Species and function lost: Role of drought in structuring stream communities

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ABSTRACT

Drought is an important natural disturbance that influences community structure by altering species composition, abundance, and richness. Human-induced alterations of the hydrologic cycle and climate change can exacerbate the impact of drought, potentially leading to species extirpations and changes in community structure. These changes in community structure can lead to substantial alterations and losses of ecosystem functions. Nutrient recycling is an important ecosystem function that helps modify rates of production and food web structure. Animals are important in cycling and storing nutrients in aquatic ecosystems through feeding, growth, and excretion. Freshwater mussels are long-lived animals, often living more than 20 years, and perform important ecosystem functions such as nutrient storage and cycling. Mussels dominate benthic biomass in many aquatic systems, and thus can be an essential component affecting nutrient dynamics. Unfortunately, they are experiencing rapid declines. In this study, we surveyed freshwater mussel populations across nine sites in three rivers in the south-central U.S. immediately before and after an exceptional, regional drought. We characterized the hydrological severity of the drought and estimated mussel biomass loss and the consequent loss of mussel-provided nutrient cycling and storage. We determined if losses differed between mussel thermal guilds and how such losses might influence nutrient dynamics and stoichiometry. Additionally, we investigated whether losses caused by the drought were intensified by different land cover types. Our surveys indicated that there were declines in both density and biomass of mussels, and greater losses were associated with areas that had less forest cover. This die-off resulted in a lower availability of N and reduced P storage by freshwater mussels in these rivers, potentially altering system nutrient availability. Additionally, our analyses showed that thermally sensitive species have lower tissue N:P. Thus, our results show that differences in species tolerance to drought may lead to varying storage and release of nutrients. Further studies incorporating net flux and storage will allow scientists to better understand the repercussions of species loss to ecosystem function.

1. Introduction

On a global scale, freshwater biodiversity is declining precipitously, with extinction rates five times higher in freshwater than in terrestrial systems (Dudgeon et al., 2006). Most of the factors underlying biodiversity loss in freshwater systems are human-derived and include water pollution, overexploitation of water resources, and habitat degradation. Climate change and human alterations to flows (e.g. water withdrawals, channelization) will potentially intensify these stressors (e.g. water temperatures, timing and magnitude of flows) (Palmer et al., 2008). Drought is an important natural disturbance that influences community structure (Boulton, 2003; Lake, 2003; McCluney and Sabo, 2012; Resh et al., 1988; Woodward et al., 2012), but human induced alterations of the hydrologic cycle can exacerbate drought impacts (Bond et al., 2008; McCluney and Sabo, 2012; Perry et al., 2012; Xenopoulos et al., 2005). Rivers around the world are drying with increasing frequency and severity (Cayan et al., 2010; Gleick, 2003; Poff et al., 1997) and this has been a major cause of biodiversity loss (Postel and Richter, 2003). There is evidence that declines in species richness and abundance alter ecosystem processes and reduce overall ecosystem function (Covich et al., 2004; Hooper et al., 2005; Kirwan et al., 2009; Vaughn, 2010), ultimately...
compromising human well-being (Cardinale, 2011). Understanding the consequences of biodiversity loss to ecosystem function is critical for predicting ecosystem change.

In both terrestrial and aquatic ecosystems, organisms directly affect nutrient dynamics by sequestering nutrients through growth and remineralizing nutrients via excretion and egestion (Vanni, 2002). The relative magnitude of consumer excretion and its potential importance to ecosystem-level nutrient cycling depends on a number of biotic and abiotic factors. Characteristics of the consumer community are clearly important, including stoichiometric requirements, size, biomass, and aggregating behavior (Capps and Flecker, 2013; McIntyre et al., 2008; Vanni, 2002). Additionally, the importance of these consumer-mediated nutrient subsidies depends on the biomass and density of the organisms (Hall et al., 2003; McIntyre et al., 2008; Moore, 2006; Small et al., 2009), ecosystem size (Benstead et al., 2010; McIntyre et al., 2008), and background nutrient conditions (Benstead et al., 2010; Wilson and Xenopoulos, 2011). Although the linkages between biodiversity and ecosystem function are an area of intense research and debate (Duffy, 2002; Schmid et al., 2009; Tilman, 1999), there are significant gaps in our understanding of how species loss and declines affect ecosystem function, particularly in freshwater systems (Covich et al., 2004; Dudgeon et al., 2006). Many studies have documented the effects of organisms on nutrient dynamics, but few have documented the effects of biomass loss (except see, McIntyre et al., 2007) and species composition changes on this important ecosystem function.

