ASSESSING THE ECOLOGICAL ROLE OF THE INVASIVE CLAM CORBICULA FLUMINEA IN SOUTHEASTERN RIVERS AND NATIONWIDE

by

WILLIAM GILES MCDOWELL II

(Under the Direction of James E. Byers)

ABSTRACT

Globally, ecosystems are facing myriad stressors, and climate change and invasive species are two of the most pervasive. Not only does the impact of each stressor need to be understood singly, but their interactions may produce novel, unexpected results. The impact of an invasive species is a function of its range, abundance, and effects. We examined the impact of an abundant and widespread invasive species, the freshwater clam *Corbicula fluminea*, by examining its range, abundance, and effects, and how these could be impacted by interactions with climate change. To understand the range of *Corbicula*, we used two species distribution modeling approaches: a logistic regression and Maximum Entropy modeling. Logistic regression indicated that climate was more important than habitat in controlling *Corbicula*'s distribution, and both models identified minimum temperature as the most important controller of *Corbicula*'s distribution. Applying the Maximum Entropy model to future climate scenarios showed large expansions of *Corbicula*'s range into New England and the northern Midwest. Thus, the impacts on rivers from climate change will be compounded by the addition of *Corbicula* and its own influences on ecosystem function. To estimate density and the impacts of *Corbicula* in the Georgia Piedmont, systematic sampling was used in four rivers spanning three of the four major watersheds in Georgia. Overall, densities ranged from 60/m^2 to 175/m^2, and published filtration, sedimentation, and excretion rates indicate that *Corbicula* play an important role in these ecosystems. The impact of *Corbicula* may be impacted by the occurrence of extreme events. During the summer of 2012, which was hot and dry, a mass mortality event occurred where over 99% of the *Corbicula* in a section of the Broad River died. As *Corbicula* is the only filter-feeding bivalve in the system with significant biomass, this event led to the near complete halting of the ecosystem services provided by bivalves. The clam population recovered within a year. Overall, *Corbicula* is having a large impact on aquatic ecosystems in the southeast. The impacts in this region could provide estimates for future scenarios in northern parts of the United States, as *Corbicula*'s distribution spreads with warming winter temperatures.

INDEX WORDS: *Corbicula*, Invasive species, Climate change, Species distribution modeling, Mass mortality

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

The Earth's ecosystems are changing. Human impacts are nearly ubiquitous, and include global changes to the nitrogen cycle, fundamental changes in habitats, and alterations of climate (Vitousek et al. 1997, Millennium Ecosystem Assessment 2003). Temperatures have risen 0.19 C per decade over the last 25 years, and sea ice is disappearing and sea levels are rising faster than predicted by climate models (Allison et al. 2009). Climate changes are already impacting species (Parmesan and Yohe 2003). Coupled with these climate changes, invasive species dominate the biota in many ecosystems (Wrona et al. 2006). The theoretical potential for interactions between invasive species and global change is well established (Rahel and Olden 2008, Hellman et al. 2008, Strayer 2010). To effectively manage changing ecosystems, ecological forecasts are critical (Clark et al. 2001), and these must incorporate the impact of the interaction between invasive species and climate change.

Impact of an invasive species, as defined by Parker et al. (1999), is a product of the range, abundance, and per capita effect of the species. A key principle of many ecological studies is scaling up small scale studies to estimate overall impacts over a larger spatial scale, especially for invasive species (Dick et al. 2002, Kercher and Zedler 2004, Barber et al. 2008). Therefore, the many small scale experiments conducted under laboratory or mesocosm conditions require solid estimates of the abundance and variability in abundance to accurately predict an invasive species overall impact. Additionally, if general rules can be determined as to what controls the abundance and distribution of the invasive species, more accurate predictions can be made to a variety of systems, without requiring labor intensive field sampling.

Invasive species can have significant impacts on ecosystem function (e.g. Gordon 1998, Strayer et. al 1999, Anderson and Rosemond 2007). Mollusks, in particular, can dominate ecosystem functions whether they are native (Covich et al. 1999, Vaughn and Hakenkamp 2001) or invasive (Heath et al. 1995, Strayer et al. 1999, Zhu et al. 2006, Caraco et al. 2007) through changing nutrient dynamics, sedimentation, and zooplankton communities (Vaughn and Hakenkamp 2001). For example, the New Zealand mud snail (*Potamopyrgus antipodarum*) has been shown to dominate nitrogen cycling in small Montana streams, supplying over two thirds of the ammonium demand in the stream through excretion thanks to extremely high densities (Hall et al. 2003). Zebra mussels (*Dreisseina polymorpha*) in the Hudson River filter 10-100% of the water column each day, reducing chlorophyll a and microzooplankton biomass by approximately 80% thanks to both high densities and high per capita filtration rates (Strayer et al. 1999). It has also been recognized that invasive species may have both positive and negative impacts on ecosystem services provided to humans, so a well-rounded approach in estimating and understanding their impacts is required (Pejchar and Mooney 2009).

Climate changes are already impacting species distributions in many ecosystems throughout North America (Parmesan and Yohe 2003). Among aquatic ecosystems, large changes in species distribution and abundance are predicted to occur over the next several decades (Wrona et al. 2006). Invasive species represent a significant component of the aquatic communities in North America, with well-documented interactions with native species (Cohen and Carlton 1998, Mack et al. 2000). Here, I attempt to understand the overall impact of a widespread, abundant freshwater invasive by assessing its range, abundance, and effects, as well as how these components might change with climate change.

Background

Corbicula is native to southeastern Asia and was first observed in the United States in the Columbia River, Washington in 1938 (McMahon and Bogan 2001). It is now found throughout a large portion of the United States (USGS NAS database). Since first being observed in Georgia in 1979, *Corbicula* has become the dominant bivalve in many southeastern rivers, replacing the native unionid mussels, although little evidence exists of competitive interactions between the two. There are several differences between the life history strategy of *Corbicula* and that of the native unionid mussels. *Corbicula* is a classic r-selected species – they have a short life span of three to five years, can reproduce at six months old, and will colonize risky habitats such as sand bars that unionids typically avoid. Additionally, as a self-fertilizing hermaphrodite, *Corbicula* has a very simple reproductive strategy (McMahon and Bogan 2001), unlike unionids which have glochidial larvae which must encyst on the gills of fish. However, *Corbicula* is also more vulnerable to many stressors than unionids, including high temperatures (Ilarri et al. 2011), low temperatures (Werner and Rothhaupt 2008), low dissolved oxygen, and desiccation (McMahon and Bogan 2001). However, unionids can live upwards of 80 years, are able to survive adverse conditions for several weeks, and have much lower reproductive outputs (McMahon and Bogan 2001). Populations of each are able to survive adverse conditions through these combinations of traits: *Corbicula* through resilience following large mortality events thanks to high reproductive rates and unionids through resistance to negative impacts from difficult environments.

Corbicula has specific traits that make it very likely to have significant impacts on Piedmont rivers and fill the role previously filled by native unionids. Specifically, it has a high filtration per biomass rate (McMahon and Bogan 2001), can remove large amounts of suspended material from the water column (Atkinson et al. 2010), and is a particle generalist (Atkinson et al. 2011). These traits, combined with its often high densities, make *Corbicula* it an important player in southeastern river ecosystems.

Additionally, research using laboratory mesocosms has shown that the nutrients released during a mass mortality event can raise ammonia concentrations to toxic levels in both the porewater and the water column (Cooper et al. 2005, Cherry et al. 2005). With increased water withdrawals, higher temperatures, and changes in the timing and magnitude of precipitation, these mass mortality events could become more common and larger in scale.

Summary of Chapters

In Chapter 2, we set out to understand what habitat and climate variables control the range of *Corbicula* by combining multiple data sources and modeling methods, including logistic regression and Maximum Entropy modeling. We found that climate variables, minimum temperature in the coldest month in particular, were more important in controlling *Corbicula*’s distribution. We applied a climate-only MaxEnt model to a suite of future climate scenarios, which predicted a large expansion of *Corbicula*’s range by the 2080s, into the Great Lakes, the northern Midwest, some river valleys in the interior Western United States, and New England.

In Chapter 3, we conducted extensive surveys in four rivers of the Georgia Piedmont to provide accurate estimates of *Corbicula* density. These estimates were then scaled up using per capita estimates of filtration. Additionally, we modeled density using habitat variables collected during these surveys, including substrate composition and depth, in order to try and forecast densities for unsurveyed rivers. Across all four rivers, *Corbicula* densities were approximately 100 individuals/m2. *Corbicula* are filtering water faster than it leaves a 10 km reach, indicating that they are playing an important role in sediment dynamics in these rivers, particularly under low summer flows. Our model identified coarse sand to cobble sized substrate as suitable for *Corbicula*, but the model explained less than 20% of the variance in density, indicating that a large degree of stochasticity or unmeasured variables influence its density.

Finally, in Chapter 4, we examined the consequences of a mass mortality event in response to extremely high temperatures and low flows in the Broad River, Georgia. During this event, over 99% of the *Corbicula* in the sampled reach died. This led to increased concentrations of phosphate and total dissolved phosphorus, but no change in nitrogen. Also, as *Corbicula* was the only filter-feeding bivalve in the system with significant biomass, this event led to the near complete cessation of the ecosystem services provided by bivalves. These events could become more common in the future, with increasing temperatures and lower precipitation frequency; another way in which climate change could alter the overall impact of *Corbicula*.

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CHAPTER 2

CLIMATE CONTROLS THE DISTRIBUTION OF A WIDESPREAD INVASIVE SPECIES: IMPLICATIONS FOR FUTURE RANGE EXPANSION[1]

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[1] McDowell, W.G., A.J. Benson, and J.E. Byers. Accepted by Freshwater Biology. Reprinted here with permission of the publisher.

Abstract

Two dominant drivers of species distributions are climate and habitat, both of which are changing rapidly. Understanding the relative importance of variables that can control distributions is critical, especially for invasive species that may spread rapidly and have strong effects on ecosystems. Here we examine the relative importance of climate and habitat variables in controlling the distribution of the widespread invasive freshwater clam *Corbicula fluminea* and we model its future distribution under a suite of climate scenarios using logistic regression and Maximum Entropy modeling (MaxEnt). Logistic regression identified climate variables as more important than habitat variables in controlling *Corbicula* distribution. MaxEnt modeling predicted *Corbicula*'s range expansion westward and northward to occupy half of the contiguous United States. By 2080, *Corbicula*'s potential range will expand 25-32%, with more than half of the continental United States being climatically suitable. Our combination of multiple approaches has revealed the importance of climate over habitat in controlling *Corbicula*'s distribution and validates the climate-only MaxEnt model, which can readily examine the consequences of future climate projections. Given the strong influence of climate variables on *Corbicula*'s distribution, as well as *Corbicula*'s ability to disperse quickly and over long distances, *Corbicula* is poised to expand into New England and the northern Midwest of the United States. Thus, the direct effects of climate change will probably be compounded by the addition of *Corbicula* and its own influences on ecosystem function.

Introduction

Changes in climate are already affecting species distributions in ecosystems throughout North America (Parmesan and Yohe 2003). Many researchers are using species distribution modeling to examine how ranges may shift. This approach has been criticized, however, because most models have not included non-climate variables, such as biotic factors like competition and predation, and abiotic factors such as habitat attributes, that could themselves influence distributions (Woodward and Beerling 1997, Pearson and Dawson 2003, Jeschke and Strayer 2008, Zarnetske et al. 2012). We must understand the relative importance of climate and non-climate variables in controlling present-day distributions in order to predict how climate changes will affect species distributions.

Making accurate ecological forecasts is a critical part of ecological research (Clark et al. 2001). Climate changes are not occurring in isolation, but rather are coupled with other stressors such as habitat loss and land-use changes, eutrophication and invasive species. In order to understand the overall impact of these changes, we must also examine their interactions. Large changes in the distribution and abundance of aquatic organisms are predicted to occur over the next several decades (Wrona et al. 2006). Understanding changes in distribution is especially important for invasive species, because they often are not yet at equilibrium, represent a significant component of aquatic communities and can interact strongly with native species (Cohen and Carlton 1998, Mack et al. 2000, Byers et al. 2002). The conceptual basis for understanding how climate change could alter distributions and impacts of invasive species is well developed (Rahel and Olden 2008, Hellman et al. 2008, Strayer 2010), but few specific predictions have been made. Important topics to consider include quantifying how an invasive species may begin to spread with warming climate (Hellman et al. 2008) and assessing how these changes in distribution will affect aquatic ecosystems. The development of a more detailed understanding of the response of invasive species to climate change is thus critical to managing their impact and limiting their further spread.

Freshwater molluscs are an ideal group on which to focus because they provide important ecosystem services such as filtration and nutrient uptake (Strayer et al. 1999, Vaughn and Hakenkamp 2001). Also, invasive freshwater molluscs have had major impacts on aquatic ecosystems, including the New Zealand mud snail *Potamopyrgus antipodarum* that dominates nutrient cycling in western United States streams (Hall, Tank, and Dybdahl 2001), zebra mussels (*Dreissena polymorpha*) that remove phytoplankton and increase water transparency in the Great Lakes and the Hudson River (Caraco et al. 1997, Hecky et al. 2004) and the golden mussel *Limnoperna fortunei* that increases transparency and decreases primary productivity in South American lakes and reservoirs (Boltovskoy et al. 2009).

Of the common aquatic invaders in the contiguous United States, the Asian clam *Corbicula fluminea* (hereafter *Corbicula*) is the most widely distributed (McMahon and Bogan 2001). Since it was first introduced to Washington State in 1938, *Corbicula* spread eastward in the 1950s and reached the southeastern United States in the 1960s (McMahon and Bogan 2001). *Corbicula* has invaded rivers throughout the United States, from southern New York to Florida on the east coast of the United States, west to Texas on the Gulf Coast, and throughout the Midwest and west coast states (McMahon and Bogan 2001). *Corbicula* can reach densities of several thousand individuals per square meter (Cohen et al. 1984, Phelps 1994, Cataldo and Boltovsky 1999, Sousa et al. 2008b) and can strongly affect river ecosystems. Documented effects include decreasing phytoplankton concentrations, reducing rates of organic matter processing and reducing the abundance of submerged aquatic vegetation through indirect effects (Cohen et al. 1984, Lauritsen 1986, Phelps 1994, Hakenkamp and Palmer 1998,).

The status of *Corbicula* as an invader that disperses rapidly, presumably aided by some means of human-mediated transport, makes it especially capable of invading new habitats as they become suitable. Therefore it is critical to understand how climate changes may alter the ability of *Corbicula* to persist in new habitats. This paper uses two different modeling approaches to determine the variables that control the distribution of *Corbicula*. First, to compare the relative importance of climate and habitat as predictors of *Corbicula* presence and absence, we constructed logistic regression models that examine all combinations of the predictor variables. Second, we created a Maximum Entropy (MaxEnt) model that only uses data on *Corbicula* presence and produces a continuous, spatially explicit prediction of suitability. To create this continuous prediction, the predictive variables must be spatially continuous, and therefore the model is limited to climate-related predictive variables. Results of the model are then used to assess likely range expansions of *Corbicula* in the United States over the coming decades.

Methods

Modeling Approaches

We modeled suitability of locations within the continental United States for *Corbicula* using a logistic regression and a MaxEnt model. The logistic regression uses a general linear model to determine the suitability of a location using known presence and absence locations. A logistic regression is ideal for modeling binary data, such as presence and absence, as it has a higher power than the analysis of transformed data (Warton and Hui 2011). The logistic regression also allowed us to include habitat variables, such as water chemistry and substrate variables that were only available as discrete data points, as well as discretized climate variables.

By including both climate and habitat variables, we could test the importance of habitat and climate factors alone and in combination. Logistic regression, however, is only able to model habitat suitability for individual points; sampling these points is labour intensive because true presence and absence points are required, and the number of sites included is much lower than for the MaxEnt model.

