Ecosystems
https://doi.org/10.1007/s10021-021-00679-9
ECOSYSTEMS

Animal-Driven Nutrient Supply Declines Relative to Ecosystem Nutrient Demand Along a Pond Hydroperiod Gradient

Jared A. Balik,[1,2]* Emily E. Jameson,[2,3] Scott A. Wissinger,[2,4]* Howard H. Whiteman,[2,5] and Brad W. Taylor[1,2]

[1]Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695, USA; [2]Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224, USA; [3]Department of Ecology and Evolutionary Biology and Department of Statistics, University of Michigan, Ann Arbor, Michigan 48109, USA; [4]Departments of Biology and Environmental Science, Allegheny College, Meadville, Pennsylvania 16335, USA; [5]Watershed Studies Institute and Department of Biological Sciences, Murray State University, Murray, Kentucky 42071, USA

ABSTRACT

In many lentic ecosystems, hydroperiod, or the duration of inundation, controls animal community composition and biomass. Although hydroperiod-imposed differences in wetland animal communities could cause differences in animal-driven nutrient supply, hydroperiod has not been considered as a template for investigating patterns of animal-driven nutrient cycling. Here, we use nutrient excretion rates (NH_4-N and SRP) and biomasses of pelagic and benthic invertebrates and salamanders and nutrient uptake rates in a simulation model to estimate animal-driven nutrient supply and pond-level demand along a hydroperiod gradient of 12 subalpine ponds in the U.S. Rocky Mountains that are vulnerable to climate change. We found that animal biomass increased with hydroperiod duration and biomass predicted animal-driven supply contributions among hydroperiod classifications (temporary-permanent). Consequently, community-wide supply was greatest in permanent ponds. Animal-driven N supply exceeded demand in permanent and semi-permanent ponds, whereas P supply equaled demand in both. Conversely, temporary ponds had large deficits in N and P supply due to lower community biomass and hydroperiod-induced constraints on dominant suppliers (oligochaetes and chironomids). The distribution of taxon-specific supply also differed among hydroperiods, with supply dominated by a few taxa in permanent ponds and supply more evenly distributed among temporary pond taxa. The absence or lower biomass of dominant suppliers in temporary ponds creates nutrient deficits and possible limitation of productivity. Thus, as climate warming causes hydroperiods to become increasingly temporary and indirectly prompts biomass declines and compositional shifts, animal-driven nutrient supply will decrease and strong nutrient limitation may arise due to loss of animal-driven supply.

Key words: Animal effects; Biogeochemistry; Climate change; Drying; Ponds; Wetlands.

Received 12 March 2021; accepted 16 June 2021

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-021-00679-9.

Author contributions JAB, BWT, and SAW conceived the study. All authors contributed to data collection. EEJ and JAB processed all water chemistry samples. JAB analyzed data, developed pond simulation model, and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Corresponding author; e-mail:* balikj3@gmail.com

HIGHLIGHTS

- Estimated animal-driven nutrient supply and pond-level demand in subalpine ponds.
- N exceeded and P matched demand in permanent, but temporary ponds had deficits.
- Temporary pond deficits result from community composition and lower animal biomass.

INTRODUCTION

In small ponds and wetlands, hydroperiod is an important dimension of water availability that controls animal biomass and community composition (Wiggins and others 1980; Schneider 1999). Ponds with temporary hydroperiods that are inundated seasonally and dry annually, or periodically via rainfall, select for invertebrate communities shaped by dispersal and taxa capable of completing larval development before drying (Schneider and Frost 1996; Wissinger and others 1999a). In contrast, ponds with longer hydroperiods (semi-permanent ponds that dry occasionally and permanent ponds that never dry) allow for multiple trophic levels with invertebrate communities adapted to cohabitation with predators (Wissinger and others 1999b; Stoks and McPeek 2003). Furthermore, permanent ponds often have greater invertebrate densities (Schneider and Frost 1996; Wissinger and others 1999a) and species richness (Chase 2007) than temporary ponds. Thus, hydroperiod maintains differences among ponds in community composition, biomass and life history traits. However, it is unclear how differences in animal communities among hydroperiod classifications affect animal-driven nutrient cycling.

Higher animal biomass in permanent relative to temporary ponds (Schneider 1999; Wissinger and others 2016) suggests greater community-wide animal-driven nutrient supply in permanent ponds (Atkinson and others 2017; Atkinson and others 2019). Yet, contrasting life history strategies and differences in community composition promote variation in nutrient excretion rates among hydroperiods that could mediate or enhance the positive effect of biomass on community-wide supply. For example, in any hydroperiod, a taxon with high excretion could make supply contributions disproportionate to their biomass (Small and others 2011). Alternatively, temporary pond taxa with rapid larval development may have lower excretion, especially of P (Elser and others 2003). Numerically dominant taxa in permanent ponds are also smaller (Wissinger and others 1999a) which could promote higher excretion (Elser and others 1996) and thus further enhance the positive effects of biomass. Although large-bodied vertebrate predators in permanent ponds could themselves make large supply contributions (Schindler and Eby 1997; McIntyre and others 2008), they also select for different invertebrate communities with lower biomass relative to temporary ponds (Wellborn and others 1996; Wissinger and others 1999a). Therefore, variation in excretion among differing communities and life history strategies complicates a first-principle prediction for greater community-wide supply in permanent ponds due to biomass alone.

Animal contributions to nutrient cycles can fulfill substantial proportions of ecosystem nutrient demand (Vanni 2002; Hall and others 2003; McIntyre and others 2008), though few studies have estimated supply contributions of all benthic and pelagic animals in lentic systems and little is known about how demand varies among hydroperiod classifications or how changes in animal communities will influence supply relative to demand (Elser and others 1988). For example, demand could increase with growing season length, resulting in greater demand in permanent ponds that could match their supply from greater animal biomass. Although supply relative to demand could be similar in temporary ponds due to lower biomass and shorter growing seasons, mismatches between supply and demand could arise due to compositional differences in their animal communities. Furthermore, permanent and semi-permanent ponds that do not dry could have some overwinter nutrient demand and interannual microbial turnover, whereas nutrient demand in temporary ponds refilled by spring melt could be lower due to nascent microbial communities.

Alternatively, periods of aerobic decay when temporary ponds are dry could stimulate greater rates of internal recycling when re-wetted. Thus, evaluating animal-driven supply relative to ecosystem demand provides important context for comparing supply among systems, but it is unclear how community-wide animal supply relative to ecosystem demand varies among hydroperiod classifications.

Here, we explored differences in animal-driven nutrient supply relative to demand along a hydroperiod gradient in subalpine ponds using a resampling-based simulation model. The model was parameterized with survey data collected from four representative ponds in each of three hydroperiod classifications. Specifically, the model leverages observed variation in physical pond characteristics, nutrient uptake rates, community composition, species relative abundances and their nutrient excretion rates to estimate nutrient supply and demand in permanent ponds that never dry, semi-permanent ponds that dry in some years and temporary ponds that dry every summer. We used these estimates to explore where along the hydroperiod gradient animal-driven supply equaled, exceeded or fell short of demand and we support these inferences with empirical estimates from the twelve ponds we sampled.

Our specific predictions were 1) community-wide animal-driven nutrient supply would increase with hydroperiod because biomass increases with permanence (Wissinger and others 2016) and is consistently a strong predictor of animal-driven supply (Carpenter and others 1985; Atkinson and others 2017). Likewise, 2) whole-pond seasonal demand would be greatest in permanent ponds due to greater area and longer hydroperiod durations. However, 3) supply would match demand in permanent and semi-permanent ponds but fall short in temporary ponds because of low biomass to drive supply. Next, we compared population-level biomass, nutrient excretion rate, time spent in the pond and their interactions in linear models of taxon-specific supply to understand what best predicts a taxon's role as a dominant nutrient supplier across hydroperiod classifications. We expected that 4) population-level biomass would be the strongest driver of taxon-specific supply and 5) salamanders would provide the largest supply contribution in permanent ponds because their biomass is comparable to the entire invertebrate community (Wissinger and others 1999a) and vertebrates drive large nutrient supplies elsewhere (Schindler and Eby 1997; McIntyre and others 2008). Finally, we predicted that 6) taxon-specific supply would be more evenly distributed in temporary ponds because drying selects for low-richness communities and taxa with similar life histories (Schneider and Frost 1996; Chase 2007) and functional roles due to niche complementarity (Loreau and Hector 2001). In contrast, permanent hydroperiods with species-rich communities could have taxa that attain high biomass and dominate function (Grime 1998).

METHODS

Site Selection and Animal Surveys

Ponds were located within the Mexican Cut Nature Preserve, a pristine, subalpine (3560 m) wilderness area owned by The Nature Conservancy and managed by the Rocky Mountain Biological Laboratory (RMBL) in the Elk Mountains of central Colorado. The Mexican Cut is a glacial cirque with 60 + kettle-pond wetland habitats, all with similar basin substrate composition and geomorphology, emergent and riparian vegetation and water chemistry (Wissinger and others 1999a). Ponds in the Mexican Cut thaw and are supplemented or refill completely via snowmelt in June and are similar to high-elevation kettle-pond wetlands throughout the Rockies and other mountainous regions (Wissinger and others 2016). For this study, we selected four representative ponds in each of three hydroperiod classifications: permanent, semi-permanent and temporary. Temporary ponds typically dry during August or earlier and semi-permanent ponds hold water through winter freeze in most years but occasionally dry in August. Montane ponds and wetlands are ideal systems for the broader study questions because their snowmelt-driven hydroperiods are expected to become increasingly temporary due to rapid climate change at high elevations (Lee and others 2015; Lund and others 2016).

Large benthic invertebrates were surveyed with single 0.33 m^2 benthic D-net sweeps at the north, east, south and west sides of each pond on July 19, 2018, following benthic census methods used for long-term population surveys in this system (Wissinger and others 1999a). Small benthic invertebrates were sampled using a 0.02 m^2 benthic core. All individuals were identified to species-level (for example, caddisfly sp.) or family level (for example, Gerridae, Hydrophilidae, Veliidae *and* so on) according to previous census methods (Wissinger and others 1999a). Average zooplankton density was estimated for each hydroperiod by pooling pond-level samples collected with a 80-µm mesh net and 2.2 L Van-Dorn following established methods for this system (Dodson 1974).