Freshwater mussels (Bivalvia: Unionidae) are one of the most imperiled faunal groups globally. In North America, approximately 70% of the more than 300 recognized species are at risk of extinction (Bogan, 2008). Mussels occur in many freshwater habitats, with the greatest abundance and diversity in medium to large rivers where they typically occur as dense, multi-species communities called mussel beds (Strayer, 2008). Previous studies have shown the importance of mussels in nutrient cycling, community structure, and food web support (Allen et al., 2012; Atkinson et al., 2010; Atkinson et al., 2013; Vaughn and Spooner, 2009). Mussels are thermally-conformers with different strategies to avoid physiological stress. More mobile species can move to deeper regions of a stream reach to survive high temperatures, while others become metabolically less active while catabolizing their energy reserves (McMahon, 2002). Regardless of their heat-avoiding strategy, no mussel can survive an extended amount of time in an isolated pool at high temperatures, low dissolved oxygen, and often high ammonia levels (Cherry et al., 2005; Gagnon et al., 2004; Golladay et al., 2004; Haag and Warren, 2008). Losses due to drought conditions can drastically reduce mussel populations which will affect mussel-provided ecosystem functions such as filter-feeding and nutrient storage and cycling.

We studied an area in the south-central U.S. in which mussels and their influence on ecosystem functions have been well documented (Allen and Vaughn, 2011; Atkinson et al., 2013; Spooner and Vaughn, 2006; Vaughn and Hakenkamp, 2001). Within this region, mussel densities have declined due to water management and several, regional droughts, with a 65% decline between the early 1990s and 2000s including both rare and common species (Galbraith et al., 2008; Vaughn and Atkinson, 2010). Additionally, community composition has shifted, with species more able to withstand warm water temperatures (thermally tolerant species) increasing in relative abundance compared to species less able to withstand warm temperatures (thermally sensitive species) (Galbraith et al., 2010; Spooner and Vaughn, 2008). In this study, we assessed the impact of an exceptionally severe drought on mussel abundance and the subsequent impacts on mussel-provided nutrient cycling and storage. Here we asked: (1) How will mussel-provided nutrient cycling and storage be impacted by losses in mussel biomass associated with drought? (2) Will particular landscape factors, such as agricultural land use, lead to drought affecting some mussel populations more than others? To address these questions, we quantified the biomass and density of mussels immediately before and after the drought, examined how changes in mussel species composition and biomass affected nutrient dynamics, and determined if land use interacted with the drought to potentially exacerbate the effects of the drought in certain locales.

2. Methods

2.1. Study area

We studied three mid-sized rivers with normally perennial flows in southeastern Oklahoma, U.S. (Kiamichi – K, Little – L, and Mountain Fork – M; Fig. 1), where previous work suggests mussels play an important role in supporting primary and secondary production (Spooner and Vaughn, 2009; Vaughn and Spooner, 2006). Here mussel beds are diverse and dense, with species composition changing longitudinally along the length of the rivers (Atkinson et al., 2012). Rivers in this region tend to be N-limited and nutrient-poor, with mussels often playing an important role in nutrient cycling and food web provisioning (Allen et al., 2012; Atkinson et al., 2013; Spooner et al., 2012).