We also created a MaxEnt model, which is a machine learning approach that uses presence-only data and spatially explicit data layers of predictive environmental variables to model species distributions (Elith et al. 2006). MaxEnt modeling outperforms other commonly used species distribution models (e.g. GARP, BIOCLIM), because it works well with incomplete data, small sample sizes and gaps, and therefore is well suited to modeling work with invasive species (Jarnevich et al. 2006, Kumar et al. 2009).

MaxEnt has two major advantages over logistic regression. First, MaxEnt is able to use presence-only records, allowing a much larger set of known *Corbicula* locations to be used. Second, with the availability of spatially explicit predictive climatic variables across a region, MaxEnt directly produces a spatially explicit output that describes how suitable an area is for *Corbicula*. Logistic regression, in contrast, makes predictions for individual points based on a broad range of site-specific habitat information, but spatial gaps in data availability limit its ability to produce a continuous spatial output. Because we elected to create a continuous MaxEnt model using climate variables, we cannot include the habitat data because continuous habitat data are generally not available. Thus unlike logistic regression, our MaxEnt model cannot readily allow comparisons of the relative importance of habitat and climate variables. By combining logistic regression and MaxEnt, however, we were able to identify habitat variables that influence *Corbicula*'s distribution that could not be included in the MaxEnt model, quantify the amount of variability in *Corbicula*'s distribution that models looking only at climate factors on *Corbicula* can explain, and create spatially explicit predictions about the potential distribution of *Corbicula* under future climate scenarios.

Data Sources

Corbicula locations

Data on known locations of *Corbicula* came from two primary sources: the Environmental Protection Agency's (EPA) Environmental Monitoring and Assessment Program (EMAP) and the United States Geological Survey's Nonindigenous Aquatic Species (NAS) Database. During the EMAP surveys, a total of 1392 stream sites in the coterminous United States were sampled by EPA staff scientists and contractors with identical methods during summer months in 2000 – 2004, with most sampling occurring in 2003 and 2004. These data are freely available for ecological modeling (Paulsen et al. 2008). The logistic regression can only use the points from the EMAP surveys, as it requires true presence and absence points. For the MaxEnt model, we combined the presence locations from the EPA EMAP surveys and the USGS NAS Database, because unlike logistic regression, a MaxEnt model does not require true absence points. This allowed us to use the locations from the USGS NAS Database, despite the lack of known absence points associated with them, increasing the overall number of *Corbicula* locations in the model by an order of magnitude. Many locations within the USGS NAS Database are clustered within small geographic areas. To prevent giving too much weight in the MaxEnt model to small areas with many known *Corbicula* locations, the list of known points was converted to a raster with the same cell size as the predictive climate variables using ArcCatalog (ESRI, Redlands, CA, USA). This raster was then converted back to a list of points.

By doing this, we ensured that no single cell had more than one location to it, reducing the total number of *Corbicula* locations from over 3,500 to approximately 2,800.

Predictive variables

During EMAP sampling a variety of data were collected, including water quality, habitat and substrate measurements (Supporting Information Appendix S1). These habitat variables were only used for the logistic regression, as they are not available for points in the USGS NAS Database, nor are these variables available in a continuous, spatially explicit data layer. Climate data were used as predictive variables in both the logistic regression and the MaxEnt modeling. We used BioClim variables, a set of seventeen climate variables that provide a continuous data layer of climatic variables that are interpolated between weather stations. BioClim variables focus on aspects that could control species distributions, such as annual temperature, timing and amount of precipitation, and extreme conditions such as high temperature in the warmest month and low temperature in the coldest month (Hijmans et al. 2005) (Supporting Information Appendix Table S2). Because the logistic regression models specific points, rather than a continuous geographic area, BioClim variable values were extracted to the sampling points from the EMAP surveys.

Multicollinearity between explanatory variables can lead to inaccurate model parameterization and the exclusion of significant predictive variables (Graham 2003). To avoid multicollinearity among the predictive variables, pairwise Pearson's correlation coefficients were calculated for all combinations of the variables, and one variable from any pair of variables with a Pearson's correlation coefficient greater than 0.7 ($r^2>0.49$) was removed from consideration (Moore and McCabe 1993). We selected the variable to remove based on biological mechanisms. For example, calcium was highly correlated with conductivity ($\rho=0.94$); from this pair, conductivity was removed, due to the documented importance of calcium concentrations for other invasive shell-building molluscs, such as the zebra mussel (Hincks and Mackie 1991, Whittier et al. 2008).

For the logistic regression, 16 habitat variables were retained following the removal of collinear pairs (Appendix A). For climate variables, which were used in both logistic regression and MaxEnt modeling, four of the original 17 remained following the removal of collinear variables (Appendix A). No habitat variables were collinear with climate variables. The four climate variables that remained were: annual precipitation, precipitation in the warmest quarter, precipitation in the driest quarter and minimum temperature in the coldest month. Maximum temperature in the warmest month was initially considered as a predictive variable, as mass mortality of *Corbicula* has been observed at high temperatures (Cohen et al. 1984, Ilarri et al. 2011) and a warming climate could increase temperatures beyond *Corbicula*'s maximum temperature of 35° C (McMahon and Bogan 2001). However, in initial model runs that included maximum temperature in the warmest month, there was a positive correlation between maximum temperature in the warmest month and *Corbicula* presence. *Corbicula* are sensitive to high water temperatures (McMahon and Bogan 2001), which can lead to mass mortality events (Cohen et al. 1984, Illari et al. 2011), and there is no clear mechanism as to why higher maximum temperatures would lead to an increased likelihood of *Corbicula* presence. More importantly, its inclusion precluded the inclusion of a related, collinear variable, namely minimum temperature in the coldest month, which has a strong effect on *Corbicula* presence and solid mechanistic underpinnings (Werner and Rothhaupt 2008). Thus, maximum temperature in the warmest month was the collinear temperature variable we excluded from the model.

Comparing Habitat and Climate Variables: Logistic Regression

To identify which individual variables should be included, we conducted a stepwise regression in R (R 2008) and evaluated candidate models with AICc, a modified version of Akaike's Information Criterion (AIC) (Akaike 1973) that is adjusted to account for a finite sample size (Burnham and Anderson 2002). This model initially considered the 16 habitat variables and the four climate variables remaining following the removal of collinear variables as described above. From the results of the stepwise regression, a list of candidate models was created using methods described in Burnham and Anderson (2002). Using model weights, variables that appeared in a total of 0.95 candidate models by weight were identified, and were classified as either "Habitat" (from the EPA EMAP surveys) or "Climate" (from BioClim variables).

To determine the relative importance of climate and habitat variables in controlling *Corbicula*'s presence or absence, three models were created: a model with only habitat variables, a model with only climate variables and a model with both climate and habitat variables. These three models were compared using AICc, model weights and pseudo-R^2, calculated for the three different models.

Spatially Explicit, Climate-Only Model: Maximum Entropy Model

We created the MaxEnt model with MaxEnt software (Version 3.3.3e, Phillips, Anderson, and Schapire 2006) using the 2800 known locations of *Corbicula* from our data sources. A MaxEnt model does not use known absence points, instead it generates pseudo-absences from a defined spatial area. This approach has been criticized, especially when it includes areas that have not been sampled or novel habitats (Peterson et al. 2007). However, given the extremely wide distribution of *Corbicula* within the United States already and because the points from the EPA EMAP surveys are part of a systematic, nationwide survey of streams and rivers, creating pseudo-absences from the entire continental United States avoids these issues (Phillips 2007). Using predictive variables input as a continuous ASCII grid, the model fits the distribution of a species over the area of the grid. A MaxEnt model uses several different methods, including linear, non-linear, hinge and threshold functions, to fit the distribution of known points the best possible way (Elith et al. 2006). MaxEnt creates a model from the predictive variables; model results range from zero to one and are interpreted using *a priori* selected thresholds based on varying levels of permissiveness. For example, the "minimum training presence" threshold is typically the lowest threshold, and therefore the most permissive threshold. Using this threshold the model output does not need to be very close to 1 in order for the area to be deemed climatically suitable, and thus it will classify a much larger area as suitable for *Corbicula* than other, more stringent (higher) thresholds. We selected three different thresholds to interpret the MaxEnt model, ranging from liberal (equate entropy of thresholded and original distributions) to conservative (equal test sensitivity and specificity).

Using current climatic data, a MaxEnt model was created using the four independent BioClim variables. If a variable did not contribute significantly to the model fit, as measured by percent contribution to the overall model fit and by permutation importance (a measure of how much the model is changed by random variation in a given variable), that variable was removed from the model and the more parsimonious model was re-run. Cross validation was performed on five replicate MaxEnt models, using 80% of the known *Corbicula* locations to train the model and the remaining 20% to test the model. Test data were sampled without replacement, so that each of the 2,800 *Corbicula* locations was used in the test set once and the training set four times. To prevent over-fitting of the response curves of predictive variables, a regularization multiplier of 10 was used. This prevented the inclusion of complicated higher order polynomial functions that, despite fitting the data better, produced response curves that were not biologically meaningful.

We applied the MaxEnt model created using current climate conditions, and using the threshold values described above, to three projections of climate in the year 2080 corresponding to different emission scenarios: A2a, which includes large human population growth, large amounts of energy use and slow technological change; A1b, which includes lower population growth, high energy use and a mix of fossil fuel and other energy sources; and finally the B2a scenario, which includes medium population growth and a mix of energy sources that is consistent with usage today (IPCC 2007). These scenarios provide a range of projected temperature increases by 2080, ranging from 2.4 C (B2a) to 3.4 C (A2a) (IPCC 2007). Although this is not the full range of projected temperature rise predicted by other models, the selected climate data have a consistent, simple, straightforward methodology for spatial downscaling (Delta Method) and use the same source model (Canadian Centre for Climate Modeling and Analysis) while varying only human population and energy sources.

Results

Comparing Habitat and Climate Variables: Logistic Regression

Stepwise regression identified nine variables that appeared in more than 95% of candidate models, by weight. Six were habitat variables (water depth, ammonium, pH, percent fine gravel, total suspended solids and percent agriculture in the catchment) and three were climate variables (minimum temperature in the coldest month, annual precipitation and precipitation in the driest quarter) (Table 2.1). When comparing the relative importance of the six habitat variables and three climate variables, the combined model, which included all nine variables, had the best fit for *Corbicula* presence and absence from the EPA EMAP data, as measured by AIC, Area Under the Curve (AUC) and pseudo-R^2 (Figure 2.1, Table 2.2). However, the climate model performed nearly as well, while the habitat-only model lagged behind both of the other two candidate models in all measures of fit (Table 2.2).

Spatially Explicit, Climate-Only Model: Maximum Entropy Model

The final MaxEnt model included three climatic variables: minimum temperature in the coldest month, precipitation in the warmest quarter and precipitation in the driest quarter (Appendix S2). Initial runs of the MaxEnt model indicated that annual precipitation, one of the four *a priori* climate variables initially considered (Appendix S2), was not a significant predictor of *Corbicula* presence or absence. Annual precipitation was removed from the model, and a final model was run. From the final model run, the replicates had an average AUC of 0.762 (out of 1) for the test data, with a standard deviation of 0.009 (Figure 2.2). Of the three variables included in the final model, minimum temperature in the coldest month was the most important by percent contribution (58.4%) and permutation importance (55), followed by precipitation in the driest quarter (27.9% contribution and 26.1 permutation importance) and finally by precipitation in the warmest quarter (13.7% contribution and 18.9 permutation importance).

Comparing the climate variables identified in the logistic model and the MaxEnt model, precipitation in the driest quarter and minimum temperature in the coldest month were identified in both models as important controllers of *Corbicula* distribution. The MaxEnt model identified precipitation in the warmest quarter as an important variable, while annual precipitation was retained in the logistic regression. Precipitation in the warmest quarter was a candidate variable for the logistic regression, but was not identified as a significant predictor of *Corbicula*'s distribution. Likewise, annual precipitation was a candidate variable in the MaxEnt model, but was not a significant predictor of *Corbicula*'s distribution using that modeling approach.

The MaxEnt model suggests that *Corbicula* is limited to southern New York and the southern extent of the Great Lakes under current climate conditions, leaving much of the Midwest climatically unsuitable (Figure 2.3a). Under all three future climate scenarios, the range is predicted to expand throughout New England, the Midwest and into the Great Lakes by 2080, or potentially sooner (Figure 2.3b, c, d). The exact range varies between the three climate scenarios, but the overall range increase is fairly consistent. Using the intermediate threshold (10% training presence) presented in Figure 2.3, *Corbicula*'s potential range is predicted to increase from 37% of the United States by area to 46, 49 or 48.5% under the B2A, A1B and A2A climate scenarios, respectively. This increase in range represents a total areal increase of 25-32% in the distribution of *Corbicula*, and this occurs despite slight range retractions in Louisiana and southern Florida under the A1B climate scenario (Figure 2.3c) and nearly all of Florida in the A2A climate scenario (Figure 2.3d).

Discussion

The distribution of the widespread invasive freshwater clam *Corbicula fluminea* is controlled both by habitat variables, such as substrate and pH, and by climate variables, indicating the potential interaction between invasive species and climate change, as predicted by many studies (Rahel and Olden 2008, Hellman et al. 2008, Strayer 2010). Within our extensive data set, climate variables are more important than habitat in driving the distribution of *Corbicula*. This supports the recent findings of Petitpierre et al. (2012) showing widespread invaders have similar climate niches in their native and invasive ranges. The clear importance of climate variables in controlling *Corbicula*'s distribution in the logistic regression makes our use of the climate-only MaxEnt model particularly appropriate. The switch to climate-only modeling with MaxEnt is also advantageous because it allows us to use the much larger set of known *Corbicula* locations where habitat factors were unmeasured. Climate envelope models are often criticized for failing to include other important variables or failing to compare the importance of climate variables relative to other biotic and abiotic factors (Pearson and Dawson 2003). By explicitly making this comparison, we have demonstrated that a climate-only MaxEnt model can capture a major portion of the variability in a species distribution at the continental scale.

Our results show that a significant expansion in *Corbicula*'s range throughout the northern and central United States is likely with future temperature increases. This may already be occurring, as a population was identified in the Merrimack River, New Hampshire, while this analysis was being conducted (New Hampshire Department of Environmental Services 2012). This range expansion could be rapid and occur soon, because climate changes appear to be occurring at the higher range of predicted temperature changes (Fasullo and Trenberth 2012). The models also identified water bodies with higher pH and fine gravel substrate as likely to be suitable for *Corbicula*, which supports previous studies that indicated *Corbicula*'s preference for sand and fine gravel substrates (McMahon 1999, McMahon and Bogan 2001). These results can help catchment managers to target and monitor vulnerable habitats. Because of this, catchment managers in New England and the northern central United States should be aware that rivers with neutral to basic pH and sandy substrate are particularly at risk of invasion. Monitoring for early detection coupled with an eradication or control plan may be able to prevent widespread establishment, especially in lentic environments, where populations of *Corbicula* have been reduced using gas impermeable barriers (Wittman et al. 2012). Given *Corbicula*'s high per biomass filtration rates (McMahon and Bogan 2001, Atkinson et al. 2010), high densities and influential impacts, newly invaded rivers could experience significant changes in energy flow and community structure, as observed in previously invaded rivers (Cohen et al. 1984, Lauritsen 1986, Phelps 1994, Hakenkamp and Palmer 1998, Sousa et al. 2008a).

Under the A2A climate scenario, the one with the highest emissions, the area deemed climatically suitable in the southeastern United States is predicted to shrink in southern Florida. The A2A projections predict a decline in precipitation in the driest quarter and an increase in overall temperature. The interaction between increasing temperatures and declining precipitation is probably responsible for the classification of this area as unsuitable according to the more conservative thresholds. There is no reason why increasing minimum temperature would lead to areas being unsuitable for *Corbicula*; however, maximum temperature and minimum temperature covary. Increased maximum temperatures and decreased precipitation could lead to mass mortality events such as those observed during periods of low water level and high temperature (Cohen et al. 1984, Ilarri et al. 2011, Bodis et al. in press, W.G. McDowell pers. obs.), due to the inability of *Corbicula* to regulate its oxygen consumption under stressful conditions (McMahon 2002). In all these observed cases, however, *Corbicula* populations quickly rebounded from the mass mortality events (and were likely sped in such recovery from fast growth in warmer water) and were not removed from a river entirely. Regarding the future suitability of southern Florida, it is important to note, however, that under the A2A climate scenario, a combination of precipitation and temperature conditions in Florida arises that does not exist in the training data, so the model results are extrapolated beyond training data and should be interpreted cautiously (Elith et al. 2006).

