Mass mortality of a dominant invasive species in response to an extreme climate event: Implications for ecosystem function

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Abstract

Impacts of invasive species on ecosystems are often context dependent, making empirical assessments difficult when climatic baselines are shifting and extreme events are becoming more common. We documented a mass mortality event of the Asian clam, *Corbicula fluminea*, an abundant invasive clam, which has replaced native mussels as the dominant filter-feeding bivalve in the southeastern United States. During an extremely hot and dry period in the summer of 2012, over 99% of *Corbicula* died in our 10-km study reach of the Broad River, Georgia. Because *Corbicula* were the only filter-feeding organism in the ecosystem with substantial biomass, their death led to the nearly complete cessation of ecosystem services provided by filter-feeding bivalves. We estimate that following the mass mortality event, turnover time within the sampling reach (reach volume/total filtration) rose from approximately 5 h to over 1200 h. In addition to the loss of filtering capacity, concentrations of total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) were also higher in areas where die-off was occurring than in an upstream area without mortality. Mass balance calculations and a manipulative mesocosm experiment predicted TDP and SRP concentrations much higher than our observed values, suggesting that rapid biotic or abiotic uptake of phosphorus may have occurred. Our study demonstrates that climate change can increase the temporal variability of populations of aquatic organisms that provide key ecosystem functions, and highlights that even pulsed, short-lived events can markedly affect systems of reduced diversity.

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 2005). Their effects on native species and community structure are widely known, but the effects of invasive species on nutrient cycling and other ecosystem functions 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 zebra mussel (*Dreissena polymorpha*) has reshaped nutrient dynamics in the Great Lakes, shifting phosphorus availability from open water areas to nearshore ecosystems thanks to its high densities and per capita filtration rates (Hecky et al. 2004).

Because 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 as native species (Byers 2002; Cox 2004). Therefore, to fully understand the impact of an invasive species, one must consider how the invasive species responds to extreme events and how these responses differ from native species. In aquatic communities, invasive species often represent a large proportion of the community diversity, 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, 2006; Vaughn and Hakenkamp 2001; Vaughn 2010; Sousa et al. 2013). In North America, the native mussels in the Unionidae family are in significant decline (Bogan 1993; Neves et al. 1997; Haag 2012). In many systems these species are no longer present due to human impacts and have been replaced by invasive filter-feeding bivalves such as the zebra mussel *D. polymorpha*

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and the Asian clam *Corbicula* sp. (McMahon and Bogan 2001). Globally, nutrient cycles in aquatic ecosystems have been dramatically reshaped by invasive bivalves, such as the golden mussel (*Limnoperna fortunei*) in South America (Cataldo et al. 2012; Boltovskoy and Correa 2015), the zebra mussel in the Hudson River (Caraco et al. 1997; Strayer et al. 2004) and the Great Lakes (Arnott and Vanni 1996; Hecky et al. 2004), and *Corbicula* sp. in both Europe (Pigneur et al. 2012) and the United States (Phelps 1994). These introduced bivalves are classic r-selected species—they are short lived, reproduce early, and are sensitive to extreme environmental conditions (McMahon 2002).

In many rivers in the southeastern United States, the native unionids are no longer abundant and instead *Corbicula* sp. are found in high densities (McMahon and Bogan 2001). Most likely *Corbicula fluminea* is the predominant species representing this genus in the southeastern United States, including in our study, because it is widespread (Leff et al. 1990; Atkinson et al. 2010 among others). However, because *Corbicula* represents a cryptic species complex and there is considerable taxonomic debate surrounding the number and identification of species within the genus (Sousa et al. 2008), we inclusively refer to it (and our study organism) as *Corbicula*. *Corbicula* is sensitive to both high temperatures (> 35°C) and low dissolved oxygen levels (< 0.5 mg L) (McMahon and Bogan 2001). Within the family Unionidae a wide range of tolerances and life history strategies is seen, but with few exceptions they are longer-lived and more tolerant of abiotic stressors such as high temperature and desiccation than are *Corbicula* (McMahon and Bogan 2001; Haag 2012). Although unionids are not immune to the effects of these stressors (*see* Haag and Warren 2008; Atkinson et al. 2014; Vaughn et al. 2015), in several cases during extreme events *Corbicula* mortality was nearly complete while some native mussels survived (Haag and Warren 2008), or *Corbicula* mortality occurred before impacts on native mussels were observed (Golladay et al. 2004), indicating *Corbicula*'s lower tolerance to these stressors. Typically, mass mortality events affecting unionids occur when rivers and streams cease to be free flowing, and form disconnected pools with extremely high temperatures (Golladay et al. 2004; Haag and Warren 2008; Atkinson et al. 2014; Vaughn et al. 2015).