2.2. Drought assessment

Whereas many drought indices use monthly hydrological measures, we used daily data in this assessment given the extreme daily flow variability (i.e. dry vs. flood) of rivers in this region and the sensitivity of mussels to extremely low flows over short periods (i.e. days). Given the highly variable response of streamflow to precipitation in this ecoregion (personal observation, Poff, 1996), as well as private upstream water diversions/abstractions, we relied primarily on streamflow rather than precipitation data to characterize hydrological drought. Nevertheless, we used weekly drought indices from the Drought Monitor (Svoboda et al., 2002) to characterize drought for each of our three study watersheds separately, where severe drought (D2) represents the <10th percentile of weekly flow. We assigned severe drought if a majority of the watershed had a D2 magnitude or higher. To be consistent with the Drought Monitor, we quantified the number of days where daily flow was below the 10th percentile on the flow duration curve. Further, we quantified the number of “no flow” (<0.01 m3/s) days because of their lethal effect on mussels.

Kiamichi River flow data were obtained from a gage (USGS 07336200) just downstream of KM2 (Fig. 1), which had continuous daily flow records for 1972 – present. Flow data for the Mountain Fork River were obtained from a gage (USGS 07338750) just upstream of MF3 (Fig. 1), which had continuous daily flow data for 1991 – present. There was not a long-term flow gage on the Upper Little River, and thus we relied on the Drought Monitor data for this watershed. Because all three watersheds are in the same physiographic region and the Little River watershed is sandwiched between the Kiamichi and Mountain Fork watersheds, we assumed that Little River flow patterns followed those of the other two rivers. Hydrological drought was assessed for the hydrological years (October 1–September 30) of 2009–2012.

2.3. Mussel Surveys

A severe hydrological drought impacted our study rivers in the summer of 2011 (Table 2). To determine the influence of this drought on mussel communities, nine mussel beds that were sampled during the summer of 2010 were resampled during the sum-
All sites were quantitatively surveyed for mussels by excavating ten 0.25-m² quadrats randomly placed within each study site. Quadrats were excavated to a depth of 15 cm, and all mussels were removed, identified to species, and measured to the nearest 0.1 mm. Length data were used to estimate tissue biomass based on previously determined length-weight regressions (Atkinson, unpublished data).

### 2.4. Storage and cycling

We measured mussel nutrient (nitrogen and phosphorus) excretion and storage rates before and after the drought. We measured nutrient excretion rates of the 6 most common species in the study area in both 2010 and 2012 (Table 1) following Atkinson et al. (2013). We used mean excretion rate values for other unmeasured species in the study area. The thermal guild rating is based on Spooner and Vaughn (2008) and unpublished data.

#### Table 1

Tissue nutrient concentration, excretion rates, and thermal guild placements for 6 of the most common species and the average found across the 9 sampling sites. The thermal guild rating is based on Spooner and Vaughn (2008) and unpublished data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean tissue %N</th>
<th>Mean tissue %P</th>
<th>N excretion rate (µmol N h⁻¹)</th>
<th>P excretion rate (µmol P h⁻¹)</th>
<th>Thermal guild</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinonaias ligamentina</td>
<td>12.04</td>
<td>2.35</td>
<td>32.00</td>
<td>1.58</td>
<td>Sensitive</td>
</tr>
<tr>
<td>Amblema plicata</td>
<td>12.32</td>
<td>1.30</td>
<td>17.36</td>
<td>1.46</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Fusconaia flava</td>
<td>12.30</td>
<td>1.40</td>
<td>13.53</td>
<td>1.46</td>
<td>Tolerant</td>
</tr>
<tr>
<td>Psychobranchus occidentalis</td>
<td>11.52</td>
<td>1.14</td>
<td>17.65</td>
<td>1.39</td>
<td>Unknown</td>
</tr>
<tr>
<td>Quadrula pustulosa</td>
<td>11.85</td>
<td>1.03</td>
<td>8.93</td>
<td>1.24</td>
<td>Sensitive</td>
</tr>
<tr>
<td>Quadrula verrucosa</td>
<td>12.11</td>
<td>1.24</td>
<td>16.96</td>
<td>1.24</td>
<td>Sensitive</td>
</tr>
<tr>
<td>Average – other mussels</td>
<td>11.81</td>
<td>1.51</td>
<td>17.74</td>
<td>1.43</td>
<td>NA</td>
</tr>
</tbody>
</table>

