

High abundance of an invasive species gives it an outsized ecological role

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Abstract

1. Many communities are shifting composition, with losses of native species and increases of non-indigenous species (NIS). At its extreme, such alteration of ecological guilds can result in simplification with a single NIS performing an ecological role once carried out by a suite of natives. This alteration has occurred in many rivers of the south-eastern U.S.A., where the invasive filter-feeding freshwater clam *Corbicula fluminea* has proliferated following the nearly complete extirpation of native mussels.
2. We investigated the factors controlling the distribution and abundance of *Corbicula*, as well as estimated the ecological service it provides via water filtration. With a nested design, we surveyed multiple transects within four to six sites within each of four rivers that spanned three large catchments in the Georgia piedmont, collecting data on *Corbicula* density and physical habitat characteristics associated with its presence.
3. We found *Corbicula* present in over half of the 1,536 sampled 0.044 m² sampled plots, 90 of the 93 transects that spanned the width of the river, and all 1–2 km sample sites, underscoring the clam's ubiquity in the study region. At the river scale, *Corbicula* densities ranged from 50–212 *Corbicula* m⁻², although individual sites ranged from 7–483 *Corbicula* m⁻². *Corbicula* was more abundant in areas with higher proportions of gravel, and less abundant with higher proportions of bedrock. A hierarchical model with river, site, and these two substrate variables explained 32% of the variation in *Corbicula* density.
4. Using observed densities and published per capita feeding rates, we calculated system-wide collective filtration rates provided by *Corbicula*. In the four rivers surveyed and based on estimated residence times for median flows for the summer of 2012, *Corbicula* is estimated to filter water as many as seven times during median flows and 18 times during minimum flows before water flows out of a 10-km reach. Due to high abundances and per biomass filtration rates, *Corbicula* plays an important role in these rivers.
5. Invasive species, biotic homogenisation, and the loss of functional redundancy may mean that many more rivers are similar to our studied rivers, with a single, often invasive, species dominating ecosystem function. Understanding the influence of biotic homogenisation on ecosystem function is of foremost importance to evaluate the resilience of natural systems.

KEYWORDS

Corbicula, density, ecosystem function, filtration, non-indigenous species

1 | INTRODUCTION

Species diversity typically has a positive effect on ecosystem function (Hooper et al., 2005; Tilman, Wedin, & Knops, 1996). However, because of complementarity and sampling effects, the identity (and not purely the number) of species included in a system can drive this positive effect (Crowl, McDowell, Covich, & Johnson, 2001; Flombaum, Aragón, & Chaneton, 2017; Gordon, 1998; Hall, Tank, & Dybdahl, 2003; Pringle, Hemphill, McDowell, Bednarek, & March, 1999). A species can particularly influence ecosystem function due to some combination of a high per capita effect, high area of occupancy, and high density (Parker et al. 1999). Increasingly the relevance of diversity's effect on function has risen because of community change and biotic homogenisation caused by introductions of non-indigenous species (NIS) and loss of natives (Byers et al., 2002; Olden & Poff, 2003). NIS can sometimes be a driver of the decline of native species and therefore the subsequent alteration of ecosystem function (Crowl, Crist, Parmenter, Belovsky, & Lugo, 2008; Vaughn, 2010); however, at other times an NIS opportunistically fills an ecological role vacated by missing native species, in which case the NIS can partially compensate for some function lost from native extirpation (Lugo, 2004; Pejchar & Mooney, 2009).

Filter feeding bivalves play critical roles in aquatic ecosystems, by providing ecosystem services such as filtration, nutrient recycling, and sediment deposition, all of which affect overall water quality (Covich, Palmer, & Crowl, 1999; Strayer, Caraco, Cole, Findlay, & Pace, 1999; Strayer, Eviner, Jeschke, & Pace, 2006; Vaughn & Hakenkamp, 2001). Alterations to the community composition of filter feeding bivalves have led to dramatic alterations to ecosystem function via the addition of NIS and subsequent changes to abundance and biomass (Caraco et al., 1997; Heath, Fahnenstiel, Gardner, Cavaletto, & Hwang, 1995; Strayer et al., 1999; Zhu, Fitzgerald, Mayer, Rudstam, & Mills, 2006) or the identity (Vaughn, Spooner, & Galbraith, 2007) or loss of native species (Vaughn, 2010). Throughout much of North America, the invasive freshwater Asian clam *Corbicula fluminea* has become the dominant filter feeding bivalve (Crespo, Dolbeth, Leston, Sousa, & Pardal, 2015), with populations reaching as far north as the St. Lawrence River (Castaneda, Hamelin, Simard, & Ricciardi, 2018) and the Great Lakes (Smith, Harris, Harris, LaBudde, & Hayer, 2018), although these populations are dependent on thermal refugia from industrial cooling. *Corbicula* may also compete with native mussels (Leff, Burch, & McArthur, 1990) and can have negative impacts on the growth and physiological condition of unionid mussels (Ferreira-Rodríguez, Sousa, & Pardo, 2018).

