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ORIGINAL PAPER

Little clams with big potential: nutrient release by invasive *Corbicula fluminea* can exceed co-occurring freshwater mussel (Unionidae) assemblages

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Abstract Animal-mediated nutrient cycling research tends to emphasize either native or invasive fauna, yet communities comprising both groups are common, and biogeochemical control may shift from native to invasive species, altering local nutrient regimes. In North American rivers, co-occurring native mussels (Unionidae) and the invasive clam, *Corbicula fluminea*, have strong nutrient cycling effects through filter-feeding and bioturbation. When these two groups co-occur, the degree to which their nutrient cycling effects differ remains unclear. We quantified bivalve density, biomass, and nutrient excretion rates at four reaches in each of two rivers once during the same year to test whether differences in density and biomass led to different spatial and temporal nutrient cycling and stoichiometry patterns for co-occurring mussels and *Corbicula*. We hypothesized high densities, coupled with small body size would elevate *Corbicula* population-level nutrient cycling rates above those of less dense assemblages of larger-bodied mussels. *Corbicula* occurred at all mussel beds and their densities generally exceeded mussel densities, but *Corbicula* biomass was consistently lower. High densities and greater mass-specific excretion rates led to *Corbicula* population-level excretion rates that were greater than or equal to mussel aggregate rates at half the reaches. Abiotic conditions limited bivalve nutrient supply relative to ambient concentrations, but their contributions increased during low flows and are likely concentrated at finer spatial scales. Our results suggest spatial variation in invasive and native trait distribution associated with phylogenetic tribes influences the potential for animal-mediated nutrient cycling to shift from native to invasive species control. Overall, our study highlights the need for new management paradigms that account for nutrient cycling by invasive species.

Keywords Body size · Consumer-driven nutrient cycling · Ecosystem function · Filter-feeders · Stoichiometry

Introduction

A primary focus of invasion biology is assessing the impacts of invasive species on ecosystem structure and function (Vitousek 1990; Parker et al. 1999). In particular, invasive animals may alter biogeochemical cycling by sequestering, remineralizing, or translocating nutrients between habitats (Crooks 2002; Atkinson et al. 2017), fundamentally altering ecosystems

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in which native species evolved (Mooney 2010). Ecosystem level impacts of invasive animals have received much attention (Capps and Flecker 2013a; Loss et al. 2013; Subalusky et al. 2021), yet there are still fundamental gaps regarding how turnover from native to invasive species influences processes such as nutrient cycling (Masese et al. 2020; Ricciardi et al. 2021). Directly comparing the possible nutrient cycling effects of invasive and native species may facilitate the development of species-specific management strategies (Pennock et al. 2018; Blanton et al. 2020) or adjustments to holistic management plans (Li et al. 2021).

Freshwater ecosystems are increasingly threatened by species introductions (Dudgeon et al. 2006; Reid et al. 2019). Habitat characteristics, tolerance to a wide range of environmental conditions, and the ability to forage at low trophic positions may favor invader establishment (Kolar and Lodge 2001; Gido and Franssen 2007). Alternatively, species traits (e.g. short life spans, rapid maturation and reproduction) and propagule pressure may also be important factors allowing species to develop invasive potential (Byers 2002; Simberloff 2009). Invasive species feeding at low trophic positions can shift nutrient limitation via differential storage and release of nutrients relative to the native fauna (Capps and Flecker 2013b; Sousa et al. 2014; Hopper et al. 2020). Research comparing nutrient cycling effects of native and invasive species in freshwater systems often concentrates on disparate taxonomic and functional groups (Scott et al. 2012), though many invaders are ecologically similar to the native fauna (Atkinson et al. 2010; Strayer and Malcom 2013). For example, invasive and native bivalve mollusks are all sedentary filter-feeders, with concentrated ecosystem effects in stream benthic habitats (Higgins and Vander Zanden 2010; Vaughn and Hoellein 2018). Similar functional classification may not equal redundancy if native and invasive species process resources differently (Atkinson et al. 2010) or maintain divergent life history strategies that effect population demographics (Hornbach 1992) that govern invader impacts. For instance, most invasive bivalves feed more generally than their native counterparts (Atkinson et al. 2011). This can lead to rapid population increase and control of ecosystem structure and function by invasive bivalves (Higgins and Vander Zanden 2010; Minaudo et al. 2021). For example, invasion by dreissenid mussels (quagga and zebra) has qualitatively altered the responses of the Great Lakes to phosphorus inputs from watersheds, generating the need for a new management paradigm for those ecosystems (Li et al. 2021). Increasing prevalence of invaded bivalve communities globally elevates the need to identify potential consequences associated with turnover of species biomass (Vaughn and Spooner 2006; Bódis et al. 2014; Sousa et al. 2014; Strayer and Malcom 2018; McDowell and Sousa 2019). Therefore, mixed communities of native and invasive bivalves present an opportunity to compare the relative influence of functionally similar native and invasive species on local ecosystem processes.

Freshwater mussels (Family: Unionidae; hereafter mussels) are relatively long lived bivalves, with life spans ranging from 4–50 years and spend that time in dense aggregations called mussel beds that are patchily distributed in streams (Haag 2012). Mussel beds are critical to productivity and biogeochemical cycling in stream (Vaughn and Hakenkamp 2001; Atkinson et al. 2013) and riparian food webs (Lopez et al. 2020). Though all mussels are filter-feeders, various morphological (e.g., body size), behavioral, and physiological traits determine their ecosystem effects (Spooner and Vaughn 2012). For example, thermally sensitive mussels filter water and release greater amounts of ammonium at higher temperatures than thermally tolerant mussels (Vaughn et al. 2004; Spooner and Vaughn 2008). The highly diverse North American unionid mussel fauna (~360 species) is mostly constrained within five distinct phylogenetic tribes (Anodontini, Amblemini, Lampsilini, Pleurobemini, and Quadrulini; Pfeiffer et al. 2019), that govern aspects of their life history and stoichiometric niches (Atkinson et al. 2020a). Therefore, classification of mussels into tribes can be useful in describing broad patterns of functional diversity among mussel beds. Additionally, mussel bed densities and species composition determine aggregate flux and stoichiometry that effect primary producer and detrital based food webs (Atkinson et al. 2013, 2021; Hopper et al. 2021). Mussel ecosystem effects vary seasonally with stream discharge conditions, but are strongest during low flows when mussels filter a greater fraction of the water passing over them and warmer temperatures increase metabolic rates (Vaughn et al. 2004; Spooner and Vaughn 2008). Moreover, mussels are among the most imperiled animals globally (Ferreira-Rodríguez et al. 2019), and are particularly threatened by functionally similar invasive species, such as *Corbicula fluminea* in North America (Ferreira-Rodríguez et al. 2018b; Haag et al. 2021).

