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Biomass loss and change in species dominance shift stream community excretion stoichiometry during severe drought

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Abstract

1. Animals contribute significantly to nutrient cycling through excretion, but most studies consider their effects under relatively benign abiotic conditions. Disturbances such as drought may alter animals' nutrient contributions through shifts in species composition and biomass. Headwater streams are particularly vulnerable to extreme climate events and thus might show rapid changes in stream biota and their ecosystem effects.
2. We tested how biomass and subsequent ecosystem effects (nutrient cycling) of an intermittent prairie stream community changed during a drought. We quantified the biomass and contributions to nutrient cycling for assemblages comprising fishes, crayfish, and tadpoles in 12 isolated pools over 3 months encompassing the harshest drought on record for Kings Creek, KS, U.S.A. We predicted that macroconsumer biomass would decline with pool surface area and that differences in macroconsumer biomass and taxonomic composition would lead to different contributions of pool assemblages to nutrient cycling.
3. The biomass of pool assemblages declined with decreasing pool size, a pattern apparently driven by mortality, emigration, or metamorphosis. We also observed a change in assemblage structure of drying pools during drought relative to pool size, shifting dominance toward species with more drought-resistant traits. Accordingly, assemblage nitrogen (N) excretion rates declined as pool biomass was reduced, leading to a 58% reduction in N available to epilithic biofilms. Phosphorus (P) excretion rates declined from June to July, but increased in August, as species with high P excretion rates maintained similar proportional biomass and biomass of a non-native fish increased. Molar N:P of pool assemblage excretion declined significantly throughout the drought and coincided with loss of southern redbelly dace (*Chrosomus erythrogaster*: Cyprinidae).
4. Animal-mediated nutrient cycling was altered by the loss of biomass and stoichiometric traits of taxa that differed in their occurrences and ability to tolerate abiotic conditions during drought. Elevated availability of dissolved N in isolated pools may increase N uptake rates by biofilms during drought conditions, indicating the importance of N excreted by aggregated macroconsumers, especially those with

unique stoichiometric traits. While the significance of shifts in the composition of freshwater communities to ecosystems is not entirely known, additional losses in ecosystem function and changes in community structure may follow episodes of severe drought.

KEYWORDS
animal-mediated nutrient cycling, global change, headwater streams, nitrogen demand, no-flow

1 | INTRODUCTION

The importance of animal-mediated nutrient cycling is now widely accepted across ecosystems (Allgeier, Burkepile, & Layman, 2017; Atkinson, Capps, Rugenski, & Vanni, 2017; Sitters et al., 2017). Animal-mediated nutrient cycling is the product of stoichiometric requirements (Capps & Flecker, 2013), biomass and density of organisms (Atkinson & Vaughn, 2015; McIntyre et al., 2008), background nutrient conditions (Wilson & Xenopoulos, 2011), and ecosystem size (Benstead et al., 2010). The influence of animals on ecosystems are often most apparent when environmental conditions aggregate biomass of dominant animal groups. For example, in stream ecosystems, excretion from aggregated animals under low flow conditions can supply a larger fraction of ecosystem nutrient demand relative to catchment run-off (Atkinson & Vaughn, 2015; Childress, Allan, & McIntyre, 2014; Grimm, 1988). However, disturbance events may exacerbate ecosystem effects of animals, because they control abundances and occurrences of species (Boulton, 2003; Lake, 2003), species trait expression, and the direction and magnitude of how species traits affect ecosystem function (Ackerly, 2003).

In streams, drought represents one extreme of the hydrological continuum. Drought severity is characterised by periods of low flows that vary in temporal extent and predictability (Lake, 2003; Lennox, Crook, Moyle, Struthers, & Cooke, 2019). Stream organisms experiencing seasonal drying have evolved adaptations to water scarcity, although these adaptations may not entirely protect them from the suite of stresses associated with drying events (Boulton, 2003). Moreover, drought is a ramp disturbance, in which the perturbation intensifies over time and may prove more challenging for organisms due to a lack of predictability in timing or duration (Lake, 2003; Lynch & Magoulick, 2016). For example, the formation of isolated pools during drought prevents the normal transport of nutrients, biota and organic matter downstream, and can produce distinct lentic conditions among pools (Lake, 2003). Algal blooms (Dahm, Baker, Moore, & Thibault, 2003), rises in conductivity and temperatures (Matthews, Surat, & Hill, 1982), and stratification (Wood, Fisher, & Grimm, 1992) may occur in isolated pools and can severely stress or kill stream biota. Under these conditions, ecosystem processes shift from being hydrologically to biologically controlled, with internal processes (e.g. sedimentation of autochthonous material, nutrient cycling, and consumption) shaping conditions in pool habitats (Tockner, Pennetzdorfer, Reiner, Schiemer, & Ward, 1999).

Prolonged periods of drying can influence biogeochemical processes underlying stream ecosystem function (Baldwin & Mitchell, 2000; Dahm et al., 2003). Drought decreases inputs of dissolved organic carbon, phosphorus (P), and nitrogen (N) to intermittent streams, leading to a shift from predominantly heterotrophic (microbial) to autotrophic organisms (Dahm et al., 2003). Subsequent low dissolved oxygen from overnight respiration can also kill some animals (Matthews & Maness, 1979; Ostrand & Marks, 2000). Stratification and/or stagnant conditions can lead to nutrient accumulation, increasing the risk of toxic algal blooms that cause further mortality of stream biota (Colley, 2004; Ha, Cho, Kim, & Joo, 1999). Mortality of fishes and invertebrate populations will, in turn, affect animal-mediated ecosystem functions such as nutrient cycling. Of the few studies that tested the impacts of droughts on stream biogeochemistry, most focus on microbial-mediated processes and responses to drought (Bayley, Schindler, Parker, Stainton, & Beaty, 1992; Morecroft, Burt, Taylor, & Rowland, 2000; Foster & Walling, 1978; Wall, Phillips, & Riva-Murray 1998; Williams & Melack, 1997).

Animal contributions to stream food web dynamics and nutrient cycles can differ during drought years or during periods of low flow (Power, Parker, & Dietrich, 2008; Vaughn, Gido, & Spooner, 2004; Wootton, Parker, & Power, 1996). The influence of drought on aquatic animals' ecosystem effects may be related to the flux of individuals or materials. For instance, consumption of resources intensifies in local patches during low-flow conditions when densities are high (Canton, Short, & Ward, 1984; Matthews & Marsh-Matthews 2003) and faeces, nutrients, and fragmented particulate organic matter tend to accumulate in isolated pools (Conallin, Hillyard, Walker, Gillanders, & Smith, 2011; King, Tonkin, & Lieshcke, 2012). Moreover, positive feedback between physiological or stoichiometric traits of animals and ambient conditions may occur until habitat conditions deteriorate beyond physiological thresholds and mortality leads to loss of animal biomass (Atkinson, Julian, & Vaughn, 2014; Boulton, 2003). Specifically, nutrient cycling rates by aquatic animals should increase with temperature as animal metabolic rates increase, causing an increase in nutrient availability, which, if converted to algal biomass, may result in oxygen depletion as increasing organic matter decomposes. Given the potential consequences of these feedbacks, understanding how drought influences animal-mediated nutrient cycling is a fundamental knowledge gap (Dahm et al., 2003; Matthews & Marsh-Matthews, 2003).