Systems dominated by *Corbicula* may be particularly sensitive to mass mortality events, potentially even when systems maintain flow, and the impact of these events are both via the release of nutrients, and via the loss of ecosystem functions provided by the *Corbicula* (e.g., filter feeding and associated water column processing). The effects of these die-offs have not previously been described on a large spatial scale, or with direct measurements of water quality impacts.

To examine the direct and indirect effects of a *Corbicula* mass mortality event, we used a combined observational and experimental approach. Specifically, we used field observations to quantify the extent of a naturally occurring mass mortality event and its water quality impacts, and scaled up the clam's known per capita effects to quantify the loss of ecosystem function associated with *Corbicula* mortality. A mesocosm experiment provided a controlled examination of water quality impacts, including the timing, amount, and form of nutrients released during a simulated mass mortality event.

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, USA. The Broad River is one of the only unimpounded rivers in Georgia, and eventually flows into Lake Strom Thurmond, an impoundment of the Savannah River. The watershed is relatively rural, 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. Within the sampling reach the river is broad (40–60 m wide), relatively shallow (0.3 m on average), and slow moving. Due to shifting substrate, black flies and caddis flies are largely absent, and dragonfly nyads are the only commonly found benthic macroinvertebrates.

The summer of 2012 was very hot, with record high air temperatures of 43°C, and below-average precipitation. From January to August, 2012, precipitation was approximately 25% 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^3 s^{-1} compared with the recorded median of 19.8 m^3 s^{-1} (from 7 years of record, 2006–2013). In the nearby Middle Oconee River, which has 76 years of records, discharge in July 2012 was the seventh lowest on record. Because of the combination of record high air temperatures and low flows, we observed water temperatures as high as 34°C in the Broad River during regular bivalve density surveys as part of a separate study. We also observed an in-flow mass mortality event where millions of *Corbicula* were dying.

To quantify the extent of the mass mortality event, we sampled a 10.4 km reach of the Broad River. Previous surveys earlier in the summer of 2012 showed that *Corbicula* is the dominant bivalve within the Broad River, averaging approximately 60 individuals m^{-2} in the river as a whole, with a range of average densities per transect from 29 clams m^{-2} to 136 clams m^{-2} (W. G. McDowell and J. E. Byers unpubl.). Although these surveys did not specifically target unionid mussels, none were found. Mass mortality of *Corbicula* was first observed on 25 July 2012 downstream of a wide (100 m), shallow (0.2 m) bedrock shoal and continued for the remaining 10.4 km sampling reach. Within this reach, the visceral masses of dead *Corbicula* were frequently observed floating

downstream. The mass mortality event appeared to have just occurred, because most *Corbicula* had visceral masses still attached to their shells and did not smell of decay. Immediately upstream of the mass mortality event neither live nor dead *Corbicula* were present, presumably due to the very fine, loose substrate at this site, which is typically not thought to be suitable habitat for *Corbicula*; in addition, no dead clam tissue was observed floating within the water column at this upstream site. However, sampling sites approximately five kilometers upstream had densities of 45 individuals m^{-2} during sampling events 2 weeks later, so *Corbicula*'s absence from this one area appears to be a localized case.

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 2 days after the initial discovery of the event, on 27 July 2012 from approximately 09:00 h to 15:00 h. 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 h following collection. Water samples were analyzed for nitrate, nitrite, ammonium, total dissolved nitrogen, soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and dissolved organic carbon at the University of New Hampshire Water Quality Analysis Laboratory using standard methods. Nitrate, nitrite, ammonium, phosphate, and TDP were measured using colorimetric methods (EPA 353.2 [both NO_3 and NO_2], 350.1, 365.3, and USGS Method 4560-03, respectively) and a Westco SmartChem discrete robotic analyzer. Total dissolved nitrogen and dissolved organic carbon (non-purgeable organic carbon) were measured using high temperature platinum-catalyzed combustion on a Shimadzu TOCV with TN module. Dissolved organic N was estimated as total dissolved N minus inorganic nitrogen. Two samples were taken upstream of the mass mortality event, while twelve were taken within the mass mortality event. Water quality measurements were compared within and upstream of the mass mortality event using an ANOVA. Spatially explicit analyses were explored, but no spatial structure was found and given the distance between samples (0.75 km) we treated sampling sites as independent measurements.