Corbicula fluminea (hereafter *Corbicula*) was introduced to North America from temperate and subtropical regions of southeastern Asia in the first half of the twentieth century and is now present on all continents except Antarctica (Crespo et al. 2015). Rapid growth and maturity, short lifespan, high fecundity, and asexual reproduction (Sousa et al. 2008b; Pigneur et al. 2011) coupled with tolerance to multiple-stressors (Sousa et al. 2008a), and human-mediated dispersal (Karatayev et al. 2007) promote its successful establishment. *Corbicula* is an efficient filter-feeder (McDowell and Byers 2019) and their colonization can alter stream benthic communities (Leff et al. 1990; Hakenkamp et al. 2001; Werner and Rothhaupt 2007; Ilarri et al. 2015) and alter mussel habitat and food availability (Darrigran 2002; Ferreira-Rodríguez et al. 2018b; Haag et al. 2021). *Corbicula* can also alter nutrient cycles where they are abundant (Lauritsen and Mozley 1989; Hakenkamp and Palmer 1999) and dense populations of mussels and *Corbicula* frequently co-occur (Vaughn and Spooner 2006; Strayer and Malcom 2013). Quantifying contributions of invasive species biomass to overall nutrient availability is key to understanding the cumulative effects resulting from spatially overlapping invasive and native bivalves.

Functionally similar native and invasive species may process resources differently (Atkinson et al. 2010), leading to altered ecosystem level biogeochemical cycling (Strayer et al. 1999). Because *Corbicula* and mussels exhibit high spatial overlap in stream reaches they can be effectively sampled simultaneously (Vaughn and Spooner 2006; Kelley et al. 2022), providing an opportunity to evaluate how diverse native assemblages and invasive species differ in nutrient cycling rates. The primary goal was to compare the biomass, densities, and subsequent nutrient cycling rates and stoichiometry of diverse assemblages of mussels and co-occurring *Corbicula* populations. We hypothesized that major differences in body size between *Corbicula* and mussels would result in aggregations with different proportional biomass of each group. Specifically, we expected biomass of larger bodied mussels to exceed *Corbicula* biomass, despite lower densities of mussels. We anticipated that allometric scaling of excretion rates would lead to lower per capita but higher mass-specific excretion rates for *Corbicula* compared to mussels (Vanni and McIntyre 2016). Given this allometric relationship, combined with high densities, we expected that *Corbicula* population-level excretion rates would exceed those of mussel assemblages. Last, we expected resource use differences would lead to interspecific differences in excretion N:P among mussel species and *Corbicula* (Atkinson et al. 2010, 2011), resulting in variable aggregate excretion N:P driven by bivalve assemblage structure.

Materials and methods

Study rivers

The Duck River and Cahaba River are located in the southeastern region of North America (Fig. 1). The Duck River is the largest tributary (watershed area 8100 km^2) to the Tennessee River and supports 68 mussel species (Ahlstedt et al. 2017). The Duck River is impounded by two major dams upstream of the reaches in this study and is a major source of drinking water to residents in the watershed. Forests and grasslands are approximately 80% of the land cover, and urban and agriculture land uses make up the rest. (Murphy et al. 2016). The Cahaba River is a large, free-flowing, tributary (watershed area 3009 km^2) to the Alabama River prior to its confluence with the Mobile River with 50 mussel species(Williams et al. 2008). The dominant land use types of the Cahaba watershed are forest, urban development, and range land, which in total account for 87% of the area, with most extensive urban and agricultural development in the upper portions of the Cahaba River (Dosdogru et al. 2020; Preetha et al. 2021). Populations of *Corbicula* have been established since at least 1964 and 1965 in both the Duck and Cahaba River, respectively (Hubricht 1966; Byrne 2015). *Corbicula* is widespread in both rivers, but little work has sought to track population densities, biomass, or subsequent ecosystem effects (but see Kelley et al. 2022).

Quantitative surveys

We surveyed stream reaches encompassing a range of mussel densities and diversity to examine

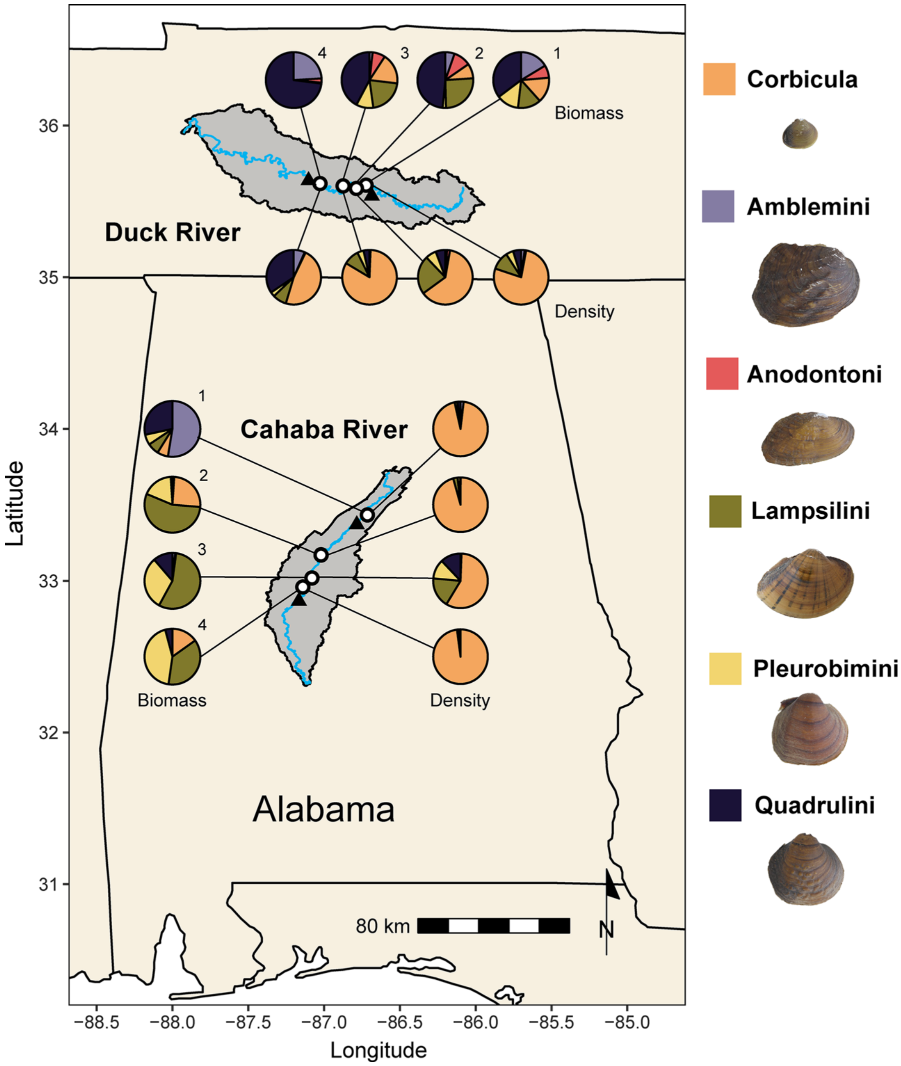

Fig. 1 Map of the study area with focal watersheds highlighted in grey. White points indicate locations of quantitative surveys and excretion measurements. Black triangles indicate USGS gages used to estimate volumetric excretion rates. Pies represent the proportional biomass or density of mussels grouped into phylogenetic tribes and *Corbicula fluminea*. Numbers correspond to site identifiers used in the text