We examined whether observed shifts in macroconsumer assemblage composition and biomass influenced animal-mediated nutrient cycling in Kings Creek (Kansas, U.S.A.), an intermittent prairie stream, during the most severe drought over the 35-year record for this system (Figure 1). We compared biomass of fishes, crayfishes, and tadpoles (hereafter macroconsumer assemblage) along a series of drying pools and estimated their contributions to nutrient cycling through excretion of N and P. Our objectives were to: (1) measure biomass of aquatic macroconsumer assemblages along a series of isolated, drying pools; (2) quantify abiotic conditions among pools and associate changes in abiotic factors with changes in taxonomic composition of pool assemblages; and (3) determine if temporal changes in macroconsumer biomass and taxonomic composition result in different flux and stoichiometric contributions to nutrient cycling through differential excretion of N and P. We hypothesised that macroconsumer biomass would decrease with pool surface area as habitat became increasingly limited and abiotic conditions (i.e. water temperatures, dissolved oxygen, and ammonium concentrations) changed. Furthermore, we hypothesised that temporal differences in macroconsumer biomass and shifts in taxonomic composition from drought-intolerant species to tolerant species would lead to different contributions of pool assemblages to nutrient cycling and stoichiometry.

2 | METHODS

2.1 | Study location and the onset of drought

Kings Creek is located on the Konza Prairie Biological Station (KPBS) in the Flint Hills region of Kansas (U.S.A.) and drains 3,487 ha of native tallgrass prairie. Tallgrass prairie is the dominant land cover type, but trees occur in riparian areas in the lower portions of the catchment. Grazing by bison (*Bison bison*) occurs in the headwaters with some row-crop agriculture also present in lower reaches of the catchment and separated from the stream with a gallery forest buffer. Long-term records of stream flow are available from the U.S. Geological Survey gaging station (no. 0678650) on Kings Creek. Although discharge at the station is intermittent, discharge is representative of the more perennial reach approximately 1.5 km downstream where our study was conducted. Discharge in Kings Creek varies annually but tends to peak during April, May, and June (Dodds, Gido, Whiles, Fritz, and Matthews, 2004). During mid- to late-summer (July–September), a lack of precipitation typically leads to drying of middle reaches in Kings Creek, while downstream reaches continue to flow. Long-term reductions to stream flow and severe drought during 2018 resulted in near-complete stream drying throughout the catchment. The middle reaches were first to dry, followed by headwater springs, and finally downstream reaches that historically flowed year-round. This main-stem perennial reach ceased to flow by early June, leading to the development of isolated pools (Figure 2).

To test our hypothesis that macroconsumer biomass would be highest in larger pools, we selected 12 isolated pools (no surface water connectivity) of varying size (surface area and depth) within the main stem of Kings Creek. These pools became isolated in early spring 2018 following sparse precipitation in winter and early spring. We sampled macroconsumers and abiotic factors within each pool monthly during June, July, and August (Table 1). Prior to sampling pools in July, we measured dissolved oxygen over a single 48 hr period (1–3 July 2018) in all 12 pools. Additionally, we logged hourly temperature in each pool throughout the study with HOBO UA-002-64 Pendant Data Loggers (Onset Computer Corporation, Bourne, MA) placed in the middle of the pool at approximately 0.5 m depth. Pool dimensions were characterised during macroconsumer assemblage sampling by measuring pool length and width at three transects (m) to calculate surface area (m^2). Depth (m) was taken at five equidistant points along each transect. We calculated pool volume (m^3) as the product of cross-sectional area and mean depth of each transect. We also obtained monthly Palmer Drought Severity Index (PDSI) values for the study region from the North American Drought Monitoring program (www.ncdc.noaa.gov). The PDSI describes regional water availability based on temperature and the balance between water supply and environmental demand and ranges from −10 to 10 (Palmer, 1965). Variation in nutrient concentrations among pools

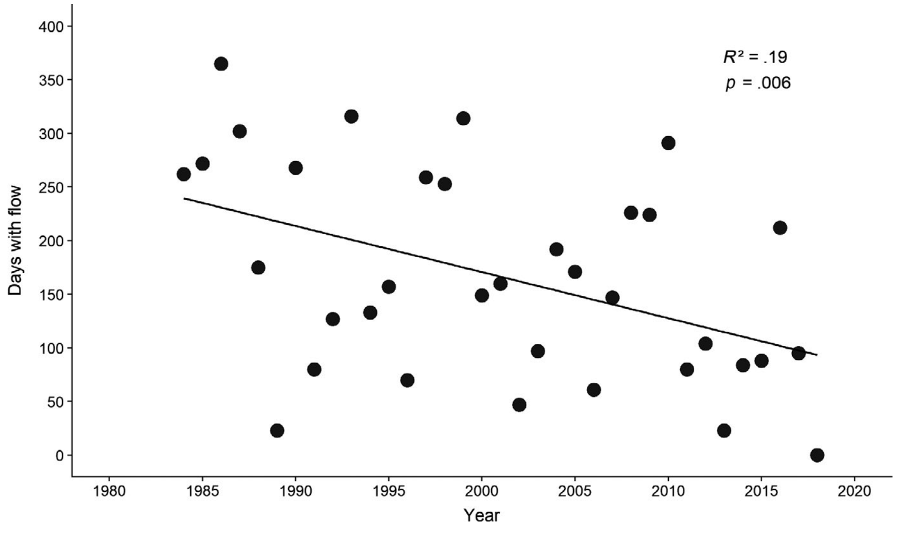

FIGURE 1 Relationship between the number of days Kings Creek (KS, U.S.A.) was flowing and time measured during the U.S. Geological Survey water year from 1983 to 2018 at gage 06879650

FIGURE 2 Time series of Pool 5 during a severe drought that impacted Kings Creek, KS, U.S.A. in summer 2018. Top photo was taken 18 June, middle photo 3 July, and bottom photo 10 July [Colour figure can be viewed at wileyonlinelibrary.com]

was quantified by collecting a 250-ml unfiltered water sample during each sampling period. Water samples were placed on ice within 30 min of collection and transported back to the laboratory, where they were kept frozen until analysis. Because ammonium (NH_4^+) can create toxic environments for aquatic animals in high concentrations via acidification following dissociation into NH_3 and H^+ (Mayes, Alexander, Hopkins, & Latvaitis, 1986), nutrient analysis focused on NH_4^+ using the indophenol blue method via an O-I Analytical Flow Solution IV autoanalyzer (APHA, 2005). We also measured soluble reactive phosphorous (SRP) using the ascorbic acid method (APHA, 2005) on the same instrument to understand variation in nutrient concentrations among pools that may be associated with changes in pool assemblage composition.