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 systematically 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 binned 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. Unattached visceral masses were not included in the counts of recently killed *Corbicula*, nor were any shells that were broken or had holes near the umbo, did not have the lustrous nacre, or were not attached at the hinge. 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 of the river 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 dead *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 those of Lauritsen (1986) for use in this study for three reasons: (1) it uses a population in the 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 as a function of *Corbicula* shell length, thereby allowing us to calculate total population filtration based on observed size distribution of *Corbicula*. In addition, 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^3 s^{-1}) to estimate the time required for *Corbicula* to filter the water within the reach. This was then compared with the residence time, which was calculated by dividing the reach volume (m^3) by the discharge values (m^3 s^{-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 to provide a time series of observations during a mortality event, we conducted a field mesocosm experiment. The 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) side-by-side spanning the channel. This

stream is suitable habitat for *Corbicula*, but densities were low (< 5 m^{-2}) prior to the experiment and were thus unlikely to affect its outcome. We created these pools by vertically 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 ($n = 3$). A fourth replicate was initiated, but it was destroyed by heavy rains and high flows on the third day and not included in any statistical analyses. To prevent impacts from previous runs of the experiment, pools were re-installed upstream for successive replicates and treatment and control pools were switched to the opposite side of the channel. We collected *Corbicula* from the Middle Oconee River, at Ben Burton Park, 1 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 a single sampling point 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 (W. G. McDowell and J. E. Byers unpubl.). This density was only about a quarter of the highest density observed in the Broad River (8400 *Corbicula* m^{-2}). Before we added *Corbicula* to the treatment mesocosm pool, *Corbicula* were killed by immersing them in a container of hot (40°C) water for 90 s. This method was observed to kill over 99% of *Corbicula* during initial trials. The water used to kill the clams was then discarded to avoid introducing any nutrient-laden water in association with the addition of dead clams.

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 min, 15 min, 30 min, 1 h, 2 h, 4 h, 8 h, 24 h, and daily thereafter, for up to 1 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 immediately following the addition of dead clams. At each time point, dissolved oxygen, temperature, and conductivity were measured using a field multi-meter (YSI 85). We also took samples for water quality measurements at each time point. As with field water quality measurements, water samples were field filtered using a pre-combusted 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 h following collection. All filters holders, 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, SRP, TDP, and dissolved organic carbon at the University of New Hampshire

Fig. 1. High density (> 1000 m^2) of dead *Corbicula* within mass mortality event in the Broad River, July 2012. The visceral mass was intact for most individuals and did not smell of decay, indicating freshly dead *Corbicula*.

Water Quality Analysis Laboratory using the same standard methods described above for field water quality surveys. Mesocosm water quality results were analyzed using a paired *t*-test comparing treatment and control pools of same experimental replicate and time point.

Results

Field density

The average density of live and dead *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, as evidenced by body and shell condition (Fig. 1). 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 km reach. Following the mass mortality event, only approximately 250,000 *Corbicula* survived (Table 1; Fig. 1). By the following summer, *Corbicula* appeared to have returned to their earlier levels based on a small number of spot density checks.

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, the entire population of *Corbicula* within the sampling reach was filtering 7.79 m^3 s^{-1} of water (Table 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 5.26 h. However,

Table 1. Summary of *Corbicula* density, abundance, and filtration rates pre- and post-mass mortality event within the sampling reach of the Broad River, GA, which was 10.33 km long, 46.7 m wide, 492,700 m², 0.3 m deep, and 147,500 m³ in volume. With an average discharge of 3.54 m³ s⁻¹ for July 2012, the residence time within the sampling reach was 11.58 h. For *Corbicula* observations, filtration rates were calculated based on Lauritsen's (1986) relationship between shell length and filtration rate and field observed lengths for individual *Corbicula*. 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 (ind. m⁻²)	Abundance	Population filtration rate (m³ s⁻¹)	Dry tissue (g m⁻²)	Mass-specific filtration rate (L h⁻¹ g⁻¹)	Time to filter reach (h)
Corbicula pre-mass mortality	191.41	94,317,595	7.79	3.49	16.29	5.26
Corbicula post-mass mortality	0.51	248,859	0.034	0.013	16.29	1210

following the mass mortality event, the overall population filtration rate dropped to 0.034 m³ s⁻¹, and the surviving *Corbicula* would take over 1200 h 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 11.58 h (Table 1).

Field water quality

Concentrations of TDP were significantly higher and concentrations of phosphate were marginally higher in the mass mortality area than upstream ($p = 0.040$ and 0.085, respectively, Fig. 2). Phosphorus concentrations were well above detection limits of 4 μg L⁻¹, and increased approximately 50% over upstream values in the study reach (Fig. 2). No significant differences were observed in any other water quality parameters, with average levels (DOC = 2.01 mg C L⁻¹, DON = 0.16 mg N

L⁻¹, NH₄ = 16 μg N L⁻¹, NO₃= 0.354 mg N L⁻¹, NO₂ = 3 μg N L⁻¹) indicative of a moderately nutrient-rich river.