The combined climate and habitat model explained a substantial amount of the variability in *Corbicula* presence and absence. Some of the remaining variability may be explained by biotic factors such as competition and predation, which are not included in these models. Within dense beds of native mussels, there are indications that competition may prevent establishment of *Corbicula* (Vaughn and Spooner 2006). When examining presence and absence on a reach or river scale, however, this is unlikely to prevent establishment of *Corbicula*. Although predation has been shown to control densities (Robinson and Wellborn 1988), there is no evidence that predators can remove *Corbicula* from a system entirely. Few barriers to *Corbicula* dispersal into suitable habitat seem to exist, given its rapid expansion in the southeastern United States following its introduction (McMahon and Bogan 2001). Because *Corbicula* can disperse widely and has been present throughout the western United States for 80 years and the eastern United States for 30 to 40 years, *Corbicula* has probably reached most of the locations that are climatically suitable for it to survive under current climate conditions. For species with a shorter invasion history or larger barriers to dispersal, it is necessary to recognize that the current distribution of the species may not reflect climatic tolerances. Because of this, species distribution models for such species are less reliable and it is critical to acknowledge the limitations of modeling in this regard.

There are two caveats to consider when interpreting our results. First, as is typical for almost all large-scale climate models for aquatic species, air temperature was used in place of water temperature in both the logistic regression and the MaxEnt models.Air temperatures typically track water temperatures well and similar approaches have been successfully used to model aquatic species including freshwater diatoms, snails, salamanders and trout (Kumar et al. 2009, Milanovich et al. 2010, Wenger et al. 2011, Blank and Blaustein 2012, Byers et al. 2013). There will be some discrepancies between air temperature and water temperature, and these differences will probably be greater for large bodies of water, systems with large amounts of ground water inputs and hot springs. In fact, these site-specific discrepancies may explain some of the outlier points, especially those in large river systems where local water temperature may be buffered against extreme fluctuations in air temperature. Given that more than 2,800 known *Corbicula* locations went into the model, it is not surprising that some of these points known to contain *Corbicula* fall outside what is considered to be a suitable climate. Nevertheless, only 3% fell outside the most liberal threshold presented. Also, it is important to recognize that significant departures from natural conditions may allow *Corbicula* to persist in environments that would otherwise be unsuitable. For example, several points in the USGS NAS Database include brief notes regarding outflow of water used in cooling operations. This warmer microclimate may allow *Corbicula* to persist in an area not predicted to be hospitable based on air temperature.

Second, our model does not make any predictions regarding densities, nor does it address how the effects of *Corbicula* on a previously colonized or newly invaded aquatic ecosystem might be altered by climate change. Density is one of the main factors controlling the impact of a nonindigenous species (Parker et al. 1999), and areas that are deemed suitable habitat may support widely varying densities of *Corbicula*. Modeling densities goes beyond the abilities of the approaches used in this paper, and presents an interesting challenge for future work. The interactions between *Corbicula* behaviour and climate change could lead to alterations in their impacts. For example, increasing temperatures could lead to higher metabolic rates and increased filtration and nutrient uptake by *Corbicula* (Spooner and Vaughn 2008). However at very high temperatures, mass mortalities of *Corbicula* can occur and may negatively affect water quality and native mussels by increasing toxic concentrations of ammonia in porewater and the water column (Cherry et al. 2005, Cooper et al. 2005). Climate change could make these events more common.

In summary, it is critical to assess the importance of climate in controlling the distribution of a species, as this dramatically affects the weight that should be given to the impacts of climate change and more local drivers. By empirically testing the relative importance of climate and carefully considering the biology of the organism being studied, we have demonstrated that *Corbicula* is likely to expand well beyond its current distribution. Already widely distributed, *Corbicula* could become nearly ubiquitous throughout the conterminous United States. MaxEnt and the freely available BioClim data make constructing a species distribution model for current and future distributions deceptively easy, and their misuse opens them up to criticism (Haegeman and Loreau 2008, Woodward and Beerling 1997). However, the combination of multiple approaches allows us to recognize what the models are capturing well and can lead to a more robust result than any single model alone.

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Table 2.1. Variables selected in stepwise regression of *Corbicula* presence. Habitat variables are from the EPA EMAP surveys and climate variables are from the BioClim dataset. All variables in this list appeared in more than 0.95 of models, by weight. The effect that an increase in the variable has on the likelihood of *Corbicula* presence is indicated in parentheses.

Habitat		**Climate**
Depth (+)	Percent Agriculture in Catchment (+)	Min. Temperature coldest month (+)
pH (+)	Percent Fine Gravel (+)	Annual precipitation (+)
Ammonium (-)	Total Suspended Solids (-)	Precipitation Driest Quarter (+)

Table 2.2. Comparisons between the three model types used in the logistic regression: habitat only (EPA EMAP data), climate data only (BioClim variables) and the combined model. By all measures the combined model performs best. However the climate-only model does a reasonable job modeling *Corbicula* presence and absence, particularly as measured by AIC and pseudo-R^2. The climate model provides the majority of the fit of the combined model despite having only half the number of variables retained in the habitat model.

	K	**AIC**	**ΔAIC**	**Weight**	**Pseudo R2**
Combined	9	695	0	1	0.41
Climate-only	3	769	74	9.00E-17	0.32
Habitat-only	6	988	293	2.00E-64	0.079

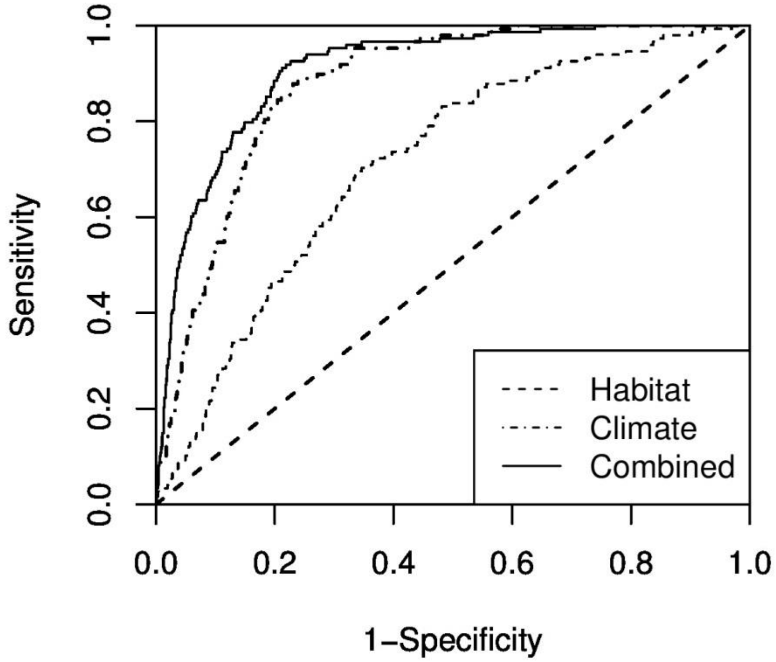

Figure 2.1. Receiver Operating Curve (ROC) for the three candidate models in the logistic regression: habitat-only (EPA EMAP data, dashed line), climate-only (BioClim data, dot and dashed line) and the combined model (solid line). Sensitivity, the proportion of points that the model identifies as suitable that are truly suitable is on the Y-axis. On the X-axis, 1 – Specificity is plotted, which is a measure of the false positive rate. The climate-only model outperformed the habitat-only model (Area Under Curve = 0.890 and 0.713, respectively). The combined model performed best (AUC=0.917), but was only slightly better than the climate-only model at predicting *Corbicula*'s presence. A perfect model would have an AUC of 1. The expected results from a random relationship are included in the 1:1 line and would have an AUC of 0.5 (large dashed line).

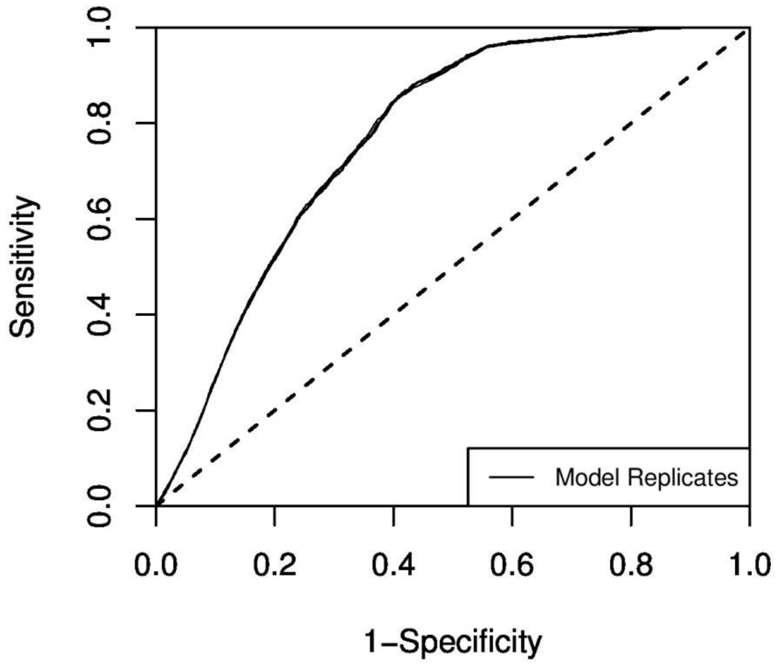

Figure 2.2. Receiver operating curve (ROC) for the five replicates of the Maximum Entropy model using the three selected BioClim variables: minimum temperature in the coldest month, precipitation in the driest quarter, and precipitation in the warmest quarter. The average Area Under Curve was 0.762, and was very consistent across the five model replicates.

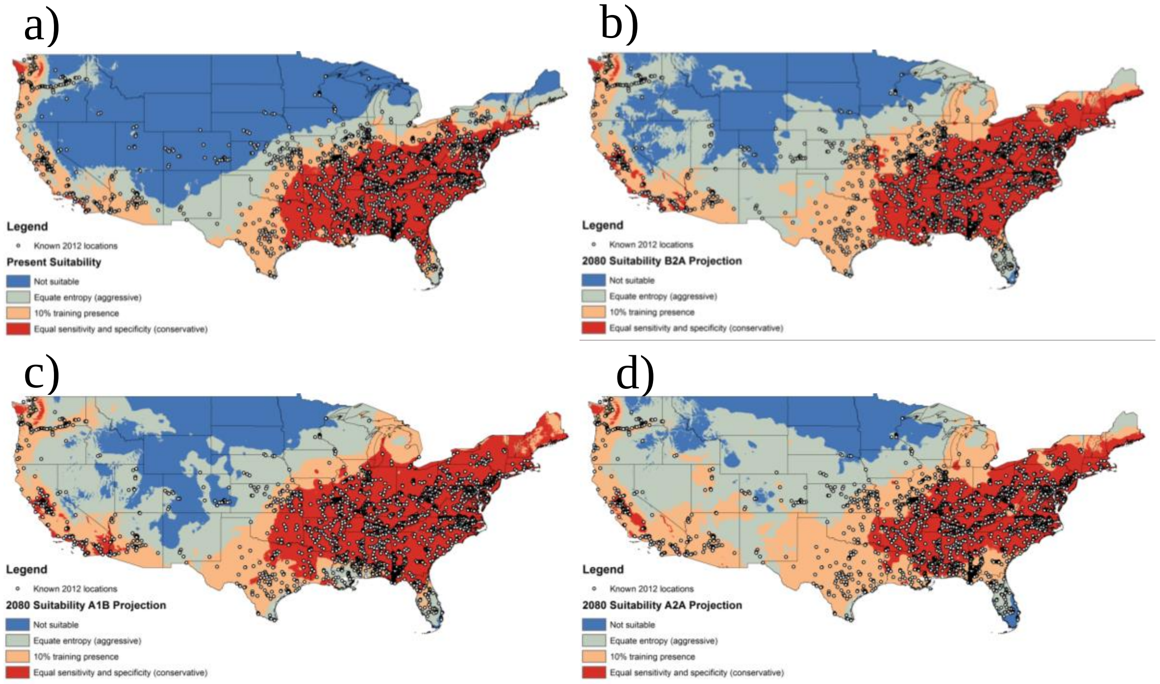

Figure 2.3. A map of modeled likelihood of *Corbicula* presence from a Maximum Entropy model based on current climate conditions of three BioClim variables: minimum temperature coldest month, precipitation in the driest quarter, precipitation in the warmest quarter (Bio 6, 17, 18) for: (a) Current climate conditions, and projected conditions in 2080 under (b) B2A emissions scenario, (c) A1B emissions scenario, and (d) A2A emissions scenario (listed in increasing warmness). The map is presented using various thresholds of suitability, as calculated by MaxEnt. Equate entropy is a more liberal threshold, which will determine a larger area to be suitable than the 10% training presence threshold or the most conservative threshold, equal sensitivity and specificity.

CHAPTER 3

CONTROLS OF DENSITY AND DISTRIBUTION OF THE ABUNDANT INVASIVE CLAM *CORBICULA FLUMINEA,* AND PROJECTIONS OF ITS ECOSYSTEM LEVEL EFFECTS[2]

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[2] McDowell, W.G. and J.E. Byers. To be submitted to *Freshwater Science*.

Abstract

Given their ubiquity, invasive species can critically affect ecosystem function. To calculate the alteration of ecosystem function, one must know an invader's per capita impacts and its abundance. Here we estimate the abundance of a widespread invasive freshwater clam, *Corbicula fluminea*, over a heterogeneous landscape and determine what physical habitat variables control its distribution. We sampled four to six sites in four rivers that spanned three large watersheds in the Georgia piedmont. Over half of all individual 0.044 m^2 sampling points and all 1-2 km sample sites had *Corbicula* present, supporting the characterization of its ubiquity in the study region. *Corbicula* densities within the rivers sampled ranged from approximately 60–175 *Corbicula* m^{-2}, but individual sites averaged as high as 483 *Corbicula* m^{-2}. *Corbicula* was more abundant in areas with higher proportions of gravel, and less abundant in areas with higher proportions of bedrock. Using spatially integrated abundance estimates from these distribution models and published per capita feeding rates, we multiplicatively scaled these up to calculate net system-wide 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 18 times over before water flows out of a 10 km reach. Given low abundances of all other filter feeding bivalves, *Corbicula* likely plays the most important role. Importantly, because *Corbicula*'s range is likely to expand with warming winter temperatures, this study could help both identify vulnerable stream habitats and forecast the impacts of new invasions in the northern United States.

Introduction

Impact, as defined by Parker et al. (1999), is the product of the range, abundance, and per capita effects of a species. A key principle of many ecological studies is scaling small-scale research to estimate impacts over a larger spatial scale, especially for invasive species (Dick et al. 2002, Kercher and Zedler 2004, Barber et al. 2008). Therefore, small scale experiments conducted under laboratory or mesocosm conditions require estimates of the abundance of invasive species to accurately predict an invasive species overall impact. Understanding the factors that influence the distribution and abundance of an invasive species enables the prediction of their impacts in unsampled systems.