Corbicula invaded the south-eastern U.S.A. in the 1960s (McMahon & Bogan, 2001) and can reach densities of several thousand per square metre in other regions (Cohen, Dresler, Phillips, & Cory, 1984; Sousa, Rufino, Gaspar, Antunes, & Guilhermino, 2008).

The historical abundance of the native pearly mussels (Unionidae) in the region is unclear; few studies on their relative abundance (Van Cleave, 1940) exist in other regions. Using harvest data, historical reports of maximum densities in mussel beds, and comparisons to relatively unimpacted systems, Strayer (2014) estimated that pristine rivers historically contained densities of 1–10 mussels/m². However, current densities of unionids are in substantial decline across the region (Neves, Bogan, Williams, Ahlstedt, & Hartfield, 1997), due to large-scale changes, such as a near complete deforestation of most piedmont catchments (Glenn, 1911). *Corbicula* has specific traits that make it very likely to be particularly impactful, as it has a high per biomass filtration rate (McMahon & Bogan, 2001) and removes a variety of particle sizes from the water column (Atkinson, First, Covich, Opsahl, & Golladay, 2011). These traits, combined with often high densities, make it an important species in altering south-eastern river ecosystems.

The first objective of this study is to provide an estimate of the density of *Corbicula* in the Georgia piedmont, as it is known to be an abundant filter-feeding bivalve in the region. Second, we scale up these measures of density to estimate *Corbicula* population sizes for a 10-km reach of four piedmont rivers. Third, through comparison of multivariate models, we determine which environmental and habitat attributes are most associated with *Corbicula* abundance. Finally, using specific physiological rates and a range of river discharges, we calculate the population level ecosystem function of water filtration currently performed by *Corbicula*.

2 | METHODS

2.1 | Study rivers

We sampled four rivers in the piedmont region of GA, U.S.A.—the Middle Oconee, the Broad, the Apalachee, and the Alcovy Rivers. These rivers are east of Atlanta, GA in the vicinity of Athens, GA (Figure 1). Within the catchments, the land use is primarily a mix of forest, agricultural pasture and cropland, with some urban areas. Athens, a small city of approximately 125,000 residents, is the only large urban area within our study region and is part of the Middle Oconee catchment. The far northern portion of the Apalachee catchment also includes a portion of Lawrence, GA, the easternmost extreme of the greater Atlanta metropolitan area. Within the sampling reaches, all rivers were free-flowing, but the Apalachee, Alcovy, and the Middle Oconee all have river impoundments. The substrate within these rivers is primarily fine sediment such as silt, sand, and gravel, though some shoals are present where larger substrate is common. These are generally turbid systems with baseline turbidities of approximately 30 NTU, and high measurements approaching 1,000 NTU (EPA STORET).



FIGURE 1 Map showing the south-eastern U.S.A., with the four studied rivers marked. From west to east, the Alcovy River (ALC), the Apalachee River (AP), the Middle Oconee River (MIDO), and the Broad River (BRO)

We selected these rivers as they vary in discharge and catchment area, which ranges from 80 to 1,031 km² above the sampling reach. Additionally, they span three large catchments in the Georgia piedmont: the Ocmulgee basin (Alcovy River), the Oconee basin (Middle Oconee and Apalachee Rivers), and the Savannah basin (Broad River). This sampling approach allows us to provide a more accurate regional estimate of *Corbicula* density and population size.