Field mesocosm experiment

Concentrations of ammonium, phosphate, and TDP peaked immediately following addition of dead *Corbicula* (Fig. 3). The concentrations for all three nutrients were significantly higher in treatment mesocosm pools (ammonium: $t = 3.48$, df = 40, $p < 0.001$; $t = 2.11$, SRP: df = 38, $p = 0.02$; TDP: $t = 2.23$, df = 36, $p = 0.016$). On average, SRP and TDP were 52 and 95 μg P L⁻¹ higher, respectively, and ammonium concentrations were 60 μg N L⁻¹ higher in treatment pools 5 min following addition. For ammonium, a secondary peak of lower magnitude (24 μg L⁻¹) occurred between 24 and 72 h, presumably as more recalcitrant tissue was decomposing. Despite the additional ammonium, there was not an additional peak in total dissolved or SRP. There were no observed
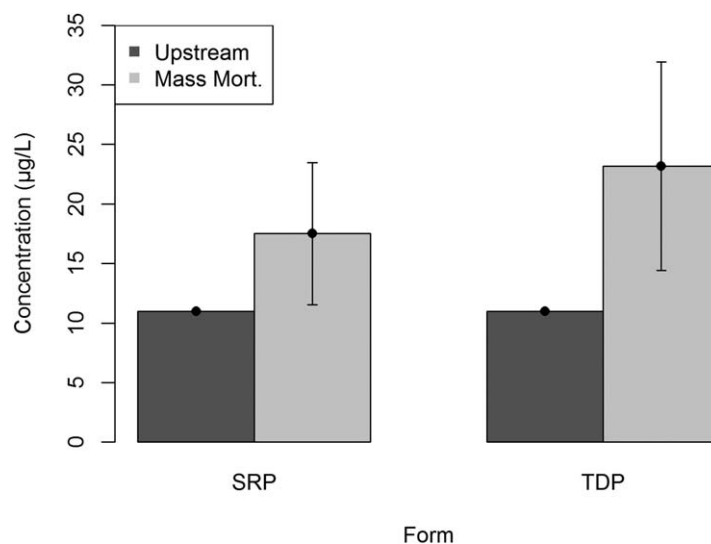
Fig. 2. Comparison of observed SRP (phosphate) and TDP within the mass mortality reach ($n = 12$) and upstream of it ($n = 2$). A one-tailed *t*-test showed that TDP was significantly higher in the mass mortality reach ($p = 0.040$), and phosphate was marginally higher ($p = 0.085$). Error bars represent one standard deviation and are zero for the upstream samples because both samples were identical.
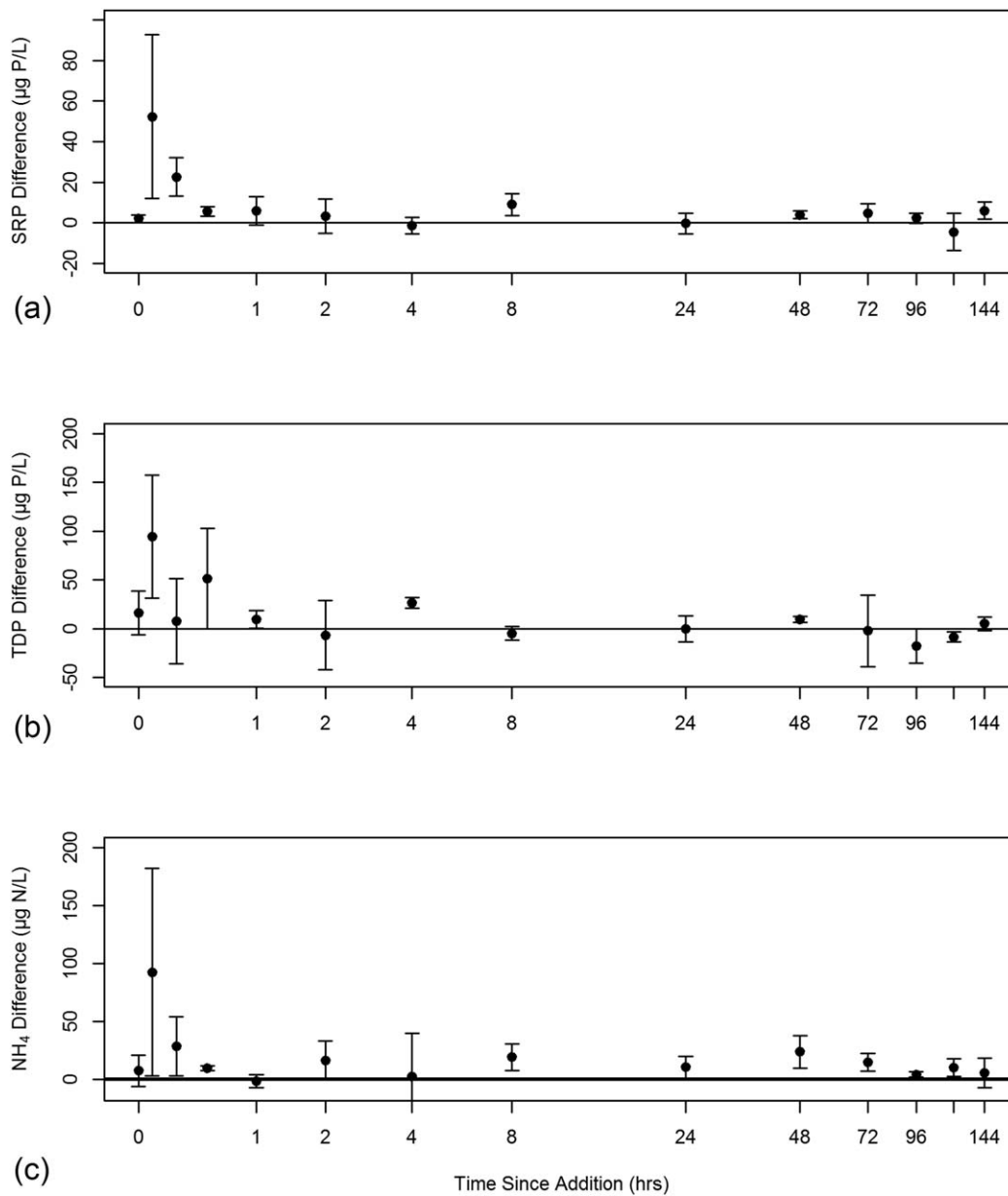
Fig. 3. Average difference in (**a**) SRP, (**b**) TDP, and (**c**) ammonium between control and treatment mesocosm pools (treatment–control). A paired *t*-test indicated that TDP and phosphate were both significantly higher in treatment mesocosms ($p = 0.016$ and 0.02, respectively). One hour was added to time since addition to use a log base 10 scale for the *x*-axis. Tick mark labels have been adjusted to account for this. Error bars represent one standard deviation.