spatial variation in mussel and *Corbicula* distribution (Fig. 1). We quantified *Corbicula* and mussel densities at four reaches in the Duck River and Cahaba River during 2020 by excavating 0.25 m^2 quadrats to 15 cm deep using a random start method (Strayer and Smith 2003). We selected reaches known to have mussels and visually determined the extent of each mussel aggregation by snorkeling. Reach lengths ranged from 40–100 m. We counted and measured all mussels along the anterio-posterior shell axis and identified them to species. We counted all *Corbicula* and measured at least 100 individuals along the anterior–posterior shell axis (mm; L_{max}) to derive size distributions for each reach. Length-mass regressions were used to estimate soft tissue dry mass of mussels (STDM [g]; Atkinson et al. 2020b) and *Corbicula*$\left(STDM = 0.86x\ 10^{-6}x\ L_{max}^{2.98}\right)$. Areal biomass was based on quadrat estimate averages (g·m^{-2}). To account for unmeasured *Corbicula* and estimate their biomass at each reach, we used average lengths from measured individuals for each reach.

Excretion measurements

We measured nitrogen and phosphorous excretion rates for 583 individuals representing 28 mussel species and 37 individual *Corbicula* across both rivers following Atkinson et al. (2013), during September 2020 when water temperatures were 19.6–22.8 °C in the Cahaba River and 20.4–27 °C in the Duck River.

Excretion rates were measured for at least 5 individuals of each species comprising approximately 80% of assemblage biomass. We collected individuals for excretion measurements during surveys. We used a toothbrush and scour pad to gently remove biofilms from shells and put them in plastic containers with 50–500 mL of filtered stream water (GF/F; 0.7 µm pore size; Millipore) depending on their size for 60–80 min (61.65 ± 4.02). Incubation times were shorter and volumes were greater for larger individuals to minimize stress and waste build up. One control container per 10 individuals was incubated simultaneously without bivalves and a subset (1 of 3 controls) had scrubbed stones collected from the stream to control for biofilm uptake. We measured individual lengths (mm) after incubation, re-filtered the water to separate biodeposits (i.e., egesta) from soluble nutrients (i.e., excreta), took 30–50 mL samples and kept them frozen (− 20 °C) until analyses. We used a Seal AQ300 discrete analyzer (Seal Analytical, Mequon, Wisconsin, USA) to analyze soluble reactive phosphorous (hereafter P) using the colorimetric method (Murphy and Riley 1962) and NH_4^+ (hereafter N) using the phenol method for filtered excretion samples (APHA 2012). Per capita excretion rates were calculated as the difference in nutrient concentration between containers with bivalves and controls while accounting for incubation time (µmol·h^{-1}).

Analysis

Spatial patterns of bivalve body size distribution

All analyses and data visualization were performed using R v. 3.6.3 (Wickham 2011; Wilke 2016; R Core Development Team 2019). Because we were interested in general body size differences between co-occurring mussels and *Corbicula*, we grouped mussels into phylogenetic tribes (Pfeiffer et al. 2019) and visualized body size distributions for mussels and the measured *Corbicula* using density ridgeline plots with 5 mm size classes (package ggridges Wilke 2018).

Bivalve nutrient excretion rates and stoichiometry

We analyzed relationships between body size (soft tissue dry mass [g]) and per capita excretion rates of N, P and N:P using linear regression (package car; Fox et al. 2018). Because we anticipated a power-law relationship between body size and excretion rates (Vanni and McIntyre 2016), we $\log_{10}$ transformed excretion rates and body size prior to analysis. Our analyses focused on interspecific comparisons using analysis of covariance (ANCOVA) with body size as a covariate using the *lm* function (Fox et al. 2018) for each river separately. When no relationship was found between excretion rates and body size, we used analysis of variance (ANOVA) to test for interspecific differences. We also calculated mass-specific excretion rates (µmol g^{-1} h^{-1}) and ratios for species grouped into phylogenetic tribes (Anodontini, Amblemini, Lampsilini, Pleurobemini, and Quadrulini; Fig. 1) to show differences among broadly classified mussels and *Corbicula*. We used the *dunn.test* function to perform Kruskal–Wallis non-parametric tests followed by multiple comparisons with Bonferroni corrections to compare differences among group mass-specific excretion rates and ratios because samples sizes among groups were highly unequal.

Aggregate density, biomass, excretion rates and stoichiometry

We tested how much density, biomass and areal N and P excretion rates differed spatially and between groups (mussels and *Corbicula*) using ANOVA. When the global ANOVA was significant ($p < 0.05$), we conducted Tukey pairwise contrast for *Corbicula* and mussels at each reach (function emmeans; Lenth 2018). To test assumptions of normality and heterogeneity of variances, we used Shapiro-Wilks test (function *shapiro.test*) and Levene's test (function *leveneTest*) in the car package (Fox et al. 2018), respectively. While biomass met test assumptions, we square root transformed density estimates and $\log_{10} + 1$ transformed Areal N and P excretion data to more closely meet assumptions of normality and equal variances and avoid $\log_{10}(0)$. We calculated log response ratios (lnRR) and standard error to visualize proportional differences in biomass, density, aggregate N and P excretion rates, and N:P for mussel assemblages and co-occurring *Corbicula* populations.