#### Table 2

Drought characteristics for the Kiamichi, Little, and Mountain Fork watersheds. The Hydrologic (Hydro) Year runs from October 1 to September 30. No flow days occur when discharge is less than 0.01 m³/s. Drought flow days occur when discharge is less than the 10th percentile on the flow duration curve, which was 0.18 m³/s for both the Kiamichi and Mountain Fork Rivers. There is not a long-term flow gage for the Upper Little River. Drought Monitor (DM) severe drought (in weeks) occurs when the drought magnitude category for a majority of the watershed was D2 or higher, which represents the 10th percentile.

<table>
<thead>
<tr>
<th>Hydro year</th>
<th>Kiamichi</th>
<th>Little</th>
<th>Mountain Fork</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No flow days</td>
<td>Drought flow days</td>
<td>DM severe drought weeks</td>
</tr>
<tr>
<td>2009</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>2010</td>
<td>1</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
<td>2011</td>
<td>52</td>
<td>146</td>
<td>17</td>
</tr>
<tr>
<td>2012</td>
<td>31</td>
<td>103</td>
<td>19</td>
</tr>
</tbody>
</table>

Fig. 1. Map of mussel sample sites surveyed in both 2010 and 2012. HOBO logger (water depth and temperature) locations and land use in the three basins are also shown. Mussel sites are arranged in numerical order from up to downstream.
sured species in the beds. For each species, we gently scrubbed the shell underwater to remove biofilm and placed the mussel in a container filled with 1000 ml of filtered river water for one hour. Empty mussel shells collected from the stream were used as a control for the presence of an object in the chambers and the potential of associated algae and bacterial fauna passing through the filter. Mussels and shells were removed from containers after an hour and then water from each container was filtered through a GF/F filter (1.0 μm pore size) to separate egestion products (i.e. biodeposits), collected on the filter, from excretion products (i.e. the filtrate – nutrients returned to the water column). Samples for total dissolved nitrogen and phosphorus were collected, acidified, and analyzed (following persulfate digestion) within 28 days of collection using a Lachat QuikChem FIA +8000 Series flow injection analyzer (Hach Company, Loveland, CO, USA).

Following the excretion experiments, a subset of mussels (those used in the experiments and other species) were placed on ice and returned to the laboratory (n = 140; Table 1). Length, total wet mass, and tissue dry mass (both soft tissue alone and soft tissue with shell) were determined for each individual. We determined soft tissue dry mass by separating the soft muscle tissue from the shell of each individual and drying it at 50 °C until mass remained constant. Total tissue biomass is the sum of the dry soft tissue and shell mass. To estimate nutrient storage of mussels, tissue-nutrient composition (%C, %N, and %P) was determined. Soft tissue (all soft tissue excluding the stomach) and shell tissue samples were analyzed on a Finnigan Delta Plus mass spectrophotometer in the University of Georgia’s Analytical Laboratory for the determination of %C and %N. For %P, samples were weighed, combusted at 550 °C for 2 h, and analyzed with H₂SO₄ digestion followed by soluble reactive phosphorus analysis (Solorzano and Sharp, 1980).