Long-term monitoring of the Arizona tiger salamander (*Ambystoma mavortium nebulosum*) population started in 1988 and is censused with PIT tags or toe clips. The Mexican Cut salamanders are facultatively paedomorphic and larvae develop into one of two adult morphs. Paedomorphs retain larval characteristics and attain sexual maturity in their natal ponds. In contrast, metamorphs transform and disperse into the terrestrial environment (Moore and Whiteman 2016). Our sampling focused on larvae and paedomorphic adults because they spend their entire life in the ponds and are keystone predators in these fishless ponds (Wissinger and others 1999b; Wissinger and others

2006). Salamanders were captured using dipnets and snout-vent length, total length, wet mass, capture date and pond were recorded. Sampling occurred daily between 15 June – 31 July. Pond-specific densities of 1 + year, 2 + year and 3 + year larval age classes and 4 + year paedomorphic adults were estimated using continuous mark and recapture and Lincoln-Peterson estimates (Whiteman and others 2012). Finally, pond-specific densities were averaged by hydroperiod for each age cohort.

Excretion and Uptake Measurements

Excretion measurements were collected following established protocols for invertebrates (Hall and others 2003; Balik and others 2018) and amphibians (Whiles and others 2009). Animals were collected and held for 0.5 to 1.5 h in plastic bags, which enabled us to measure ambient excretion rates while minimizing stress or starvation effects. All invertebrate excretion measurements were conducted by placing bagged animals in shaded areas of each pond to maintain ambient temperature. Ambient water temperatures varied by less than 4 °C among replicates for each taxon. The number of individuals (1–80) and the volume of filtered pond water (100–200 mL) were adjusted per the taxon's size. Invertebrates used for excretion measurements were dried for 48 h at 60 °C to measure dry mass. Excretion measurements were opportunistically collected for each taxon from various ponds throughout the summer and we assume that they were representative of each taxon's excretion in other ponds within the system across the season, which Balik and others (2018) previously demonstrated for the trichopteran (larval caddisfly) taxa. We collected 3–15 replicate excretion measurements for each taxon (223 total replicates across all taxa). During each sampling effort, we also included 2–4 controls without any animals to measure changes in ambient nutrient concentrations (52 total controls across all sample dates).

Salamanders used for excretion incubations were processed in a nearby shaded tent (Hansen Weatherport, Delta, Colorado, the USA) to minimize handling, thermal and oxygen stress. We collected 35 replicate salamander excretion measurements by placing individuals in 1 L of filtered pond water. Individual salamander dry mass was estimated using wet mass and a conversion factor of 0.233 (Hairston and Hairston 1987).

To estimate taxon-specific excretion, we measured differences in ammonium-nitrogen (NH_4^+-N) and soluble reactive phosphorus (SRP) in filtered water collected before and after incubation (0.5–1.5 h). All water samples were collected and filtered using a syringe and inline filter holder containing a 25 mm Gelman AE glass fiber filter and kept cool in the field then stored in a refrigerator until analysis the following morning. For all excretion and uptake measurements, we analyzed NH_4^+-N following a standard fluorometric method on a Turner Designs Trilogy Fluorometer Model # 7200 (Sunnyvale, CA, the USA; Taylor and others 2007). SRP samples were analyzed following standard methods on a Thermo Scientific GENESYS 10S UV–VIS Spectrophotometer (Waltham MA, the USA; Ostrofsky and Rigler 1987).

We estimated pond-level nutrient demand by collecting nutrient uptake measurements from two compartments within the ponds. The first compartment included demand by the water column and benthic substrates. Following a protocol adapted from Stanley and Ward (1997), paired open-bottom clear plastic cylinders (12.5 cm diameter, 1 mm wall thickness) were gently pressed into the benthic substrates in three to four locations without sedge around each pond. Cylinder water depth was measured to calculate volume and estimate the nutrient addition required to increase concentration 7–10 × above ambient by pipetting small volumes (200 µL to 3 mL) of 100 mg/L NH_4-N and PO_4-P solutions made from NH_4Cl and Na_2HPO_4. Immediately after adding NH_4 or PO_4, a meter stick was used to gently mix the added nutrients throughout the cylinder water column without disturbing the benthic substrates. Samples were collected following 0, 15, 30, 60 and 120 min. Uptake rates were estimated by fitting exponential decay models to the decline in nutrient concentration over time. Slopes were expressed as ug N or P m^{-2} d^{-1} in statistical analyses to test for differences among depths and hydroperiod classifications prior to use in the simulation model.

The second compartment included nutrient demand by microbial biofilms growing on submerged sedge (*Carex aquatilis*) in the littoral zone. Small amounts of submerged, senesced sedge (< 10 g) were transferred to plastic bags, and water samples were collected prior to, immediately after and one hour after adding nutrients to increase concentrations 7–10 × above ambient. Uptake was calculated as the decline in concentration during incubation divided by sedge mass (ug N or P g $sedge^{-1}$ d^{-1}).

Physical, chemical and biological uptake mechanisms have a nonlinear asymptotic response to elevated nutrient concentrations, and therefore, this single-addition method may underestimate uptake (O'Brien and Dodds 2007). To address this concern, we also collected uptake measurements in both compartments using higher additions (20–50 × ambient) and found no difference in uptake (Water Column P: $F_{1,42} = 0.018$, $p = 0.895$; Water Column N: $F_{1,42} = 0.423$, $p = 0.519$; Sedge P: $F_{1,10} = 1.4455$, $p = 0.257$; Sedge N: $F_{1,10} = 0.390$, $p = 0.547$), suggesting that uptake kinetics were saturated at our lower nutrient additions. Therefore, these uptake rates are likely conservative estimates of demand.

Pond Parameters

Characteristics of four ponds in each of the three hydroperiod classifications were used to parameterize hydroperiod-specific normal distributions of hydroperiod duration, pond area, habitable littoral benthic area, sedge coverage and sedge biomass for random sampling in the simulation model (Table 1). Hydroperiods were recorded with WT-HR Mark 3 data loggers (TrueTrack). The twelve ponds were mapped using Trimble GeoXT GPS units (< 50 cm accuracy), and areas were calculated using ESRI Arcmap 10 (DelVecchia and others 2019). Most benthic invertebrates congregate within approximately 3 m of interior pond edges at the Mexican Cut, which are shallow littoral zone habitats often characterized by live emergent sedge, senesced sedge detritus and high light availability. This nearshore microhabitat area was quantified by creating 3 m inverse buffers within each pond (Figure1A). Because pond shape varies, the inverse buffer areas were used to calculate littoral benthic area as a proportion of total area (Figure1B). Finally, we combined measurements of sedge areal coverage and biomass to account for hydroperiod-imposed differences in pond-level sedge biomass. First, approximate total area of sedge within each pond was calculated by measuring area of 3–20 sedge patches (for example, 1 m × 3 m) around pond perimeters, with the number of estimates depending on pond size and sedge contiguousness. Next, senesced sedge was clipped from 3–5 randomly selected 0.01 m^2 areas in each pond and massed separately after drying for 48 h at 60 °C to estimate senesced sedge biomass per m^2.

Simulation Model Framework for Estimating Community-Wide Excretion and Demand

We estimated average community-wide animal-driven nutrient supply and pond-level nutrient demand in permanent, semi-permanent and temporary ponds using a simulation model (Figure1). Each iteration simulates one pond in each of the three hydroperiod classifications, providing N and P supply estimates for all taxa in the community (Figure1C), along with estimates of pond-level nutrient demand from the benthic substrates and water column (Figure1D) as well as from sedge biofilms (Figure1E). The simulation operates by drawing random samples from hydroperiod-specific distributions parameterized by our physical pond parameter, animal survey, nutrient excretion and uptake rate datasets.

First, pond parameter distributions (Figure1B, Table 1) were randomly sampled to simulate one pond of each hydroperiod. In summers when semi-permanent ponds do not dry, their hydroperiods are determined by spring melt and winter freeze, resulting in the same annual hydroperiod as permanent ponds. Thus, if the randomly sampled semi-permanent hydroperiod was longer than that of the permanent pond, which was possible due to overlapping hydroperiod distributions, the permanent pond's hydroperiod was used for both hydroperiod classifications during that iteration.

Next, a set of taxon-specific parameters were randomly sampled for each taxon (Figure1C). Each taxon's densities were drawn from unique distributions for each hydroperiod classification. These distributions were prepared by averaging inverte-

Table 1. Summaries of Hydroperiod-Specific Parameters used in the Simulation Model.

Hydroperiod	Hydroperiod (d)	Pond area (m^2)	Littoral benthic area (% total area)	Sedge coverage (% total area)	Sedge biomass (g/m2)
Permanent	(165 ± 22)	(2147 ± 2167)	(0.28 ± 0.17)	(0.12 ± 0.14)	(167 ± 99)
Semi-permanent	(150 ± 20)	(455 ± 360)	(0.44 ± 0.09)	(0.14 ± 0.19)	(146 ± 74)
Temporary	(50 ± 19)	(104 ± 83)	(0.76 ± 0.18)	(0.37 ± 0.26)	(100 ± 85)

Distributions are parameterized as normal distributions with (mean ± 1 standard deviation).Permanent hydroperiod distributions were generated from ponds 1, 3, 5 and 12 at the Mexican Cut preserve, semi-permanent from ponds 6, 8, 10 and 44 and temporary from ponds 13, 15, 22 and 42.