2.2 | Assemblage composition and biomass variation among pools

We used one or more seine hauls (4.6 × 1.8 m, 3.2-mm mesh) to sample the entire length of each pool and estimate macroconsumer biomass. Given the severity of the drought, we chose seining rather than electrofishing to minimise stress to macroconsumers. Similar to previous studies (Allen et al., 1992), seining was effective when pools were narrow and isolated, limiting the ability of macroconsumers to escape around the seine. We identified, enumerated, and measured (total lengths; mm) all fish, crayfish, and tadpole species. At a later date, we determined capture efficiencies (*q*) using a two-pass closed population mark-recapture approach at seven of the study pools. Individuals collected during the first pass were identified to species, measured and marked with a clip on the caudal fin or uropod (crayfishes) prior to being returned to the pool. We resampled each pool several hours later after allowing for remixing to occur using identical methods. Because recaptures for some species were insufficient to predict *q* in some pools (Table S1), we averaged *q* across species and used linear regression to test the significance of the relationship between *q* and pool volume. Raw values for *q* were arc-sine square-root transformed to meet assumptions of normality and heterogeneity. Because regression analysis indicated *q* significantly declined in pools with greater volume (p = 0.04, R^2 = 0.52), we estimated capture

TABLE 1 Abiotic and biotic characteristics monitored in 12 isolated pools in Kings Creek during a severe drought in 2018. Abbreviations represent dry pools (D) or periods when data loggers were not deployed (ND). SRP, soluble reactive phosphorous

		Pool											
Abiotic factor	**Month**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Surface area (m^2)	June	87.8	46.8	117.9	83.5	46.8	27.5	74.8	31.8	46.8	35.8	67.1	81.4
	July	69.1	16.8	84.8	50.9	D	4	38.6	15.2	31	D	47.3	54.3
	August	56	17.3	92.2	11.5	D	D	34.9	10.9	39.9	D	55.8	70.1
Temperature range (°C)	June	20.6–29.7	22.7–37.5	17.9–27.9	19.5–27.9	19.0–35.4	19.9–27.9	19.25–33.7	18.8–37.9	19.5–40	23.0–40.8	21.5–32.5	16.1–21.8
	July	24.3–28.7	18.4–39.2	17.8–28.7	16.2–33.9	D	17.8–28.7	18.9–39.4	19.3–39.5	21.5–41.8	D	19.7–32.6	16.4–24.5
	August	ND	18.6–22.8	17.9–22.3	16.3–21.5	D	D	19.4–22.9	19.4–28.5	ND	D	19.8–22.7	16.7–19.2
NH_4^+ (μmol/L)	June	37.2	54.8	615.7	50.8	524.1	89.2	48.6	48.4	110.1	89.2	35.5	30.7
	July	30.9	1457.5	116	1723.5	D	1106.5	59.9	41.6	1574.7	D	30.6	24
	August	117.3	238.6	105.1	939.4	D	D	235.7	115.4	200.6	D	161	92.4
SRP(μmol/L)	June	27.8	173.4	12.4	21.5	54.1	87.3	21.7	18.6	42.9	148.2	53	42.4
	July	46	145.9	17.7	201.5	D	99	114.6	43.7	183.88	D	42.5	20.7
	August	34	287	16.7	101.2	D	D	60.3	119.9	128.5	D	49.5	27.3
Biotic factor													
Biomass (g/m^2)	June	245.1	30.9	512.7	50.5	34.4	59.1	250.7	93.6	14.2	10.0	10.4	7.5
	July	94.3	20.5	58.8	14.8	D	0.4	49.3	25.8	9.0	0.3	14.2	20.3
	August	41.1	2.0	33.6	40.6	D	D	8.6	6.7	13.0	D	13.2	7.2
Density (individuals/m^2)	June	397.0	38.1	610.7	42.7	36.0	31.0	200.7	68.3	13.9	10.3	15.1	9.9
	July	70.1	25.6	75.5	12.5	D	0.5	71.0	41.8	43.7	0.2	32.7	17.5
	August	23.6	18.3	43.0	33.2	D	D	75.5	45.8	28.5	D	19.9	22.7

efficiencies for each of the 12 pools during the three sampling periods using the linear model: $\sin^{-1}\sqrt{(q)} = -0.00338 \times \text{volume} + 0.85$. Back-transformed modelled capture efficiencies for pools in Kings Creek were similar to those of Allen et al., (1992) and ranged from 0.19 to 0.55. Modelled capture efficiencies were applied to the relative abundance of species captured during standardised sampling to estimate absolute abundances for all species. Length-mass regressions from a subset of individuals collected on-site or previously collected individuals of the same species or genus (K. Gido, unpublished data) were used to estimate wet mass of all captured individuals (Table S2). Per capita biomass (g/m^2) was estimated for each pool separately as the product of the absolute abundance estimate and the mean predicted mass of individuals collected divided by the area of their respective pool. These biomass estimates were calculated during June, July, and August 2018.

2.3 | Estimating animal-mediated nutrient cycling among pools

We hypothesised spatial and temporal differences in the distribution of biomass and taxonomic composition would lead to different contributions of macroconsumer assemblages to nutrient cycling. To test this hypothesis, individual excretion rates were measured for five fish, two tadpole, and one crayfish species that comprised >80% of total biomass across pools. Individual excretion rates were measured for at least eight individuals of each species (Table 2) during June as we did not expect excretion rates to change over the course of the study. Macroconsumers were collected from pools using a seine and placed in a cooler with water from the pools and allowed to recover for 15 min. Individuals were then placed in a plastic container with 100–200 ml of filtered stream water depending on the size of the individual (GF/F; 0.7 µm pore size; Whatman, Buckinghamshire, UK) and incubated for at least 1 hr. Following excretion measurements, we recorded total length (mm) and wet mass (g) for all individuals. Water samples were collected at the end of each trial and kept frozen until analyses. Nutrient analyses focused on NH_4^+ and SRP. Analyses were performed using the indophenol blue and ascorbic acid methods for NH_4^+ and SRP, respectively, using an O-I Analytical Flow Solution IV autoanalyser (APHA, 2005). Excretion calculations were based on the difference between nutrient concentrations of identical containers incubated simultaneously with and without macroconsumers.

Spatially explicit species composition and biomass data were used to compare variation in assemblage nutrient excretion rates among 12 isolated pools for our three discrete sampling periods during the drought. We applied excretion estimates to areal biomass estimates to derive areal excretion rates (µmol m^{-2} hr^{-1}) for each assemblage during each sampling period. The estimated excretion rates of N and P for each macroconsumer assemblage were used to calculate assemblage excretion N:P molar ratios. We then compared assemblage areal excretion rates and N:P across the gradient of macroconsumer biomass to detect changes in their contributions to nutrient cycling in isolated pools.