2.2 | Field density surveys

For each river, we examined 4–6 sites for *Corbicula* density. We selected sites based on availability of access to the river, but ensured that the two habitat types, sandy run and bedrock shoals habitats, were included in our sampling. To help avoid spatial autocorrelation, sampling sites were separated by at least 2 km. All rivers were wadeable and were sampled during low and medium flow conditions due to safety concerns. Within each site, we sampled three to six systematically spaced transects that spanned the width of the river. After randomly selecting a starting point for the first transect, transects within a site were systematically spaced at least the width of the river apart (25–100 m, depending on the river). This design resulted in sampling a randomly placed systematic grid at each site that was scaled to the size of the river at that site. Along each transect, we took approximately 25 samples for *Corbicula* density using a 0.044 m² stove pipe corer to a depth of up to 5 cm (when sufficient substrate existed), with sample points ranging from 1–4 m apart, depending on the wetted width of the river. Typically, we used four transects per site, but in narrower smaller rivers, each transect contained fewer sampling points, so we completed additional transects

per site. We chose our coring method to prevent small *Corbicula* from washing out of the sampling area when the sediment was disturbed. We sieved each sample using a 2 mm sieve to help find any *Corbicula* within the sample and quantify the substrate. At each sample point, we recorded physical habitat characteristics, including water depth and substrate composition in the first 5 cm. As *Corbicula* only burrows to shallow depths (McMahon & Bogan, 2001), only sediment near the surface should affect their density and distribution. In total, we sampled 1,536 points for substrate and *Corbicula* density. We counted all *Corbicula* within the 0.044 m² stove pipe corer and used a ruler to bin individual *Corbicula* into 5 mm size classes by shell length (extra small: <10 mm, small: 10–15 mm, medium: 15–20 mm, and large: 20+ mm).

We visually estimated percent substrate composition within the sample area (0.044 m² and 5 cm deep) for five different categories: fines (clay and silt, <0.062 mm), sand (fine sand, sand, and coarse sand, 0.062–2 mm), gravel (fine gravel, gravel, and coarse gravel, 2–64 mm), large (cobble and boulder, 64–256 mm), and bedrock (>256 mm). Although this estimation is less accurate than sieving and weighing samples, this approach allowed us to collect substrate data for all sample points, rather than a subset. We also used broad categories of substrate in order to reduce the likelihood of misclassifying substrate. In bedrock dominated areas where <5 cm depth of substrate was sampled, we assumed the remainder of the substrate was bedrock. Our use of the 2 mm sieve also allowed clear differentiation between substrate that was sand and fine compared to gravel, large, or bedrock.

2.3 | Estimating abundance

We calculated abundance estimates by multiplying the average density, the average river width, and the length of the river from the upstream-most sampling reach to the downstream-most reach. For the abundance calculations, we estimated the uncertainty by calculating bootstrapped 95% confidence intervals using the *boot* package in R and 10,000 replicates. To quantify densities accurately, no samples were excluded from these estimates, even those from air-exposed or unsuitable habitat, unlike the density model described below.

2.4 | Density model

We constructed a hierarchical mixed model using R 3.3.3 (R Core Team 2017, R Foundation for Statistical Computing, Vienna, Austria) to predict *Corbicula* density using river and site (nested within river) as random effects, and water depth and substrate composition as fixed effects. This method includes the preservation of spatial structure at both the site and river level and does not assume independence of sampling points. Preliminary analyses showed that with site and river in the model as a random factor, sampled points along transects within a site were independent. Due to the large number of sample points (1,536), all of these variables could easily be included without over parameterising the model ($n > K \cdot 10$, Moore & McCabe, 1993; Burnham & Anderson, 2002). Prior to inclusion in the

TABLE 1 Summary of rivers and observed densities during summer of 2012

River	Sites	Xsects	Reach length (km)	Avg. width (m)	Avg. depth (m)	Corbicula density (m^{-2})			Estimated Corbicula abundance in reach	Filtration/10 km (m^3/s)
						Avg. (95% CI)	Site min.	Site max.		
Alcovy	4	22	10.4	8.20	0.15	50.4 (35.5–71.3)	6.8	199.9	4,298,112	0.353
Apalachee	4	20	44.3	24.94	0.19	112.2 (86.3–133.4)	13.6	269.7	123,963,272	4,149
Broad	5	21	16.4	43.76	0.26	65.2 (54–71.4)	46.1	97.2	46,791,692	2,518
Middle Oconee	6	30	28.8	46.49	0.24	212.3 (163.5–269.2)	21.8	483.2	284,251,018	6,742

Corbicula densities are based on average densities from field, and we calculated the estimated *Corbicula* within the reach by multiplying the density by the reach length and average width. Collective filtration was calculated by using our observed size specific densities and published length/filtration relationships (Lauritsen, 1986). We normalised collective filtration rates to a 10-km reach to ensure comparability across rivers.