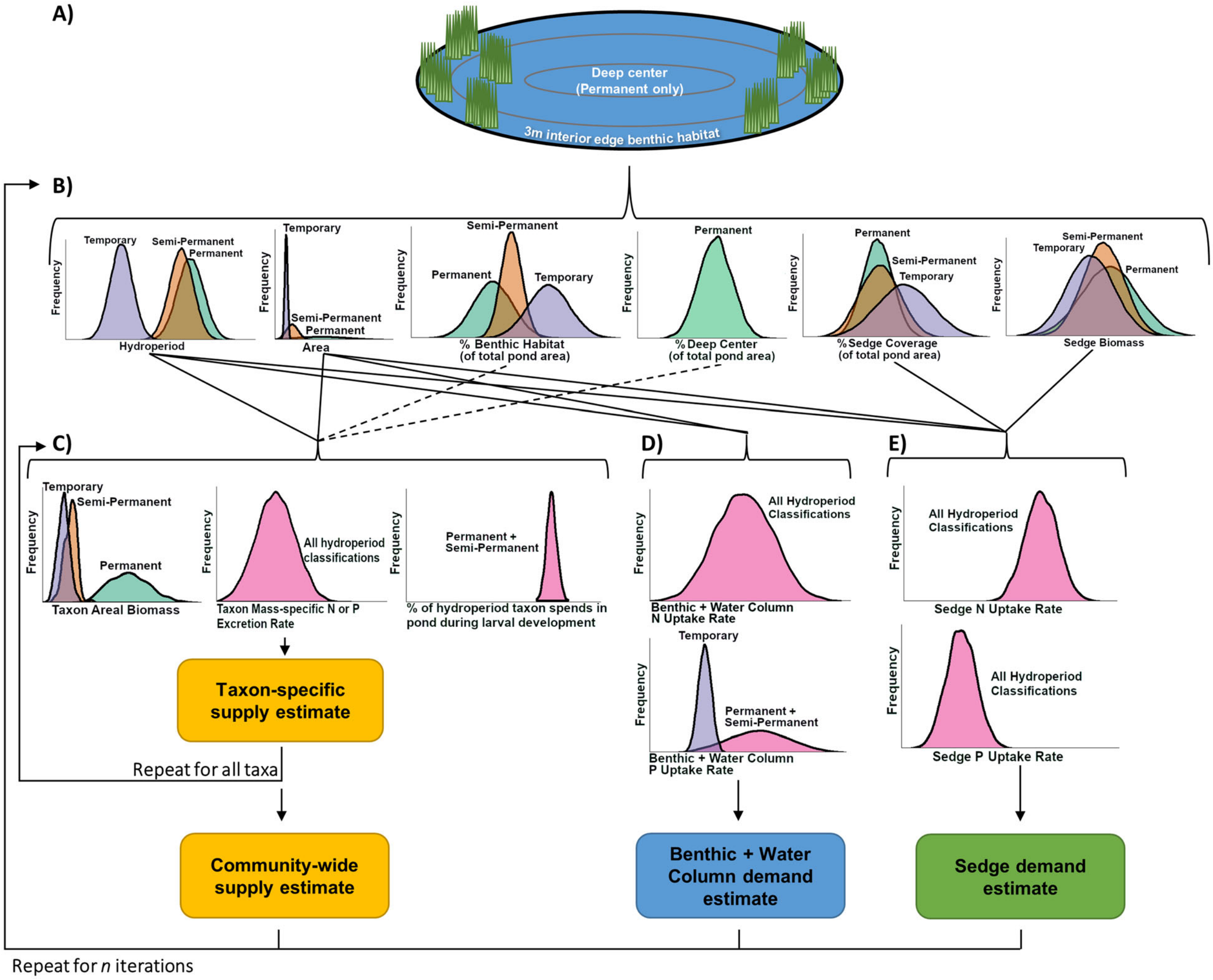


Figure 1. Conceptual diagram of the simulation model. **A** An idealized ''average'' pond at the Mexican Cut Nature Preserve. In all three hydroperiod classifications, littoral benthic invertebrates typically inhabit a ~ 3 m wide interior region around the pond perimeter. Most pond surface area is shallow depth (~ 0.5 m) in all hydroperiod classifications, but maximum depths of permanent ponds range from 1.5–3 m. During each iteration, **B** hydroperiod-specific pond parameters (Table 1) are randomly sampled to simulate one pond of each hydroperiod classification. **C** Taxon-specific supply estimates are calculated for each hydroperiod classification by multiplying randomly sampled hydroperiod, benthic area, areal biomass and mass-specific excretion rates and for permanent and semi-permanent hydroperiods, a taxon-specific percent of hydroperiod spent in larval development. Benthic area is determined by taxon life history, calculated for littoral benthic invertebrates as the product of pond area and % littoral benthic area. For chironomids and oligochaetes in permanent ponds, habitable area is pond area minus the product of pond area and % deep center area. For chironomids and oligochaetes in other hydroperiod classifications and zooplankton and salamanders in all hydroperiods, habitable area is pond area. **D** Benthic substrate and water column demand are the product of hydroperiod, area and randomly sampled benthic and water column uptake rates. **E** Senesced sedge demand is the product of hydroperiod, area, % sedge coverage, sedge areal biomass and sedge uptake rates.

brate densities were across the four census samples by pond, then averaging by hydroperiod to generate λ values (of hydroperiod-specific average density) that parameterize hydroperiod-specific Poisson distributions of invertebrate densities. In contrast, each taxon's mass-specific excretion rates were drawn from the same taxon-specific distributions for all three hydroperiods. Although excretion could vary among ponds and over time due to differences in diet or temperature, we collected replicate excretion measurements opportunistically from multiple ponds and often on different days. Furthermore, the trichopteran taxa have consistent excretion among ponds with differing hydroperiods from about 2900–3500 m elevation across the season (Balik and others 2018).

Thus, we assume that the taxon-specific variation we measured is representative across hydroperiods with potentially variable food resources over the season. We measured N and P excretion of 34 of 40 invertebrate taxa which comprise 98.7% of invertebrate biomass across the three hydroperiods. The six taxa for which we did not measure excretion were omitted from the simulation. If a negative excretion value was randomly sampled, which is possible for some taxa with low mean excretion rates with high variance, their excretion was set to zero for that iteration. Taxon-specific distributions of the percent of hydroperiod spent in a pond represent how long each taxon spends in a permanent or semi-permanent pond relative to the total hydroperiod (S. Table 1; mean values range from 35 to 100%). These distributions were generated from personal observations (J.A. Balik and B.W. Taylor) and the literature searches (Dodson 1975; Wissinger and others 1999a; Babler and others 2008). For temporary ponds, percent of hydroperiod spent in pond was always set to 100 because hydroperiod directly determines time spent in the pond for all taxa, as organisms generally emerge near pond drying or do not survive (Greig and Wissinger 2010).

Each taxon's life history (for example, benthic vs water column) and the pond hydroperiod classification determined how their supply contribution was calculated. For littoral benthic invertebrates, which congregate in about the 3-m wide nearshore area surrounding the interior pond perimeter (Figure 1A), supply was calculated as:

Littoral benthic invertebrate supply contribution

$$\left[\frac{ug\,N\,or\,P}{Pond*Summer}\right]=pond\,area\left[\frac{m^2}{Pond}\right]*\%\,benthic\,area*density\left[\frac{individuals}{m^2}\right]*mean\,mass\left[\frac{mg\,animal}{individual}\right]*hydroperiod\left[\frac{d}{Summer}\right]*\%\,hydroperiod\,spent\,in\,pond*excretion\,rate\left[\frac{ug\,N\,or\,P}{mg\,animal*d}\right]$$

Here, densities are converted to biomass using taxon-specific mean mass constants previously used to estimate whole-pond biomass (Wissinger and others 1999a).

Next, for chironomids and oligochaetes which are distributed throughout the pond basin, except for the deep center areas of permanent ponds (Figure 1A; Babler and others 2008), supply contributions were calculated as:

Chironomid and oligochaete supply contributions in permanent ponds

$$\left[\frac{ug\,N\,or\,P}{Pond*Summer}\right]=\left(pond\,area\left[\frac{m^2}{Pond}\right]*(1-\%\,deep\,center)\right)*density\left[\frac{individuals}{m^2}\right]*mean\,mass\left[\frac{mg\,animal}{individual}\right]*hydroperiod\left[\frac{d}{Summer}\right]*\%\,hydroperiod\,spent\,in\,pond*excretion\,rate\left[\frac{ug\,N\,or\,P}{mg\,animal*d}\right]$$

where "% deep center" is a random sample from a distribution of percent permanent pond area deeper than 1.5 m generated from depth measurements (DelVecchia and others 2019). Because semi-permanent and temporary ponds do not have center areas deeper than 1.5 m, chironomid and oligochaete supply contributions in these hydroperiods were calculated in the same manner as for zooplankton and salamanders, which are evenly distributed throughout all ponds:

Chironomid and oligochete supply contributions in semipermanent and temporary ponds, and of zooplankton and salamanders in all hydroperiods

$$\left[\frac{ug\,N\,or\,P}{Pond*Summer}\right]=pond\,area\left[\frac{m^2}{Pond}\right]*density\left[\frac{individuals}{m^2}\right]*mean\,mass\left[\frac{mg\,animal}{individual}\right]*hydroperiod\left[\frac{d}{Summer}\right]*\%\,hydroperiod\,spent\,in\,pond*excretion\,rate\left[\frac{ug\,N\,or\,P}{mg\,animal*d}\right]$$

Finally, community-wide animal-driven supply was the sum of all taxon-specific contributions.

To estimate nutrient demand, random samples were drawn from normal distributions generated from our uptake rate measurements in the benthic substrates plus water column (Figure 1D) and sedge compartments (Figure 1E). Uptake rates did not differ across the season (benthic substrates plus water column P: $F_{1,42} = 0.45$, $p = 0.51$; benthic substrates plus water column N: $F_{1,43} = 0.02$, $p = 0.89$; Sedge P: $F_{1,10} = 1.13$, $p = 0.31$; Sedge N uptake: $F_{1,10} = 0.02$, $p = 0.90$) or among depths (benthic substrates plus water column P: $F_{1,42} < 0.01$, $p = 0.99$; benthic substrates plus water column N: $F_{1,43} = 1.99$, $p = 0.17$), so measurements were pooled. However, benthic substrates plus water column P uptake rates were 52% slower in temporary ponds than in semi-permanent and permanent ponds ($F_{2,5} = 7.04$, $p = 0.04$), so temporary ponds used a unique distribution, whereas semi-permanent and permanent ponds were pooled (Figure1D). There were no differences among hydroperiods in benthic substrates plus water column N, sedge N and sedge P uptake rates, so all three hydroperiods drew from the same distributions (Water column N: $F_{2,5} = 0.02$, $p = 0.98$; Sedge N: $F_{2,2} = 0.03$, $p = 0.79$; Sedge P: $F_{2,2} = 0.14$, $p = 0.88$; Figure1D, E). Benthic substrates plus water column demand was estimated as:

$$\begin{aligned}
&\textit{Benthic substrates plus water column demand} \\
&\left[\frac{ug\ N\ or\ P}{Pond * Summer}\right] = benthos\ plus\ water\ column \\
&uptake\ rate\left[\frac{ug\ N\ or\ P}{m2 * d}\right] * hydroperiod\left[\frac{d}{Summer}\right] \\
&* pond\ area\left[\frac{m^2}{Pond}\right]
\end{aligned}$$

whereas sedge biofilm demand was estimated as:

$$\begin{aligned}
&Sedge\ demand\left[\frac{ug\ N\ or\ P}{Pond * Summer}\right] \\
&= sedge\ uptake\ rate\left[\frac{ug\ N\ or\ P}{gsedge * d}\right] \\
&* hydroperiod\left[\frac{d}{Summer}\right] \\
&* pond\ area\left[\frac{m^2}{Pond}\right] * \%\ coverage * sedge\ biomass\left[\frac{g}{m2}\right]
\end{aligned}$$

The supply and demand estimates presented here were based on 100,000 iterations. Mean pond-level supply and demand estimates did not increase between 10,000 and 100,000 iterations, suggesting they had reached an asymptote (P flux means: $t_{11} = -1.84$, p = 0.09; N flux means: $t_{11} = -1.49$, $p = 0.17$). Supply and demand estimates are presented in two different units (predictions 1–3; Figure2). First, areal daily estimates (mg N or P $\text{m}^{-2}\ \text{d}^{-1}$) standardize fluxes by pond area and hydroperiod duration (Figure2A, B). Second, whole-pond seasonal estimates (kg N or P $\text{pond}^{-1}\ \text{season}^{-1}$) are conservative estimates of total fluxes that incorporate differences among hydroperiods in pond area and hydroperiod duration (Table 1; Figure2C, D). Although nutrient turnover rates in each compartment could provide further context to our estimates, we do not have the nutrient storage data required to estimate mass balance. Because whole-pond seasonal estimates represent among hydroperiod variation in a given taxon's contribution to supply, they were used to test drivers of taxon-specific contributions (prediction 4) and to compare taxon-specific contributions among taxa (prediction 5) and distributions of rank-order taxon-specific supply estimates among hydroperiods (prediction 6).

