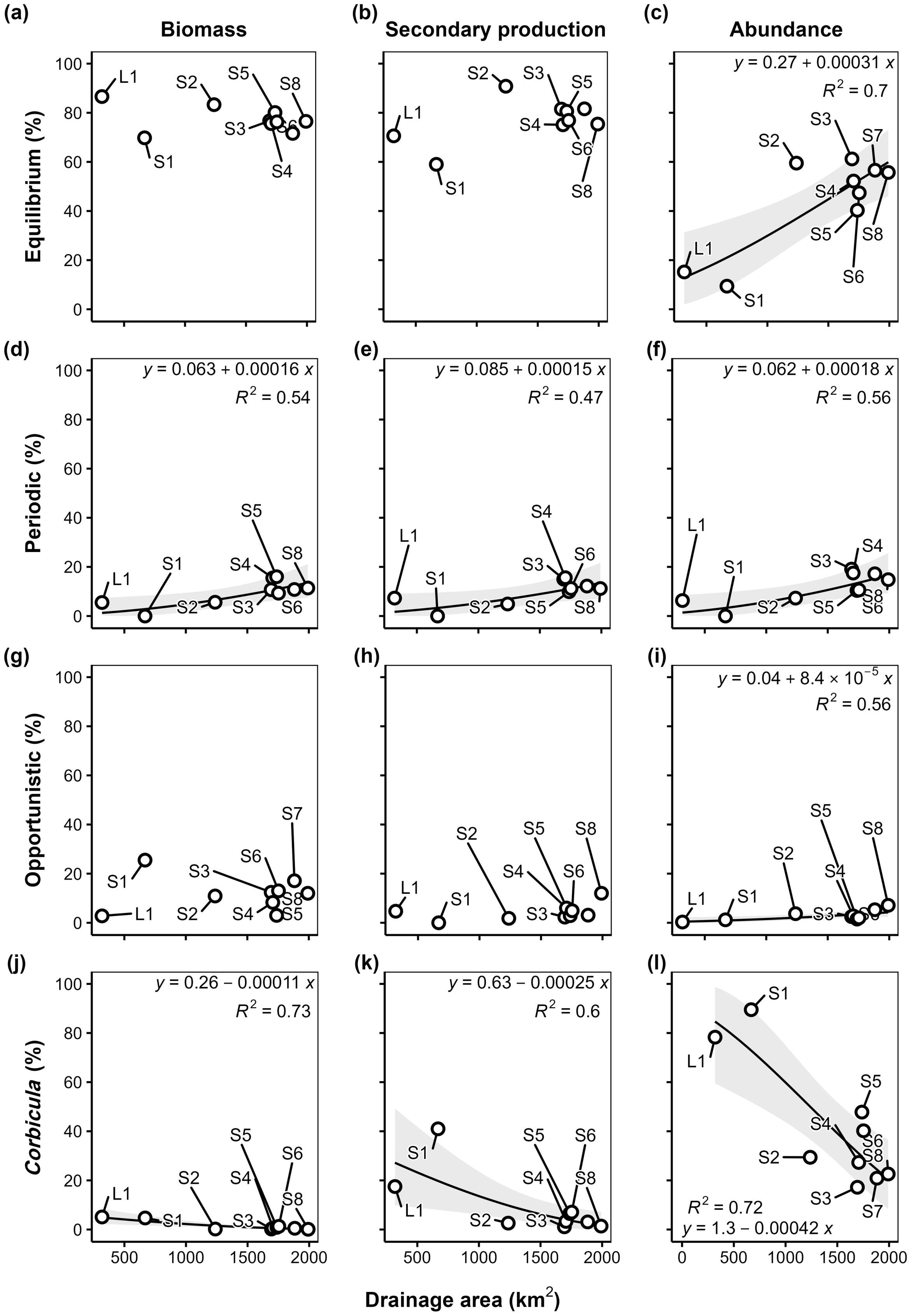

FIGURE 4 Proportional biomass (a, d, g, j), proportional secondary production (b, e, h, k), and relative abundance (c, f, i, l) contributed by different life history strategies and *Corbicula fluminea* to mussel assemblages across sites with varying drainage area in the Sipsey–Lubbub system. The *y* term in all equations represents the arcsine transformed proportion value from the back-transformed *y* axis.