2.4 | Measuring N demand by epilithic biofilms during drought

Our study focused on N excretion relative to demand because previous studies of N cycling in Kings Creek indicate organisms are N limited (O'Brien & Dodds, 2008). To obtain an estimate of N demand, which we could compare to estimates of animal-mediated excretion, we measured NH_4^+ uptake by epilithic biofilms during July 2018 in two (Pools 3 and 4) of the 12 isolated pools by incubating cobbles in $^{15}N\text{-}NH_4^+$. We collected cobbles randomly from each pool and placed them inside sealed recirculating chambers (described by Rüegg, Brant, Larson, Trentman, & Dodds, 2015) filled with stream water enriched with $^{15}N\text{-}NH_4^+$ by adding 100 µL of $^{15}NH_4Cl$ stock solution (stock solution = 77.6 mg/L 98% $^{15}NH_4Cl$, Sigma-Aldrich, St. Louis, Missouri, U.S.A.) to 15 L of stream water in a bucket. This produced a total NH_4^+ increase of <2% above ambient conditions. We maintained constant temperature with

TABLE 2 Per capita nutrient excretion rates (mean ± *SD*) for nine aquatic animals found in 12 isolated pools of Kings Creek, U.S.A. during 2018. Excretion rates for *G. affinis* includes both male and female individuals. The symbol † indicates fish species and ‡ indicates crayfish. *Tadpoles* combines excretion rates of *Acris crepitans* and *Lithobates pipiens*

Species	*n*	N excretion rate (µmol g^{-1} hr^{-1})	P excretion rate (µmol g^{-1} hr^{-1})	Excretion N:P (Molar)
Campostoma anomalum†	10	1.86 (0.61)	0.21 (0.15)	18.70 (16.52)
Chrosomus erythrogaster†	24	1.37 (0.31)	0.07 (0.04)	25.40 (11.82)
Etheostoma spectabile†	10	1.97 (0.40)	0.20 (0.06)	10.86 (3.16)
Gambusia affinis†	15	0.45 (0.17)	0.20 (0.12)	4.37 (4.12)
Luxilus cornutus†	8	1.40 (0.43)	0.11 (0.03)	13.37 (4.64)
Semotilus atromaculatus†	9	1.47 (0.50)	0.12 (0.06)	19.18 (16.00)
Orconectes nais ‡	11	0.70 (0.19)	0.01 (0.00)	140.80 (77.04)
Tadpoles	17	1.00 (0.50)	0.10 (0.11)	21.77 (20.40)

the pool by partially submerging chambers ($n = 6$ for Pool 4; $n = 5$ for Pool 3) during incubations to control temperature fluctuation. Flow velocity was maintained near 1–3 cm/s to mimic stream conditions while promoting mixing of water in the chambers. We stopped incubations within 3–7 hr by rinsing cobbles with unenriched stream water to remove unincorporated ^{15}N and cobbles were kept on ice for processing within 24 hr. We also collected reference cobbles ($n = 3$ per pool) to correct for background ^{15}N of epilithic biofilms. We scrubbed cobbles with a steel-bristle brush and rinsed them with deionised water to create one composite sample per chamber. Next, we digitally photographed each cobble to measure projection area with image processing software (ImageJ, Schneider, Rasband, & Eliceiri, 2012). Subsamples were filtered onto pre-weighed glass fibre filters (Whatman GF/F) then oven-dried at 50–60°C for at least 24 hr. We analysed dried samples for δ^{15}N on a mass spectrometer (ThermoFinnigan Delta Plus) in the Stable Isotope Mass Spectrometer Laboratory at Kansas State University.

We calculated NH_4^+ uptake rates as the difference in ^{15}N content between reference epilithic biofilms and biofilms from each of the chambers collected at the end of incubations. The change in ^{15}N content during incubation ($\Delta^{15}N$) was calculated as:

$$\Delta^{15}N = \frac{\left(\mathrm{MF}_{\mathrm{final}} - \mathrm{MF}_{\mathrm{background}}\right) * N}{A * t}$$

Where $\mathrm{MF}_{\mathrm{final}}$ is the mole fraction of ^{15}N in biofilm material after incubations, $\mathrm{MF}_{\mathrm{background}}$ is the mole fraction of ^{15}N in reference biofilm material, N is the mass of total N in epilithic biofilms in the chamber, A is the projection area of cobbles in the chamber, and t is incubation time. Finally, we calculated total uptake of NH_4^+ into epilithic biofilms using measured values of the mole fraction of $^{15}N\text{-}NH_4^+$ in chamber water ($\mathrm{MF}_{\mathrm{chamber}}$):

$$\mathrm{Uptake} = \frac{\Delta^{15}N}{\mathrm{MF}_{\mathrm{chamber}}}$$

2.5 | Analyses

2.5.1 | Macroconsumer composition and biomass variation among pools

All analyses were performed in R version 3.5.1 (R Core Team, 2018). We hypothesised that macroconsumer biomass (g/m^2) would decrease with pool surface area (m^2) as habitat became limited and abiotic conditions became increasingly harsh. We tested for temporal differences in macroconsumer biomass among drying pools using analysis of covariance (ANCOVA) with biomass as a response variable, sample period as a fixed effect and surface area as a covariate. We tested if assumptions of normality and heterogeneity of variances were met using Shapiro–Wilks tests and Levene's tests, respectively, before conducting statistical tests. It was necessary to $\log_{10}$ transform biomass data to meet assumptions of normality and heterogeneity of variances.

We used canonical correspondence analysis (CCA, ter Braak, 1987) in the package *vegan* (Oksanen et al., 2019) to summarise spatial and temporal variability in pool assemblage structure and to evaluate the relationship between abiotic environmental variables (NH_4^+, SRP, pool surface area, and maximum monthly temperature) and variation in pool assemblage structure, using species-specific biomass estimates for each sampling period. We chose to exclude DO from this analysis because all 12 pools experienced severe hypoxia (<2 mg/L; McNeil & Closs, 2007) overnight during our single diel monitoring period, and there was little variation among pools. Canonical correspondence analysis is a multivariate ordination technique that selects a linear combination of environmental variables to maximise the dispersion of species scores, while preserving χ^2 distances among samples, and thus reflects differences in proportional abundance of species across samples (Gauch, 1982). Axes lengths provide a measure of faunal turnover, and sample scores separated by four standard deviations should have few species in common or major shifts in species dominance (Gauch, 1982; ter Braak, 1987). This analysis is visualised as a diagram with vector arrows that represent the relative importance of environmental factors in describing variation among pool assemblages. Rare species (<5 occurrences across pools) were excluded from these analyses because their occurrence in samples could be random and not represent true differences in macroconsumer biomass across space or time. We combined biomass of northern cricket frog (*Acris crepitans*: Hylidae) and northern leopard frog (*Lithobates pipiens*: Ranidae) because *A. crepitans* only occurred in one pool but was the dominant macroconsumer biomass and would have been removed otherwise. This resulted in a core community of 10 species. Monte Carlo simulations (999 iterations) were used to test whether eigenvalues from the CCA were significantly ($p < 0.05$) greater than those generated from a randomised matrix. Prior to CCA, variance inflation factors were used to check variables for multicollinearity. All values were < 10 so we concluded that multicollinearity was minimal.