Nutrient excretion rates were calculated based on the difference in dissolved nutrient concentrations between the control and mussel containers following the 1-h incubation. Excretion rates for each species at a site were calculated as the product of population density and per capita excretion rates. Areal excretion rates were determined by summing the nutrient excretion rates per m² for each species at an individual site. Areal excretion was multiplied by bed area to yield aggregate excretion rates of N and P for each bed (μmol nutrient h⁻¹). Areal storage by each species was calculated as the product of biomass per m² and %nutrient composition of the tissue (both shell and soft tissue) and then summed for all species. We determined total storage by multiplying the areal storage by the total area of the mussel bed.

2.5. Ecosystem function

To determine the impact of species loss on ecosystem function, we quantified the areal nutrient storage, areal nutrient excretion, and total nutrient storage provided by each mussel bed prior to (2010) and following the drought (2012). Areal excretion is the excretion rate per unit area (μmol nutrient m⁻² d⁻¹) and the areal storage is the amount of nutrients stored in mussels per unit area (μmol nutrient m⁻²). We used the survey data from both sampling periods to estimate areal excretion, areal storage, total remineralization, and total storage of N and P for each site. We then compared the data from the two sampling periods to determine the change in these mussel-provided ecosystem functions. We also calculated areal storage N:P and excretion N:P (molar) for all mussel beds across the two sampling years. Additionally, we investigated the role of community composition, particularly the proportion of thermally sensitive species. We used ordinary least squares regression to investigate the effect of individual species on N:P excretion, and if tissue stoichiometry, specifically tissue N:P, was a good predictor of N:P. We also determined if areal storage N:P and excretion N:P varied across the two sampling years using paired t-tests. To determine if drought impacts were influenced by land cover, we first used Moran’s I to see if there was spatial autocorrelation across sites, and then used Pearson correlation to examine the association between land use, stream temperature, and mussel biomass loss. We examined the relationship between forest and agriculture land coverage in the watershed and stream temperature at all the sites with HOBO loggers, and then we examined the relationship between water temperature, forest coverage, and change in mussel biomass. Stream water temperature was calculated as the mean water temperature at these sites from 1 August 2011 until 30 Sept 2011. Proportion data were arcsine square root transformed to meet assumptions of normality (Gotelli and Ellison, 2004). All statistical analyses were done in R v2.15.1 (R Development Core Team, 2012).

3. Results

3.1. Drought characteristics

The drought of 2011–2012 reached the magnitude of exceptional (D4), the most severe category identified by the U.S. Drought Monitor. In the two years preceding the 2010 mussel surveys, none of the watersheds experienced severe drought (Table 2). Between the 2010 and 2012 mussel surveys, each watershed was in severe drought for approximately 40 weeks. The 2011–2012 drought caused reaches along the three rivers to change from continuously flowing to a series of shallow, isolated pools in which water temperatures sometimes exceeded 40 °C. Many sections also ceased flowing. The Kiamichi River had 84 days of no flow (<0.01 m s⁻¹) during the period of study, all occurring after the mussel surveys of 2010. Flow in the Mountain Fork River never ceased, but it dropped below 0.02 m s⁻¹ for 26 days during 2011–2012. The lowest discharge on the Mountain Fork in 2009 and 2010 was
While continuous flow data are not available for Little River, numerous field visits and HOBO logger depth data revealed that flow was absent between mid-July and late August during 2011 and 2012. In sum, the mussel surveys of 2010 followed a relatively drought-free and temperate period, but the 2012 mussel surveys followed a year of extremely low flows and lethal water temperatures in the three rivers.

3.2. Density and biomass changes

Population densities at survey sites ranged from 4.8 to 19.6 individuals m$^{-2}$ across both years. Mean soft-tissue dry mass for the beds ranged from 0.4 to 22.2 g m$^{-2}$ and estimated total mussel bed biomass ranged from 102.5 to 4190 g dry tissue (shell + soft tissue) m$^{-2}$. Mussel abundance declined considerably between the two sampling intervals (Fig. 2A and B). We measured a significant decline in density between 2010 and 2012 ($W = -32.0$, $Z = -2.24$, $p = 0.02$, Fig. 2A), with an average decline of 3.03 ± 1.09 individuals m$^{-2}$ (mean ± SE). Accordingly, we found a significant decline in biomass ($W = -45.0$, $Z = -2.67$, $p = 0.004$; Fig. 2B) with an average decline in 593.1 ± 171.0 g mussel m$^{-2}$, which was a 28.7 ± 6.1% reduction in soft tissue biomass across the sites between the two years.