be explained by variation in body size among the most abundant taxa across sites. Longitudinal changes in the abundance and density of *Corbicula* are likely responsible for the fact that mussel density was related to production, but not to biomass; our post hoc analysis using only native unionid mussel species suggested a strong positive relationship between density and biomass. *Corbicula* are smaller than most adult unionid mussels and have rapid growth with short tissue turnover times and high production-to-biomass (P:B) ratios that are typical of small-bodied organisms (Huryn & Benke, 2007; Sousa, Antunes, et al., 2008; Sousa, Nogueira, et al., 2008). As a result, when *Corbicula* density increases, assemblage production and density increase at a faster rate than biomass, which decouples the positive relationship of assemblage density from biomass but not from production.

Production by invasive consumers such as *Corbicula* can be orders of magnitude higher than the values we report here, with profound impacts on ecosystem functioning (Benke & Huryn, 2010; Hall et al., 2003). Notably, mean *Corbicula* P:B ratio and turnover times in our study (0.701 year^{-1} and 521 days, respectively) were considerably lower than the estimates reported elsewhere in the literature (2.89–5.00 year^{-1} and 73–126 days) (McMahon, 2002; Sousa, Nogueira, et al., 2008). *Corbicula* densities are lower in the Sipsey than several other southeastern US rivers (Kelley et al., 2022), and it is possible that they may also grow more slowly in the Sipsey River than elsewhere, especially if competition for resources with native unionid mussels constrains *Corbicula* growth. However, some of the disparity between our estimate and others may derive from the methods used to calculate secondary production. *Corbicula* can spawn multiple times per year, so other studies have used repeated sampling over the course of the year and cohort-based calculations to quantify *Corbicula* production (Dolbeth et al., 2012; Sousa, Antunes, et al., 2008; Sousa, Nogueira, et al., 2008). Unionid mussel turnover times are estimated to be much longer than a year (1790–2849 days), and they typically only spawn once per year (McMahon, 2002; Ollard & Aldridge, 2022; Sousa, Antunes, et al., 2008), so we used an annual sampling scheme to characterize their production. P:B cannot exceed 1 using an annual sampling scheme, so *Corbicula* production would be underestimated if they produced multiple cohorts each year. However, a post hoc inspection of the size structure of *Corbicula* populations at our study sites suggested that the presence of two cohorts was unlikely (Appendix S1: Figure S4). If we are underestimating *Corbicula* production, then the species likely played an even more important role than is apparent from the data reported here in driving assemblage production. Estimating production by this invasive species was not the primary impetus for the present study but is seemingly an important research avenue moving forward.

Although it is difficult to disentangle the influences of species richness and mussel density due to the strong correlations between different components of diversity in natural assemblages, we hypothesize that the observed increases in mussel biomass and production with species richness may be related to positive species interactions such as niche partitioning and facilitation (Loreau & Hector, 2001). Such positive interactions are known to occur in mussel assemblages, and the strength of these positive interactions may increase with richness (Allen et al., 2012; Morales et al., 2006; Quinn & Ackerman, 2014; Sánchez González et al., 2023; Sansom et al., 2022; Vaughn et al., 2007). However, verifying the mechanisms behind BEF relationships requires manipulative experimentation where ecosystem function is quantified across single-species and multispecies treatments (e.g., Cardinale et al., 2002). The slow-growing nature of most mussel species makes experimental testing of BEF relationships for mussel biomass and production time-consuming, but a properly designed multiyear experiment could validate whether richness and density are independent drivers of mussel biomass and production. Even without the ability to firmly assign a mechanism to the BEF relationships of production and biomass with species richness in mussel assemblages, the observational data we have presented support the relevance of species richness to ecosystem matter and energy flows—although this relationship is surely mediated by mussel density as well.