2.5.2 | Animal-mediated nutrient cycling among pools

We tested for interspecific differences in NH_4^+ and SRP (hereafter N and P) excretion rates for all species. Size scaling of N and P was visualised using least-squares regression of $\log_{10}$ transformed excretion rates against $\log_{10}$ transformed wet mass. When slopes for individual species were equal (overlapping confidence intervals), we used ANCOVA to test for interspecific differences of $\log_{10}$ transformed excretion rates, using $\log_{10}$ transformed wet mass as a covariate. If no relationship was observed between excretion rates and the covariate, we used ANOVA to test for interspecific differences in excretion rates. Differences among species excretion N:P were assessed using ANOVA. A Tukey pairwise test for multiple comparisons was used if the test indicated differences in excretion among species' excretion N:P.

We tested how changes in areal biomass influenced nutrient cycling rates of pool assemblages using ANCOVA models with areal N excretion and areal P excretion as response variables, sample period as a fixed effect and biomass as a covariate. Areal N and P were $\log_{10}$ transformed prior to analyses to meet assumptions of normality and heterogeneity of variances. Macroconsumer excretion N:P was $\log_{10}$ transformed to improve normality and meet assumptions of heterogeneity, and differences among macroconsumer assemblage excretion N:P throughout the drought were assessed using regression.

We compared relative supply of N to demand across study pools by examining the ratio of N areal excretion rates to N uptake rates. It was necessary to $\log_{10}$ transform N uptake data to meet assumptions of normality and heterogeneity. We tested for differences in N uptake rates between the two pools using a *t*-test. We found no difference in N uptake rates between pools (see Results), therefore we assumed that uptake rates were representative of all other pools. Finally, we used ANCOVA with sample period as a fixed effect and biomass as a covariate to test whether macroconsumer contributions to N cycling changed during drought. Proportional N excretion data were arc-sin square-root transformed prior to analysis to ensure that assumptions of normality and heterogeneity were met.

3 | RESULTS

3.1 | Drought-induced changes in assemblage composition and pool conditions

A total of 16,426 individuals representing 19 species was captured across the 12 pools throughout the study. Fishes comprised the majority of biomass in 10 of 12 pools during June, but crayfish or tadpoles were the dominate biomass in four of the nine remaining pools in August (Figure S1) In June, southern redbelly dace (*Chrosomus erythrogaster*: Cyprinidae) was the most abundant fish (69% of individuals captured), the dominant biomass in eight of the 12 pools, and the only fish species to occur in all pools (Figure S1). However, as the drought continued, the biomass of *C. erythrogaster* decreased, was completely lost from some pools by July and constituted the dominant biomass of only three pools in August. One species, water nymph crayfish (*Orconectes nais*: Cambaridae), was ubiquitous in June and was captured in nine (of 10) or eight (of nine) pools in July and August, respectively (Figure S1). One pool was dominated by *A. crepitans* during June and July, but their abundance was reduced during August when western mosquitofish (*Gambusia affinis*: Poeciliidae) numerically dominated, comprising >40% of macroconsumer biomass (Figure S1). Due to either mortality, emigration (crayfish or tadpoles only), or metamorphosis (tadpoles only), biomass of nearly all native species declined from June to August. In contrast, *G. affinis* biomass increased to >20% of assemblage biomass in four pools where the species was <1% of biomass in June. None of the species comprised >11% of sampled biomass remaining in pools.

Severe drought conditions (PDSI between −3 and −4) persisted throughout the study resulting in increasing temperatures and habitat reductions. Consequently, one pool dried completely before July sampling (Figure 2), and two more pools dried by August. Canonical correspondence analysis characterised the association between assemblage structure and abiotic conditions across the 12 pools and three sample periods (Figure 3). The first and second axes cumulatively explained 85.2% of the constrained variation among pools and sample periods. Pool surface area ($F_{1,27} = 4.89$; $p = 0.02$), and SRP ($F_{1,27} = 5.09$; $p = 0.02$) were the most important explanatory variables in the CCA, while temperature ($F_{1,27} = 1.91$; $p = 0.09$) and NH_4^+ concentrations ($F_{1,27} = 0.85$; $p = 0.44$) were less clearly associated with differences in macroconsumer assemblage composition. Pools with higher axis 1 scores reflected increased abundance of *C. erythrogaster* in larger pools with lower water temperatures. In contrast, lower axis 1 scores were typical of smaller pools having higher SRP concentrations and warmer temperatures characteristic of conditions in July and August. *Gambusia affinis* was the most abundant fish species in August and was reflective of small pools with lower axis 1 scores. Tadpoles had the lowest CCA axis 1 and 2 species scores because they were abundant in pools with higher concentrations of SRP. Differences in assemblage structure resulted in separation of assemblages during June (larger pools) having generally higher axis 1 scores compared to July and August (smaller pools), which had lower axis 1 scores.

3.2 | Animal-mediated nutrient cycling

Size-scaling of N excretion rates was significant for all species ($p < 0.05$, Table S3). ANCOVA revealed the relationship between N excretion

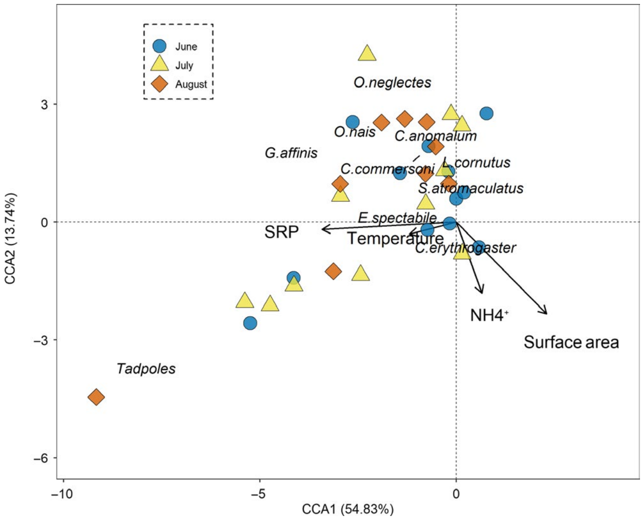

FIGURE 3 Canonical correspondence analysis of the aquatic animal community (i.e. fishes, crayfishes and tadpoles) across 12 isolated pools in Kings Creek, KS, U.S.A. sampled during June, July, and August 2018. The first and second axes had eigenvalues of 0.185 and 0.064, respectively. The species score for tadpoles combines biomass of *Acris crepitans* and *Lithobates pipiens*. Labels for environmental vectors: Temperature is the maximum temperature (°C) measured for each pool during each month; NH_4^+ is μmol/L of ammonium measured from water samples during each sample period; and volume was measured at each sampling period (m^3). One pool dried completely before July sampling and two pools dried before August sampling ($n = 32$) [Colour figure can be viewed at wileyonlinelibrary.com]