Scaling bivalve effects to the ecosystem

To understand variability in aggregate excretion as mediated by temporal variability in discharge and the fraction contributed by mussels and *Corbicula* biomass, we calculated volumetric excretion rates and turnover distances for each group during the time of year when water temperatures were within the range of those measured during excretion trials. Volumetric excretion rates combine benthic area (A: length × width), volume (V: length × cross-sectional area) and travel time (T: length/water velocity) of each reach: $E_V = (E_A \times A \times T)/V$. Volumetric excretion ($E_v$) describes average additions of dissolved nutrients ($\mu mol \cdot L^{-1}$) by excretion in a reach assuming perfect mixing and no uptake (McIntyre et al. 2008). Excretion turnover distance (m) is the distance required for excretion to turn over the ambient nutrient pool completely and is calculated by dividing ambient nutrient concentration by E_V and multiplying by the reach length (m). E_v and excretion turnover distances were calculated from 1 May 2020 through 31 August 2020 for two reaches in the Duck River (Duck 1 and Duck 4) and two reaches in the Cahaba River (Cahaba 1 and Cahaba 4). We numbered reaches consecutively from up-to-downstream for ease of explanation. Following the analysis of aggregate nutrient release, these four reaches were selected because they had opposing patterns of nutrient release by *Corbicula* and mussels (See Results), providing an opportunity to highlight how shifting from native to invasive species dominance would influence local nutrient availability. We used discharge data (Q = volume/travel time through a reach) from USGS gages near Columbia (USGS gage 03,599,500) and Milltown, Tennessee (USGS gage 03599240) for Duck River reaches and Centerville, Alabama (USGS gage 02424000) and Cahaba Heights, Alabama (USGS gage 02,423,425) for Cahaba River reaches. These gages provide a reasonable estimate of discharge at each site because they are located within 4 km of each site and there are no major tributaries between the gage and the respective sites. Additionally, to place estimated excretion rates in the context of long term seasonal temperature variation, we calculated the mean of the maximum daily water temperature for each month using data collected from a nearby USGS gage (02423496, Hoover, AL) for the Cahaba (1990–2020), and data from a HOBO temperature logger deployed near the Duck 3 site during 2018–2019.

Results

Spatial variation of bivalve body sizes, density, and biomass

General patterns

Corbicula lengths ranked the lowest among bivalves in both rivers (Fig. 2) but were smaller in the Cahaba River (mean ± SD = 12.6 ± 4.6 mm) compared to the Duck River (mean ± SD = 16.5 ± 6.6 mm; $F_{10,3076} = 541.7$, $p = 0.02$). *Corbicula* had greater

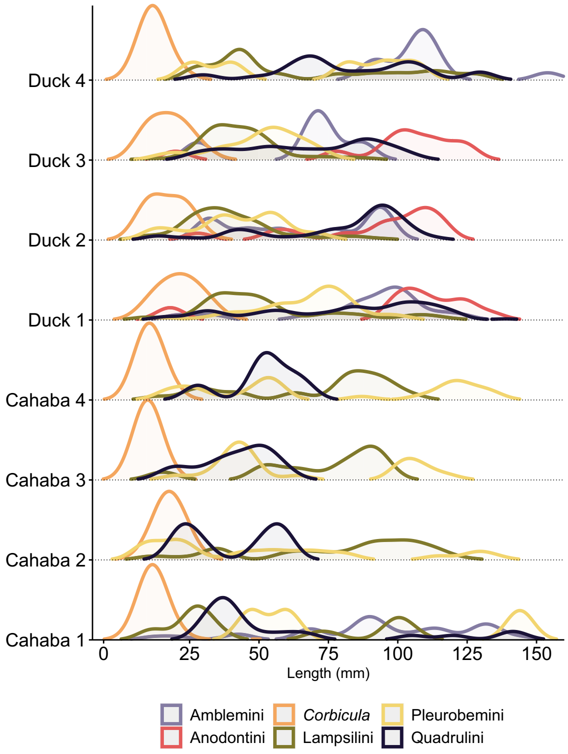

Fig. 2 Length frequency distributions (5 mm bins) for *Corbicula* and five phylogenetic tribes for mussels. Sites are numbered consecutively from upstream to downstream for each river. Note this analysis is exploratory and mean to illustrate body size differences between broadly classified mussels and *Corbicula*

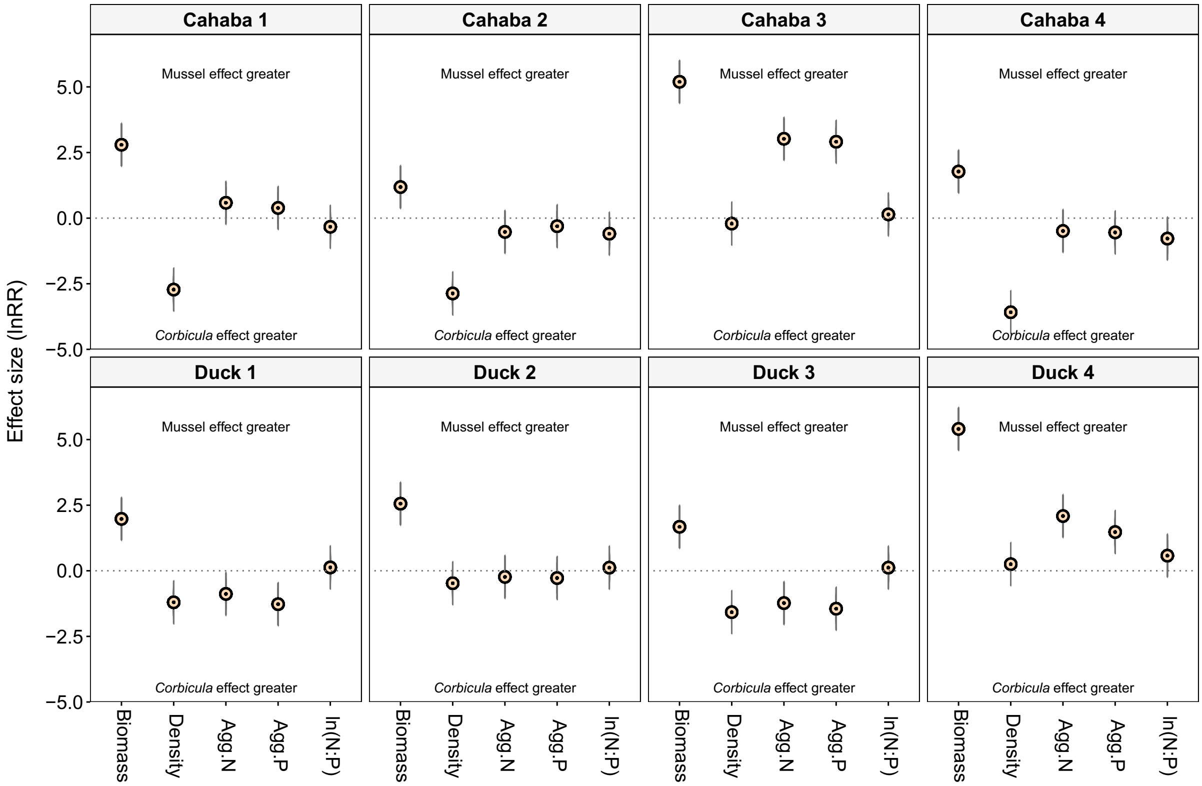

Fig. 3 Effect size of biomass, density, aggregate areal N excretionrates, aggregate areal P excretion rates, and aggregate areal excretion N:P from four mussel bed reaches in the Cahaba and Duck Rivers, USA. Dotted lines in each panel indicate net zero of each taxonomic group's effect such that positive values indicate greater mussel biomass, density, excretion rate, and N:P and negative values indicate greater *Corbicula* biomass, density, excretion, and N:P at a reach. Separate boxplots of each response variable are available as Online Resources 8–1

densities compared to mussels in each river (Figs. 1, 3). However, densities within and among reaches were highly variable for *Corbicula* and mussels ($F_{7,1256} = 21.15$, $p < 0.001$; Online Resource 8). Areal mussel biomass typically exceeded *Corbicula* ($F_{7,1256} = 11.63$, $p < 0.001$; Online Resource 9).