3.3. Ecosystem function

Due to mussel mortality, there was a reduction in mussel-provided ecosystem functions (Fig. 3). Both N and P areal excretion were reduced following the drought. Nitrogen areal excretion declined significantly by 52.5 ± 18.4 μmol N m$^{-2}$ h$^{-1}$ ($t$-test; $t_8 = 2.86$, $p = 0.02$), which was a 22% average decline in mussel N excretion across the sites (Fig. 2C). We found that P areal excretion rates declined by 3.1 ± 1.1 μmol P m$^{-2}$ h$^{-1}$, which is equivalent to a 15% average decline in mussel P areal excretion across the sites, but this change was not statistically significant ($t_8 = 2.05$, $p = 0.07$; Fig. 2D).

Mussel soft tissue ranged from 10.1–13.9% (mean 11.9%) N and 0.7–2.7% (mean 1.4%) P. Shell tissue ranged from 1.5–3.1% (mean 1.9%) N and 0.05–0.21% (mean 0.08%) P (Table 1). We found a significant 30% decline in N areal storage, equating to an average loss of 13.5 ± 4.2 g N m$^{-2}$ ($t_8 = 3.21$, $p = 0.01$). Phosphorus storage by mussels was also significantly reduced by 30%, equivalent to a loss of 4.9 ± 1.5 g P m$^{-2}$ ($t_8 = 3.28$, $p = 0.01$). Total nutrient storage of these mussel beds ranged from 1.1–682.3 kg N and 0.3–240.3 kg P, with significant declines between the two sampling periods.

3.4. Species-specific changes

Overall, densities of both thermally sensitive and tolerant mussel guilds declined between the two sampling periods, but there were no significant differences in the absolute decline between the two guilds ($t_{14} = -0.14$, $p = 0.89$; Fig. 3A). While the relative abundance of thermally sensitive species (e.g., *Actinonaias ligamentina*) decreased across sites during the drought relative to thermally tolerant species (e.g. *Amblema plicata*) (Fig. 3B), this trend...
was not significant ($t_{14} = -0.98, p = 0.34$). However, our data indicate that the loss of a higher proportion of thermally sensitive mussel individuals is affecting stream ecosystem function through changes in areal N:P excretion. Mussel bed areal excretion N:P increased with the proportion of thermally sensitive species in a bed in both 2010 and 2012, although these patterns were not significant likely due to our small sample size ($r^2 = 0.38, y = 9.5x + 26.6, p = 0.08$; 2012: $r^2 = 0.20, y = 8.29x + 21.6, p = 0.22$). Yet, the N:P of mussel bed areal excretion declined significantly between 2010 and 2012 ($W = -45.0, Z = -2.66, p = 0.004$; Fig. 3D) and was strongly correlated to areal tissue N:P in both 2010 ($r^2 = 0.58, y = -1.6x + 61.32, p < 0.02$; Fig. 3D) and 2012 ($r^2 = 0.53, y = -2.0x + 63.95, p < 0.03$; Fig. 3D), suggesting changes in nutrient availability occurred across the two years.

### 3.5. Land use and temperature

Our data did not exhibit spatial autocorrelation across the sites in the proportion of agriculture in the watershed ($I = 0.06, p = 0.37$). Mean stream water temperature decreased with increasing forest coverage in the watershed ($r = -0.70, p = 0.01$; Fig. 4A). Biomass losses were not significantly correlated with increasing mean stream temperature ($r = -0.58, p = 0.18$; Fig. 4B). Smaller reductions in biomass of mussels between the sampling periods were positively correlated to forest cover ($r = 0.67, p < 0.05$; Fig. 4C), while greater losses in biomass were associated with higher agricultural land cover ($r = 0.77, p = 0.04$).