differences between treatment and control pools for concentrations of nitrate, nitrite, total dissolved nitrogen, dissolved organic nitrogen, and dissolved organic carbon. Dissolved oxygen levels were consistently lower in the treatment mesocosm with the dead clams ($t = 5.38$, df $= 36$, $p < 0.001$, Fig. 4) but never dropped below 5.3 mg L^{-1}; the largest difference in dissolved oxygen concentration between treatment and control of dissolved oxygen (0.6 mg L) were observed at the 24- and 72-h measurements.

Discussion

This study provides the first quantitative, whole-reach assessment of an inflow mass mortality event of *Corbicula*, the dominant filter-feeding bivalve in most rivers in the southeastern United States. Documenting the response of *Corbicula* to climatic extremes is central to understanding the ecosystem-level effects of this invasive species. Within the Broad River, unionid mussels are functionally extirpated
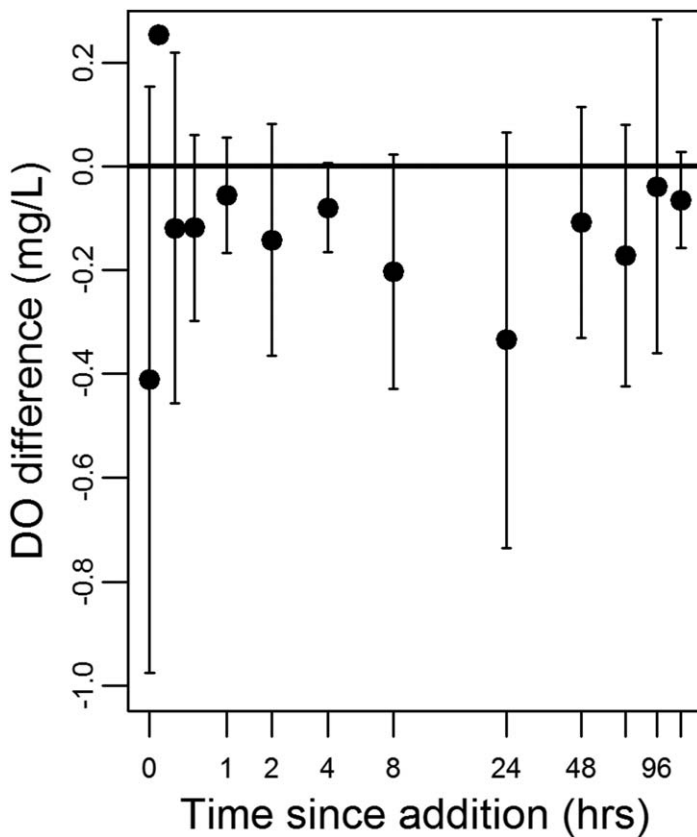
Fig. 4. Average difference in dissolved oxygen between treatment and control mesocosms ($n = 3$ for all points except $t = 0$ and 120 ($n = 2$) and $t = 0.083$ (5 min, $n = 1$). A paired *t*-test showed that DO was significantly lower in treatment mesocosms ($p < 0.001$), however, absolute DO concentrations never dipped below 5.30 mg L^{-1}. One hour was added to time since addition to use a log base 10 scale for the *x*-axis. Tick mark labels have been adjusted to account for this. Error bars represent one standard deviation.