Cahaba River mussel size distribution

Amblemini (only represented by *Amblema plicata*) was abundant at only Cahaba 1 and spanned the full range of lengths (mean ± SD = 90 ± 34.2 mm; Online Resource 2). Lampsilini was represented by 10 species in the Cahaba River (mean ± SD = 72.9 ± 30.4 mm), yielding lengths that spanned the entire distribution, but still with clear peaks. Lampsilini body sizes peaked approximately 75 mm due to highly abundant *Lampsilis ornata*. However, Cahaba 1 had higher abundances of small *Leptodea fragilis* (mode approximately 30 mm) representing the Lampsilini. Three species represented the Pleurobemini in the Cahaba River. Modes around 100 mm are *Elliptio crassidens*, modes around 50 mm are *Pleurobema decisum* and *Fusconaia cerina*, while *F. cerina* also falls within the smaller class around 20 mm. Quadrulini was represented by four species (mean ± SD = 49.0 ± 26.1 mm). *Cyclonaias asperata* was the only Quadrulini present all reaches in the Cahaba River with a mode at 50 mm.

Duck River mussel size distribution

Anodontini (mean ± SD = 87.3 ± 27.5 mm), represented by two species, only occurred in the Duck River and was represented most by the large bodied *Lasmigona costata*. Amblemini (*A. plicata*) was present at all reaches, often with a dominant length class around 90 mm (mean ± SD = 87.2 ± 27.5 mm), although smaller length classes were observed in lower abundances. Lampsilini was represented by 21 species (mean ± SD = 45.8 ± 20.6 mm), with most individuals having small body lengths (maximum of approximately 45 mm). Seven Pleurobemini species were found in the Duck River. The most abundant species and representative of the largest class was *Eurynia dilatata* (mode of approximately 70 mm) except at the most downstream site where it did not occur. The less common *Pleurobema dolabelloides*, *P. oviforme*, and *Pleuronaia barnesiana* were in smaller length classes of Pleurobemini. Quadrulini comprised seven species (mean ± SD = 76.9 ± 27.4 mm) and was evenly represented across reaches by *C. tuberculata* (mode of approximately 80 mm), *C. pustulosa* (mode of approximately 50 mm), and *Theliderma cylindrica* (mode of approximately 85 mm).

Bivalve nutrient excretion rates and stoichiometry

Cahaba River

Per capita excretion rates varied from 2.57–9.49 μmol·h^{-1} for N, and 0.36–2.24 μmol·h^{-1} for P for *Corbicula* (Online Resource 3). Per capita excretion rates for Cahaba mussels ranged from < 0.01- 8.7 μmol N·h^{-1} and < 0.01–0.82 μmol P·h^{-1}. Regression across the entire Cahaba River data set (including both bivalve groups) indicated body mass was a strong predictor for N ($F_{1,185}$ = 386.9, $p < 0.001$, $R^2 = 0.67$), and P ($F_{1,185}$ = 106.9, $p < 0.001$, $R^2 = 0.36$) excretion rates. Body mass (F_1 = 632.63, $p < 0.001$) and species identity (F_{14} = 9.19, $p < 0.001$) separately explained variation for N excretion rates, but did not interact ($F_{1,14}$ = 1.20, $p = 0.28$). The interaction between species identity and body mass clearly explained P excretion rates ($F_{14,157}$ = 2.47, $p = 0.03$) using ANCOVA. Differential scaling of N and P (Online Resource 3, 4) yielded wide ranges of excreted N:P ratios for *Corbicula* (3.54–108.8) and mussels (0.91–1711.35). Mass-specific N excretion rates ($\chi^2 = 49.86$, $p < 0.001$) and P excretion rates ($\chi^2 = 50.86$, $p = < 0.001$) were variable among bivalve groups. Pairwise comparisons indicated *Corbicula* mass-specific N and P excretion exceeded all mussels ($p < 0.001$), while mussel tribes were similar to each other ($p > 0.05$). Excretion N:P stoichiometry varied among groups ($\chi^2 = 17.51$, $p = 0.002$). *Corbicula* excretion stoichiometry was lower than Lampsilini (z = − 2.82, $p = 0.02$), and Quadrulini (z = − 346, $p = 0.003$). Pleurobemini had lower excretion N:P compared to Quadrulini (z = − 2.94, $p = 0.02$).

Duck River

Corbicula per capita excretion rates ranged from 0.23–1.62 μmol·h^{-1} for N and 0.11–0.35 μmol·h^{-1} for P (Online Resource 3). Per capita excretion rates for mussels ranged from < 0.01 –14.49 μmol N·h^{-1} and < 0.01–12.54 μmol P·h^{-1}. Body mass was strongly related to N ($F_{1,310}$ = 241.6, $p < 0.001$, $R^2 = 0.44$) and P ($F_{1,310}$ = 65.16, $p = 0.001$, $R^2 = 0.17$) excretion rates when using regression across the complete Duck River data set. As in the Cahaba, ANCOVA revealed strong species effect (F_{16} = 7.26, $p < 0.001$) and body mass effects (F_1 = 323.40, $p < 0.001$), but the interaction term did not explain N excretion rates ($F_{16,278}$ = 1.29, $p = 0.19$), while P excretion rates were clearly explained by the interaction between species identity and body mass ($F_{16,278}$ = 1.99, $p = 0.01$). Interspecific scaling of N and P yielded a range of excreted N:P ratios for *Corbicula* (1.08–4.79) and mussels (0.10–91.38) and the regression across the complete data set showed a clear but highly variable relation between N:P and body mass ($F_{1,310}$ = 17.45, $p < 0.001$, $R^2 = 0.05$). Excretion N:P was explained by a species and body mass interaction ($F_{1,310}$ = 3.77, $p < 0.001$, $R^2 = 0.23$). Mass-specific N excretion rates ($\chi^2 = 61.49$, $p < 0.001$; Online Resource 5) and P excretion rates ($\chi^2 = 41.57$, $p = < 0.001$; Online Resource 5) varied among bivalve groups. *Corbicula* mass-specific N and P excretion rates exceed those of all mussel tribes ($p < 0.001$; Online Resource 5). Lampsilini N mass-specific excretion rates were greater than Amblemini (z = -3.34, $p = 0.01$) and Quadrulini (z = 5.72, $p < 0.001$). Lampsilini P mass-specific excretion rates exceeded Amblemini (z = − 3.18, $p < 0.01$) and Anodontini (z = − 2.88, $p < 0.03$). Excretion N:P varied among groups ($\chi^2 = 14.67$, $p = 0.01$; Online Resource 5). Pairwise comparisons indicated this was driven by increased N:P for Anodontini compared to Quadrulini (z = 3.20, $p = 0.01$).