Invasive species can substantially affect ecosystem functions (e.g. Gordon 1998, Strayer et. al 1999, Anderson and Rosemond 2007). Mollusks, in particular, can dominate ecosystem functions whether they are native (Covich et al. 1999, Vaughn and Hakenkamp 2001) or invasive (Heath et al. 1995, Strayer et al. 1999, Zhu et al. 2006, Caraco et al. 2007) through changing nutrient dynamics and zooplankton communities (Vaughn and Hakenkamp 2001). For example, the New Zealand mud snail has been shown to dominate nitrogen cycling in small Montana streams, supplying over two thirds of the ammonium demand in the stream through excretion due to extremely high densities (Hall et al. 2003). Zebra mussels in the Hudson River filter 10-100% of the water column each day, reducing chlorophyll a and microzooplankton biomass by approximately 80% (Strayer et al. 1999). Invasive species may have both positive and negative impacts on ecosystem services provided to humans, so an unbiased approach in estimating and understanding their impacts is required (Pejchar and Mooney 2009).

In Georgia piedmont rivers, one of the most abundant and widespread invasive is the Asian clam *Corbicula fluminea*. *Corbicula* invaded southeastern United States in the 1960s

(McMahon and Bogan 2001) and can reach densities of several thousand per square meter in other regions (Cohen et al. 1984, Phelps 1994, Cataldo and Boltovsky 1999, Sousa et al. 2008). The native filter-feeding bivalves, the previously abundant and diverse native pearly mussels (Unionidae), are declining throughout the region, primarily due to unrelated anthropogenic stressors such as increased sediment loading and dam construction (Neves et al. 2007). The declines of this diverse group of bivalves has left *Corbicula* as the only filter feeding bivalve with notable biomass within many southeastern rivers.

Corbicula has specific traits that make it very likely to have significant impacts on piedmont rivers and fill the role previously filled by native unionids. Specifically, it has a high biomass-specific filtration per biomass rate (McMahon and Bogan 2001) and is a particle generalist (Atkinson et al. 2011). These traits, combined with often high densities, make it an important player in altering southeastern river ecosystems.

Because of *Corbicula*’s high densities and high per capita and per biomass measures of filtration *Corbicula* is poised to play a dominant role in ecosystem function in Georgia piedmont rivers, and therefore impact water quality. This is of practical importance, as 61% of the human population in Georgia is served by surface water supplies (Barber et al. 2009), and is likely higher for the piedmont region. Although *Corbicula* is known to be throughout the Georgia piedmont, few, if any, estimates of density are available.

The objective of this study is to provide an estimate of the density of the invasive clam *Corbicula fluminea* in rivers in the Georgia piedmont, and how this density is affected by habitat attributes. This approach allows good estimates of density and abundance to be made quickly over a larger spatial scale than is possible to survey extensively. This model would also allow for prediction of invasibility to be applied to specific areas, given certain habitat attributes. Finally, we convert densities to measures of ecosystem function and compare values to the function that native species could have hypothetically provided.

Methods

Rivers Studied

Four rivers were sampled in the piedmont region of Georgia – the Middle Oconee, the Broad, the Apalachee, and the Alcovy rivers. We selected these rivers as they vary in watershed area, ranging from 80 km^2 to 1031 km^2 above the sampling reach, and discharge. Additionally, they span three large watersheds 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. Of the four rivers, all have impoundments that span the width of the river except for the Broad, however, within the sampling reaches all rivers were free-flowing.

Field Density Surveys

For each river, 4-6 sampling sites were examined for *Corbicula* density. These sites were selected to ensure a diversity of habitats were sampled, specifically sandy run habitats and bedrock shoals habitats, and that sampling sites were separated by at least 2 km. Within each site, 4 – 6 systematically spaced transects which spanned the width of the river were sampled. These transects were 25 – 100 m apart, depending on the width of the river, after an initial starting point was randomly selected. Along each transect, approximately 25 samples for *Corbicula* density were taken, with sample points ranging from 1 – 4 m apart, depending on the wetted width of the river. All rivers were wadeable, allowing a 0.044 m^2 stove pipe corer to be used for sampling. This method was used to prevent small *Corbicula* from washing out of the sampling area when the sediment was disturbed. At each sample point, physical habitat characteristics were recorded, including depth and substrate composition in the first five centimeters. As *Corbicula* burrows very shallowly in sediment (McMahon and Bogan, 2001), only sediment near the surface should alter their density and distribution. Percent substrate composition was estimated for five different categories by visual estimation and spot checks of individual particles: 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 (coble and boulder, > 64 mm), and bedrock. During density surveys, individual *Corbicula* were binned into 5 mm size classes by shell length (extra small: <10 mm, small: 10-15 mm, medium: 15-20 mm, and large: 20+ mm). At each sampling site, a subset of individuals was saved for size measurements to the nearest hundredth of a millimeter, to ensure that field size classifications were accurate. We treat these measurements as absolute density, rather than relative density, as all transects and sampling points were randomly selected within a site.

Estimating Abundance

Absolute abundance estimates were calculated by multiplying the average density, the average width, and the length of the river from the upstream most sampling reach to the most downstream reach. To avoid extrapolation, density estimates outside this area were not calculated. To accurately capture the occurrence of unsuitable habitat, no within-channel points were excluded from this estimate, unlike the density model described below.

Quantifying Filtration

Filtration rates were estimated using published filtration rates from Lauritsen (1986). Although other estimates of filtration are available (e.g. Way et al. 1990, Viergutz et al. 2012), we selected this study for three reasons: 1) it uses a population in North Carolina, which is likely from the same invasive lineage as the Georgia population (Lee et al. 2005); 2) the study was conducted under North Carolina summer water temperatures, which are similar to those observed in Georgia; and 3) it provides a regression of *Corbicula* shell length compared to filtration rate, allowing us to calculate specific rates, thereby accounting for differences in Corbicula size to estimate population specific filtration rates. The relationship between *Corbicula* dry weight and filtration rates is strong (Lauritsen 1986, Leff et al. 1990). We calculated and used a size class-specific filtration rate for each size class (< 10 mm, 10-15 mm, 15-20 mm, 20+ mm). To determine the relative importance of filtration rates relative to residence time within the reach, we used a similar approach to studies examining the impact of eastern oysters (zu Ermgassen et al. 2013) by treating the sampling reach as a distinct water body. We estimated the total volume using average width and depth measurements from density surveys. Using the total volume in the sampling reach and discharge values from USGS stream gages, we estimated the residence time within a 10 km portion of the reach under three different conditions for the summer of 2012: median, low, and high flows. All gages were located within the sampling reach, or within 10 river kilometers. We then used calculated filtration rates for the sampling reach, again normalized to a 10 km subsection, and the residence time to calculate a turn-over ratio within a 10 km reach. These values were standardized for a 10 km reach to ensure that values were comparable between rivers. The values represent the number of times the river is being filtered (in terms of the volume of water theoretically processed) by *Corbicula* within the 10 km reach under different flow conditions.

Density Model

A hierarchical mixed model was constructed using R 3.03 (R 2008) to predict *Corbicula* density using river and site (nested within river) as random effects, and depth and substrate composition as fixed effects. Due to the large number of sample points (1536), all of these variables could be included without over parameterizing the model (n>K*10, Moore and McCabe 1993). Prior to inclusion in the model, a Pearson's correlation matrix was constructed for the substrate categories, and any variables that had a correlation of greater than 0.7 were removed (Moore and McCabe 1993); however, no substrate variables were correlated. 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 utilize this habitat. However, any point that was submerged and had any amount of non-bedrock substrate was left in the model. An initial model containing all variables was constructed. Using the MuMIn package in R, models were constructed using all possible combinations of variables, and model weights were calculated for each possible model, using AICc. AICc was used, rather than AIC, as it controls for sample size (Moore and McCabe 1993). We used model averaging to calculate the average standard beta estimate and its associated error for each predictor variable across all possible models. To determine the overall fit of the model, as well as the relative contribution of random (site and river) and fixed (substrate) factors, a marginal and conditional R^2 was calculated. The marginal R^2 measures the variability in the data that is explained by fixed factors, while the conditional R^2 measures the variability in the data explained by fixed and random factors (Nakagawa and Schielzeth 2013).

Results

Field Density Surveys

A total of 19 sites were sampled in the four different rivers, using 93 transects (Table 3.1). The maximum observed density for a single sampling point was 8409 *Corbicula* m^{-2} at Ben

Burton Park, in the Middle Oconee River. This site also had the highest per transect density (1,114 m^{-2}) and the highest overall site density observed (270 m^{-2}).

Overall, averaging across all sites within each river, *Corbicula* density was highest in the Middle Oconee River (176 m^{-2}), followed by the Apalachee River (134 m^{-2}), and the Broad and Alcovy rivers (65 m^{-2} and 62 m^{-2}, respectively) (Table 3.2). However, densities ranged substantially between sites (Table 3.2, Table 3.3). Across all rivers, 100% of sampling sites, 98% of transects, and 55% of sampling points within the wetted width had *Corbicula* present.

Estimating Abundance

Using field measured wetted width and reach length (Table 3.1), as well as the average density across all sites within a river, we estimated the total number of *Corbicula* in each sampling reach (Table 3.2). These estimates ranged from 5.3 million to 235 million, based on variations in density, width, and sampling reach length.

Quantifying Filtration

Filtration rates calculated using size-specific filtration rates and estimated abundances for a 10 km reach ranged from 0.353 – 6.742 m^3s^{-1} (Table 3.2). Based on these 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 3.4). Under low flows observed in the summer of 2012, these values could have been as high as 18.3 times for the Apalachee River, which had very high *Corbicula* densities and a long residence time. Under high flow conditions, turnover rates were lower as a function of decreased residence time, ranging from 0.04 – 1.7. Residence times exceeded the time to filter the water within a 10 km reach (turn-over ratio >1) for all rivers under low flow conditions and three of the four rivers under median flow conditions (Figure 3.1).

Predictive Model

Initial model runs showed that depth was not a significant predictor of *Corbicula* density. In order to include as many sample points as possible, depth was removed as a predictor variable in future model runs. 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 beta estimates from model averaging for these variables did not cross zero (Figure 3.2). Gravel and bedrock were also the most important predictor variables, by cumulative model weight, at 1 and 0.953, respectively (Table 3.5), followed by sand (0.429), large (cobble and boulder, 0.293), and fines (0.292). No one single model was clearly superior, as the highest model weight was 0.305, for a model containing bedrock and gravel substrate proportions, as well as site and river as random effects (Table 3.6). 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 condition R^2 to 0.317. The difference in conditional and marginal R^2 indicates that the fixed factors (substrate) explain approximately the 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 models. Across all candidate models, marginal R^2 ranged from 0.130 - .143 and conditional R^2 ranged from 0.284 – 0.322 (Table 3.6).

Discussion

Corbicula clearly play an important role in southeastern 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 turn-over ratios within a 10 km reach were as high as 18 times before water flows out of the reach. These high turn-over ratios should lead to lower abundances of meiofauna in the water column and lower turbidity. The combination of clearer water, and warmer temperatures, which are commonly associated with summer low flow conditions, could help lead to higher primary productivity during low flows. This impact should be particularly significant for episammic and epilithic periphyton that would not be consumed by *Corbicula*. 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 (Strayer et al. 1999, Caraco et al. 2007).

The filtration rates and turn-over ratios provide a tractable summary of the overall impact of a filter feeder which is often used in estuary studies (e.g. zu Ermgassen et al 2013), but there are several important caveats associated with these estimates. First, it is critical to recognize that the turn-over ratio is directly impacted by the length of reach selected. As reach length increases, both *Corbicula* filtration rates (in m^3s^{-1}) and reach volume increase linearly, assuming that width, depth, and density are constant. However, longer reaches have a longer residence time, as flow is constant but volume is increasing. Therefore, longer reaches will have a higher turn-over ratios, as Corbicula will have a longer time to act on water parcels passing through the reach. In a river ecosystem, the relevant length for the reach 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. This length 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 likely increase, thereby increasing the volume. Therefore, our estimates of the impacts of *Corbicula* under higher flow conditions are an underestimate of their true impacts. We did not account for any water withdrawals or losses in our sampling reaches, so flow estimates are likely to be slightly overestimated for the portion of the sampling reach upstream of the gauge, and slightly underestimated for portions downstream of the gauge. Despite these caveats, the calculation provides an estimate to enable relative comparisons of the ecological role of *Corbicula* among these reaches.

Our calculation also assumes 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 biota 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 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 et al. 1990). Under higher flow conditions, it is likely there will be more suspended sediment in the water, further decreasing the already lower turn-over ratios.

The average density and maximum density of *Corbicula* observed in the Georgia piedmont compare similarly to densities across the United States and Europe. Belanger et al. (1985) found maximum densities of 2,286 m^{-2} 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 United States, 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 et al. 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 beta estimate for the percent of sand. In areas dominated by bedrock, a higher proportion of sand would likely make the point more suitable for *Corbicula*, as it would provide more usable substrate. However, in sandy run and bar habitats, areas that are primarily sand are likely to be geomorphically active. In these habitats, disturbance could displace *Corbicula* and wash them downstream, especially given that they burrow very shallowly in the sediment (McMahon and 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.

Our results demonstrate how ubiquitous *Corbicula* is in this region, being found in over half of all sample points. Prior to this study, there were no known *Corbicula* points in the USGS Nonindigenous Aquatic Species database between Atlanta, GA and Athens, GA. Additionally, the only points in the Georgia piedmont were in the Chattahoochee River basin, the one major watershed of Georgia that was not sampled in our surveys (USGS 2014). This difference between the database records and common knowledge of the region is an important reminder that a lack of sampling or reporting can lead to significant discrepancies between known and actual distributions for invasive species, even for a well-established invasive species. However, this result is not surprising; it has been locally well known that *Corbicula* is established in the region (Grubaugh and Wallace 1995, M. Freeman, pers. comm.).

Overall, densities appear to be primarily controlled by variables other than substrate that are unaccounted for in our analysis. The importance of substrate composition is equally important as intrinsic differences between the rivers. These results suggests that knowing the general substrate of a river, combined with limited sampling within the river to provide an estimate of the random effect of river, would provide a rough estimate of absolute *Corbicula* density and abundance. However, the model's conditional R^2 value, which accounts for both random and fixed variables, was only 0.32, leaving almost two thirds of the variability in *Corbicula* density unaccounted for, so these estimates would be imprecise. The relatively low R^2 for the model and the river specific differences in shoals habitats make it difficult to extrapolate over the entire region without further field surveys.

On a per individual basis, *Corbicula* is providing a similar amount of filtration to what native mussels would have provided, as per capita filtration rates are similar between *Corbicula* and unionids (McMahon and Bogan 2001). However, because *Corbicula* are much smaller than native mussels (McMahon and Bogan 2001), on a biomass basis, they are providing much more filtration than native mussels would have. 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 and Hakenkamp 2001). Although there are fingernail clams (*Sphaeriidae*) present in small numbers from surveys, due to their small maximum size (<10 mm, McMahon and Bogan 2001) and the fact that the services provided by filter feeding bivalves are exponentially related to size (e.g. Lauritsen 1986), they are unlikely to have a major impact on ecosystem function. From a human perspective, under baseline conditions *Corbicula* may be serving human needs better than native mussels. Sixty-one percent of the population of Georgia relies on surface water supplies (Barber et al. 2009), and the higher removal rate of sediment by *Corbicula* than native mussels would make it easier and less costly to utilize these resources. However, these services are 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 declines of *Corbicula* occur. For example, *Corbicula* is sensitive to high temperatures and low dissolved oxygen concentrations that native unionid mussels would be able to tolerate (McMahon and Bogan 2002). During the summer of 2012 water temperatures reached 35 C and a mass mortality event was observed, killing more than 99% of the *Corbicula* in a reach (McDowell et al. in prep). This event caused the ecosystem functions and services provided by *Corbicula* to effectively cease, whereas in an intact, diverse native community many species would have been able to survive the poor conditions (McMahon and Bogan 2001).

Given *Corbicula*'s regional status as a nearly ubiquitous invasive species, high densities across all rivers surveyed, and large per capita impacts, it is clear that this single species is having a large impact (sensu Parker et al. 1999) on these aquatic ecosystems. Understanding these impacts in other areas where *Corbicula* is well established will also allow us to better forecast the future, as *Corbicula*'s range expands with warming winter temperatures (McDowell et al. 2014). As the only filter feeding bivalve in many southeastern rivers, these functions are extremely important. However, these impacts are also extremely temporally variable, so monitoring water temperatures and populations of *Corbicula* in the future is also critical to understanding their ecological role in the future.