and none were detected during our surveys, therefore the ecosystem services provided by filter-feeding bivalves (Vaughn and Hakenkamp 2001) are exclusively provided by *Corbicula*. No other filter-feeding organisms were found during the surveys—very few benthic macroinvertebrates were found, and those found were exclusively dragonfly nyads. With the mass mortality event of Corbicula, this means that the ecosystem functions provided by filter-feeding bivalves as a whole effectively cease. This can be seen with the summer low flow turnover time rising from 5.26 h before the mass mortality event to over 1200 h (Table 1).

The biomass of unionid mussels, both historical and extant, within the piedmont region of the southeastern US is poorly described, as is the biomass of the invasive *Corbicula*. This lack of basin-wide data makes it difficult to develop quantitative comparisons of the importance of *Corbicula* to that of native unionids. However, within the southeastern United States as a whole, declines of unionid mussels have

been documented over the last few decades and they have been extirpated from many systems (Neves et al. 1997). In rivers such as the Broad River, *Corbicula* is currently the most widespread filter feeder with significant biomass, and *Corbicula* has been hypothesized to compensate for lost unionid biomass, given their similar ecological roles (Vaughn and Hakenkamp 2001). Under baseline conditions without mass mortality events, *Corbicula* provides four times as much filtration per unit biomass (16.3 L h^{-1} g^{-1}; Table 1) as a composite of 12 unionid species in Oklahoma (3.93 L h^{-1} g^{-1}) (Vaughn et al. 2015). Although this comparison is coarse, it suggests that *Corbicula* is currently playing an important ecological role in rivers such as the Broad, but that extreme events can quickly reduce their numbers and thus significantly alter their importance in the river ecosystem.

Extreme events can have negative impacts on the native unionid mussels as well as the invasive *Corbicula*. Recent literature, however, shows that both the severity of the extreme event that elicits mass mortality and the magnitude of the response to the extreme event differ greatly from our observations of a *Corbicula* mortality event within a free flowing river. For example, during a severe multi-year drought in Oklahoma, several rivers became a series of disconnected pools with water temperatures reaching over 40°C (Galbraith et al. 2010; Atkinson et al. 2014). Unionid mussel populations declined by 60% during these extreme events (Vaughn et al. 2015). Golladay et al. (2004) and Haag and Warren (2008) both observed declines in unionid mussel populations ranging from 30% to 90% and 65% to 83% during droughts in the southeastern United States, but only in non-flowing sites; at sites that maintained flow, populations were steady or even increased in response to the drought. In contrast, *Corbicula* appears far more sensitive. In the Broad River over 99% of *Corbicula* died during the mass mortality event, which peaked in temperature at 34°C and remained free-flowing throughout the summer of 2012.