Aggregate excretion fluxes and stoichiometry

General patterns

Areal N excretion rates varied spatially and were greater at Duck River aggregations compared to those of the Cahaba River ($F_{7,1256} = 16.27$, $p = 0.001$; Fig. 3). Areal P excretion rates by *Corbicula* and mussels also varied across sites ($F_{7,1256} = 16.25$, $p < 0.001$), but were only significantly different at Duck River sites (Fig. 3). Variable areal N and P excretion rates among sites gave way to a range of N:P ratios for *Corbicula* and mussels among sites with inconsistent differences between the groups in both rivers ($F_{7,1256} = 20.62$, $p < 0.001$; Fig. 3).

Cahaba River

Corbicula densities exceeded mussels at the two most upstream (Cahaba 1, t = 8.55, $p < 0.001$; Cahaba 2, t = 10.74, $p < 0.001$) reaches by approximately 20-fold and Cahaba 4 by more than 50-fold (t = 11.12, $p < 0.001$ Fig. 3, Online Resource 8), but the two groups were similar at Cahaba 3 (t = 0.23, $p = 0.82$). Cahaba River mussel biomass was approximately three-fold greater than *Corbicula* at the upstream reach, Cahaba 1 (t = − 5.48, $p < 0.001$) and approximately five-fold at the third reach (t = 6.66, $p < 0.001$), but was similar at Cahaba 2 (t = − 0.65, $P = 0.52$) and Cahaba 3 (t = − 1.48, $p = 0.14$; Online Resource 9). Areal N excretion rates of mussels were lower than *Corbicula* at Cahaba 3 (t = − 4.34; $p < 0.001$), but the opposite was true at Cahaba 2 (t = 2.84; $p = 0.05$), while areal N rates at the most upstream ($t = -0.65$; $P = 0.52$) and downstream site were similar between groups (t = 1.82; $p = 0.07$; Online Resource 10). Pairwise comparisons did not yield clear differences between mussel and *Corbicula* areal P excretion for any reaches (Online Resource 11). *Corbicula* had greater areal excretion N:P ratios at both upstream reaches (Cahaba 1; t = 6.498; $p < 0.001$, Cahaba 2: t = 7.74; $p < 0.001$) and the most downstream site (t = 9.46; $p < 0.001$) compared to mussels, but were similar at Cahaba 3 (t = 0.004; $p = 0.96$; Online Resource 12).

Duck River

Density of *Corbicula* exceeded mussels at the most upstream reach by threefold (t = 5.44, $p < 0.001$) and the Duck 3 reach by fivefold on average (t = 8.69, $p < 0.001$; Fig. 3). Densities of *Corbicula* and mussels were similar at Duck 2 (t = 1.24, $p = 0.22$) and Duck 4 (t = − 0.34, $p = 0.73$; Online Resource 8). *Corbicula* biomass (range of means 0.08–5.61 $g \cdot m^{-2}$) was lower than mussel biomass (range of means 15.24–40.54 $g \cdot m^{-2}$) at all sites ($p < 0.001$; Online Resource 9). *Corbicula* areal N excretion rates were greater at the upper most site (t = 4.42, $p < 0.001$) and site 3 (t = 5.11, $p < 0.001$). Moreover, mussel areal N rates were marginally higher at Site 2 (t = − 1.78, $p = 0.07$) and significantly greater than *Corbicula* at Site 4 (t = -5.97, $p < 0.001$; Online Resource 10). Areal P excretion for *Corbicula* was greater at Duck 1 (t = 7.23, $p < 0.001$) and Duck 3 ($t = 8.81$, $p < 0.001$), but lower than mussels at Duck 2 (t = − 2.12, $p = 0.03$) and Duck 4 (t = − 5.05, $p < 0.001$; Online Resource 11). Only the most downstream reach in the Duck River had strong differences between *Corbicula* and mussel excretion N:P, with mussels excreting more N relative to P ($t = -2.48$, $p = 0.03$; Online Resource 12).

Bivalve volumetric excretion

General patterns

Expressing nutrient excretion as volumetric units highlighted the influence of stream flow on bivalve mediated fluxes of N and P, such that nutrient flux and discharge were inversely related (Fig. 4). Estimated bivalve contributions were low, with volumetric excretion making up < 1% of ambient concentrations in the four reaches we modeled.

Cahaba River

At the average discharge 1 May 2020 to 31 August 2020 of 3.3 $m^3 s^{-1}$, volumetric N excretion for *Corbicula* (approximately 39% of aggregate N; approximately 33% of aggregate P) and mussels at Cahaba 1 were 0.88 and 0.15 nmol L^{-1}, while volumetric P excretion was 0.03 and 0.02 nmol L^{-1}, respectively (Fig. 4). Even combining E_v of both groups would require approximately 38 km for the bivalve

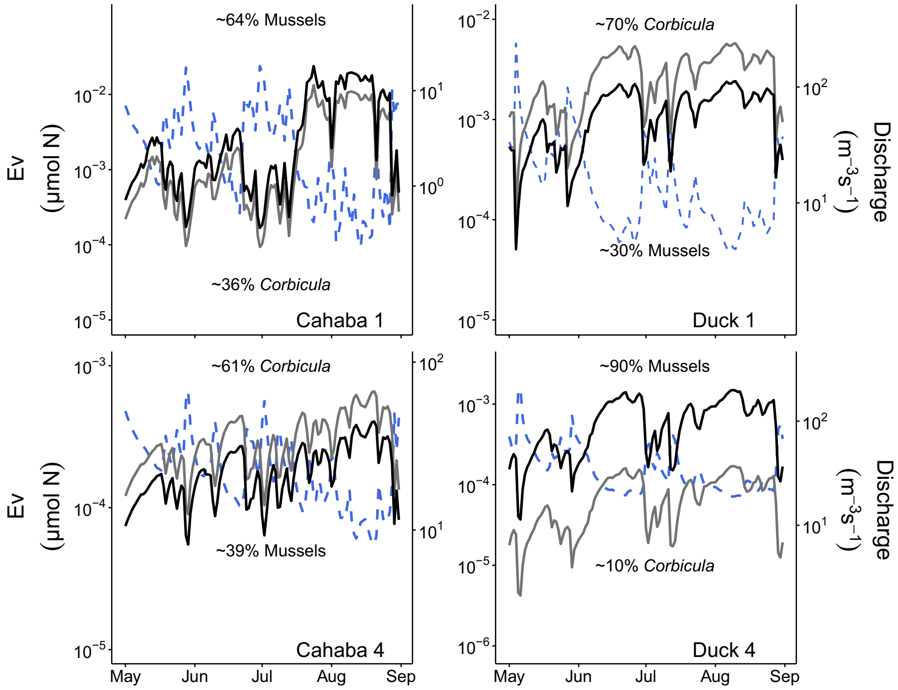

Fig. 4 Volumetric excretion (E_V) of nitrogen (N) during 01 May 2020 to 31 August 2020 in relation to discharge (shown on second y-axis, with blue dashed line) at two Cahaba River reaches and two Duck River reaches. Percentage of each group's contribution to aggregate volumetric N excretion is presented as text on each panel