and mass for non-native *G. affinis* was significantly different than other species and increased more than proportionately with wet mass (Table S3). However, the per capita N excretion rate of *G. affinis* was less than half of all native fishes, crayfishes and tadpoles (Table 2). Only four fish species, *C. erythrogaster*, *G. affinis*, common shiner (*Luxilus cornutus*: Cyprinidae), and creek chub (*Semotilus atromaculatus*: Cyprinidae) showed significant size-scaling for P excretion rates ($p < 0.05$, Table S3). ANCOVA testing for interspecific differences in P excretion rates showed that *C. erythrogaster* and *S. atromaculatus* increased proportionately with wet mass (Table S3). *Orconectes nais* per capita excretion rate was nearly 10-fold lower (0.01 µmol g^{-1} h^{-1}) than other species (Table 2). No species showed size-scaling between excretion N:P and wet mass. However, excretion N:P differed significantly among species ($F_{7, 96} = 25.70$, $p < 0.001$). Post hoc tests indicated *O. nais* excreted at higher N:P relative to other species. *Gambusia affinis* had significantly lower N:P than all other species (Table 2).

3.3 | Drought-induced changes in biomass and animal-mediated nutrient cycling

Macroconsumer biomass was generally greater in pools with larger surface area (slope = 0.85, $F_{1, 26} = 12.14$, $p = 0.002$) and this pattern was consistent across months (Figure 4a). Temporally distinct macroconsumer biomass mediated the differences in areal N excretion rates among pools ($F_{2, 26} = 9.61$, $p = 0.001$), with greater N excretion rates occurring in June when macroconsumer biomass was highest (Figure 4b). In contrast, P areal excretion rates increased during August when assemblages had higher proportional biomass of species that excreted P at higher rates, such as *G. affinis* ($F_{2, 26} = 8.02$, $p = 0.002$; Figure 4c; Figure S1). Accordingly, molar N:P of macroconsumer excretion decreased significantly throughout the drought ($R^2 = 0.18$, $F = 6.58$, $p = 0.02$; Figure 5).

3.4 | N demand by epilithic biofilms and macroconsumer excretion relative to demand

Uptake rates by epilithic biofilms varied between 17 and 2102 µmol NH_4^+-N m^{-2} h^{-1} among chambers. However, we found no difference in N uptake among the two pools ($t = -0.78$, df = 8, $p = 0.46$). Mean N uptake by epilithic biofilms was 826 µmol NH_4^+-N m^{-2} hr^{-1} (SE = 190 µmol NH_4^+-N m^{-2} hr^{-1}) for 11 chambers. Overall, macroconsumer contributions to N cycling through N excretion diminished over the course of the drought ($F_{3, 27} = 22.85$, $p = 0.005$; Figure 6). Their contributions were greatest in June (mean = 38% of demand) but varied widely (2.7–139%) among pools. Decreasing macroconsumer biomass led to a 58 and 95% reduction in N contributions

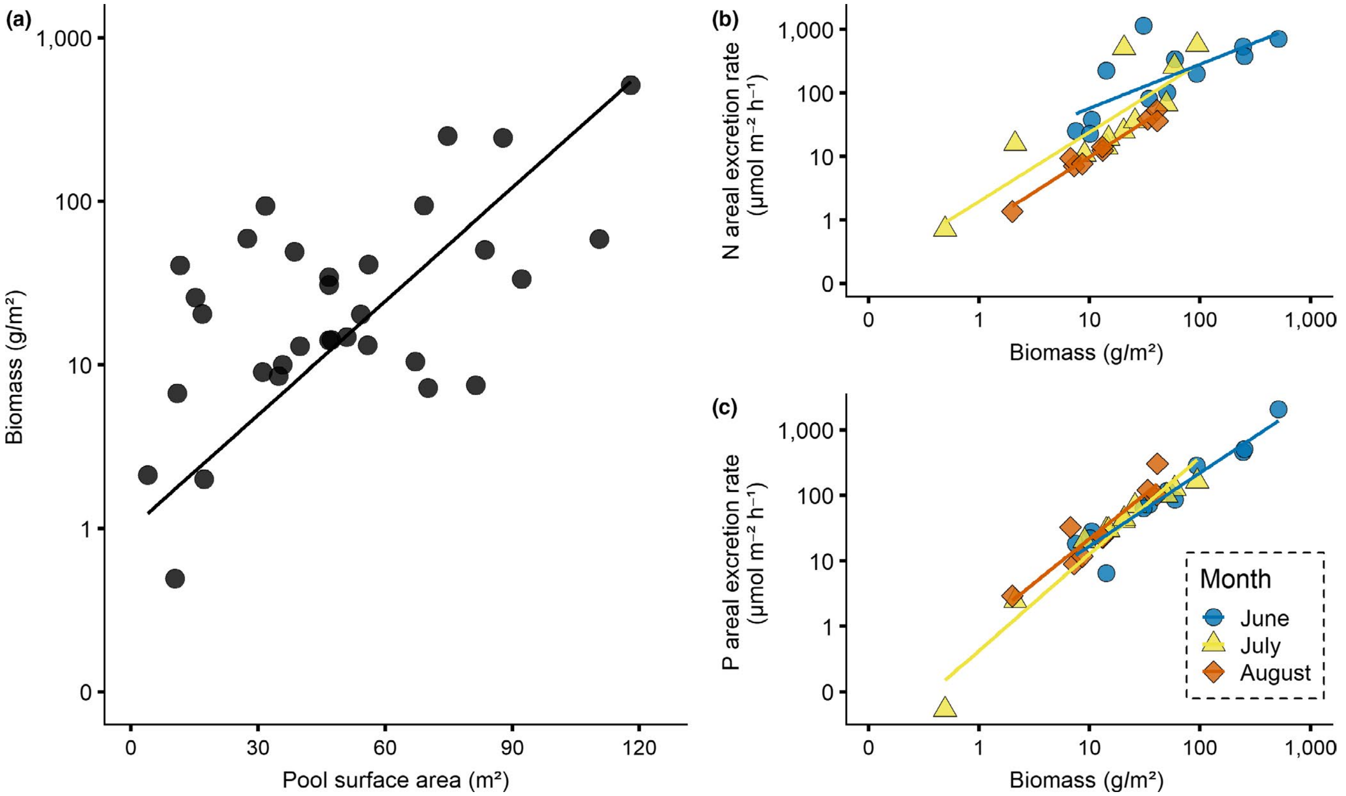

FIGURE 4 Relationship between pool assemblage biomass and surface area (a). Relationship between pool assemblage biomass and assemblage N areal excretion (b) and P areal excretion (c) rates from 12 isolated pools in Kings Creek, KS, U.S.A. sampled during June, July, and August 2018. Data are presented on log scaled axes. One pool dried completely before July sampling and two pools dried before August sampling ($n = 32$) [Colour figure can be viewed at wileyonlinelibrary.com]