Although the simulation model is conceptually similar to a bootstrap, we sampled hydroperiod-specific distributions generated from our field data rather than resampling our pond-level datasets for three reasons. First, within a hydroperiod classification, there is substantial variation in pond area and sedge coverage (Table 1). Simulating many ponds across the observed range of physical pond parameter distributions better characterized average supply and demand within each hydroperiod. Second, long-term invertebrate surveys demonstrate that dominant taxa are interannually consistent (for example, chironomids, oligochaetes, larval caddisflies), but interannual variation in abundance of other taxa can be high (Wissinger and others 2016). Thus, the simulation model leverages variation in abundance among multiple ponds within each hydroperiod classification to predict nutrient supply of an ''average'' community in each hydroperiod. Third, invertebrate communities were surveyed for a subset of the ponds with physical datasets (10 of 12 ponds in Table 1). Only the overlapping subsets of animal and physical datasets could be resampled in a true bootstrap, whereas the simulation used the entirety of both datasets to estimate average supply and demand for each hydroperiod. Finally, to support inferences drawn from the simulation, the same calculations described above were used to estimate empirical supply and demand for each survey pond in areal daily units.

Statistical Analyses

The simulation model and all statistical analyses were performed in R 4.0.2 (R Core Team 2019). To guide preparation of water column and sedge uptake rate distributions for the simulation model, mixed models were used to test for differences in uptake among sample dates, depths, hydroperiod classifications and nutrient spike volumes as fixed effects and pond as a random effect (Pinhero and others 2019). Empirical estimates of supply relative to demand were compared among hydroperiods with ANOVA and post hoc Tukey's HSD. Simulation model supply estimates were used in linear models to evaluate drivers of taxon-specific whole-pond seasonal supply across hydroperiods (Prediction 4) by comparing AIC scores among reduced models (Akaike and others 1998). Distributions of taxon-specific supply estimates from the simulation model were compared among hydroperiods (Pre-

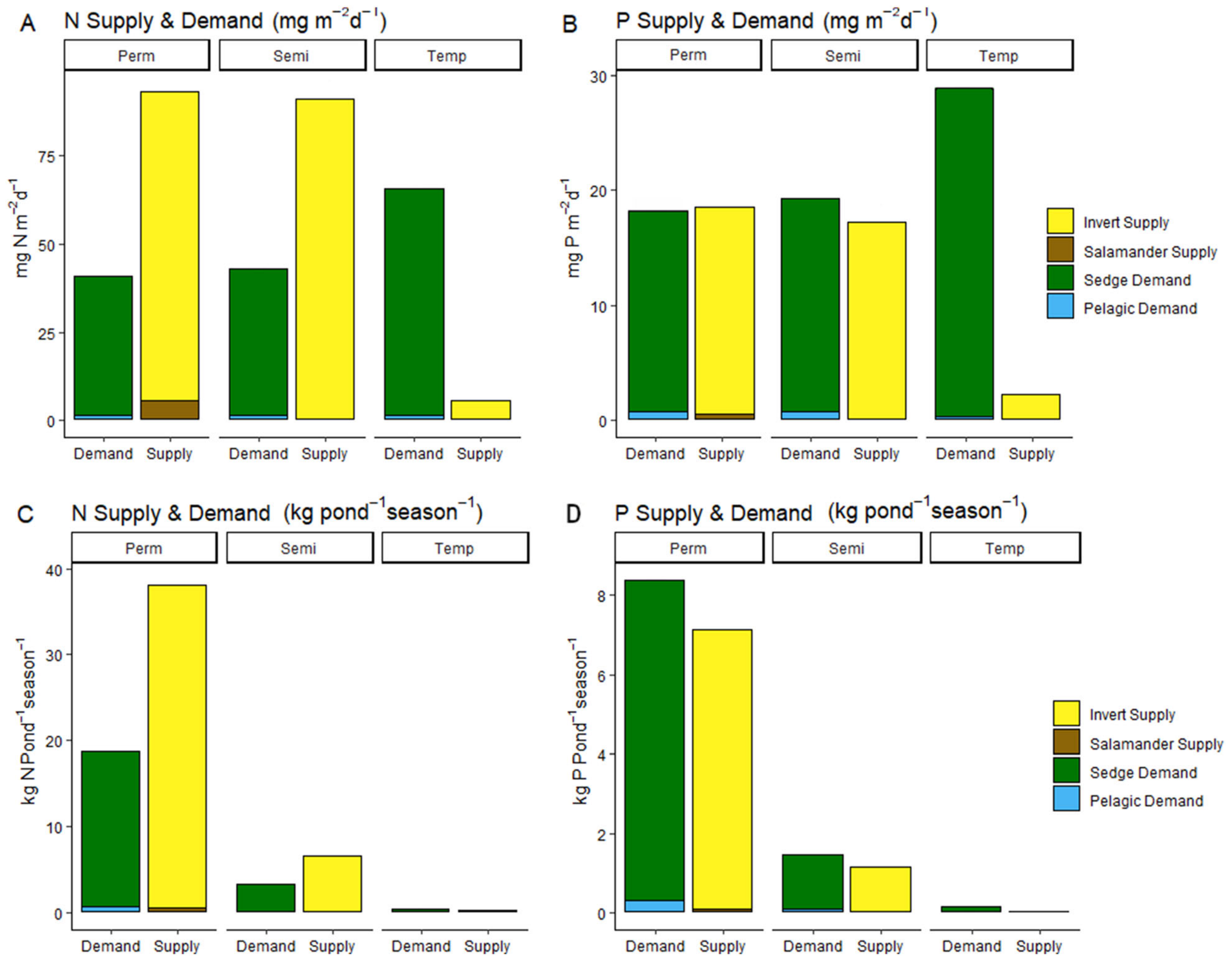


Figure 2. Mean estimates of N and P supply and demand from the simulation model. Panels **A** and **B** present estimates of each rate in units of mg N or P m^{-2} d^{-1}. Panels **C** and **D** scale estimates to seasonal whole-pond rates (kg N or P $pond^{-1}$ $season^{-1}$) to demonstrate effects of differences in pond area and season length among hydroperiod classifications. Error bars are omitted because the simulation ran until the mean supply and demand estimates were stable, and thus, variance was low.

diction 6) with a Kolmogorov–Smirnov (KS) test and multiple KS test p values were Bonferroni adjusted. Lastly, to assess differences in how evenly supply was distributed among taxa, skewness of mean rank-order taxon-specific supply distributions were calculated for each hydroperiod (Meyer and others 2019).

RESULTS

Nutrient Supply and Demand Across a Hydroperiod Gradient

Empirical estimates of supply relative to demand differed among hydroperiods (Table 2; N: $F_{2,7} = 11.98$, $p = 0.006$; P: $F_{2,7} = 11.23$, $p = 0.007$). Empirical estimates of N supply relative to demand did not differ between permanent and semi-permanent hydroperiods and averaged 188% of demand, but N supply in temporary hydroperiods only met 18% of demand (HSD < 0.05). Likewise, empirical estimates of P supply relative to demand did not differ between permanent and semi-permanent hydroperiods and averaged 99% of demand, but P supply in temporary hydroperiods only met 15% of demand (HSD < 0.05). Molar N:P of empirical supply and demand estimates did not differ among hydroperiods (Supply: $F_{2,7} = 0.07$, $p = 0.928$; Demand: $F_{2,7} = 0.31$, $p = 0.740$), and supply N:P was 187% of demand N:P.