model, we constructed a Pearson's correlation matrix for the substrate categories to determine if any variables had a correlation >0.7 and needed to be removed due to collinearity (Moore & McCabe, 1993); however, no substrate variables were correlated enough to require exclusion. To improve the fit of these models, we excluded points that were known a priori to be unsuitable: those that were dry and exposed at the time of the survey and those that were entirely bedrock, as a burrowing clam would not be able to utilise this habitat. However, we retained any points that were submerged and had any amount of non-bedrock substrate, including points with a small amount of sand over bedrock. Using the MuMIn package in R, we constructed models using all possible combinations of variables, and model weights were calculated for each model, using a modified version of the Akaike Information Criterion (AIC), AICc. AICc was used instead of AIC, as it controls for sample size, though given our large sample size the difference between the two measures was likely to be minimal (Moore & McCabe, 1993). We used model averaging to calculate the average standard β estimate and its associated error for each predictor variable across all possible models. For each variable included in the models, we calculated its cumulative model weight, which is the sum of Akaike weights across all models that included that particular variable. If a variable appears in all candidate models, its cumulative model weight would be 1.0. To determine the overall fit of the model, as well as the relative contribution of random factors (site and river) and fixed (water depth and substrate) factors, we calculated the marginal and conditional R^2 . The marginal R^2 measures the variability in the data that is explained by fixed factors (such as substrate), while the conditional R^2 measures the variability in the data explained by fixed and random factors (such as site and river; Nakagawa & Schielzeth, 2013).

2.5 | Quantifying filtration

We estimated filtration rates in a reach using our observed *Corbicula* size specific densities and filtration per organism from Lauritsen (1986). We selected this estimate because it provides size specific (by length) estimates of filtration using a population from North Carolina that is probably from the same invasive lineage as the Georgia piedmont (Lee, Siripattrawan, Ituarte, & Ó Foighil, 2005) and was conducted under similar water temperatures. We calculated and used a size class-specific filtration rate for each size class (<10 , 10–15, 15–20, 20+ mm), using the midpoint of each class (7.5, 12.5, 17.5, 22.5 mm), with filtration rate (FR) as an exponential function of shell length (SL), specifically, $FR = 3.534SL^{1.723}$ (Lauritsen, 1986). We then multiplied these filtration rates for an individual of a given size class by the total number of individuals in that size class within a 10-km river reach, based on our density survey results to yield a measure of *Corbicula*'s collective filtration rate (F).

To determine the ratio of collective filtration rates relative to residence time within the reach, we used a similar approach to Dame (1996), which has also been used in studies examining the impact of native mussels in Oklahoma rivers (Vaughn, Gido, & Spooner, 2004) and eastern oysters (zu Ermgassen, Spalding, Grizzle, & Brumbaugh,

2013). We estimated the total volume using average river width and water depth measurements from density surveys. We recorded river discharges (Q) in cubic meters per second, using USGS stream gages. All gages were within the sampling reach, or within 10 river km. Using these discharge values, our calculated collective filtration estimates (F , also in m^3/s) data, we divided the hydraulic residence time of water (volume/ Q) within a 10-km portion of the reach by the time needed to filter the water within the 10-km reference reach (volume/ F , in s). Thus, this number estimates the number of times the water in the reach is being filtered by *Corbicula* as it passes through a 10-km reach by calculating the unitless ratio of residence time over filtration time; for simplicity, we have labelled this ratio as the turnover ratio. We calculated turnover ratios for a 10-km segment in each river using two different approaches. First, we examined the turnover ratios under three different empirically observed flows from 1 June to 31 August 2012: the median, maximum, and minimum, thus providing the full range of turnover ratios experienced during the season. We also constructed a kernel density function in R to describe the distribution of turnover ratio using daily flow discharge measurements from the summer of 2012.