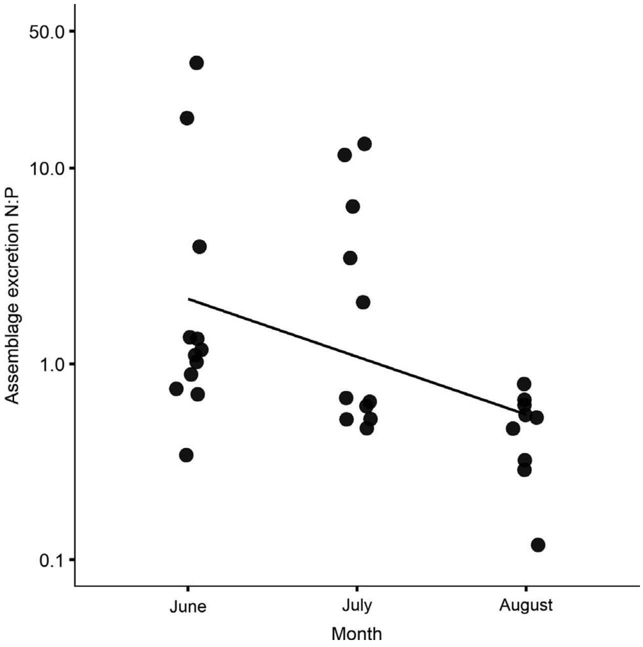

FIGURE 5 Assemblage excretion N:P (molar) presented on log scaled axis for 12 isolated pools in Kings Creek, KS, U.S.A. sampled during June, July, and August 2018. Points are jittered to prevent overlap. One pool dried completely before July sampling and two pools dried before August sampling (*n* = 32)

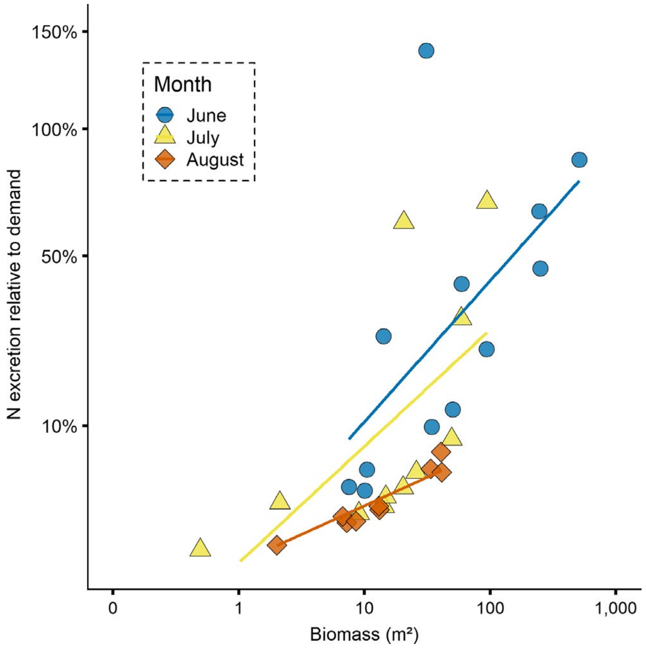

FIGURE 6 Relationship between biomass and assemblage N areal excretion rates relative to epilithic biofilm uptake rates for three sampling periods during a severe drought for 12 isolated pools in Kings Creek, KS, U.S.A. sampled during June, July, and August 2018. Data are presented on log scaled x-axis and square-root scaled y-axis. One pool dried completely before July sampling and two pools dried before August sampling (*n* = 32) [Colour figure can be viewed at wileyonlinelibrary.com]

from June to July (July mean = 16% of demand), and from June to August (August mean = 2% of demand), respectively.

4 | DISCUSSION

Our study quantified shifts in the ecosystem effects of aquatic macroconsumers resulting from biomass loss and shifts in dominance of species in isolated pools during a severe drought. Diminishing pool surface area caused large reductions in per capita biomass of macroconsumers and subsequent changes to animal-mediated nutrient cycling. For example, we saw a large decline in N (average of 91% among pools) and P excretion (average of 45% among pools) by macroconsumers following drought-related reductions in biomass and alterations to species dominance patterns. Variable abiotic conditions among isolated pools led to the initial macroconsumer assemblage of each pool, but pool surface area had the greatest influence on changes in taxonomic and functional composition of pool assemblages. These changes were driven by the complete loss or massive decline of *C. erythrogaster* and the recruitment of *G. affinis* during drought. In general, macroconsumer assemblages in isolated pools exhibited a nested pattern of species richness; species remaining at the end of the drought were a subset of the species present in the pool at the beginning of the drought. In contrast to the other species, *G. affinis* is a non-native fish in this catchment and appeared to proliferate under conditions brought on by drought (Casterlin & Reynolds, 1977; Hubbs, 2000), becoming abundant in four pools by August. Furthermore, pools with higher concentrations of SRP were associated with high biomass of *G. affinis*. Thus, our study highlights the potential for drought to influence the stability and function of ecosystem processes, such as nutrient cycling, by shifting species' roles according to their ability to tolerate conditions that are unsuitable for many species.

Excretion by macroconsumers was a major source of N to epilithic biofilms at the beginning of drought, contributing nearly 40% of demand (averaged across pools). Macroconsumer biomass primarily mediated N availability, with a reduction in areal excretion rates coinciding with biomass declines. Specifically, *C. erythrogaster* was the majority of biomass in most pools at the outset of the drought and excreted N at a relatively high rate. Major biomass reductions throughout the drought led to a 58% reduction (averaged across pools) in macroconsumer contributions to N demand, so only 2% of demand was met by excretion in August. Our measured N uptake rates by biofilms from pools were much higher compared to N uptake measured for comparable pools under baseflow conditions for Kings Creek (O'Brien & Dodds 2008). In contrast, Dodds et al. (2000) found uptake rates in Kings Creek to be higher than our measurements. This contrast is probably because their whole stream addition experiment included riffles, where uptake rates are generally higher (O'Brien & Dodds 2008). Thus, high rates of N uptake may be driven by elevated availability of dissolved N present in isolated pools compared to baseflow, indicating the importance of N excreted by aggregated macroconsumers, especially those with unique stoichiometric traits such as *C. erythrogaster*, to microbial-mediated processes such as decomposition during drought conditions.