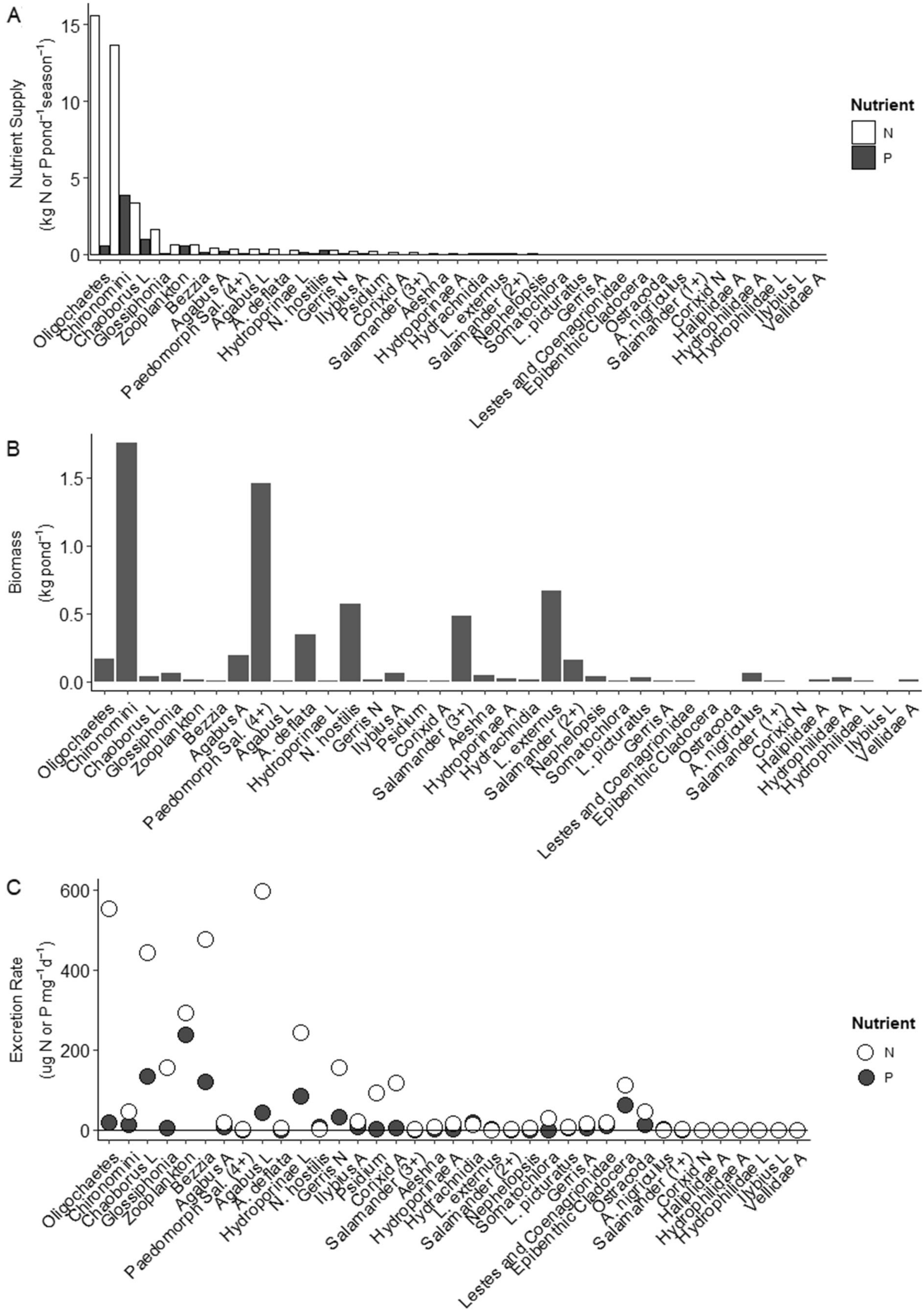
Mean areal daily estimates from the simulation model demonstrate that empirical patterns along the hydroperiod gradient prevail after considering each hydroperiod's various possible combinations and permutations of pond area, hydroperiod duration and animal communities (Figure2A, B). The simulation model's mean estimate of areal daily N supply was 221% of demand in permanent and semi-permanent hydroperiods, but only 9% of demand in temporary hydroperiods. Areal daily P supply was 101% and 86% of demand in permanent and semi-permanent hydroperiods but only 8% of demand in temporary hydroperiods. Thus, when fluxes are standardized for pond area and hydroperiod duration, N and P supplies meet comparable proportions of their respective demand in permanent and semi-permanent ponds, whereas in temporary ponds, both nutrients meet much lower proportions of demand. In turn, molar N:P of areal daily supply was 233% of demand N:P in permanent and semi-permanent hydroperiods, but only 112% of demand N:P in temporary (Table 2).

The simulation model's mean estimates of whole-pond seasonal N and P supply followed similar patterns after accounting for pond area and hydroperiod duration (Figure2C, D). Whole-pond seasonal N supply estimates were 203% of demand in permanent and semi-permanent ponds and 25% of demand in temporary ponds. Whole-pond seasonal P supply estimates were 85%, 78% and 22% of demand in permanent, semi-permanent and temporary hydroperiods, respectively. Thus, whole-pond seasonal N and P supply and demand estimates decreased along the hydroperiod gradient from permanent to temporary.

Table 2. Empirical Pond Supply and Demand Estimates in Units of mg N or P m^{-2} d^{-1} and Molar N/P Ratios and for all Ponds with 2018 Invertebrate Survey Data.

Hydroperiod	Pond	N Supply (mg N m^{-2} d^{-1})	N Demand (mg N m^{-2} d^{-1})	P Supply (mg P m^{-2} d^{-1})	P Demand (mg P m^{-2} d^{-1})	N:P Supply (molar)	N:P Demand (molar)
Perm	MC1	11.60	6.12	2.23	2.89	20.85	4.68
	MC3	69.12	38.78	34.21	30.91	4.47	2.77
	MC5	65.68	33.81	9.80	15.20	14.82	4.92
	MC12	17.70	20.07	7.95	9.02	6.58	4.92
	Empirical Mean ± 1 SE	41.02 ± 15.29	24.69 ± 7.35	13.5 ± 7.35	14.5 ± 6.02	11.68 ± 3.79	4.32 ± 0.52
	Simulation Mean ± 1 SE	99.59 ± 0.73	41.99 ± 0.11	19.09 ± 0.09	18.86 ± 0.05	11.54 ± 0.02	4.92 ± 0.01
Semi	MC6	52.51	16.83	6.76	6.62	17.18	5.62
	MC8	22.40	9.38	26.51	27.00	1.87	0.77
	MC10	50.34	31.64	10.40	6.92	10.70	10.11
	Empirical Mean ± 1 SE	41.75 ± 8.4	19.28 ± 5.67	14.56 ± 5.25	13.51 ± 5.84	9.92 ± 4.44	5.50 ± 2.70
	Simulation Mean ± 1 SE	91.06 ± 0.21	44.34 ± 0.11	17.22 ± 0.04	19.92 ± 0.05	11.69 ± 0.01	5.11 ± 0.01
Temp	MC13	5.39	11.01	2.34	4.33	3.57	5.62
	MC15	10.44	57.41	2.02	19.86	11.43	6.39
	MC22	9.54	70.99	2.65	29.48	7.96	5.32
	Empirical Mean ± 1 SE	8.46 ± 1.35	46.47 ± 15.73	2.67 ± 0.33	17.89 ± 6.34	7.65 ± 2.27	5.78 ± 0.32
	Simulation Mean ± 1 SE	5.8 ± 0.02	66.78 ± 0.18	2.27 ± 0.01	29.2 ± 0.08	5.65 ± 0.00	5.06 ± 0.01

Estimates from the simulation model are also presented in the same units for comparison (Figure2A, B).


A
Nutrient Supply
(kg N or P pond^{-1}season^{-1})
0
5
10
15
Nutrient
N
P
Oligochaetes
Chironomini
Chaoborus L
Glossiphonia
Zooplankton
Bezzia
Agabus A
Paedomorph Sal. (4+)
Agabus L
A. deflata
Hydroporinae L
N. hostilis
Gerris N
Ilybius A
Psidium
Corixid A
Salamander (3+)
Aeshna
Hydroporinae A
Hydrachnidia
L. externus
Salamander (2+)
Nephelopsis
Somatochlora
L. picturatus
Gerris A
Lestes and Coenagrionidae
Epibenthic Cladocera
Ostracoda
A. nigriculus
Salamander (1+)
Corixid N
Haliplidae A
Hydrophilidae A
Hydrophilidae L
Ilybius L
Vellidae A
B
Biomass
(kg pond^{-1})
0.0
0.5
1.0
1.5
Oligochaetes
Chironomini
Chaoborus L
Glossiphonia
Zooplankton
Bezzia
Agabus A
Paedomorph Sal. (4+)
Agabus L
A. deflata
Hydroporinae L
N. hostilis
Gerris N
Ilybius A
Psidium
Corixid A
Salamander (3+)
Aeshna
Hydroporinae A
Hydrachnidia
L. externus
Salamander (2+)
Nephelopsis
Somatochlora
L. picturatus
Gerris A
Lestes and Coenagrionidae
Epibenthic Cladocera
Ostracoda
A. nigriculus
Salamander (1+)
Corixid N
Haliplidae A
Hydrophilidae A
Hydrophilidae L
Ilybius L
Vellidae A
C
Excretion Rate
(ug N or P mg^{-1}d^{-1})
0
200
400
600
Nutrient
N
P
Oligochaetes
Chironomini
Chaoborus L
Glossiphonia
Zooplankton
Bezzia
Agabus A
Paedomorph Sal. (4+)
Agabus L
A. deflata
Hydroporinae L
N. hostilis
Gerris N
Ilybius A
Psidium
Corixid A
Salamander (3+)
Aeshna
Hydroporinae A
Hydrachnidia
L. externus
Salamander (2+)
Nephelopsis
Somatochlora
L. picturatus
Gerris A
Lestes and Coenagrionidae
Epibenthic Cladocera
Ostracoda
A. nigriculus
Salamander (1+)
Corixid N
Haliplidae A
Hydrophilidae A
Hydrophilidae L
Ilybius L
Vellidae A

◂**Figure 3.** Estimates of **A** mean taxon-specific contributions to whole-pond seasonal nutrient supply in a permanent pond, with each taxon's **B** biomass and **C** excretion rates from 100,000 simulation iterations. Bar or point height gives mean estimate and error bars are omitted because the simulation ran until mean supply estimates were stable and variance was low. Taxa sorted by rank-order contribution to N supply in each panel.

Predicting Taxon-Specific Nutrient Supply Estimates Across Hydroperiod Classifications

Along the hydroperiod gradient from temporary to permanent, the variation in taxon-specific contributions to supply ranged from one to five orders of magnitude (Figures3A, 4A, 5A). Taxonomic identity, population biomass, mass-specific excretion rate and larval development length were all included in linear models of taxon-specific N and P supply among the three hydroperiod classifications (S. Table 2). Relative to the selected models, reduced models with population biomass removed had the largest increases in AIC, indicating biomass was the strongest predictor of taxon-specific supply contributions among hydroperiods (S. Table 3).

Likewise, removal of population biomass caused the largest reductions in model R^2 relative to the selected models (S. Table 3), ranging from 2.7–5.6 × greater reductions in model R^2 than when N excretion rate or taxonomic identity was removed from the taxon-specific N supply model and 8 × greater than when taxonomic identity was removed from the taxon-specific P supply model.