3 | RESULTS

3.1 | Field density surveys

A total of 19 sites were sampled in the four different rivers, using 93 transects (Table 1). Across all rivers, 100% of sampling sites, 98% of transects, and 55% of sampling points within the wetted width had *Corbicula* present. Across all sample points, the mean *Corbicula* density was 125 individuals/ m^2 (108–150 individuals/ m^2 95% confidence interval). However, densities ranged substantially between

ivers and sites (Table 1 and Supporting Information Table S1). Overall, averaging across all sites within each river, mean *Corbicula* density was highest in the Middle Oconee River (212 individuals/ m^2 , 163.5–269.2: 95% confidence interval), followed by the Apalachee River (112 individuals/ m^2 , 86–133), and the Broad (65 individuals/ m^2 , 54–71) and Alcovy Rivers (50 individuals/ m^2 , 36–71; Table 1). The maximum observed density for a single sampling point was 8,409 *Corbicula* m^{-2} at Ben Burton Park, in the Middle Oconee River. This site also had the highest overall site density observed (483 individuals/ m^2), as well as the highest transect density (1,114 individuals/ m^2) and the highest overall site density observed.

3.2 | Estimating abundance

Using field measured wetted width and reach length, as well as the average density across all sites within a river, we estimated the total number of *Corbicula* in each sampling reach (Table 1). These estimates ranged from 5.3 million to 236 million individuals, based on variations in density, width, and sampling reach length.

3.3 | Density model

Initial model runs showed that water depth was not a significant predictor of *Corbicula* density and we removed it as a predictor variable in future model runs. The model containing bedrock and gravel substrate proportions, as well as site and river as random effects, had the highest model weight at 0.305 (Table 2). This model had a marginal R^2 , a measure of fit using only fixed effects, of 0.141; the inclusion of random effects of river and site increased the conditional R^2 to 0.317. The difference in conditional and marginal R^2 indicates that the fixed factors (substrate) explain approximately the

TABLE 2 Summary of all candidate models (weight > 0.01) from hierarchical modelling of *Corbicula* density

Variables included	df	AICc	Δ AICc	Weight	Cond. R^2
BR, gravel	6	17815.2	0	0.305	0.317
BR, gravel, sand	7	17816.1	0.90	0.195	0.322
BR, fines, gravel	7	17817.2	1.98	0.113	0.318
BR, gravel, large	7	17817.3	2.02	0.111	0.317
BR, gravel, large, sand	8	17817.9	2.71	0.079	0.322
BR, fines, gravel, sand	8	17818.0	2.79	0.076	0.322
BR, fines, gravel, large	8	17819.2	4.00	0.041	0.318
BR, fines, gravel, large, sand	9	17819.7	4.44	0.033	0.322
Fines, gravel, large, sand	8	17820.9	5.67	0.018	0.294
Gravel, large, sand	7	17821.9	6.66	0.011	0.292
Fines, gravel, sand	7	17821.9	6.70	0.011	0.294

We considered any model with a Δ AICc < 7 as a candidate model (Burnham & Anderson, 2002). BR = bedrock, fines = silt and clay, large = cobble and boulder. We included river and site in all models as random effects.

same amount of variability in density as the random factors (site and river); however, even with both fixed and random factors, two thirds of the variability in density remain unexplained by the model. Across all candidate models, marginal R^2 ranged from 0.130 to .143 and conditional R^2 ranged from 0.284 to 0.322 (Table 2).

The model averaged results indicated that higher densities of *Corbicula* were associated with a higher proportion of gravel and a lower proportion of bedrock, as the confidence intervals for the standard β estimates from model averaging for these variables did not cross zero (Table 3). As indicated by their model weights, gravel (cumulative model weight = 1) was included in every top model and bedrock (cumulative model weight = 0.953) was included in nearly every one (Table 3); these were clearly superior to sand (0.429), large (cobble and boulder, 0.293), and fines (clay and silt; 0.292).

3.4 | Quantifying filtration

Collective filtration rates calculated using size-specific filtration rates and estimated abundances for a 10-km reach ranged from 0.353 to 6.74 m^3/s (Table 1). Based on these collective filtration rates and the estimated water residence time, *Corbicula* turned the water over 0.59–7.33 times as it passed through the 10-km reach at median summer flows in 2012, as measured by USGS stream gages (Table 4). Under the lowest flows observed in the summer of 2012, we calculated river specific turnover ratios that ranged from 1.27 to 18.3 (Table 4, Figure 2), with the highest turnover ratio for the Apalachee River, which had very high *Corbicula* densities and a long residence time. Under high flow conditions, turnover rates were lower, ranging from 0.04 to 1.72. Residence times exceeded the time to filter the water within a 10-km reach (turnover ratio > 1) for all rivers under low flow conditions and three of the four rivers under median flow conditions (Table 4); however, three of the four rivers also experienced higher discharge rates than collective filtration rates (turnover ratio < 1) during high flow conditions (Table 4, Figure 2), including turnover ratios of 0.09 for the Broad River and 0.04 for the Alcovy River under the maximum observed discharge for the summer of 2012.