In contrast to N, P excretion by assemblages was only initially reduced with biomass loss and tended to increase in small pools remaining in August. Macroconsumer assemblages at the end of the drought had higher proportional biomass of species that excreted P at higher rates. Variation in functional traits (e.g. those associated with resource acquisition and assimilation) among animals can influence animal-mediated nutrient cycling because food quality and quantity can strongly influence growth, reproduction and body stoichiometry. Species remaining at the end of the drought were potentially capable of acquiring and assimilating food in isolated pools, reducing the need to retain P. For example, when preferred prey are scarce, white sucker (*Catostomus commersoni*: Catostomidae) consume high amounts of detritus but their growth is substantially reduced; however, when benthic microcrustaceans are readily available, they reject detritus completely (Ahlgren, 1990). Increasing biomass of *G. affinis*, in combination with the high per capita P excretion of this species, appears to have contributed to the rise of macroconsumer P excretion in August. Previous experimental work demonstrated Cuatro Cienegas mosquitofish (*Gambusia marshii*: Poeciliidae) retain more P when fed reduced rations of food compared to those allowed to feed *ad libitum* (Moody et al., 2018). Thus, we hypothesise that macroconsumers with higher P excretion rates during the drought were able to acquire and assimilate food in isolated pools, reducing P retention in these species.

Loss of biomass and shifts in assemblage structure over the course of the drought led to a decline in assemblage excretion N:P. Macroconsumer excretion was measured near the beginning of this study (late June) and may not reflect physiological consequences of thermal stress and starvation such as when organisms catabolise their tissues and excrete at higher N:P (Spooner & Vaughn, 2008). For example, *C. erythrogaster*, had the highest excretion N:P compared to other species and dominated assemblage biomass in June. This species is thermally sensitive (Frenette 2019) and typically occupies permanent headwater reaches maintained by cool groundwater springs (Kansas Fishes Committee, 2014). Thermal and hypoxia tolerance traits for *Campostoma anomalum* (Family: Cyprinidae), *C. commersoni*, *Etheostoma spectable* (Family: Percidae), *G. affinis* and *S. atromaculatus* measured in other systems, prevent stress or population loss during drought and might explain the relatively lower N:P excreted by these species, compared to *C. erythrogaster* (Otto, 1973; Smale and Rabeni, 1995; Matthews et al., 1982; Hubbs, 2000). Furthermore, stoichiometric models predict reductions in consumption rates can increase excretion N:P (Moody et al., 2018) and certain animals may be limited by resource availability during drought, which may also explain the high excretion N:P of the herbivorous minnow *C. erythrogaster* in our study (mean = 25.4) compared to other studies (mean = 9.8, *SD* = 2.7, *n* = 10; McManamay, Webster, Valett, & Dolloff, 2010). Reduced foraging is expected to increase nutrient use efficiency and decrease excretion rates as an adaptive response to the extrinsic mortality threat posed by predators (Dalton & Flecker, 2014). The relatively low excretion rates measured for some taxa during drought compared to other studies (Vanni & McIntyre, 2016) may signal reduced food consumption during drought conditions similar to reductions during predation threat, but further tests of this hypothesis are needed.

The development of distinctive lentic conditions and local extinction of some species formed unique assemblages among the 12 pools, with potentially important consequences to ecosystem processes. The majority of assemblages at the end of the study comprised subsets of species that occurred in large pools at the beginning of the study. However, a single pool, was dominated by the tadpole *A. crepitans* during June and July comprising 94 and 98% of assemblage biomass, respectively. By August, this species was nearly absent from the pool when *G. affinis* numerically dominated (40% of assemblage biomass). In contrast to fish, tadpole biomass was probably reduced by an environmentally cued developmental switch to adult frogs that may have emigrated rather than died (Crump, 1989; Gerlanc and Kaufman, 2005). In addition to metamorphosing tadpoles, decomposing fishes or those eaten by terrestrial predators might also represent a net loss of nutrients to these systems. However, differences in fish and amphibian life histories might affect their role as short-term or long-term nutrient sinks during severe drought.

The supply ratios of nutrients limiting primary producers and bacteria can depend on the stoichiometric traits of dominant animal groups (Elser, Elser, MacKay, & Carpenter 1988, Elser et al., 1995). While fish biomass decreased during drought, crayfishes maintained relatively high biomass and probably serve as important nutrient cyclers in isolated pools during severe drought. For example, previous work investigating somatic stoichiometry of crayfish (Evans-White & Lamberti, 2005) indicated that they might act as P sinks in isolated pools given their relatively high excretion N:P and low N:P tissue stoichiometry. Although crayfish stoichiometry may vary during base-flow conditions, we predict that nutrients controlled by crayfishes may be important to ecosystem functions, including microbial respiration and leaf decomposition in isolated pools dominated by this group (Rosemond, Pringle, Ramírex, Paul, & Meyer, 2002). Other aquatic macroinvertebrates not quantified in our study can maintain high densities during stream drying (Boulton & Lake, 1992) and their contributions to nutrient cycling may exceed that of the macroconsumers measured here (Atkinson et al., 2019; Balik, Taylor, Washko, & Wissinger, 2018). Regardless, our study contributes evidence that the relative dominance of broad taxonomic groups (e.g. crustaceans or fishes) may have a prominent influence on stream nutrient dynamics and food web interactions, especially during periods of drought. Future work should focus on interactions among groups within whole communities to understand their influence on nutrient cycling (Atkinson et al., 2019; Hopper et al., 2018).

With expectations of a drier future for this region, we should anticipate significant changes to stream food webs and nutrient dynamics as events, such as that documented here, appear more frequently and with greater intensity (Dai, 2013; Diffenbaugh, Swain, & Touma 2015; Langerwisch et al., 2013; Mishra & Singh, 2011). Physiological tolerance and stoichiometric traits could be combined with population vital rates to assess and predict the immediate and lasting consequences of such disturbances to stream nutrient dynamics (Dubose, Vaughn, Atkinson, & Golladay 2019). Organismal traits including thermal tolerance, feeding, and life history have previously been used to evaluate risks to both drought and climate change (Chessman, 2013; Villnäs et al. 2012; Wenger et al., 2011), and thermal tolerance may drive changes in community composition as climate change takes hold and anthropogenic modifications to hydrologic regimes continue (Perkin et al., 2017; Spooner & Vaughn, 2008). Although the full implications of shifts in the composition of freshwater communities to ecosystems are not known, previous works in this system indicate populations of native fishes are resilient to disturbances and will recover quickly if the disturbance magnitude is within historic ranges (Whitney, Gido, Martin, & Hase, 2016). Our study fills a fundamental knowledge gap by illustrating that biomass loss and shifts in dominance of species with varying stoichiometric traits alter the availability of nutrients in a prairie stream during severe drought, which may result in altered ecosystem function.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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