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Table 3.1. Summary of characteristics of rivers sampled during summer of 2012 flow conditions.

River	**Sites**	**Tran-sects**	**Reach Length (km)**	**Avg. Width (m)**	**Avg. Depth (m)**	**Reach Vol. (m^3)**	**Observed Flow (Q) Summer 2012 (m^3s^{-1})**		
							Low	**Median**	**High**
Alcovy	4	22	10.4	8.20	0.15	12716.6	0.057	0.283	8.495
Apalachee	4	21	44.3	24.94	0.19	211106	0.227	0.566	2.407
Broad	5	21	16.4	43.76	0.26	183556	1.982	4.248	28.317
Middle Oconee	6	30	28.8	46.49	0.24	327105	0.991	2.124	12.743

Table 3.2. Summary of *Corbicula* densities observed in the four rivers sampled, as well as the minimum and maximum densities observed at each site within a river.

River	**Reach Length (km)**	***Corbicula* density (m^{-2})**			***Corbicula* / km**	***Corbicula* Abundance in Reach**	**Filtration (m^3s^{-1}/10 km)**
		Avg.	**Site Min.**	**Site Max.**			
Alcovy	10.4	61.65	6.82	199.87	505,664	5,258,907	0.353
Apalachee	44.3	133.78	13.64	269.73	3,340,071	147,965,164	4.149
Broad	16.4	64.65	46.09	97.17	2,829,053	46,396,479	2.518
Middle Oconee	28.8	175.97	21.76	483.20	8,181,518	235,627,718	6.742

Table 3.3. Summary of individual sampling sites and metadata.

River	**USGS Gage #**	**Site**	**Lat.**	**Long.**	**# of Xsects**	**Avg. Width (m)**	**Avg. Depth (m)**	**Transect *Density* (*Corb*. m^{-2})**			**Sample Point Max Density (*Corb*. m^{-2})**
								Min.	**Avg.**	**Max.**	
Alcovy	02208150	Brooks Road	33.9434	-83.9168	6	8.5	0.166	3.8	27.3	54.0	227.3
Alcovy	02208150	Freeman's Mill Park	33.9644	-83.9244	4	8.6	0.098	132.6	194.2	420.5	909.1
Alcovy	02208150	New Hope Road	33.9172	-83.8881	6	7.9	0.182	0.0	12.1	22.7	90.9
Alcovy	02208150	US 29	33.9786	-83.9394	6	7.9	0.145	0.0	6.8	18.6	113.6
Apalachee	02219000	d/s 441 bridge	33.7190	-83.4342	5	38.5	0.278	9.3	13.1	17.3	90.9
Apalachee	02219000	Moores Ford Bridge	33.8551	-83.5757	4	19.0	0.214	58.1	193.9	311.7	1522.7
Apalachee	02219000	SR 11 bridge	33.9001	-83.7232	8	11.1	0.158	22.7	53.0	134.3	363.6
Apalachee	02219000	US 78	33.8815	-83.5912	3	31.2	0.112	90.9	230.6	283.3	909.1
Broad	02191300	Broad River Outpost	34.1810	-83.1453	5	58.8	0.250	76.1	92.0	117.0	454.5
Broad	02191300	Freeman Cabin	34.2313	-83.1639	4	42.6	0.393	44.5	50.3	58.4	386.4
Broad	02191300	Slow Water kayak	34.2483	-83.1762	5	25.2	0.180	27.1	45.2	136.4	840.9
Broad	02191300	SR 172 bridge	34.1566	-83.0827	3	69.7	0.304	29.4	50.0	73.9	545.5
Broad	02191300	US 29	34.2398	-83.1785	4	22.6	0.259	49.6	65.7	95.2	431.8

River	USGS Gage #	Site	Lat.	Long.	# of Xsects	Avg. Width (m)	Avg. Depth (m)	Transect Density (*Corb*. m^{-2})			Sample Point Max Density (*Corb*. m^{-2})
								Min.	Avg.	Max.	
Middle Oconee	02217500	Ben Burton Park	33.9610	-83.4415	6	72.1	0.197	187.5	483.2	1114.6	8409.1
Middle Oconee	02217500	Bot. Gardens	33.8994	-83.3862	5	30.5	0.367	12.3	66.2	125.8	636.4
Middle Oconee	02217500	Broad St	33.9455	-83.4240	5	26.4	0.328	14.1	34.7	77.7	454.5
Middle Oconee	02217500	Tallassee Shoals	33.9881	-83.4985	5	54.6	0.288	60.6	260.3	602.9	3022.7
Middle Oconee	02217500	Vaughn Road	33.9606	-83.4616	5	30.3	0.430	46.5	148.7	263.0	750.0
Middle Oconee	02217500	Whitehall Forest	33.8776	-83.3507	4	65.0	0.108	8.6	21.5	34.6	136.4

Table 3.4. Summary of filtration rates and turnover ratios under different flow (Q) rates. All values are normalized to a 10 km sampling reach, to standardize 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. Unsurprisingly, these impacts are larger under low flow conditions, when all turn over ratios are greater than one, and less during high flow conditions. However, in the Apalachee River, which has a combination of high densities of *Corbicula* and a long residence time, *Corbicula* still filter water in a 10 km reach more than once even under the highest flow conditions observed in July 2012.

	Low Q		**Median Q**		**High Q**	
River	**Residence Time (hrs)**	**Turn-over ratio**	**Residence Time (hrs)**	**Turn-over ratio**	**Residence Time (hrs)**	**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

Table 3.5. Summary of cumulative model weights, or relative value index, across all candidate models from hierarchical modeling of *Corbicula* density. Large substrate consists of cobble and boulder. Cumulative model weights for individual variables range from 0 – 1, with 1 indicating that the variable was present in all models, by weight.

Variable	**Cumulative model weight**
Gravel	1.000
Bedrock	0.953
Sand	0.429
Large	0.293
Fines	0.292

Table 3.6. Summary of all candidate models (weight>0.001) from hierarchical modeling of *Corbicula* density.

Variables included	**df**	**logLik**	**AICc**	**ΔAICc**	**Weight**	**Marg. R^2**	**Cond. R^2**
BR, Gravel	6	-8901.6	17815.2	0	0.305	0.141	0.317
BR, Gravel, Sand	7	-8901.0	17816.1	0.90	0.195	0.143	0.322
BR, Fines, Gravel	7	-8901.6	17817.2	1.98	0.113	0.141	0.318
BR, Gravel, Large	7	-8901.6	17817.3	2.02	0.111	0.141	0.317
BR, Gravel, Large, Sand	8	-8900.9	17817.9	2.71	0.079	0.143	0.322
BR, Fines, Gravel, Sand	8	-8900.9	17818.0	2.79	0.076	0.143	0.322
BR, Fines, Gravel, Large	8	-8901.6	17819.2	4.00	0.041	0.141	0.318
BR, Fines, Gravel, Large, Sand	9	-8900.8	17819.7	4.44	0.033	0.143	0.322
Fines, Gravel, Large, Sand	8	-8902.4	17820.9	5.67	0.018	0.134	0.294
Gravel, Large, Sand	7	-8903.9	17821.9	6.66	0.011	0.133	0.292
Fines, Gravel, Sand	7	-8903.9	17821.9	6.70	0.011	0.134	0.294
Gravel, Sand	6	-8905.2	17822.6	7.32	0.008	0.130	0.284

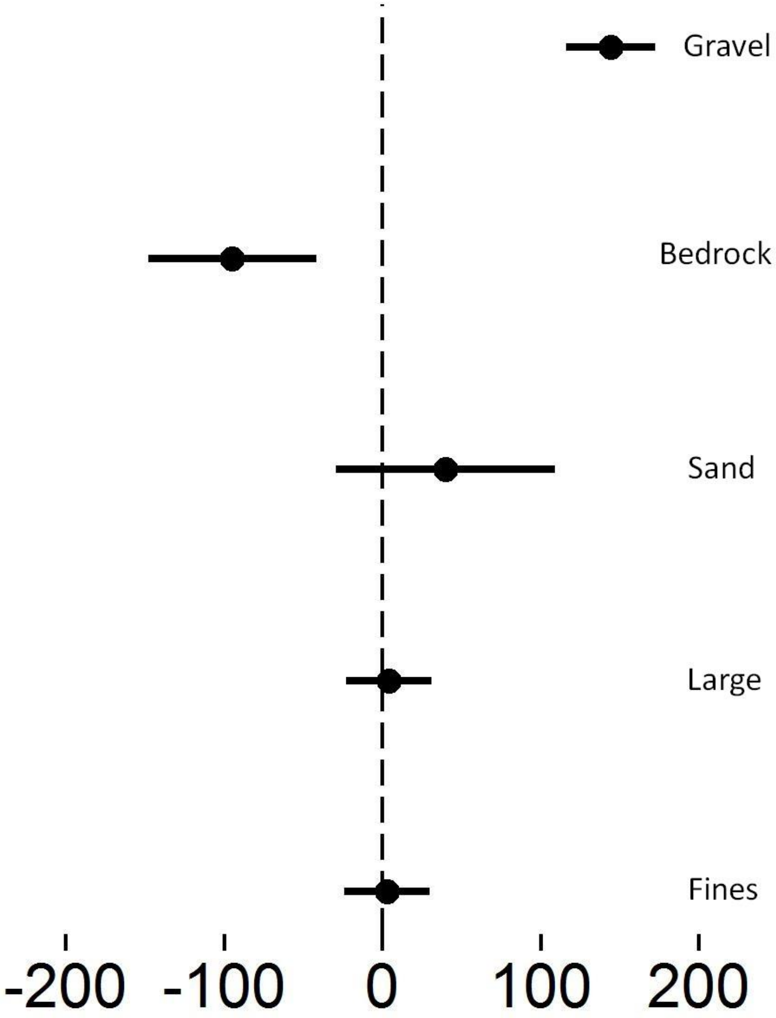

Figure 3.1. Summary of standard beta estimates of substrate variables from hierarchical modeling results. Variables are ranked from top to bottom in terms of importance, and those to the right of zero were associated with higher *Corbicula* densities, while those to the left were associated with negative *Corbicula* densities. Error bars represent the confidence interval of the standard beta estimate; for confidence intervals that span zero, the variable may not have an effect on *Corbicula* abundance.

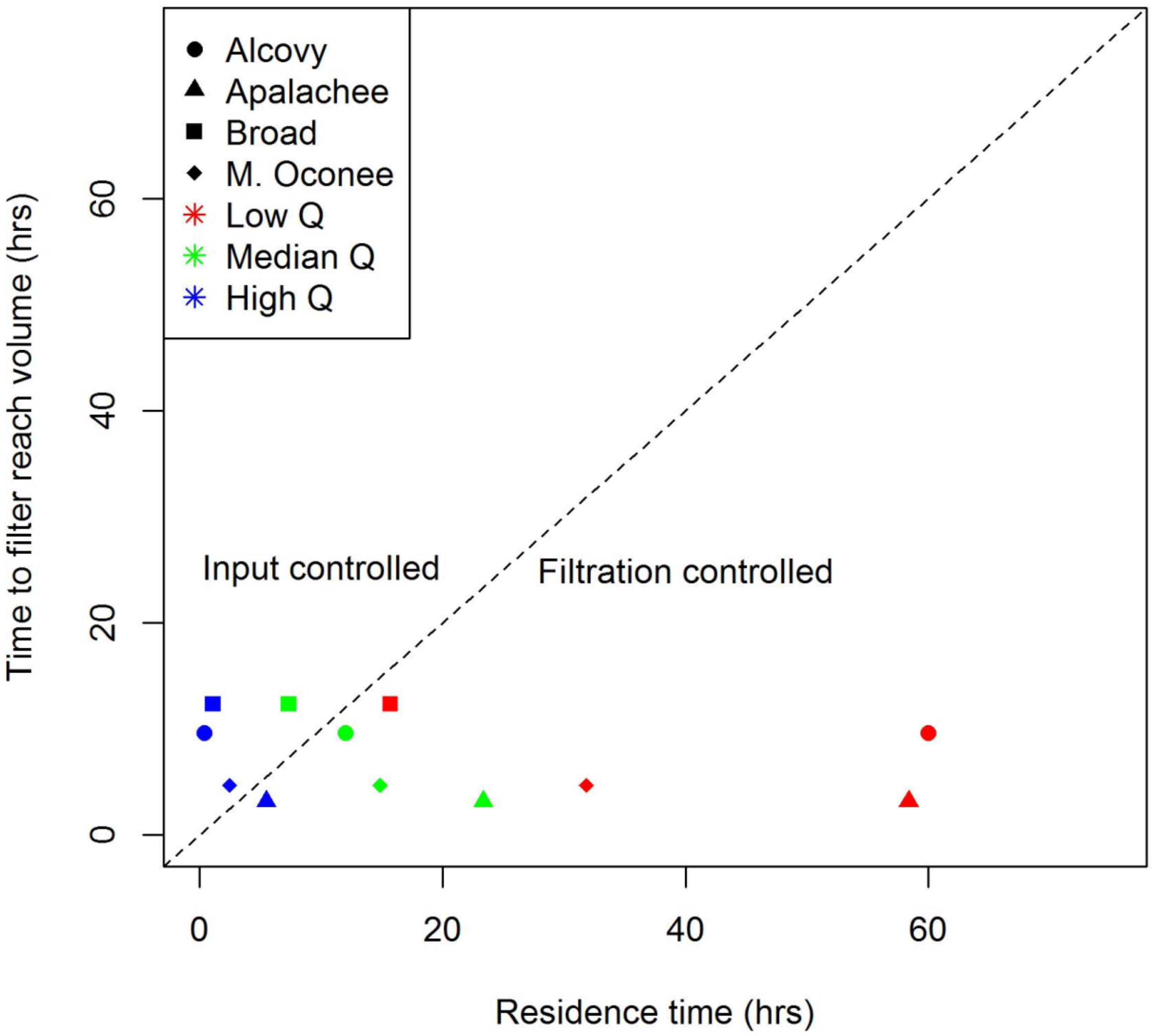

Figure 3.2. Plot of water residence time in a standard 10 km reach vs filtration by *Corbicula* within the same distance in four different Georgia piedmont rivers under three different flow conditions. Red, green, and blue points represent minimum flows, median flows, and maximum observed flows in the summer of 2012, respectively. All flows are actual flows observed at USGS stream gauges. The black line is the 1:1 line; above the line, water is leaving the reach faster than it is being filtered (turn-over ratio < 1) and below the line water is being filtered faster than (turn-over ratio > 1). Only under observed maximum observed flows in the summer of 2012 is a 10 km segment not controlled by *Corbicula* filtration.

CHAPTER 4

MASS MORTALITY OF AN INVASIVE SPECIES IN RESPONSE TO AN EXTREME CLIMATE EVENT[3]

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[3] McDowell, W.G., W.H. McDowell, and J.E. Byers. To be submitted to *Biological Invasions*.