With nearly all the filter-feeding biomass concentrated in a single species sensitive to high temperatures, the Broad River ecosystem is therefore extremely susceptible to a nearly complete loss of biofiltration within the affected reach, causing a shift from a consumer-controlled ecosystem, where the hydrologic residence time was greater than the time for the *Corbicula* to filter the entire reach volume, to one controlled by inputs. Although other studies have documented the massive effects that invasive bivalves can have on an ecosystem through interactions with native communities (Caraco et al. 1997; Strayer et al. 1999, 2006), in this case, *Corbicula* may be providing services that native species would have otherwise provided. Because the unionids were in decline in the region prior to the invasion of *Corbicula* (Neves et al. 1997), *Corbicula* appears to have replaced an important ecosystem service, rather than displacing a native species. The (temporary) loss of nearly all the *Corbicula* in the river means the full loss of filter feeders, along with the important
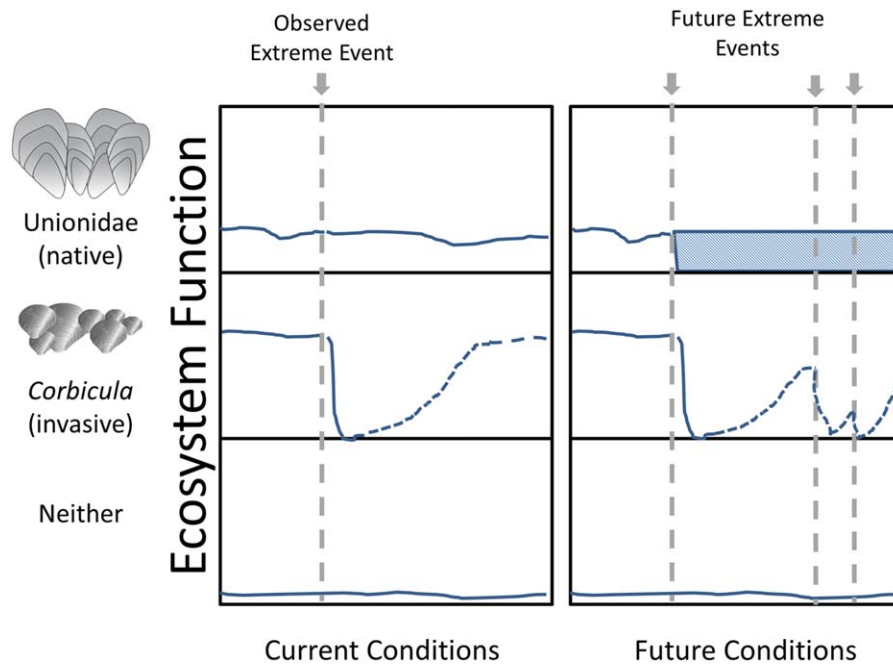
Fig. 5. Conceptual diagram of ecosystem function provided by filter-feeding bivalves prior to, and following an extreme event under current climate conditions (first column) and projected conditions where extreme events are more frequent (second column). Under baseline conditions, *Corbicula* provide more ecosystem function than an intact community of native mussels (unionids) would were they present, due to high filtration rates per unit biomass and higher densities. Following an extreme event in the Broad River, nearly all *Corbicula* died, but native mussels would have been able to survive this event. Within 1 year, populations of *Corbicula*, and therefore the ecosystem function provided, returned to pre-mortality levels (dashed lines indicate potential recovery trajectory). However, under future climate scenarios these extreme events are likely to become more common, leading to more frequent mortality events which may reduce *Corbicula* populations, and therefore diminish the ecosystem functions associated with them. The impact of future extreme events on native mussels is less predictable (denoted by shaded area) and may depend on the severity of the events. As many rivers in the southeastern United States are similar to the middle panel now, we should expect large variance in filtration control and periodic pulsed nutrient releases. [Color figure can be viewed at wileyonlinelibrary.com]

ecosystem function they provide, until its populations can rebound.

The mesocosm results support our contention that the measured increase in P in the Broad River was specifically due to mass mortality of *Corbicula*. In 2013, a non-die off year, phosphorus concentrations downstream of the sampling reach were measured monthly by the Georgia Department of Natural Resources and were below their detection limit of approximately 4 μg soluble reactive P L^{-1} (EPA Method 365.1). Values that we measured in 2012 for SRP were well above this detection limit, ranging from 11 to 40 μg L^{-1}, and were at least 3–10 times higher than those observed in 2013. This year-to-year change in SRP, when combined with the significant upstream-downstream increase in TDP that we measured during the mortality event, provides strong evidence that *Corbicula* mortality can alter phosphorus dynamics at the scale of a large river reach.

Our combined mesocosm and field data can be used to assess the magnitude of the nutrients and organic matter released by *Corbicula* mass mortality. At the whole river scale, the biomass of dead clam dry tissue (1714 kg for the

reach) would contain 751 kg of carbon, 180 kg of N (10.48% N), and 44.9 kg of P (2.62% P) (using values for clam elemental content from Atkinson et al. 2010 and unpubl.). These nutrients would increase river concentrations by 1.82 mg L^{-1} for carbon, 0.204 mg L^{-1} for nitrogen, and 51.3 μg L^{-1} for phosphorus, using the volume of the sampling reach plus river flow over the 2 days required for soft tissue to decay following the mortality event. Only an increase in phosphorus was observed, however, and the magnitude of this increase (12.3 μg L) was much lower than predicted by the mass balance calculations. The lack of any significant increase in concentrations of dissolved organic carbon, dissolved organic nitrogen, or inorganic nitrogen in the Broad River and differences between these estimated values and field observations suggest that in-stream uptake of carbon and nutrients may be occurring soon after *Corbicula* decay or that peak concentrations were missed during sampling. Microbial assimilation or denitrification could both result in a loss of C and N from the rapidly decomposing *Corbicula* soft tissue, resulting in lower observed concentration of C and N than would be expected based on the stoichiometry of *Corbicula* tissue and the observed phosphorus

concentrations. The rapid uptake of nutrients 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). In particular, nutrients could have been released directly into sediment pore water or taken up by sediment microbes and thus would not have been detected in our water column measurements.

Nitrogen and phosphorus in shells could also have longer-term impacts on nutrient cycling within the system. Shell fragments can persist for years within the river (Strayer and Malcom 2007), and using observed size classes we estimate that the mass mortality event added approximately 130,000 kg of dead shell. While data on shell stoichiometry are not available for *Corbicula*, unionid species contain approximately 1% N and 0.01% P by mass (Christian et al. 2008) indicating that *Corbicula* shells could play an important long-term role in nutrient cycling following a mortality event.