Our prediction that opportunistic and periodic life history strategists would contribute proportionally more biomass and secondary production at upstream sites, with a shift toward more biomass and production from equilibrium strategists farther downstream, was not supported (P_3). We detected increases in periodic strategist biomass and production, and in the relative abundance of all three life history strategies increased from upstream to downstream, but these longitudinal patterns were only evident when *Corbicula* was included in the life history analysis. Life history strategies explained very little longitudinal variation in biomass, production, and abundance when only native unionid mussels were analyzed. Thus, the apparent increases in periodic strategist biomass and production, and in equilibrium, periodic, and opportunistic strategist abundance, were actually artifacts of a longitudinal decrease in *Corbicula* biomass, production, and abundance.

Unstable conditions at upstream sites should be conducive to taxa with traits that facilitate recolonization after disturbance (Pease et al., 2012; Randklev et al., 2019; Townsend & Hildrew, 1994). High *Corbicula* densities at upstream sites might therefore be explained by the *Corbicula* life cycle, which shares some traits with the opportunistic strategy, including high reproductive rates and rapid growth—traits that also make it a prodigious invader of freshwater ecosystems worldwide (Crespo et al., 2015; Sousa, Antunes, et al., 2008; Sousa, Nogueira, et al., 2008). *Corbicula* may also compete directly with native mussels for food and impair juvenile mussel growth (Ferreira-Rodríguez, Fandiño, et al., 2018; Ferreira-Rodríguez, Sousa, et al., 2018; Haag et al., 2021). However, it remains unclear whether and how negative species interactions with *Corbicula* manifest at the assemblage level, as high *Corbicula* abundance occurs in regions with both declining and stable native mussel populations, across a broad range of stream sizes and environmental conditions (Crespo et al., 2015; Ferreira-Rodríguez et al., 2022; Haag, 2019). Further, the fact that we did not observe any longitudinal change in the biomass, production, or relative abundance of opportunistic, periodic, or equilibrium strategists casts doubt on the explanations above. It seems more likely that the range of stream size that we studied was insufficient to capture enough variation in habitat stability to generate shifts in mussel life history strategy composition (Haag, 2012), as most biomass and production came from equilibrium and periodic strategists across all sites. By broadening the gradient of stream sizes included in our life history analysis, we might be able to detect clearer links between life history traits and secondary production. What is clear from our life history trait analysis is that an invasive species seems to have effect traits that are associated with patterns of biomass, production, and other key ecosystem functions (e.g., Hopper et al., 2022). This is especially important given that invasive species are a global threat to freshwater assemblages and to biodiversity in general (Reid et al., 2019; Strayer, 2010). Invasive species are therefore likely to become increasingly important in driving ecosystem function.

The results of the present study highlight the generality of the SAR and the importance of assemblage density effects in BEF studies using observational data. Efforts to disentangle the importance of species richness from those of density and abundance in natural assemblages are ongoing and involve a range of mathematical and statistical approaches (Genung et al., 2020; Hopper et al., 2023; van der Plas, 2019; Winfree et al., 2015). We also highlight the need for a more thorough understanding of how the interplay between species' functional response and effect traits strengthen or weaken their impacts on ecosystem function. We saw the important effects of an invasive species on biomass and production, but the life history strategy framework did not help clarify which functional response traits might underlie those effects at the scale of our study. Accurate characterization of the impacts that invasive species have on ecosystem function and the traits that regulate the strength of these impacts should therefore be a priority. This study thus demonstrates the utility of observational field data in understanding fundamental ecological patterns in freshwater animal assemblages, and the need for a sound understanding of how organisms' functional traits regulate their relationships with the environment at different scales.

AUTHOR CONTRIBUTIONS

Jonathan W. Lopez and Carla L. Atkinson conceived the study ideas. Jonathan W. Lopez led the data analysis and wrote the initial draft of the manuscript. Carla L. Atkinson and Garrett W. Hopper led the mussel surveys. Angela K. Burrow and Wendell R. Haag developed the methodology and code for estimating secondary production with input from Carla L. Atkinson. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lopez et al., 2024) are available from Figshare: https://doi.org/10.6084/m9.figshare.24968958.

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SUPPORTING INFORMATION

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

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