aggregation to turnover N and approximately 820 km to turnover P. For the Cahaba 4 where mean discharge was 22.52 m^3 s^{-1}, volumetric N excretion was 0.19 and 0.31 nmol L^{-1}, while volumetric P was 0.02 and 0.01 nmol L^{-1} for mussels and *Corbicula*, respectively. *Corbicula* contributed to approximately 61% of aggregate N (Fig. 4) and 21% of P excretion at Cahaba 4 reach. Bivalve aggregate excretion turnover distances were approximately 112 km for N and ~ 850 km for P. Water temperature in the Cahaba River ranged from 9.2 to 28.7 °C, with lower temperature corresponding to winter months and higher temperatures corresponding to summer months (Online Resource 13).

Duck River

Volumetric excretion for mussels was 1.19 nmol L^{-1} N and 0.27 nmol L^{-1} P and for *Corbicula* was for 2.67 nmol L^{-1} N and 1.12 nmol L^{-1} P at Duck 1 reach (Fig. 4) when mean discharge was 20.22 $m^3 \cdot s^1$. Aggregate turnover distance was ~ 38 km for N and ~ 96 km for P. *Corbicula* was ~ 66% of aggregate N and > 90% of P excretion at Duck 1. Duck 4 had a mean discharge of 26.19 $m^3 \cdot s^{-1}$. *Corbicula* volumetric excretion was 0.07 nmol L^{-1} N and 0.03 nmol L^{-1} P, whereas mussel volumetric excretion was 0.66 nmol L^{-1} N and 0.11 nmol L^{-1} P. Combined aggregate excretion had turnover distances of approximately 172 km for N and > 1000 km for P. *Corbicula* was 10% of aggregate N and approximately 2% of aggregate P excretion at this reach (Fig. 4). Water temperature in the Duck River ranged from 9.5 to 26 °C, with lower temperature corresponding to winter month and higher temperatures corresponding to summer months (Online Resource 13).

Discussion

Identifying invasive species that alter processes governed by native faunal groups is key to the development of targeted management programs that improve or maintain ecosystem function (Pergl et al. 2020; Li et al. 2021). We examined the potential of an established invasive bivalve species to influence local nutrient availability through excretion of N and P compared to an ecologically similar native faunal group in two rivers by combining spatially explicit biomass estimates and measured per capita excretion rates. Overall, *Corbicula* occurred at greater densities, but mussels typically exceeded the invader in biomass due to their larger body sizes (Figs. 2, 3). We observed that *Corbicula* nutrient fluxes exceeded or equaled those of mussels at half of the reaches given their high mass-specific excretion rates. Collectively, we demonstrate that small-bodied animals invading into low trophic positions have the potential to control fluxes and stoichiometry of nutrients even in the presence of high-biomass aggregations of functionally similar native animals.

Corbicula was widespread and reached high densities in mussel beds throughout the Cahaba and Duck Rivers. Evidence regarding whether *Corbicula* and mussels can successfully co-exist in North American rivers is often conflicting (Vaughn and Spooner 2006; Kelley et al. 2022). Although *Corbicula* was considered established in these rivers more than 50 years ago, complete accounts of *Corbicula* invasion timing and quantitative population estimates are rarely available where mussels are found. Although our estimates represent a snapshot in time, our study captures spatial patterns of density and biomass among reaches where *Corbicula* potentially interact with mussels. *Corbicula* is widespread throughout both systems and local populations often exceed densities of co-occurring native mussel assemblages. Widespread habitat alterations such as dams and water quality degradation, that harm native mussel communities (Galbraith and Vaughn 2011; Gascho Landis et al. 2013) likely promotes *Corbicula* establishment in these rivers (Byers 2002; MacDougall and Turkington 2005). Similar niche requirements, higher tolerance to some stressors (Ferreira-Rodríguez and Pardo 2017), and asexual reproduction (Pigneur et al. 2014) could also aid *Corbicula* colonization into habitats where mussels are declining (Strayer et al. 1999). Whereas *Corbicula* is more tolerant to many stressors, they are quite vulnerable to high temperatures and low dissolved oxygen which can lead to mass mortality events resulting in water quality issues that can harm mussel populations (McDowell and Sousa 2019). Yet, *Corbicula* populations have the ability to recover shortly following disturbances, while mussel populations may take decades to reach pre-disturbance abundances due to their slow maturation (McMahon and Bogan 2001; Haag 2012). Altogether, increasing *Corbicula* abundances should be alarming because mussel-provided ecosystem services subsequently decline or may become controlled by high densities of *Corbicula*.

Small-bodied *Corbicula* had lower per capita excretion rates, but higher mass-specific excretion rates compared to all mussels. Body size is the most important axis of biodiversity and controls the degree to which animals influence nutrient cycling (Hall et al. 2009). For most aquatic animals, the relationship between body size and excretion rates increases less than isometrically due to the strong link with metabolism, which scales at 3/4 power of body size but can vary among taxonomic groups (Allen and Gillooly 2009). Bivalves in our study spanned a wide range of scaling exponents but most met what is expected by the metabolic theory of ecology (Online Resource 2, 3, and 4) and were within the range reported in global analyses of aquatic invertebrate excretion rates (Vanni and McIntyre 2016). Although other factors (e.g., temperature) influence metabolism and subsequent nutrient release by animals (Atkinson et al. 2017), our study emphasizes how changing size structure associated with an abundant invasive species may shift animal-mediated nutrient cycling (Minaudo et al. 2021; Li et al. 2021).

Combining per capita excretion rates with biomass estimates allowed us to evaluate spatial variation in animal-mediated nutrient cycling of co-occurring invasive and native bivalves in two different rivers. *Corbicula* areal N excretion rates often exceeded mussels. Because small animals have higher metabolism and, therefore, higher mass-specific excretion rates, when total biomass is equal, fluxes from an assemblage with small animals may exceed an assemblage with large animals (Hall et al. 2009; Vanni and McIntyre 2016). Our result of greater N excretion by high density, but low biomass populations of *Corbicula* in the presence of low density, high biomass mussel aggregations supports this concept. Areal P excretion rates were similar between mussels and *Corbicula* in the Cahaba River, but differed spatially in the Duck River, with mussels only exceeding *Corbicula* at the most downstream site with comparatively low *Corbicula* density.