High concentrations of un-ionized ammonia are lethal to unionid mussels (Newton et al. 2003; Wang et al. 2007) and the release of ammonia during *Corbicula* mass mortality events has been identified as a potential mechanism by which *Corbicula* could have negative impacts on native mussels (Cherry et al. 2005; Cooper et al. 2005). Our results suggest this is unlikely to be occurring in the Broad River, however. The maximum concentration of ammonia in our sampling reach of the Broad River can be calculated from the maximum measured concentration of ammonium (26 μg L^{-1}), the maximum temperature observed during the field surveys (35°C), and the highest pH observed during summer months (7.7, EPA STORET 2014). This calculation yields an estimate of 1.39 μg L^{-1} of unionized ammonia, well below the LC$_{50}$ for unionid glochidia (11 μg L^{-1}), which was the most sensitive mussel life stage tested by Cherry et al. (2005). While this may be an underestimate if our sampling missed the ammonium peak, even in the mesocosm experiment, which had a higher density of *Corbicula* than the field sampling reach, more stagnant water, and a much more frequent sampling schedule, the maximum observed ammonium concentration of 208 μg L^{-1} yields an estimated concentration of 11.1 μg L^{-1} of unionized ammonia, barely above the LC$_{50}$ for unionid glochidia. Under the median summer pH value of the Broad River (7.3, EPA STORET 2014), instead of the maximum pH used in the previous calculation, we estimate unionized ammonia concentrations reached 4.89 μg L^{-1} in the mesocosms. Thus, *Corbicula* mortality events have the potential to create lethal concentrations of unionized ammonia for native unionids only in stagnant water bodies with extremely high *Corbicula* densities or high pH.

Any reduction in dissolved oxygen levels due to *Corbicula* decomposition following a mass mortality event is unlikely to directly affect the few unionid mussels that remain in the Broad River. Although DO levels were significantly lower when large numbers of dead *Corbicula* were added to our experimental mesocosm, the absolute levels were still adequate for aerobic organisms. Furthermore, unlike *Corbicula*, unionids can slow or nearly stop their metabolism in response to low dissolved oxygen conditions (McMahon and Bogan 2001). Although we did not observe hypoxic levels of DO, the decrease associated with decay of *Corbicula* could be larger under very stagnant conditions; modest flow, as used in the experimental mesocosm pools, appears to be sufficient to minimize the likelihood of anoxic conditions during a mass mortality event.

Despite the magnitude of the mortality event that we have documented, *Corbicula*'s unusual biology makes it unlikely that this level of mortality would result in its exclusion from the river. *Corbicula* has an extremely high fecundity and is a self-fertilizing hermaphrodite that reproduces via androgenesis in its invasive range, allowing populations to rebound quickly from a small number of individuals (McMahon 2002). In fact, follow-up visits indicated that densities returned to pre-mass mortality levels by the summer of 2013, mirroring the rapid population recovery observed following a mass mortality event in Portugal (Ilarri et al. 2011). However, these newly recruited clams may not be providing the same levels of ecosystem function, as individuals were smaller on average than prior to the mass mortality event (W. G. 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 2001).

Conclusions

Replacement of native biota by opportunistic invasive biota may come at a cost of decreased system resistance to extreme events. In the case of *Corbicula*, its high fecundity appears to allow population levels to rebound quickly following a catastrophic mass mortality event such as the one we have documented. *Corbicula* biomass is thus inherently more variable than the native fauna that it has replaced, with concomitant effects on ecosystem services such as the water filtration that these bivalves provide (Fig. 5). This heightened sensitivity, but strong resilience to extreme events primes this system for repeated mass mortality events, particularly with forecasted temperature increases (IPCC 2007). Given that *Corbicula*'s range is predicted to expand (McDowell et al. 2014), understanding its impact under both baseline and extreme conditions is key to assessing its ecological role. In the face of more common extreme events, the ability of a species or species assemblage to tolerate high temperatures becomes even more important to the overall stability of the system. Invasive species often have high growth rates (Rejmanek and

Richardson 1996), and this may in fact reduce the evolutionary value of tolerance to stressful conditions (McMahon 2002), leading to less resistance to perturbations, but more resilience. Our results also tend to support the general principle that decreased biodiversity tends to make ecosystem functions less stable and less resistant to perturbation from extreme events (Tilman and Downing 1994). As an increasing number of systems lose native species and are dominated by non-natives, the systems become more reliant on the ecosystem services provided by non-natives and may simultaneously become more susceptible to enhanced variability.

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Conflict of Interest

None declared.