Distributions of Taxon-Specific Nutrient Supply along a Hydroperiod Gradient

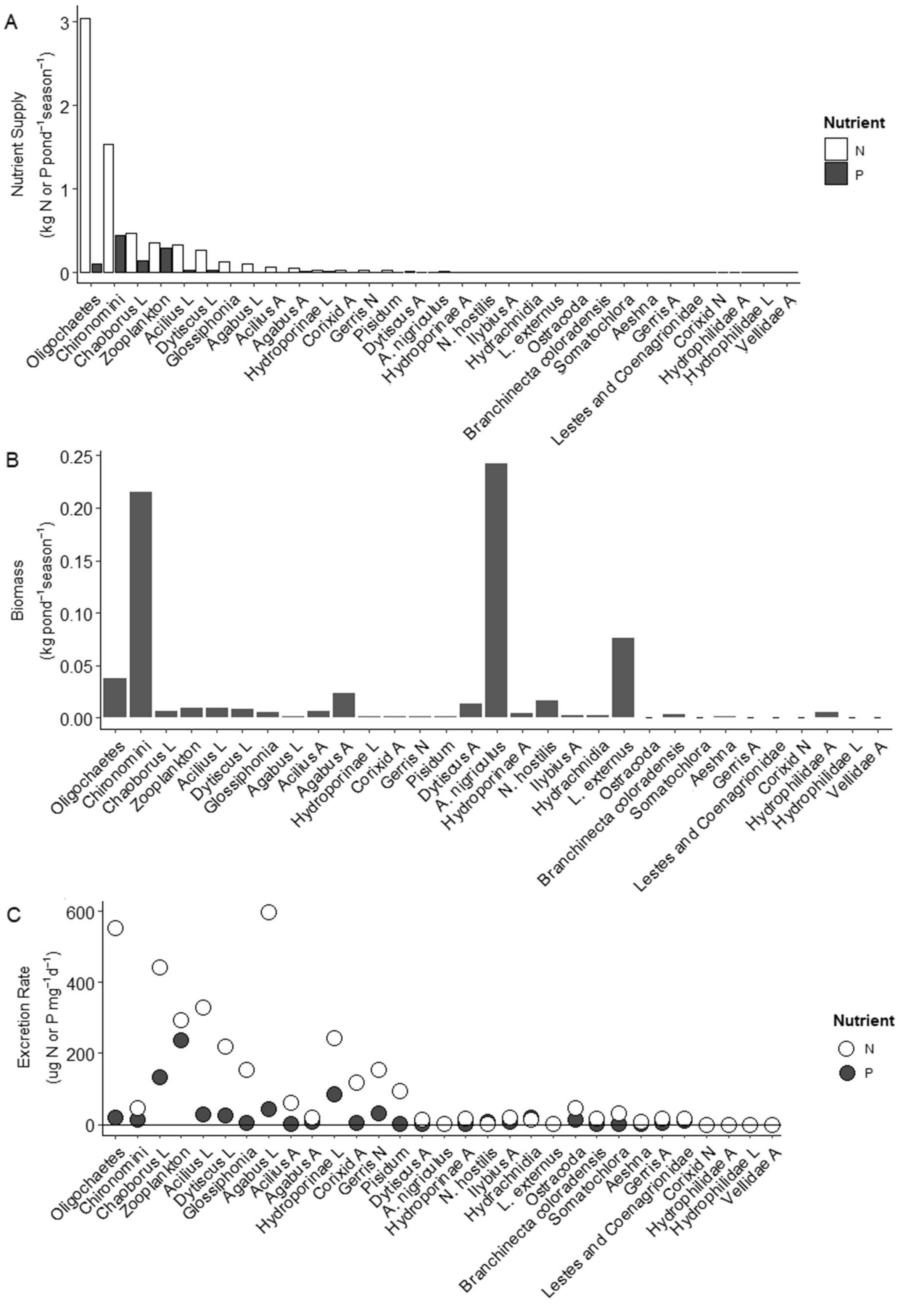
The distributions of rank-order taxon-specific supply within each hydroperiod revealed the extent to which functionally dominant taxa drive community-wide supply (Figures3A, 4A, 5A). Distributions of rank-order taxon-specific N supply differ between permanent and semi-permanent hydroperiods (KS Distance = 0.38, $p = 0.043$) and between semi-permanent and temporary (KS Distance = 0.52, $p = 0.039$). Distributions of rank-order taxon-specific P supply did not differ between permanent and semi-permanent hydroperiods (KS Distance = 0.31, $p = 0.191$) or between semi-permanent and temporary (KS Distance = 0.37, $p = 0.349$). However, distributions for rank-order taxon-specific N and P supply both differ between permanent and temporary hydroperiods (N: KS Distance = 0.74, $p < 0.001$; P: KS Distance = 0.62, $p < 0.001$). N and P supply was more evenly distributed among taxa in temporary (Skewness: N = 0.437, $P = 1.659$) than in permanent (Skewness: N = 3.24, $P = 4.40$) or semi-permanent hydroperiods (Skewness: N = 3.39, $P = 2.827$).

DISCUSSION

Community-Wide Nutrient Supply along a Hydroperiod Gradient

Here, we show that ponds with longer hydroperiods (that is, greater water availability) have larger animal-driven nutrient supply and greater demand. Specifically, whole-pond seasonal estimates demonstrate that cycling rates increase with pond size and hydroperiod duration; permanent pond cycling rates were 5–10 × greater than these of semi-permanent and temporary ponds. In turn, areal daily estimates demonstrate that the N surpluses and P supply relative to demand were similar between permanent and semi-permanent ponds. However, temporary ponds had large supply deficits for both nutrients. These differences in supply relative to demand among hydroperiods (permanent and semi-permanent vs temporary) are consistent with the absence of a dominant N and P supplier (oligochaetes) and a large reduction in the biomass of another (chironomids) in temporary ponds, rather than temporary pond taxa having overall lower excretion rates.

Although population-level biomass was the best predictor of supply across hydroperiod classifications, within a hydroperiod, variation in excretion rates and time spent in the pond mediated the role of animal biomass in driving supply and consequently taxonomic identity or functional traits improved supply predictions despite being less useful predictors across hydroperiods. For example, although salamanders had similar biomass to the invertebrate community in permanent ponds, they also had much lower excretion. Consequently, invertebrates supplied approximately 157 × more P and 74 × more N than salamanders. Finally, taxon-specific supply was distributed more evenly in temporary ponds, confirming that supply was dominated by a few key taxa in permanent ponds (oligochaetes and chironomids). This suggests that unexpected species losses are more likely to have a large impact on supply in temporary ponds if other taxa do not replace lost biomass. As permanent hydroperiods become increasingly temporary due to climate-driven declines in water availability (Lund and others 2016), our estimates suggest that


A
Nutrient Supply
(kg N or P pond^{-1}season^{-1})
0
1
2
3
Nutrient
N
P
Oligochaetes
Chironomini
Chaoborus L
Zooplankton
Acilius L
Dytiscus L
Glossiphonia
Agabus L
Acilius A
Agabus A
Hydroporinae L
Corixid A
Gerris N
Pisidum
Dytiscus A
A. nigriculus
Hydroporinae A
N. hostilis
Ilybius A
Hydrachnidia
L. externus
Ostracoda
Branchinecta coloradensis
Somatochlora
Aeshna
Gerris A
Lestes and Coenagrionidae
Corixid N
Hydrophilidae A
Hydrophilidae L
Vellidae A
B
Biomass
(kg pond^{-1}season^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
C
Excretion Rate
(ug N or P mg^{-1}d^{-1})
0
200
400
600
Nutrient
N
P

◀**Figure 4.** Estimates of **A** taxon-specific contributions to whole-pond seasonal nutrient supply in a semi-permanent pond, with each taxon's **B** biomass and **C** excretion rates from 100,000 simulation iterations. Bar or point height gives mean estimate and error bars are omitted because the simulation ran until mean supply estimates were stable and variance was low. Taxa sorted by rank-order contribution to N supply in each panel. Note: the different scales of the y-axes compared to Figure3.

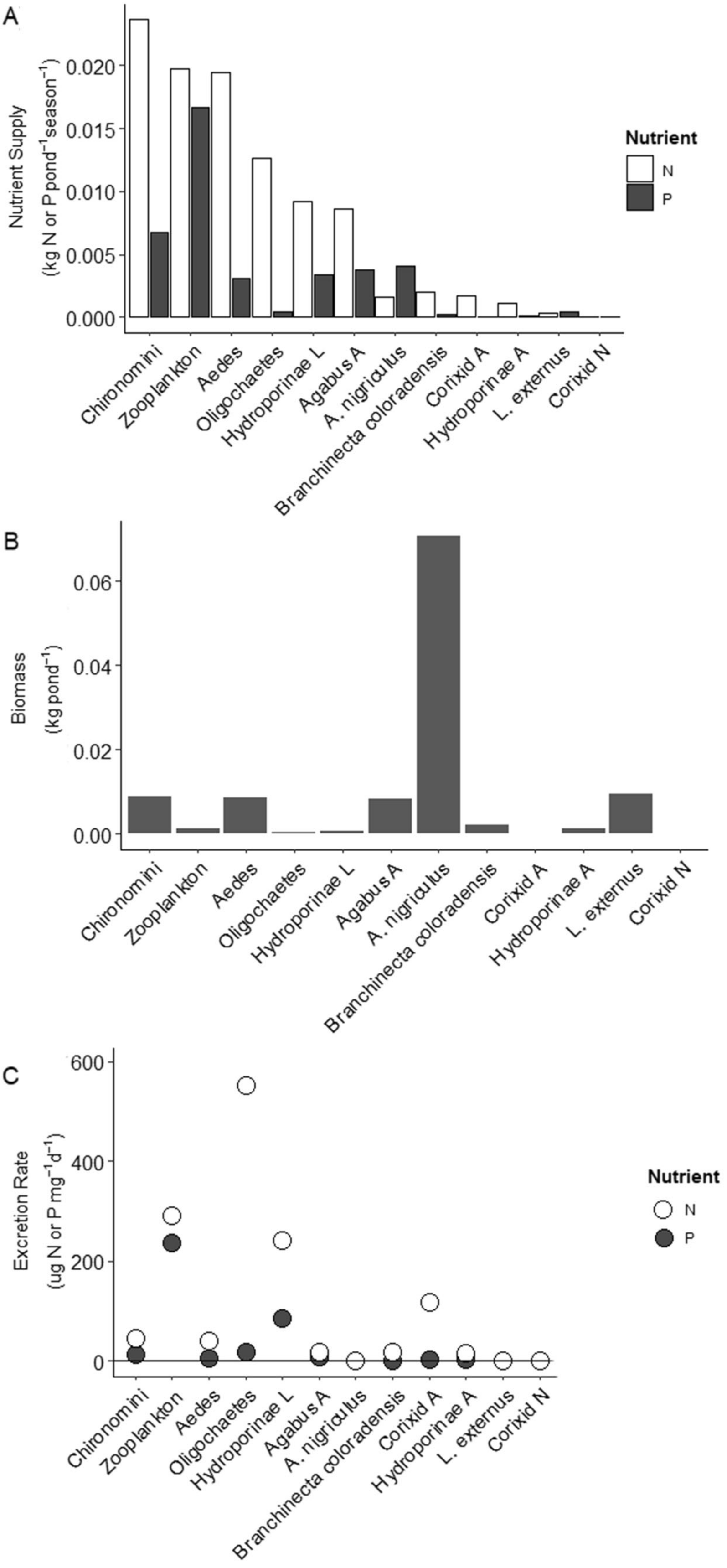
animal-driven supply will decrease relative to demand. Consequently, ponds with formerly permanent or semi-permanent hydroperiods and surplus or adequate nutrient supplies will become increasingly nutrient limited.