### 4. Discussion

Our study provided a quantitative assessment of how river ecosystem function can change and is changing in response to the continued loss of freshwater mussels, one of the most imperiled faunas globally (Lydeard et al., 2004). Drought caused a large reduction in freshwater mussel populations, and our results indicate that declining mussel abundance reduces both nutrient recycling and storage within stream systems. Some nutrient storage will be maintained because of the relatively slow dissolution of shell material (Gutierrez et al., 2003; Strayer and Malcom, 2007) which may constitute a nutrient sink in the system (Vanni et al., 2013). However, the loss of living mussels results in the immediate loss and decomposition of nutrient-rich, soft tissue (Atkinson et al., 2013) and declines in the ecosystem functions provided by the living mussels such as water filtration (Vaughn, 2010) and nutrient remineralization (Atkinson et al., 2013). As an example, we saw a dramatic decline in nitrogen remineralization by mussels (average of 22%) due to drought related losses in mussel biomass.

Rivers in our study region are N-limited (Atkinson et al., 2013) and N provided by mussel remineralization has been shown to move into primary producers and consumers and support the food web (Allen et al., 2012; Atkinson et al., 2014). These mussel-

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Fig. 3. (A) The density of the two mussel thermal guilds, thermally sensitive and thermally tolerant, in 2010 and 2012. There was a decline in the density in both the sensitive and tolerant thermal mussel guilds between 2010 and 2012. (B) The average relative abundance of thermally sensitive species at the sampling sites declined between 2010 and 2012, while tolerant species increased slightly in relative abundance. (C) The relationship between the proportion of thermally sensitive species in a mussel bed to the areal excretion N:P. We observed lower areal excretion N:P in 2012 in comparison to 2010, however this was not significant ($p = 0.10$). (D) Areal excretion N:P was significantly related to the areal tissue N:P of the bed. The dashed arrows indicate changes in 2-dimensional space of storage and excretion N:P at each site between 2010 and 2012.
derived nutrients influence community structure of benthic primary producers (Allen et al., 2012; Atkinson et al., 2013) and fuel primary and secondary productivity (Howard and Cuffey, 2006; Spooner and Vaughn, 2006; Vaughn and Spooner, 2006). Thus, the declines we observed in mussel biomass and ecosystem processes could lead to significant changes in stream function. A recent meta-analysis showed that the impact of species loss on ecosystems could be as great as effects of environmental change (Hooper et al., 2012). Our results suggest the loss of mussels would lead to large changes in nitrogen and phosphorus cycling in these systems. Undoubtedly, environmental change often leads to species loss, thus the total change in ecosystem function is a consequence of both environmental change and species loss. Future droughts and further losses of mussels could have dire consequences and may lead to an altered stable state (i.e., changes in nutrient availability) in these rivers.

Our results, in combination with those of previous studies (Gagnon et al., 2004; Golladay et al., 2004; Haag and Warren, 2008; Shea et al., 2013), show that severe drought has a detrimental effect on mussel communities. Given the life history of most mussel species, long-lived and slow growing (Haag, 2012), the rate of recovery of mussels in drought-impacted areas is likely low, especially compared to mobile, shorter-lived, and more rapidly reproducing faunal groups such as insects and fish (Dewson et al., 2007; Matthews and Marsh-Matthews, 2003). We observed declines in the biomass of all species, regardless of how rare or common they were, as has also been documented for a previous drought in our study region (Galbraith et al., 2010) and for droughts in other systems (Haag and Warren, 2008). We also observed changes in community structure, with the relative abundance of thermally sensitive species declining more than thermally tolerant species. Although this pattern was not significant here, it was previously documented in our study region and found to be significant over longer periods (Galbraith et al., 2010). Comparisons across sites revealed repeated patterns in ecosystem function (i.e., reduced remineralization N:P between years), but also underscore the complexity of predicting ecosystem-level effects of extirpations from species-rich natural communities. For example, mussel densities did not change between the two sampling years at K2, but biomass decreased presumably due to larger individuals being more sensitive to low flow conditions. This decline in biomass led to declines in both nutrient recycling and storage and these mussel-provided functions will likely take a long time to recover.