TABLE 3 Summary of cumulative model weights and standard β values, across all candidate models from hierarchical modelling of *Corbicula* density

Variable	No. of Models	Cumulative model weight	Standard β (\pm SE)
Gravel	11	1.000	144 (\pm 14.2)
Bedrock	8	0.953	-90.5 (\pm 27.1)
Sand	7	0.429	17.1 (\pm 34.9)
Large	6	0.293	1.15 (\pm 13.7)
Fines	6	0.292	0.827 (\pm 13.8)

Model weights for individual variables range from 0 to 1, with 1 indicating that the variable was present in all of the 11 candidate models (weight > 0.01), by weight. In the averaged model, only gravel and bedrock were significant predictors of *Corbicula* abundance, and therefore are the only predictor variables with standard β estimates that do not span zero.

4 | DISCUSSION

Corbicula clearly plays an important role in south-eastern rivers, given that water within a given reach is filtered multiple times as it passes through. The importance of this role is particularly marked during low flow conditions, when turnover ratios within a 10-km reach were as high as 18 times before water flows out of the reach. These high turnover ratios should lower abundances of plankton and invertebrates in the water column. Similar effects have been observed with *Corbicula* in the Potomac River (Cohen et al., 1984; Phelps, 1994) and zebra mussels in the Hudson River, New York (Caraco et al., 1997; Strayer et al., 1999).

The collective filtration rates and turnover ratios provide a tractable summary of the overall impact of a filter feeder which is often used in estuary studies (zu Ermgassen et al., 2013), but there are several important caveats associated with these estimates. First, it is critical to recognise that the turnover ratio is directly impacted by the length of reach selected. As reach length increases, the collective *Corbicula* filtration rates (in m^3/s) increases linearly, while discharge (Q) remains the same. In a river ecosystem, a sensible length for comparison would be the entire river length. However, calculating the turnover time for an entire river would require extrapolating our data well beyond our sampling reaches. Instead, we elected to present these values over a 10-km reach. Choosing a common length provides a standardised measure of comparison between rivers, and also ensures that we do not extrapolate beyond our sampling reach, while also including a long enough sampling area where we would expect a diversity of habitats and substrates. Additionally, we held the volume in a given reach constant under different flows, whereas in reality depths and widths are dynamic properties, increasing during high flows and decreasing during low flows. While turnover ratio is a volume independent metric, because it is the ratio of collective filtration rate and discharge, it is important to recognise this simplification.

Filtration by *Corbicula* is admittedly only one of several potential controllers of organic matter and particles in these systems. Phytoplankton production and allochthonous inputs can add organic matter within our sampling reach, and ultimately filtration and turnover rates make sense in an absolute sense only when comparing them to the net balance of these inputs. By contrast, sedimentation and filtration by other consumers could remove organic matter and particles. We believe collective contributions by other filter-feeders are very low. Previous studies on one of our study rivers found 14.6 ± 13.21 (± 1 SD) collector-filterer benthic insects/ m^2 with a biomass of $7.3 \text{ g} \pm 6.8 \text{ m}^{-2}$ within bedrock shoals habitat (Grubaugh & Wallace, 1995). Sandy areas have been noted for having little insect production (Ligon, Dietrich, & Trush, 1995), so reach-wide, the areal biomass would be substantially lower. Thus, the abundance and biomass of collector-filterers were an order of magnitude lower than what we measured for *Corbicula*. Given these details, insects appear to play a small role in filtration.

We also did not account for any water withdrawals or losses in our sampling reaches, but to our knowledge the only significant water

TABLE 4 Summary of filtration rates and turn-over ratios under the median, minimum, and maximum observed flow (Q) rates in each of the four rivers from the summer of 2012 (1 June–31 August)

River	Minimum Q		Median Q		Maximum Q	
	Residence time (hr)	Turn-over ratio	Residence time (hr)	Turn-over ratio	Residence time (hr)	Turn-over ratio
Alcovy	59.97	6.24	11.99	1.25	0.40	0.04
Apalachee	58.38	18.32	23.35	7.33	5.49	1.72
Broad	15.68	1.27	7.32	0.59	1.10	0.09
Middle Oconee	31.83	6.80	14.86	3.17	2.48	0.53

All values are normalised to a 10-km sampling reach, to standardise comparisons between sites of equal distance. At median flow rates in three of the four rivers sampled, *Corbicula* turns the water column over more than once in a 10-km reach. Turn-over ratios were above one under low flow conditions in all four rivers and below one under high flow conditions in three of the four rivers.