Abstract

Extreme events are becoming more common with climate change. The impacts of extreme events could be exacerbated by reactions of non-indigenous invasive species that have little to no evolutionary history in the systems where they are now embedded, and may not have the same tolerances to extreme episodic events. Understanding how the responses of invasive species differ from those of native species in the ecosystem, is critical to ecological forecasting. In rivers throughout the southeastern United States, *Corbicula* is an abundant invasive species that has many documented impacts. However, *Corbicula* may have additional impacts associated with the occurrence of extreme events. Because of their unpredictable nature, the effects of extreme events on aquatic communities are difficult to quantify using field observations. During the summer of 2012, which was hot and dry, a mass mortality event occurred where over 99% of the *Corbicula* died in the Broad River, Georgia. However, temperatures were not high enough to kill native mussels. We assessed the impacts of this event using in situ water quality measurements and calculations to estimate the effects of the loss of *Corbicula* on the system, as well as a manipulative mesocosm experiment. Concentrations of total dissolved phosphorus (TDP) were significantly higher and concentrations of phosphate were marginally higher in areas where a die-off was occurring, but no differences were observed in ammonium, nitrate, total dissolved nitrogen, and dissolved organic carbon. Despite the statistically significant increase, TDP and phosphate concentrations were lower than predicted by mass balance calculations. These differences may be due to biotic uptake, particularly of phosphorus; this hypothesis is supported by lower dissolved oxygen concentrations in treatment pools in the mesocosm experiment. Mesocosm results indicate that nutrients are released in approximately 48, indicating that these mass mortality events likely lead to short term nutrient pulses. Also, as *Corbicula* were

the only filter-feeding bivalves in the ecosystem with significant biomass, this event led to the nearly complete removal of the ecosystem services provided by bivalves, such as filtration. This temporal variability in ecosystem function could have significant effects on aquatic ecosystems, especially if they become more frequent in the future.

Introduction

Extreme events are becoming more common with climate change, and have the potential to interact with other stressors on ecosystems. Invasive species are one of the most pervasive stressors of ecosystems worldwide (Vitousek et al. 1997, Millennium Ecosystem Assessment 2003). Their effects on native species and community structure are widely known, but the effects of invasive species on ecosystem processes are not as well documented (Strayer et al. 1999, Hecky et al. 2004). The impacts of invasive species are a function of their range, abundance, and per capita effects (Parker et al. 1999), which are often determined by the relationships among their species traits, the traits of other species in the ecosystem, and the abiotic conditions in their novel range. For example, the invasive perennial cheat grass, *Bromus tectorum*, burns readily, creating an alternate fire regime in western grasslands (D'Antonio and Vitousek 1992, Billings et al. 1994). In aquatic ecosystems, the zebra mussel (*Dresseina polymorpha*) has reshaped nutrient dynamics in the Great Lakes, shifting phosphorus availability from open water areas to nearshore ecosystems (Hecky et al. 2004).

Because these non-native invasive species have not evolved in the ecosystems where they are becoming established, they may not have the same tolerances to extreme episodic events in their new range (Cox 2004). Invasive species thus might have different responses to these events than native species. Non-native fish can be at higher densities in low-flow years in California (Propst and Gido 2004) and in Portugal (Bernardo et al. 2003). In contrast, the invasive marine crab *Petrolithses armatus* suffers significant mortality during extremely cold winters, which can create a cascade of effects (Canning-Clode et al. 2011). Additionally, drought may force native fishes into reservoir habitats which they can be preyed upon by invasive piscivores (Matthews and Marsh-Matthews 2003). The effects of non-native species on aquatic communities and ecosystems can thus be substantial during climatic extremes.

Native and Invasive Freshwater Bivalves in the United States

In aquatic communities, invasive species represent a large proportion of the community, and some have been shown to have large-scale ecosystem effects. Many of those with the largest impacts are mollusks, because freshwater mollusks play a critical role in aquatic ecosystems by providing ecosystem services such as filtration, nutrient uptake, and sedimentation all of which affect overall water quality (Strayer et al. 1999, Vaughn and Hakenkamp 2001, Strayer et al. 2006). The native mussels in the Unionidae family are classic K-selected species – they are long lived, can tolerate desiccation or periods of low dissolved oxygen for extended periods of time, and can tolerate temperatures up to 40^{o}C (McMahon and Bogan 2001). However, in many systems these species are no longer present due to human impacts (Bogan 1993, Neves et al. 1997) and have been replaced by invasive filter-feeding bivalves such as the zebra mussel *Dreissena polymorpha* and the Asian clam *Corbicula fluminea* (McMahon and Bogan 2001), hereafter *Corbicula*. Both of these introduced bivalves are classic r-selected species – they are short lived, reproduce early, and, despite their success, are sensitive to extreme environmental conditions (McMahon 2002).

In some rivers in the southeastern United States, the native unionids have been replaced by the Asian clam, *Corbicula* (McMahon and Bogan 2001). *Corbicula* is sensitive to both high temperatures (>35 ^{o}C) and low dissolved oxygen levels (<0.5 mg/L) (McMahon and Bogan 2001). In contrast, the native mussel *Elliptio complanata*, a common species throughout the region, can survive higher temperatures and low dissolved oxygen concentrations for weeks at a time by shutting down its metabolism, allowing it to survive transient periods of low dissolved oxygen (McMahon and Bogan 2001).

Because of their sensitivity to extreme events, mass mortality events of *Corbicula* have been noted during extreme conditions in European rivers (Ilarri et al. 2011, Sousa et al. 2012); however, these have been associated with stranding on sand bars or stagnant pools. Experiments have demonstrated that mass mortality events in stagnant waters could lead to toxic levels of ammonia for native mussels in stagnant waters (Cooper et al. 2005, Cherry et al. 2005). Native mussels are not invulnerable to these events, but due to their much higher tolerances to high temperature and low dissolved oxygen, mass mortality events have only been described during extreme drought in stagnant pools (Vaughn et al. in review). Therefore, these mortality events are more likely to be a novel event in ecosystems resulting from the invasion of *Corbicula,* especially given predicted climatic changes in extreme temperatures and droughts (Hopkinson et al. 2013). For *Corbicula*, the effects of this phenomenon have not previously been described on a large spatial scale, with in situ water quality measurements.

To examine the effects of a *Corbicula* mass mortality event, we used both field observations and in-situ mesocosm experiments. We used field observations to quantify water quality impacts and the extent of the mass mortality event, which was then scaled up to measures of ecosystem function. A mesocosm experiment allowed for a more sustained and controlled examination of the timing, amount, and fate of nutrients released during a mass mortality event as well as direct effects on dissolved oxygen.

Methods

Field Density and Water Quality Surveys

The Broad River, an approximately 100 km long tributary of the Savannah River, is located in the piedmont region of northeastern Georgia. The Broad River is one of the only unimpounded rivers in Georgia, and eventually flows into Lake Strom Thurmond. The watershed is relatively undeveloped, with forested lands and agriculture, and poultry production in particular, the primary land uses (Molinero and Burke 2009). The substrate is primarily silt, sand and fine gravel, except in occasional bedrock-controlled shoals.

The summer of 2012 was very hot, with record high air temperatures of 43 ^{o}C, and very little precipitation. From January to August, 2012, the precipitation was almost 200 mm below the 30- year average at the nearby Athens, GA weather station. This led to low discharge in the Broad River, approximately 2.8 m^3s^{-1} compared to the recorded median of 19.8 m^3s^{-1} (from seven years of record). In the nearby Middle Oconee River, which has 76 years of record, discharge in July 2012 was the 7th lowest on record. Because of the combination of record high air temperatures and low flows, we observed water temperatures as high at 34 ^{o}C in the Broad River during regular density surveys as part of a separate study. We also observed an in-flow mass mortality event where thousands of *Corbicula* were dying.

To quantify the extent of the mass mortality event, we sampled a 10.4 km reach of the Broad River extensively, from the confluence with the Hudson River to the Highway 281 bridge crossing, approximately 65 km upstream of its confluence with the Savannah River at Lake Strom Thurmond. Within this reach, and the Broad River as a whole, *Corbicula* is the dominant bivalve, averaging approximately 60 m^{-2} in the river as a whole with a range of densities from 29 m^{-2} to 136 m^{-2} in early summer of 2012 (McDowell and Byers, in prep.). Although these surveys did not specifically target unionid mussels, none were found. The mass mortality event was initially observed on July 25th, 2012 and appeared to have just occurred, as most *Corbicula* had visceral masses still attached to the shells and did not smell of decay.

To determine the impact of this mass mortality event on water quality, we took water samples at a total of 14 sampling stations within the sampling reach two days after the mortality event, on July 27th, 2012. During this survey many *Corbicula* with visceral mass still attached to the shell were observed, so the impacts of the mass mortality event were clearly still ongoing. Water quality sampling stations were systematically spaced approximately 0.75 km apart over the 10.4 km sampling reach and were not selected based on proximity to any aggregations of dead *Corbicula*. At each station, all measurements were taken mid-channel. Temperature and conductivity were measured in situ using a Yellow Springs Instrument model 85 meter. Water samples were field filtered using an ashed Whatman GF/F glass fiber filter (0.7 µm nominal pore size) and kept on ice until they could be frozen, no more than 12 hrs following collection. Water samples were analyzed for nitrate, nitrite, ammonium, total dissolved nitrogen, soluble reactive phosphorus, total dissolved phosphorus, and dissolved organic carbon at the University of New Hampshire Water Quality Analysis Laboratory using standard methods. Total dissolved forms of nitrogen and phosphorus would include more complex organic molecules that would likely be a recent input into the system from decaying clams. Bacteria can break down these organic nutrients into soluble reactive phosphorus (phosphate) and mineral nitrogen (nitrate and ammonium) under typical conditions. Ammonium is of particular interest, as it is a proxy for ammonia, which is highly toxic to native unionid mussels (Cherry et al. 2005, Cooper et al. 2005). DOC is a good proxy for the overall release of organic matter from decaying clams, and decomposition of this organic carbon results in oxygen demand that can reduce dissolved oxygen levels to harmful levels. Water quality measurements were compared within and upstream of the mass mortality event using an ANOVA.

To determine how many *Corbicula* died during the mass mortality event, a total of nine density transects were made, approximately 1 km apart. As with water quality sampling points, density transects were selected based on distance along the river, not on the presence of any dead *Corbicula*. At each density transect, five density sample measurements were taken at even intervals across the river. Using a stove pipe corer (0.044 m^2) to delineate the sample point area and a 3 mm Perspex mesh sieve to filter the contents, all *Corbicula* were counted and placed into one of four 5-mm size classes (0-10 mm, 10-15 mm, 15-20 mm, 20+ mm). Only live clams and clams that were freshly killed were counted in these surveys. A clam was considered freshly killed if it still had its visceral mass attached to the shell or if the shell was still attached at the hinge and the inner nacre was lustrous and shiny. Any shells that were broken or had holes near the umbo, did not have the lustrous nacre, or were not attached at the hinge were considered older shells, and were not included in the counts of recently killed *Corbicula*. Because *Corbicula* shells are fairly fragile and will break apart easily, we believe this measure to be a conservative estimate of the number of *Corbicula* that died during the mass mortality event. At each transect the wetted width was measured using a laser range finder. To calculate the total number of *Corbicula* that died during this event, we multiplied the average density of *Corbicula* at the nine density transects, the average wetted width of the river, and the length of the sampling reach.

Estimating Filtration

The abundance and size distribution of *Corbicula* were used to estimate total filtration rates using previously published size-specific filtration rates for this species (Lauritsen 1986). Although other estimates of filtration are available (e.g. Way et al. 1990, Viergutz et al. 2012), we selected Lauritsen (1986) in this study for three reasons: 1) it uses a population in piedmont region of North Carolina, which is likely from the same invasive lineage as the Georgia population (Lee et al. 2005); 2) the study was conducted under North Carolina summer water temperatures, which are similar to those observed in Georgia; and 3) it provides an estimate of filtration rate versus *Corbicula* shell length, thereby allowing us to calculate total population filtration based on observed size distribution of *Corbicula*. Additionally, we estimated the total volume of water within the reach, using the average observed depth, width, and the length of the sampling reach. We divided the reach volume (m^3) by the filtration rate (m^3s^{-1}) to estimate the time required for *Corbicula* to filter the water within the reach. This was then compared to the residence time, which was calculated by dividing the reach volume (m^3) by the discharge values (m^3s^{-1}) from a nearby USGS stream gauge (02191300).

Field Mesocosm Experiment

To better track the fate of nutrients released during a mass mortality event, as well as providing a time series of observations during a mortality event, we conducted a field mesocosm experiment. The field mesocosm experiment was conducted in Big Creek, Athens, Georgia. This small, sandy creek was selected because of similar substrate characteristics as the Broad River, and it was small enough to set up two artificial pools (0.34 m^2) spanning the channel. We created these pools by inserting a plywood frame, which was made waterproof using a heavy duty PVC pond liner, into the sandy substrate. A small tube was installed at the downstream end of the pool to provide an outflow point for sample collection. A treatment and control pool, which were on opposite sides of a small sand bar, were used for each run of the experiment, which was blocked by time (n=3). To prevent impacts from previous runs of the experiment, pools were installed upstream for successive replicates and placed on the opposite side of the sand bar.

We collected *Corbicula* from the Middle Oconee River, at Ben Burton Park, one day before the experiment. A total of 735 *Corbicula* were added to each treatment mesocosm, a density (2200 m^{-2}) that approximates the high densities of live *Corbicula* (95% percentile) observed in the Middle Oconee and Broad Rivers during sampling prior to the mortality event in the summer of 2012 (McDowell and Byers, in prep.). This density was only about a quarter of the highest density observed in the field (8,400 *Corbicula* m^{-2}). Before we added *Corbicula* to the treatment mesocosm pool, *Corbicula* were killed by immersing them in hot (40 ^{o}C) water for one to two minutes. This method was observed to kill over 99% of *Corbicula* during initial trials. Warm water used for immersion was then drained away to minimize nutrients leaching into the water prior to addition.

To measure changes in water quality following the addition of dead clams, we collected water samples at several time points: a pre-experiment baseline (t0), five minutes, 15 minutes, 30 minutes, 1 hour, 2 hours, 4 hours, 8 hours, 24 hours, and daily thereafter, for up to one week or until significant rains caused water levels in the stream to rise, destroying the pools. To capture any rapid release of nutrients, sampling was more frequent following addition of dead clams. At each time point, dissolved oxygen, temperature, and conductivity were measured using a field multi-meter (YSI 85). The YSI 85 was calibrated at the beginning of each run of the mesocosm, and as needed afterwards (typically every 2-3 days). We also took samples for water quality measurements at each time point. As with field water quality measurements, water samples were field filtered using an ashed Whatman GF/F glass fiber filter (0.7 µm nominal pore size) and kept on ice until they could be frozen, no more than 4 hrs following collection. All filters, sample syringes, and vials were acid washed prior to use, then were washed three times with distilled water, then three times with sample water immediately before the sample was taken. Samples were taken from the mesocosm outflow, if there was flow, and from the downstream end of the pool if there was not. Water samples were analyzed for nitrate, nitrite, ammonium, total dissolved nitrogen, soluble reactive phosphorus, total dissolved phosphorus, and dissolved organic carbon at the University of New Hampshire Water Quality Analysis Laboratory using standard methods.

Results

Field Density

The average density of *Corbicula* within the sampling reach was 191 m^{-2}. Most of these were in the extra small (< 10 mm shell length) and small (10-15 mm shell length) size class. 99.94% of the total *Corbicula* found were freshly killed. Using the average width of the Broad River, *Corbicula* density, and the length of the sampling reach, we estimate that a pre-mortality population of 94.4 million *Corbicula* existed in the 10.4 kilometer reach. Following the mass mortality event, only approximately 250,000 *Corbicula* survived (Table 4.1).

Estimating Filtration

Using published size-specific filtration rates (Lauritsen 1986) and size class data collected during the density surveys, we estimate that prior to the mass mortality event, *Corbicula* were filtering 8.02 $m^3s^{-1}$of water (Table 4.1). With an average width of 46.7 m, a 10.33 km sampling reach, and an average depth of 0.306 m, the reach held approximately 147,500 m^3 of water. Prior to the mortality event, the 94.4 million *Corbicula* would filter the water within about 5.1 hours. However, following the mass mortality event, the overall filtration rate dropped to 0.3 m^3s^{-1}, and the surviving *Corbicula* would take over 1,200 hours to filter the entire volume of the reach. In comparison, given the observed median discharge in July 2012, the month immediately prior to the mass mortality event, the residence time within the reach was approximately 11.6 hours (Table 4.1).