Biomass Predicts Supply Across Systems and Traits Provide Informative Context within a System

Consistent with our first and fourth predictions, population biomass was the best predictor of a taxon's contribution to community-wide supply. Consequently, supply increased along the hydroperiod gradient from temporary to permanent as community biomass increased. There is ample precedent that animal biomass is a powerful predictor of supply in lakes (Carpenter and others 1985; Schindler and Eby 1997), streams (McIntyre and others 2008; Benstead and others 2010) and marine systems (Allgeier and others 2017). Furthermore, because hydroperiod is functionally analogous to the amount or duration of water availability in terrestrial systems (Western 1975; Newman and others 2006), water availability could provide a generalizable framework for predicting biomass-driven animal effects on nutrient cycling and identifying systems where climate-induced changes in water availability could impact nutrient cycles.

However, within a given ecosystem (here, each hydroperiod classification), variation in functional traits such as mass-specific excretion rate can mediate the role of biomass as a driver of a taxon's contribution to supply. For example, a taxon with high biomass and slow excretion can contribute little to supply (for example, Figure4; paedomorphic and 3 + salamanders, *A. nigriculus, L. externus*), or a taxon with low biomass and fast excretion can make a large contribution (for example, Figure5; zooplankton). This interaction explains a result that conflicts with our fifth prediction regarding the importance of salamanders in permanent pond nutrient cycling. We expected that salamanders would dominate permanent pond supply because of their high biomass, which on average is half of the entire invertebrate community (mean = 2.1 kg salamanders vs mean = 4.2 kg invertebrates). However, estimates of salamander N and P supplies were less than 1.5% of invertebrate supply. This is surprising because vertebrates are often assumed to contribute large fluxes due to their biomass dominance and because they tend to have higher mass-specific excretion relative to invertebrates (Vanni and McIntyre 2016). Nonetheless, low salamander excretion rates are consistent with several aspects of their natural history at the Mexican Cut. Specifically, adult salamander growth rates are low, and larval development is protracted relative to lower elevations due to short growing seasons (for example, 3 months) and cold water temperatures that slow metabolisms and reduce activity (Whiteman and others 2012). Thus, coupled with their long lifespans (15 + years), salamanders at the Mexican Cut are likely a nutrient sink. Although vertebrate and invertebrate supply contributions are not often directly compared (Carpenter and others 1992; Attayde and Hansson 1999; Devine and Vanni 2002), there is some precedent for invertebrates providing larger contributions than vertebrates even when their population biomasses are similar (Atkinson and others 2019). Here, salamanders provide an example of how the interaction between high population biomass and low excretion produces a comparatively low supply contribution that would be greatly overestimated from biomass alone.

The taxon-specific nutrient supply contributions made by other biomass-dominant taxa provide further insight to the importance of the interaction between biomass and excretion. In permanent ponds, biomass-dominant chironomids supply 35% of community-wide N and 55% of P supply. This adheres to the mass-ratio hypothesis from the plant productivity literature, which predicts that overall ecosystem processing or functioning is determined by a dominant taxon's functional trait (Grime 1998). However, this is not always the case, as demonstrated by taxon-specific supply estimates in temporary ponds. Here, biomass dominant *A. nigriculus* contributes only 2% and 10% of community-wide N and P supply. In contrast, zooplankton, which have 57-fold less biomass than *A. nigriculus* in temporary ponds, contributes 20% and 43% of N and P supply owing to their comparatively higher excretion. Thus, predictions generated using the mass-ratio hypothesis are often useful, and however, variation in a key functional trait


A
Nutrient Supply
(kg N or P pond^{-1}season^{-1})
0.000
0.005
0.010
0.015
0.020
Nutrient
N
P
Chironomini
Zooplankton
Aedes
Oligochaetes
Hydroporinae L
Agabus A
A. nigriculus
Branchinecta coloradensis
Corixid A
Hydroporinae A
L. externus
Corixid N
B
Biomass
(kg pond^{-1})
0.00
0.02
0.04
0.06
Chironomini
Zooplankton
Aedes
Oligochaetes
Hydroporinae L
Agabus A
A. nigriculus
Branchinecta coloradensis
Corixid A
Hydroporinae A
L. externus
Corixid N
C
Excretion Rate
(ug N or P mg^{-1}d^{-1})
0
200
400
600
Nutrient
N
P
Chironomini
Zooplankton
Aedes
Oligochaetes
Hydroporinae L
Agabus A
A. nigriculus
Branchinecta coloradensis
Corixid A
Hydroporinae A
L. externus
Corixid N

◀**Figure 5.** Estimates of **A** taxon-specific contributions to whole-pond seasonal nutrient supply in a temporary pond, with each taxon's **B** biomass and **C** excretion rates from 100,000 simulation iterations. Bar or point height gives mean estimate and error bars are omitted because the simulation ran until mean supply estimates were stable and variance was low. Taxa sorted by rank-order contribution to N supply in each panel. Note: the different scales of the y-axes compared to Figure3.

(here, nutrient excretion) among taxa can ameliorate the importance of biomass dominance. Furthermore, among communities with low richness (for example, temporary ponds with one-third as many taxa), dissimilarity in a key functional trait is likely more informative than species number for predicting each community's functional contributions (Heemsbergen and others 2004).

In addition to functional traits like nutrient excretion, taxonomic identity and natural history provide valuable context for interpreting estimated contributions. For example, oligochaetes and chironomids drive large proportions of N supply in permanent and semi-permanent hydroperiods (35% and 23%). These taxa live in pond sediments, where their excreta likely enrich sediments and are subsequently buried, bound or gradually released (Devine and Vanni 2002; Hölker and others 2015; Herren and others 2017). This may reconcile the estimated N surplus with ambient water chemistry, as ponds in and near the Mexican Cut are considered oligotrophic (Wissinger and others 1999a; Elser and others 2009) with water column NH_4-N of 2.4 ± 0.17 ug/L and NO_3-N of 67.8 ± 4.8 ug/L (mean ± SE) over the summer across all hydroperiod classifications. Likewise, chironomid and oligochaetes cumulatively contribute 62% and 47% of P supply in permanent and semi-permanent ponds. This large proportion of P supply entering the system slowly via bioturbation-driven sediment release (Hölker and others 2015) or binding to iron near the sediment–water interface under well-mixed aerobic conditions (B.W. Taylor unpub.) is also consistent with low water column SRP concentrations averaging 2.2 ± 0.4 ug/L over the summer across all hydroperiods and could contribute to P limitation previously measured in and around the Mexican Cut (Elser and others 2009). Indeed, a greater relative demand for P was apparent in both empirical and simulation estimates, as molar N:P of community-wide supply was greater than demand N:P in all hydroperiod classifications.

Differences in chironomid and oligochaete abundance among hydroperiod classifications also explain the transition from N surplus in permanent and semi-permanent hydroperiods to a deficit in temporary hydroperiods. First, oligochaetes supplied the most N in permanent and semi-permanent ponds but are not present in temporary ponds. Second, chironomids in temporary ponds only attain 0.7% and 5% of their biomass in permanent and semi-permanent ponds, limiting their ability to contribute large amounts of nutrients. Although the ability of animal communities to contribute to nutrient cycling is well-recognized (Vanni 2002), there are few examples of systems where one taxon dominates supply (but see Hall and others 2003; McIntyre and others 2008; Small and others 2011). Together with previous work quantifying their nutrient fluxes (Tatrai 1986; Devine and Vanni 2002; Hölker and others 2015), this switch from N surplus to deficit along the hydroperiod gradient suggests that oligochaetes and chironomids could fulfill essential roles in driving ecosystem-level N supply.

Climate Change and Animal-Driven Nutrient Supply in High-Elevation Ponds

Climate warming and associated changes in precipitation are causing hydroperiods of high-elevation wetlands to become increasingly temporary (Lee and others 2015; Lund and others 2016). Here, as ponds shift from permanent to temporary, they shift from an N supply surplus to a deficit and from sufficient P supply to a deficit. This occurs because hydroperiod directly controls community composition. Consistent with increasing species evenness from permanent to temporary ponds (Wissinger and others 1999a), N and P supply are dominated by few taxa in permanent and semi-permanent ponds and are distributed more evenly in temporary ponds. Thus, if compositional changes result in reduced abundance of dominant taxa there could be large effects on community-wide supply as ponds transition toward temporary. Additionally, even though salamanders directly contribute very little to supply, their role in structuring the invertebrate community in permanent ponds (Wissinger and others 1999a) is similar to that of fish in mountain lakes (Schindler and others 2001) and could have large indirect effects on animal-driven supply that could be lost when historically permanent ponds begin to dry.

Here, our estimates suggest that as climate warming reduces water availability and causes biomass declines and compositional shifts in animal communities, nutrient limitation may arise due to loss of animal-driven supply. Furthermore, the framework of water availability determining animal biomass distribution and contributions to nutrient cycles across the landscape could be generalizable to other systems, allowing us to predict how climate-driven shifts in water availability could alter nutrient cycles. For example, droughts may reduce ungulate contributions to grassland nutrient cycles by reducing populations and altering dispersal (Augustine and McNaughton 2007). These effects could even cross ecosystem boundaries, as wildebeest mass drownings at river crossings provide substantial energetic and nutrient subsidies to aquatic systems but do not commonly occur during low water (Subalusky and others 2017). Likewise, droughts could disrupt nutrients transported by migratory taxa such as salmon or waterfowl (Greer and others 2007; Isaak and others 2007).