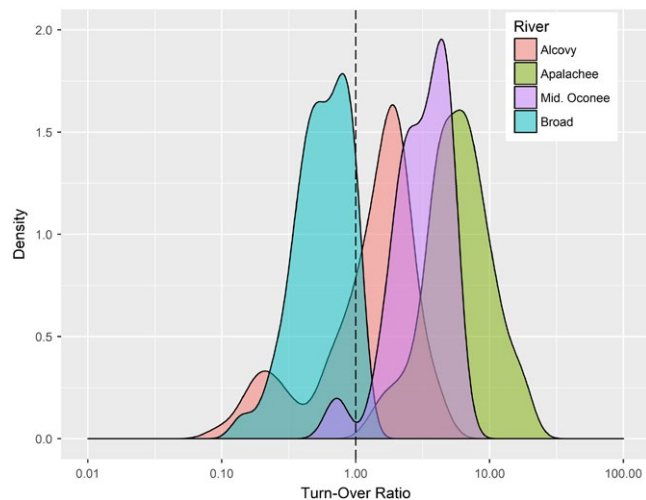


FIGURE 2 Density function of turnover ratio (F/Q) of *Corbicula* in a standard 10-km reach in four different Georgia piedmont rivers based on: daily discharge (Q) observed at nearby USGS stream gages during conditions of June, July, and August 2012 and calculated collective filtration rates based on size specific densities (Table 4). The dashed vertical line ($x = 1$) is a useful reference point to indicate where water is leaving the reach at the same rate it is being filtered and the turn-over ratio is 1. Values <1 indicate that water is leaving the reach faster than it is being filtered and >1 indicate that water is being filtered faster than it is leaving the reach. The Broad River is the only river with its median and mode below one; however, even it at the lowest flows observed in the summer of 2012, experienced turn-over ratios >1 (the right-most tail of its distribution). Note the x-axis is on a log scale

withdrawal was located just downstream of the Middle Oconee Ben Burton Park site (Supporting Information Table S1) and upstream of the USGS gage we used in our flow analysis. While there are several small creeks entering our sample reaches, there are no major confluences within our sampling reaches. Despite these caveats, the calculation provides an estimate to enable relative comparisons of the ecological role of *Corbicula* among these reaches.

It is also assumed that all water within the reach is equally likely to be filtered and that *Corbicula*'s filtration rate is constant under all flow conditions. As a benthic dwelling organism, *Corbicula* is

filtering water more frequently from the benthic boundary layer, and therefore, removing disproportionately more of the seston from that portion of the water column. However, *Corbicula* has had water column wide impacts on much larger rivers than those sampled in this survey, such as increased water clarity and declines in chlorophyll a in the Potomac River (Phelps, 1994). *Corbicula* is likely to be able to have impacts throughout the entire water column in the sampled rivers. Finally, *Corbicula*'s filtration rates are altered by the amount of suspended sediment in the water column (Way, Hornback, Miller-Way, Payne, & Miller, 1990). Under higher flow conditions, it is likely there will be more suspended sediment in the water, further decreasing the already lower turnover ratios.

The average density and maximum density of *Corbicula* observed in the Georgia piedmont are similar to reported densities across the U.S.A. and Europe. Belanger, Farris, Cherry, and Cairns (1985) found maximum densities of 2,286 to 11,522 m^{-2} in Virginia rivers and Pigneur et al. (2014) found densities between 50 and 900 m^{-2} in European rivers. In the western U.S.A., densities were slightly lower—reaching a site wide maximum of 201 m^{-2} in the San Joaquin River and its tributaries in the Central Valley of California (Brown, Thompson, Higgins, & Lucas, 2007), compared to our maximum site average of over 500 m^{-2} in the Middle Oconee River. The substrate preference for *Corbicula* was slightly coarser than that observed by Belanger et al. (1985); however, in California, higher densities and biomass of *Corbicula* were associated with larger median substrate size (Brown et al., 2007). This preference for coarser substrate may be due to factors that covary with substrate composition. Under certain circumstances, sand appears to be an important predictor of *Corbicula* density, as shown by the very high variability and large confidence interval in the standard β estimate for the percent of sand. We observed that in shoals habitats with bedrock as the dominant substrate type, areas with sand often had very high *Corbicula* densities. One example of this is the Ben Burton Park site on the Middle Oconee River, where we found the highest densities at the point, transect, and site levels. However, in sandy run and bar habitats, areas that are primarily sand are likely to be unstable. In these habitats, disturbance could displace *Corbicula* and wash them downstream, especially given that they burrow very shallowly in the sediment (McMahon & Bogan, 2001). Finer sediment is likely