Field Water Quality Results

Concentrations of total dissolved phosphorus were significantly higher and concentrations of phosphate were marginally higher in areas where a die-off was occurring ($p=0.040$ and 0.085, respectively, Figure 4.1), but no differences were observed in any other water quality measurements (DOC, TDN, DON, nitrate, and ammonium). Despite the statistically significant difference, TDP and phosphate concentrations were low overall (max of 40 and 36 $\mu g\ L^{-1}$, respectively).

Mesocosm Experiment Results

Concentrations of ammonium, phosphate, and total dissolved phosphorus peaked immediately following addition of dead *Corbicula* (Figure 4.2, 4.3). The concentrations for all three nutrients were significantly higher in treatment mesocosm pools. On average, phosphate and total dissolved phosphorus were 52 $\mu g\ N\ L^{-1}$ and 95 $\mu g\ N\ L^{-1}$ higher, respectively, and ammonium concentrations were 94 $\mu g\ N\ L^{-1}$ higher in treatment pools five minutes following addition. For ammonium, a secondary peak of lower magnitude (24 $\mu g\ L^{-1}$) occurred between 24 and 72 hours, presumably as more recalcitrant tissue was decomposing. Despite the additional ammonium, there was not an additional peak in total dissolved phosphorus or phosphate. There were no observed differences between treatment and control pools for concentrations of nitrate, nitrite, total dissolved nitrogen, and dissolved organic nitrogen. Dissolved oxygen levels were consistently lower in the treatment mesocosm with the dead clams (Figure 4.5, $p<0.001$). Overall, dissolved oxygen levels were 0.27 $mg\ L^{-1}$ lower in the treatment mesocosm than the control, with the largest difference occurring eight hours to 72 hours following the addition of dead clams, when dissolved oxygen levels were 0.4 mg L^{-1} lower in treatment pools, on average. The peak difference in dissolved oxygen in the three replicate runs was 1.21 mg L^{-1}, at the 24 hr sample point. Despite the declines in dissolved oxygen concentrations, conditions remained oxic, with a minimum concentration of 5.30 mg L^{-1}. In a fourth mesocosm run, which was excluded from analysis because it was destroyed by high flows following a storm after only two days, dissolved oxygen concentrations dropped below 0.5 mg L^{-1} for the day one and two measurements.

Discussion

The response of *Corbicula* to climatic extremes is central to understanding the ecosystem-level effects of this invasive species. Because native unionid mussels have already been lost from many rivers in the Georgia piedmont due to sedimentation and other anthropogenic impacts (Neves et al. 1997), *Corbicula* is the most widespread significant filter feeder in the region. Others have hypothesized that *Corbicula* (Vaughn and Hakenkamp 2001) may compensate for lost unionid biomass, given their similar roles. Under baseline conditions, *Corbicula* provides similar or potentially higher filtration rates than an intact assemblage of native mussels would provide (Figure 4.5), due to high per capita and per biomass filtration rates (McMahon 1991). Our results demonstrate, however, a great deal of intra-annual temporal variability in the effectiveness of this compensation, as *Corbicula* was not able to withstand high water temperatures (Figure 4.5). With all the filter-feeding biomass in the Broad River concentrated in one species sensitive to high temperatures, this leads to a near cessation of filtration within the reach. In the mass mortality event documented here, nearly all *Corbicula* were lost from the system due to high temperatures. As a result, the reach shifted from a consumer controlled ecosystem, as the residence time was greater than the time for the *Corbicula* to filter the entire reach volume, to one controlled by inputs. While other studies have shown the massive changes that invasive bivalves can have on an ecosystem through interactions with native communities (Strayer et al. 1999, Caraco et al. 2006, Strayer et al. 2006), in this case, *Corbicula* may be providing services that native species would have otherwise provided. Therefore, the loss of nearly all the *Corbicula* in the river means that this entire class of organism, along with the important ecosystem function they provide, is eliminated from the system.

In addition to the loss of filtration, the death of millions of *Corbicula* would lead to the pulsed release of large amounts of nitrogen and phosphorus into the Broad River. Field measured values of phosphate were at least three to five times higher than monthly background measurements taken in 2013 just downstream of the sampling reach, from the EPA STORET database, all of which were below the detection limit of approximately 4 µg L^{-1}. This may indicate that during 2012 there may have been an additional mortality event upstream, however, we found no direct evidence of upstream mass mortality events.

In the Chesapeake Bay, the decline of the filter feeding Eastern oyster, *Crassostrea virginica*, led to a wide range of changes, from reduced top down control of phytoplankton to ecosystem level consequences such as reduced connections between the benthic and pelagic food webs (Coen et al. 2007). Additionally, oyster densities at historical levels could help mitigate anthropogenic eutrophication (Cerco and Noel 2007). As southeastern rivers are already high in nitrogen and extremely turbid, the loss nutrient uptake provided by *Corbicula* could lead to decreased surface water quality in downstream reservoirs, such as Lake Strom Thurmond.

The release of phosphorus and nitrogen during a mass mortality event could stimulate primary productivity during the low flow conditions typical of mortality events, particularly as southeastern rivers are often phosphorus limited (Elder 1985, Mainstone and Parr 2002). A mass balance approach indicates that there could be biotic uptake occurring in both the field and the mesocosm experiment. Using published dry tissue weight calculations (Lauritsen 1986), *Corbicula* tissue nitrogen content (Atkinson et al. 2011), and the nitrogen to phosphorus ratio for similar invasive species (Arnott and Vanni 1996), we estimate that 197 kg of nitrogen and 27 kg of phosphorus were released during the field mass mortality event. Assuming that *Corbicula* tissue would decay in approximately 48 hours, which matches both field and mesocosm observations, the reach volume calculated earlier, and the observed discharge during the mass mortality event, these inputs would have increased the concentration of nitrogen and phosphorus by 0.224 mg/L N and 30.9 µg/L of P. However, the average concentration of total dissolved phosphorus within the mass mortality event was only 12 µg/L higher than upstream of the event, and total dissolved nitrogen concentrations were unchanged. Additionally, phosphorus concentrations in the mescosom were lower than expected based on tissue stoichiometry and the observed nitrogen concentrations, as there was no secondary peak following dead *Corbicula*. The lack of a secondary phosphorus peak in the mesocosm experiment could be due to rapid biological uptake. The Broad River, and rivers in the region in general, have low concentrations of phosphorus; in monthly water quality surveys, phosphate and total dissolved phosphorus was below detection limits for all of 2013 (EPA STORET). There results, coupled with the drop in dissolved oxygen, indicate that productivity is being stimulated, presumably due to the phosphorus addition.

High concentrations of toxic unionized ammonia during mass mortality events have been identified as a potential way *Corbicula* could have negative impacts on native mussels (Cherry et al. 2005, Cooper et al. 2005). Our results do not support this as a plausible mechanism in the

Broad River, however. To translate the concentration of ammonium into ammonia, we used the maximum temperature observed during the field surveys of 35° C, the maximum pH observed in the Broad River in the EPA STORET database (8.50, EPA STORET 2014), and the maximum observed field and mesocosm concentrations of ammonium (26 and 208 μg L^{-1}, respectively), which would give us a theoretical maximum for unionized ammonia. This calculation estimated that only 0.007 μg L^{-1} of ammonia would be present in the field samples, and 0.055 μg L^{-1} in the mesocosm sample. Both of these are well below the LC_{50} for unionid glochidia (0.11 μg L^{-1}), the most sensitive life stage tested by Cherry et al. (2005). However, in more basic water bodies, this ammonia toxicity could be more problematic; if the pH were increased to 9, the maximum observed concentration of ammonium in the mescosom (208 ug L^{-1}) would just reach the LC_{50} for unionid glochidia (Cherry et al. 2005).

The reduction in dissolved oxygen levels following a mass mortality event is unlikely to direct affect the few unionid mussels that remain in the Broad River. Unlike *Corbicula*, unionids can shut down their metabolism in response to low dissolved oxygen conditions. However, this could have impacts on less tolerant organisms such as benthic macroinvertebrates, particularly ones that cannot quickly move out of affected reaches. Given that these mass mortality events occur when water temperatures are very high and dissolved oxygen levels are low, the mass mortality events could exacerbate already stressful conditions by further depressing dissolved oxygen concentrations.

Despite the magnitude of this mortality event, *Corbicula*'s unusual biology makes it unlikely to be excluded from the river. *Corbicula* has an extremely high fecundity and is a self-fertilizing hermaphrodite in its invasive range, allowing populations to rebound quickly from a small number of individuals (McMahon 2002). In fact, follow up visits indicate that densities returned to pre-mass mortality levels by the summer of 2013 (McDowell, pers. obs), indicating a great deal of resilience by *Corbicula*. These may not be providing the same levels of ecosystem function, however, as individuals were smaller on average than prior to the mass mortality event (McDowell, pers. obs). In contrast, native mussels would be more resistant to these mass mortality events, due to generally higher temperature tolerances (McMahon and Bogan 2002), but can occur under extreme drought (Vaughn et al. in review). Although *Corbicula* would persist in ecosystems, their densities, and therefore the services provided, would be highly variable in time, whereas an intact community of native mussels would provide more consistent services. These mass mortality events in *Corbicula* could also lead to selection for more tolerant individuals, given the extremely high selection coefficient for any individuals that can withstand higher temperatures. However, *Corbicula* in its invasive range reproduces clonally, and so there is extremely limited genetic diversity within a river system (Pigneur et al. 2012).

The life history traits of *Corbicula* suggest that its presence will interact with global climate change to produce novel, extreme events. The southeastern United States is projected to have hotter, drier summers in the future, which could make these mass mortality events a common occurrence. Temperature measurements from the Broad River watershed showed water temperatures above 30 ^{o}C three times since 2000 – twice in 2002 and once in 2009. In 2002, the entire state was under drought conditions, and 34% of the state was under an exceptional drought, the highest category; in 2009, the drought was much less severe, with only 44% of the state under drought conditions, but no areas under exceptional drought. However, in the other years there were several weeks with much more severe drought conditions that did not lead to high water temperatures, indicating that the frequency of droughts is not limiting the occurrence of high water temperatures, and therefore *Corbicula* mass mortality events. That could change with the forecasted increase of 2 – 5 ^{o}C in annual temperature for the southeastern United States, as well as a large increase in the number of days with air temperatures above 32 ^{o}C (USGCRP 2009). While the mass mortality of an invasive species might generally be considered a positive thing, these events represent the loss of the only remaining abundant filter feeder and thus could have major impacts on the system, both directly through release of nutrients, and indirectly, through the loss of this filter feeding capacity. Because of the generally higher tolerances of native mussels, a more intact bivalve community would have tolerated these extreme events better. Decreased biodiversity tends to make function less stable and resistant to perturbation from extreme events (Tilman and Downing 1994). Additionally, a more intact bivalve community could lead to improvements in water quality, via niche partitioning of preferred particle sizes (Cardinale 2011), leading to increased clarity and nutrient uptake.

Mass mortality events may occur with other invasive bivalves in the future. The zebra mussel and the quagga mussel (*Dreissena rostriformis bugensis*), two other widespread invasive filter feeding bivalves, have lower temperature tolerances than native unionid mussels (Spidle et al. 1995, McMahon 2002). With extreme climate events predicted to become more common, these mass mortality events could be a frequent occurrence in any invaded aquatic ecosystem.

Replacement of native biota by opportunistic invasive biota may come at a cost of decreased system resistance to extreme events. *Corbicula* populations are able to recover from extremely high mortality rates, however, presumably thanks to high reproductive rates and colonization from unaffected upstream populations. This lack of resistance, but strong resilience to extreme events primes this system for repeated mass mortality events, particularly with forecasted temperature increases (IPCC 2007). This could lead to large amounts of temporal variability, both intra- and inter-annual, in the services provided by *Corbicula*, depending on the time since the last mortality event. There is a synergism between invasive species and climate change (Hellman et al. 2008). In the face of more common extreme events, the ability of species to tolerate high temperatures becomes more important to the overall stability of the system. In the case of filter feeding bivalves, the invasive species which come to dominate many systems are generally very susceptible to extreme temperatures and therefore the services provided by these species will likely become unstable.

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Table 4.1. Summary of *Corbicula* density, abundance, and filtration rates pre- and post-mass mortality event. Prior to the mass mortality event, the time to filter the water volume within the reach was lower than the residence time, indicating that *Corbicula* could potentially control abundance of particulate organic matter, plankton, and zooplankton abundance in the water column. Following the mass mortality event, nearly all filtration stopped and the time to filter the reach volume was two orders of magnitude higher than the residence time.

	Density (*Corb.* $^{m-2}$)	**Abundance**	**Filtration (m^3s^{-1})**	**Time to filter reach (hrs)**	**Residence Time (hrs)**
Pre-Mass Mortality	191.41	94,317,595	8.02	5.11	11.58
Post-Mass Mortality	0.51	248,859	0.033	1248	11.58

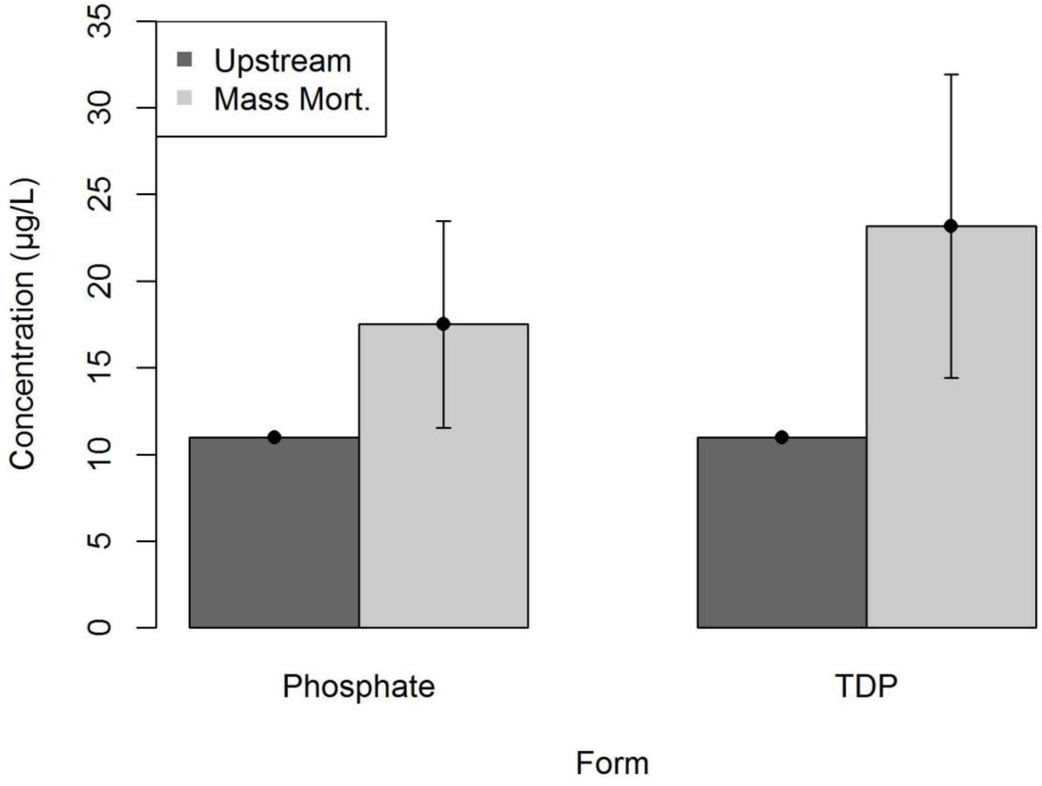

Figure 4.1. Comparison of observed phosphate phosphorus and total dissolved phosphorus within the mass mortality reach (n=12) and upstream of it (n=2). A one-tailed t-test showed that total dissolved phosphorus was significantly higher in the mass mortality reach (p=0.040), and phosphate was marginally higher (p= 0.085). Error bars represent one standard deviation and are zero for the upstream samples because both were identical.