Species loss is not random. In the rivers we studied, mussel thermal traits govern mussel physiology and thus mussel tolerance to high temperatures as well as temperature-dependent nutrient excretion rates (Spooner and Vaughn, 2008; Galbraith et al., 2010). As some species decrease in relative abundance and others increase, changes in nutrient cycling and storage will likely occur (Spooner and Vaughn, 2008). The thermal trait relationships established for many of the mussels in these streams could be used to predict future trait-based vulnerability to climate change. Thermal and stoichiometric traits combined could be used to assess and predict future changes in stream nutrient dynamics. This approach is not new. Traits including heat tolerance, feeding, and life history have already been used to assess risk to both drought and climate change (Chessman, 2013; Villnas et al., 2012; Wenger et al., 2011), and thermal tolerance may drive community composition in a changing climate and hydrologic regime (Spooner and Vaughn, 2008). For example, river size and flow permanence are key factors controlling aquatic food chain length, with shorter food chain lengths in smaller rivers that dried more frequently (Sabo et al., 2010; Woodward et al., 2012). More research is necessary to understand how species traits are distributed to make better predictions regarding how species composition may change in the future and the consequential impact on ecosystem function and structure.

Land cover change in combination with a changing climate and water management could significantly alter community structure and lead to declines (Galbraith et al., 2010). In our study, stream temperature was correlated to land cover: sites with higher percentages of watershed forest coverage had lower stream temperatures. Temperature and the density and biomass loss of mussels
were uncorrelated (likely due to low sample size, N = 7), but we did see a significant negative relationship between forest coverage and change in mussel biomass. Land cover influences stream temperature, with higher water temperatures typically associated with lower forest cover (Poole and Berman, 2001; Quinn et al., 1997; Sponseller et al., 2001). Forest cover can mitigate the effects of drought and heat waves by reducing ground/water surface insolation and moderating soil water temperatures (Poole and Berman, 2001). Previous studies have linked long-term declines in mussel species richness to changing land use practices and increased nitrogen concentrations (Arbuckle and Downing, 2002; Poole and Downing, 2004). The losses seen in these previous studies may not only be linked to nutrient or sediment runoff but also to alterations in thermal regime resulting from land cover change.

Future droughts, likely intensified by greater human water demand, could lead to further species losses, changes in community structure, and degraded ecosystem function (Palmer et al., 2008). Indeed, climate change threatens most ecosystems and is predicted to alter freshwater biogeochemical processes, primary and secondary productivity, food-web structure, species ranges, population dynamics and species interactions, and large-scale patterns of freshwater biodiversity (Carpenter et al., 1992; Heino et al., 2009; Perkins et al., 2010; Sabo et al., 2010). Drought is predicted to become more frequent and intense in our study region and the southern U.S. with climate change (Seager and Vecchi, 2010). Because the rivers in this study are threatened by planned municipal water extractions (Oklahoma Water Resources Board, 2011) and further dam construction (Galbraith et al., 2010; Vaughn and Taylor, 1999), an understanding of factors influencing species loss is critical to future river management plans. Interactions between species loss and environmental changes are important for understanding net effects on ecosystem processes because both will often occur simultaneously (Dudgeon et al., 2006). The full ramifications of past losses of freshwater mussels are not known, but our results suggest that the loss of this faunal group would alter the storage and availability of nutrients in riverine ecosystems, which would lead to further losses in ecosystem function and changes in community structure.

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Appendix A. Supplementary material

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References


