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

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A B S T R A C T

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., 2012, 2005; Kirwan et al., 2009; Vaughn, 2010), ultimately

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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 et al., 2008). Mussels are thermo-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 et al., 1996). 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" ($<0.01\ \mathrm{m^3/s}$) 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 gauge (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-