Areal excretion N:P for *Corbicula* was typically greater than that of mussels in the Cahaba River, but similar in the Duck River. This pattern resulted from similar body size-scaling of per capita N and P excretion rates between Cahaba mussels and *Corbicula* combined with greater densities of *Corbicula*. This means that greater densities and mass-specific excretion rates of N and P in the Cahaba River *Corbicula* populations influence aggregate nutrient fluxes, not stoichiometric differences between mussels and *Corbicula*. Differential per capita excretion scaling for *Corbicula* compared to mussels in the Duck River elevated P excretion relative to N, reducing *Corbicula* N:P. Similarities between Duck River *Corbicula* and mussel areal N:P resulted from an approximately tenfold greater flux of both N and P from *Corbicula* populations, while stoichiometry remained stable. Resource quality, physiology, and life history differences among *Corbicula* populations in the region may have contributed to such differences in per capita excretion rates. For example, a stable isotope analysis of *Corbicula* and a dominant mussel species (*Elliptio crassidens*) suggested a more generalized feeding strategy and increased N release in biodeposits (feces and pseudofeces) for *Corbicula* (Atkinson et al. 2010). Furthermore, Lauritsen and Mozley (1989) attributed seasonal differences in N excretion rates for a single population of *Corbicula* to gametogenesis and metabolic adjustments by individuals to resource quality and temperature. Additionally, there is variability in *Corbicula* reproductive cycles that may influence temporal variation in nutrient release, with some studies indicating two reproductive peaks per year in North America, while other suggest a single peak (Hornbach 1992). Stoichiometric traits, such as nutrient storage and excretion rates, could be combined with population vital rates to evaluate and forecast the immediate and long-term effects of invasive and native species to nutrient dynamics (Sharitt et al. 2021).

Biomass distribution, functional trait composition, stoichiometric requirements and environmental context all modulate the contributions of animal communities to biogeochemical cycling (Hopper et al. 2018; Subalusky and Post 2019). Volumetric excretion rates for bivalve aggregations (combined *Corbicula* and mussels) were very low, never exceeding 1% of ambient concentrations. Previous work demonstrates that dense aggregations of mussels and other aquatic animals can generate biogeochemical “hotspots” (McIntyre et al. 2008; Atkinson and Vaughn 2015), where nutrient regeneration rates are high relative to demand (McClain et al. 2003). Bivalve aggregations in our study had similar biomass as other studies (Atkinson et al. 2020a; Hopper et al. 2021), but the estimated mussel excretion contributions here were a small fraction of ambient nutrient concentration comparatively. For example, excretion by mussel aggregations from five rivers in the southeastern region of North America exceeded background N concentrations and were 20% of ambient P concentrations on average (Hopper et al. 2021). Small contributions to ambient conditions appeared to be driven by discharge associated with comparatively larger stream sizes that increase the volume of water over the animals and the lower water temperatures during our excretion measurements. Water temperature also can play a role because it governs invertebrate metabolism and mussel excretion rates and ratios can shift seasonally, with asymmetric responses by co-occurring species (Vaughn 2010; Atkinson and Vaughn 2015). Our field excretion measurement approach did not enable a robust analysis of interspecific responses to water temperature gradients. Still, a key factor for predicting biological rates to temperature increase is their $Q_{10,}$ which indicates the relative change of a rate between two temperatures that differ by 10 °C. Generally, biological rates, such as excretion, increase by 1.5 × to 3 × with a 10 °C increase, but vary greatly among species (Clarke 2004). Our excretion measurements took place when water temperatures were typically highest or within 5 °C of maximum seasonal water temperatures (Online Resource 13), thus we expect the estimated contributions of bivalves in our study to be within the typical range for the Duck River, but lower in the Cahaba River. Nevertheless, the greater aggregate excretion at lower discharge supports other work showing that animal-mediated nutrient cycling effects vary with ecosystem size (Vaughn et al. 2004; Benstead et al. 2010). While bivalve aggregations in these rivers may not be a major source of nutrients at broad spatial scales when discharge is high and water temperatures are low, their effects may be stronger during warmer summer base flow conditions and concentrated locally in benthic habitats (Spooner and Vaughn 2012).

Shifts in community composition of freshwater systems are commonplace and likely to continue with global change (Tonkin et al. 2019). For example, more frequent and severe stream drying events will undoubtedly reduce flows and increase temperature that could harm mussels, but may be less detrimental to *Corbicula* (Ferreira-Rodríguez et al. 2018a). Still, low stream discharge can strand or cause water temperature to exceed tolerances of *Corbicula,* leading to mass mortality events that release pulsed fluxes of dissolved nutrients (Cherry et al. 2005; Cooper et al. 2005; McDowell et al. 2017; McDowell and Sousa 2019). Physiological tolerance of mussels to desiccation and high temperatures can be greater than *Corbicula*, but mussels can experience mass mortality when temperature is high and discharge is low (Vaughn et al. 2015; DuBose et al. 2019). Because *Corbicula* has asexual reproduction and matures rapidly (< 1 year), compared to mussels that mature much slower (6–10 years), it seems likely that *Corbicula* may be more resilient to such low flow disturbances and recover quickly (Sousa et al. 2008b; Haag 2012). Therefore, we expect that differential responses of mussels and *Corbicula* to anticipated climate change scenarios increase the likelihood of shifting control of local nutrient cycling toward *Corbicula*.

To completely understand the implications of animal community shifts to ecosystems, it is necessary to refocus or expand monitoring efforts to include invasive species populations (Ruaro et al. 2021), especially those overlapping with imperiled fauna such as mussels. The many functional roles performed by mussels (Vaughn and Hakenkamp 2001; Vaughn 2018) may be replaced by other filter feeders (Minaudo et al. 2021; Li et al. 2021), but may not be as stable and differ in impact. Previous work indicates mussels are declining, sometimes for unknown reasons (Haag 2019). If *Corbicula* harms mussels, invades into previously occupied mussel habitats, or becomes more widespread, a lack of information on their distribution will only impede efforts to mitigate mussel declines, protect remaining habitat and associated ecosystem services. Our study illustrates that increasing densities of a small bodied invasive species has the potential to alter nutrient cycling compared to native species and highlights variable stoichiometric traits within a functional feeding group.

Authors' contributions GWH and CLA conceived the idea; GWH and JKB collated and analyzed the data and drafted the manuscript; GWH, CLA, ISG, JRB, MEK, and MBL conducted field excretion measurements and surveys. CLA and JDL supervised and provided support. All authors provided input on the manuscript and approve the submitted version.

Data availability Streamflow data are publicly available at https://waterdata.usgs.gov/nwis/rt Survey and excretion data are available at the Open Science Framework https://doi.org/10.17605/OSF.IO/F2NRW.

Code availability No custom code used.

Declarations

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

Consent to participate Freshwater mussel collection was conducted under USFWS permit #TE68616B-1, TWRA permit #1807, ALCDNR permit #2020097718468680.

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