to have lower dissolved oxygen in the interstitial water and, given that dissolved oxygen may be limiting under extreme circumstances, *Corbicula* in finer sediment may experience higher mortality under stressful conditions.

Although river, site, and substrate can explain nearly one third of the variation in *Corbicula* density, two thirds of its variation is still unexplained. Furthermore, the marginal R^2 that measures the variability in the data that is explained by fixed factors—in this case, substrate—was only 14%. Factors that have been found to influence *Corbicula* abundance in other studies include temperature (McDowell, McDowell, & Byers, 2017; Smith et al., 2018), the density of native mussels (Vaughn and Spooner 2006), the abundance of fish predators (Robinson & Wellborn, 1988), and water level fluctuations (Werner & Rothhaupt, 2008).

Other anthropogenic impacts in these rivers have led to major declines in unionid densities, so *Corbicula* is the only species providing the critical ecosystem functions associated with their functional group, such as filtration (Vaughn & Hakenkamp, 2001). Because unionids are in dramatic decline throughout the entire south-eastern U.S.A. due to unrelated anthropogenic stressors, such as increased sediment loading and dam construction (Neves et al., 1997), *Corbicula* is the only filter-feeding bivalve with notable biomass within many south-eastern rivers. A broader survey of the region would also allow the impact of climate and geographic factors, such as altitude or bioclimatic variables, on density to be explored, which was not possible given the scope of our study. Bioclimatic variables, particularly minimum temperature, control *Corbicula*'s distribution within the U.S.A. (McDowell, Benson, & Byers, 2014). This increases the importance of understanding what controls the density and distribution of *Corbicula*, as well as understanding its impact on aquatic ecosystems. However, the ecosystem functions and services are now concentrated within a single species, rather than spread out across an extremely diverse group. By having the services provided within a single species, the overall ecosystem services could be temporally variable, should population decline of *Corbicula* occur.

Episodic (but temporary) *Corbicula* mass mortality events have been documented in a variety of systems globally (Bodis, Toth, & Sousa, 2014; Ilarri, Antunes, Guilhermino, & Sousa, 2011; Werner & Rothhaupt, 2008), including in Georgia (McDowell et al., 2017). The loss of *Corbicula* would cause the ecosystem functions and services provided by filter feeding bivalves to vary temporally with variations in *Corbicula* populations sizes (Strayer et al., 2017), whereas a river with an intact, diverse native mussel community would not experience as large a fluctuation. This change in variability would be a product of both *Corbicula*'s sensitivity to stressors relative to native mussels (Haag, 2012), and also the inherent difference in the stability and the response to stressors of a diverse community compared to one dominated by a single species (Tilman et al., 1996).

The importance of understanding the role of *Corbicula* in the studied rivers goes well beyond the Georgia piedmont. Rivers throughout the world are losing native mussel species, and *Corbicula* is likely to spread poleward with warming winter

temperatures (Crespo et al., 2015; McDowell et al., 2014). In the future, many more rivers will probably look like Georgia piedmont rivers—large amounts of sedimentation, low native mussel diversity and biomass, and abundant *Corbicula*. Understanding these impacts in other areas where *Corbicula* is well established will allow us to better forecast the future state of rivers. Lessons from *Corbicula*'s dominance in these systems apply more broadly, as the challenges of invasive species, biotic homogenisation, and the loss of functional redundancy are not unique to rivers, nor aquatic ecosystems as a whole (McKinney & Lockwood, 1999) and currently are reshaping ecosystems globally (Olden, 2006). Understanding the confluence between biotic homogenisation and ecosystem function is critical to both direct conservation research and forecast the future states of ecosystems (Olden, Poff, Douglas, Douglas, & Fausch, 2004).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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