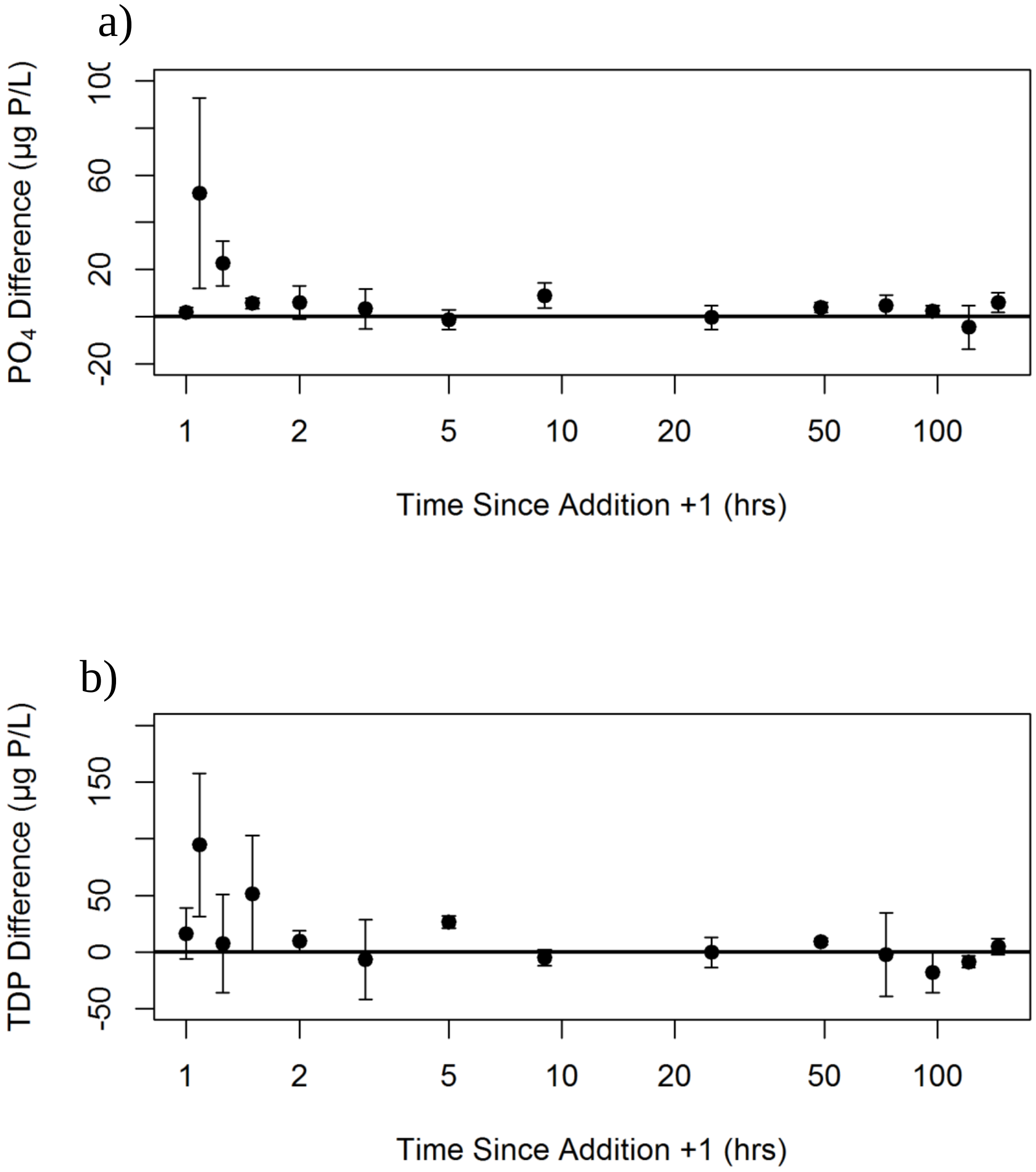

Figure 4.2. Average difference in a) total dissolved phosphorus and b) phosphate between control and treatment mesocosm pools (treatment – control). A paired t-test indicated that total dissolved phosphorus and phosphate were both significantly higher in treatment mesocosms (p=0.016 and 0.002, respectively). One hour was added to time since addition in order to use a log scale for the x-axis. Error bars represent one standard deviation.

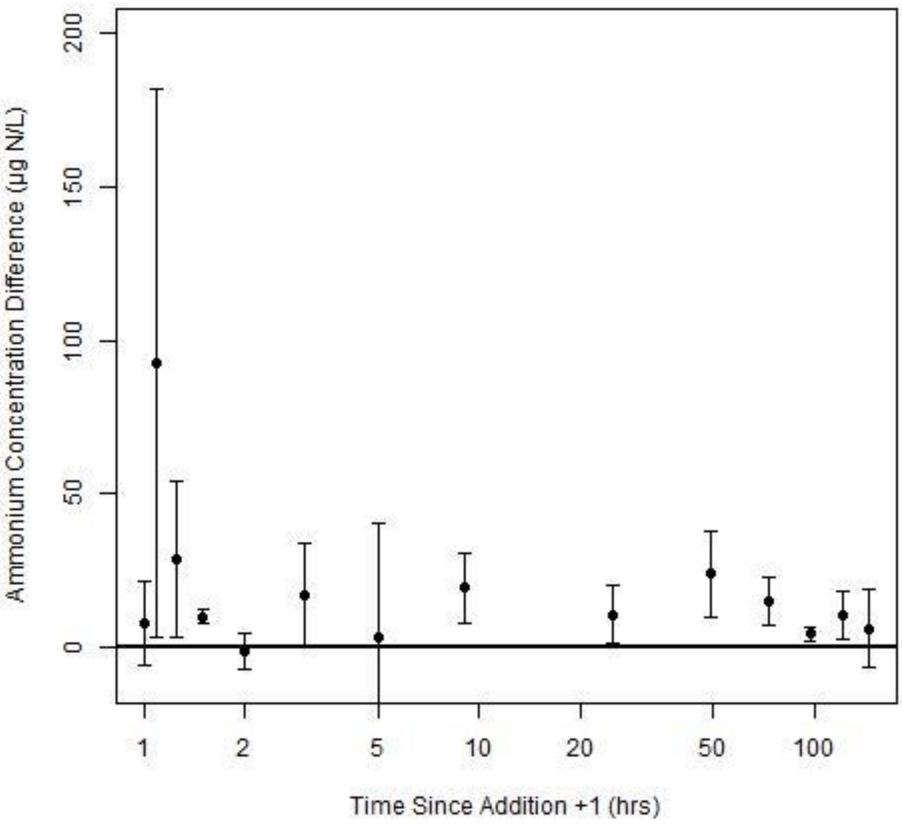

Figure 4.3. Average difference in ammonium concentrations between treatment and control mesocosms. A paired t-test indicated that ammonium concentrations were significantly higher in treatment mesocosms (p<0.001). One hour was added to time since addition in order to use a log scale for the x-axis. Error bars represent one standard deviation.

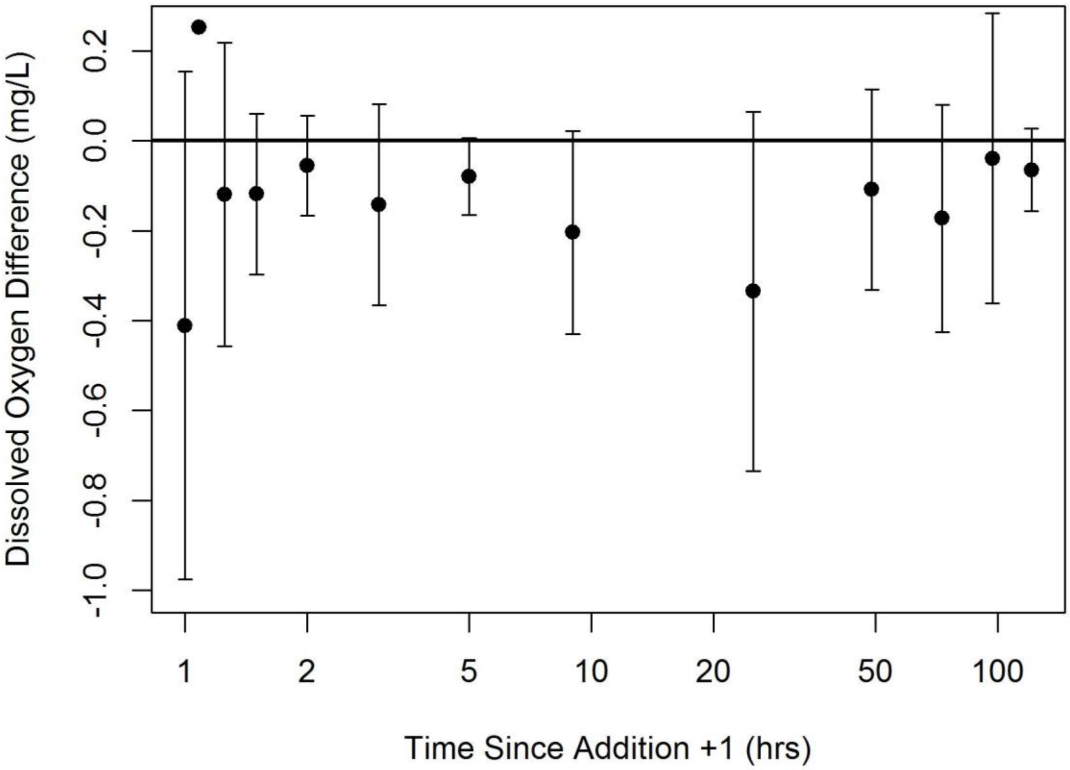

Figure 4.4. Average difference in dissolved oxygen between treatment and control mesocosms (n=3 for all points except t=0, 120, and 144 which have two and t=0.083 (5 minutes), which has one). A paired t-test showed that DO was significantly lower in treatment mesocosms (p<0.001). One hour was added to time since addition in order to use a log scale for the x-axis. Error bars represent one standard deviation.

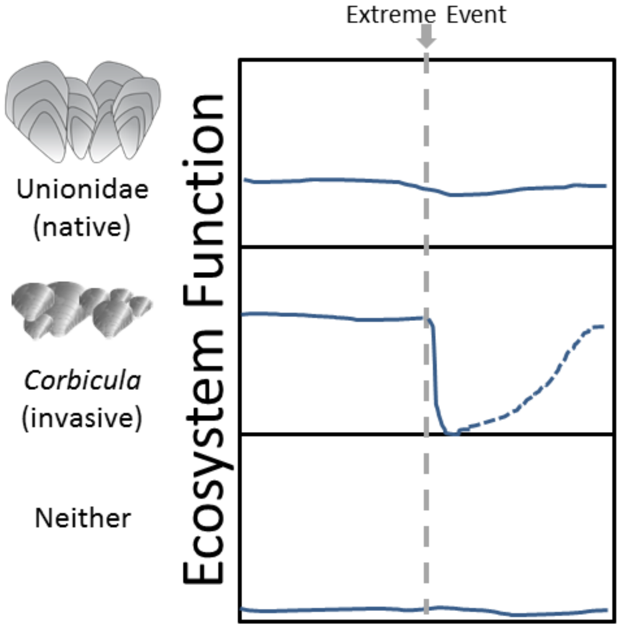

Figure 4.5. Conceptual diagram of ecosystem function provided by filter feeding bivalves prior to, and following an extreme event. Under baseline conditions, *Corbicula* provide more ecosystem function than an intact community of native mussels (unionids) would, due to high filtration rates per unit biomass. Following an extreme event, nearly all *Corbicula* died, leading to but native mussels would have been able to survive this event. Within one year, populations of *Corbicula*, and therefore the EF provided, returned to pre-mortality levels. As many rivers in the southeastern United States are similar to the middle panel now, we should expect large amounts of variance in filtration control and periodic pulsed nutrient releases, whereas the native dominated system was more robust to such stressors.

CHAPTER 5

CONCLUSIONS

In order to understand the overall impact of the invasive clam *Corbicula fluminea*, we set out to determine what its range is, how many are present in the Georgia Piedmont, and what impacts the *Corbicula* are having. Based on our distribution modeling, *Corbicula*'s distribution is likely controlled by climate variables more than habitat variables, such as substrate or water quality. *Corbicula* is likely to expand into the Great Lakes, northern Midwestern United States, and New England by 2080, and this expansion is likely to occur even under the most conservative carbon emissions scenarios. This represents an expansion of approximately 25% over their current range, and by 2080 up to 50% of the coterminous United States will be climatically suitable. Given *Corbicula*'s ability to disperse rapidly over long distances, the climatic suitability will likely determine their future range. Our habitat modeling indicates that areas with fine substrate and a high pH are especially likely to be invaded.

Throughout the Georgia Piedmont, *Corbicula* is extremely widespread and abundant, averaging about 100 individuals/m^2 across the four rivers sampled. As *Corbicula* prefers finer sediment, such as coarse sand, it is well suited to thrive in human impaired rivers that are full of fine sediment, unlike native Unionid mussels. *Corbicula* filter over 100% of the water column as it passes through a 10 km reach in three of the four rivers sampled, thanks to high densities and per capita filtration rates.

However, unlike native mussels, *Corbicula* are very sensitive to high temperatures and low dissolved oxygen concentrations. This led to a mass mortality event in one sampled river where over 99% of the *Corbicula* died. This led to a pulse of nitrogen and phosphorus, which in turn could lead to an increase in primary productivity and potentially an algal bloom in downstream reservoirs. Additionally, because native Unionids have declined substantially in this river, the loss of *Corbicula* meant that the important ecosystem functions provided by filter feeding bivalves nearly ceased. Estimated Filtration, for example, dropped from approximately 7.78 m^3s^{-1}, to 0.02 m^3s^{-1} following the mass mortality event.

In the future, the impacts of *Corbicula* will likely grow. With warming temperatures, the number of rivers invaded by *Corbicula* will likely increase. Additionally, warmer summer temperatures in the southeastern United States combined with less frequent precipitation events could increase the frequency of mass mortality events.

All told, *Corbicula* is an invasive species that is widespread, abundant, and has different life history characteristics than similar native species. As a classic r-selected species, it reproduces early in life, tends to reach high densities, has a short life span, and susceptible to adverse conditions. This dissertation provides a snapshot of the current impact of *Corbicula* in the southeastern United States, but also provides a glimpse into the future for uninvaded regions that may become suitable, and for southeastern rivers as mass mortality events become more common.

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APPENDIX A: FULL LIST OF VARIABLES CONSIDERED FOR DISTRIBUTION MODELING

Table S1. Full list of EPA EMAP habitat variables considered. Variables that were selected for inclusion in the final logistic regression model are marked with a †.

General Variables

Canopy cover midchannel	Canopy cover on bank	Average Depth†
Average Width	Percent urban land use in watershed	Percent agriculture land use in watershed†
Percent forest land use in watershed	Watershed area	

Water Quality

pH†	Total suspended solids†	Ammonium†
Conductivity	Total phosphorus	Nitrate
Turbidity	Calcium	Total nitrogen

Substrate

Percent Sand	Percent Course Gravel	Percent Fine (silt or finer)
Percent Fine Gravel†	Percent Bigger Coarse Gravel (>16 mm)	

Table S2. List of environmental variables from the BIOCLIM dataset used in the MaxEnt model. Bold font indicates variables that were significant predictors of *Corbicula* presence in the final MaxEnt model run; † superscript indicates variables included in the final logistic regression model comparisons.

BIOCLIM predictor variables	
1. annual mean temperature	10. mean temperature of warmest quarter
2. mean diurnal range temperature	11. mean temperature of coldest quarter
3. isothermality	12. annual precipitation†
4. temperature seasonality	13. precipitation of wettest month
5. maximum temperature of warmest month	14. precipitation of driest month
6. **minimum temperature of coldest month**†	15. precipitation seasonality
7. temperature annual range	16. precipitation of wettest quarter
8. mean temperature of wettest quarter	17. **precipitation of driest quarter**†
9. mean temperature of driest quarter	18. **precipitation of warmest quarter**
	19. precipitation of coldest quarter