Furthermore, climate-driven changes in water availability are already commonly linked to other ecosystem functions, particularly primary productivity. For example, changing water availability will impact primary productivity in agricultural systems, forests and grasslands (Fay and others 2008; Rosenzweig and others 2014). In many of these studies, potential for consequent changes in energy and material flow is acknowledged but not quantified. Identifying systems where water availability is linked to animal-driven nutrient cycling could provide additional rationale for protecting species or water availability in systems threatened by climate change. Thus, there is precedent for using water availability to predict primary productivity and associated functions, but the potential of this currency for anticipating changes in animal-driven N and P cycling remains underutilized.

ACKNOWLEDGEMENTS

We thank the Rocky Mountain Biological Laboratory for logistic support and The Nature Conservancy for access to the Mexican Cut Nature Preserve. We thank Austyn Long for assistance sampling sedge and Kevin Gross for helpful discussions on the simulation. Comments from Chelsea Little, Bobbi Peckarsky and four anonymous reviewers greatly improved the manuscript. Balik was supported by an NSF Graduate Research Fellowship, a Southeast Climate Adaptation Science Center Global Change Fellowship, a Colorado Mountain Club Foundation Al Ossinger Fellowship and a RMBL Graduate Fellowship from the Snyder Endowment. Wissinger was funded by NSF DEB 1557015. Whiteman was funded by NSF DEB 1354787. Jameson was funded by NSF REU supplement 1819108 to Taylor. Additional funding was provided by NSF DEB 1556914, REU supplement 1721812 and North Carolina State University.

Declarations

Conflict of interest The authors declare no conflicts of interest.

REFERENCES

Akaike H, Parzen E, Tanabe K, Kitagawa G. 1998. Selected papers of Hirotugu Akaike. Springer Science & Business Media.

Allgeier JE, Burkepile DE, Layman CA. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Glob Chang Biol 23:2166–2178.

Atkinson CL, Alexiades AV, MacNeill KL, Encalada AC, Thomas SA, Flecker AS. 2019. Nutrient recycling by insect and fish communities in high-elevation tropical streams. Hydrobiologia 838:13–28.

Atkinson CL, Capps KA, Rugenski AT, Vanni MJ. 2017. Consumer-driven nutrient dynamics in freshwater ecosystems: from individuals to ecosystems. Biol Rev Camb Philos Soc 92:2003–2023.

Attayde JL, Hansson L-A. 1999. Effects of nutrient recycling by zooplankton and fish on phytoplankton communities. Oecologia 121:47–54.

Augustine DJ, McNaughton SJ. 2007. Interactive Effects of Ungulate Herbivores, Soil Fertility and Variable Rainfall on Ecosystem Processes in a Semi-arid Savanna. Ecosystems 9:1242–1256.

Babler AL, Solomon CT, Schilke PR. 2008. Depth-specific patterns of benthic secondary production in an oligotrophic lake. Journal of the North American Benthological Society 27:108–119.

Balik JA, Taylor BW, Washko SE, Wissinger SA. 2018. High interspecific variation in nutrient excretion within a guild of closely related caddisfly species. Ecosphere 9.

Benstead JP, Cross WF, March JG, McDowell WH, RamÍRez A, Covich AP. 2010. Biotic and abiotic controls on the ecosystem significance of consumer excretion in two contrasting tropical streams. Freshwater Biology 55:2047–2061.

Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Carpenter SR, Kraft CE, Wright R, He X, Soranno PA, Hodgson JR. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. The American Naturalist 140:781–798.

Chase JM. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences 104:17430–17434.

DelVecchia AG, Balik JA, Campbell SK, Taylor BW, West DC, Wissinger SA. 2019. Carbon Dioxide Concentrations and Efflux from Permanent, Semi-Permanent and Temporary Subalpine Ponds. Wetlands 39:955–969.

Devine JA, Vanni MJ. 2002. Spatial and seasonal variation in nutrient excretion by benthic invertebrates in a eutrophic reservoir. Freshwater Biology 47:1107–1121.

Dodson SI. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605–613.

Dodson VE. 1975. The distribution and habitat separation of three corixids (Hemiptera: Heteroptera) in western Colorado. Freshwater Biology 5:141–150.

Elser JJ, Acharya K, Kyle M, Cotner J, Makino W, Markow T, Watts T, Hobbie S, Fagan W, Schade J. 2003. Growth rate–stoichiometry couplings in diverse biota. Ecology Letters 6:936–943.

Elser JJ, Dobberfuhl DR, MacKay NA, Schampel JH. 1996. Organism size, life history and N: P stoichiometry: toward a unified view of cellular and ecosystem processes. BioScience 46:674–684.

Elser JJ, Elser MM, MacKay NA, Carpenter SR. 1988. Zooplankton-mediated transitions between N-and P-limited algal growth. Limnology and Oceanography 33:1–14.

Elser JJ, Kyle M, Steger L, Nydick KR, Baron JS. 2009. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. Ecology 90:3062–3073.

Fay PA, Kaufman DM, Nippert JB, Carlisle JD, Harper CW. 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Global Change Biology 14:1600–1608.

Greer AK, Dugger BD, Graber DA, Petrie MJ. 2007. The effects of seasonal flooding on seed availability for spring migrating waterfowl. The Journal of Wildlife Management 71:1561–1566.

Greig HS, Wissinger SA. 2010. Reinforcing abiotic and biotic time constraints facilitate the broad distribution of a generalist with fixed traits. Ecology 91:836–846.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Hairston NA, Hairston NG. 1987. Community ecology and salamander guilds: Cambridge University Press.

Hall RO Jr, Tank JL, Dybdahl MF. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1:407–411.

Heemsbergen DA, Berg MP, Loreau M, Van Hal JR, Faber JH, Verhoef HA. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306:1019–1020.

Herren CM, Webert KC, Drake MD, Jake Vander Zanden M, Einarsson Á, Ives AR, Gratton C. 2017. Positive feedback between chironomids and algae creates net mutualism between benthic primary consumers and producers. Ecology 98:447–455.

Hölker F, Vanni MJ, Kuiper JJ, Meile C, Grossart H-P, Stief P, Adrian R, Lorke A, Dellwig O, Brand A. 2015. Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems. Ecological Monographs 85:333–351.

Isaak DJ, Thurow RF, Rieman BE, Dunham JB. 2007. Chinook salmon use of spawning patches: relative roles of habitat quality, size and connectivity. Ecological Applications 17:352–364.

Lee SY, Ryan ME, Hamlet AF, Palen WJ, Lawler JJ, Halabisky M. 2015. Projecting the Hydrologic Impacts of Climate Change on Montane Wetlands. PLoS One 10: e0136385.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Lund JO, Wissinger SA, Peckarsky BL. 2016. Caddisfly behavioral responses to drying cues in temporary ponds: implications for effects of climate change. Freshwater Science 35:619–630.

McIntyre PB, Flecker AS, Vanni MJ, Hood JM, Taylor BW, Thomas SA. 2008. Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. Ecology 89:2335–2346.

Meyer D, Dimitriadou E, Hornik K, Weingessel A, Leisch F. 2019. e1071: Misc Functions of the Department of Statistics, Probability Theory Group, TU Wien.

Moore MP, Whiteman HH. 2016. Natal philopatry varies with larval condition in salamanders. Behavioral Ecology and Sociobiology 70:1247–1255.

Newman BD, Wilcox BP, Archer SR, Breshears DD, Dahm CN, Duffy CJ, McDowell NG, Phillips FM, Scanlon BR, Vivoni ER. 2006. Ecohydrology of water-limited environments: A scientific vision. Water Resources Research 42.

O'Brien JM, Dodds WK. 2007. Ammonium uptake and mineralization in prairie streams: chamber incubation and short-term nutrient addition experiments. Freshwater Biology 0: 071026235033002-???

Ostrofsky ML, Rigler FH. 1987. Chlorophyll–phosphorus relationships for subarctic lakes in western Canada. Canadian Journal of Fisheries and Aquatic Sciences 44:775–781.

Pinhero J, Bates D, DebRoy S, Core Team R. 2019. nlme: Linear and Nonlinear Mixed Effects Models.

Rosenzweig C, Elliott J, Deryng D, Ruane AC, Müller C, Arneth A, Boote KJ, Folberth C, Glotter M, Khabarov N. 2014. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. Proceedings of the National Academy of Sciences 111:3268–3273.

Schindler DE, Eby LA. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. Ecology 78:1816–1831.

Schindler DE, Knapp RA, Leavitt PR. 2001. Alteration of Nutrient Cycles and Algal Production Resulting from Fish Introductions intoMountain Lakes. Ecosystems 4:308–321.

Schneider DW. 1999. Snowmelt ponds in Wisconsin: influence of hydroperiod on invertebrate community structure. Invertebrates in freshwater wetlands of North America: Ecology and management: Wiley, p299–318.

Schneider DW, Frost TM. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15:64–86.

Small GE, Pringle CM, Pyron M, Duff JH. 2011. Role of the fish Astyanax aeneus (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. Ecology 92:386–397.

Stanley EH, Ward AK. 1997. Inorganic nitrogen regimes in an Alabama wetland. Journal of the North American Benthological Society 16:820–832.

Stoks R, McPeek MA. 2003. Predators and life histories shape Lestes damselfly assemblages along a freshwater habitat gradient. Ecology 84:1576–1587.

Subalusky AL, Dutton CL, Rosi EJ, Post DM. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. Proc Natl Acad Sci U S A 114:7647–7652.

Tatrai I. 1986. Rates of ammonia release from sediments by chironomid larvae. Freshwater Biology 16:61–66.

Taylor BW, Keep CF, Hall RO Jr, Koch BJ, Tronstad LM, Flecker AS, Ulseth AJ. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence and standard additions. Journal of the North American Benthological Society 26:167–177.

Vanni MJ. 2002. Nutrient Cycling by Animals in Freshwater Ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Vanni MJ, McIntyre PB. 2016. A global database of nitrogen and phosphorus excretion rates of aquatic animals. Ecology 98:1475.

Wellborn GA, Skelly DK, Werner EE. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Western D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. African Journal of Ecology 13:265–286.

Whiles MR, Huryn AD, Taylor BW, Reeve JD. 2009. Influence of handling stress and fasting on estimates of ammonium excretion by tadpoles and fish: recommendations for designing excretion experiments. Limnology and Oceanography: Methods 7:1–7.

Whiteman HH, Wissinger SA, Denoël M, Mecklin CJ, Gerlanc NM, Gutrich JJ. 2012. Larval growth in polyphenic salamanders: making the best of a bad lot. Oecologia 168:109–118.

Wiggins GB, Gb W, Rj M, Im S. 1980. Evolutionary and ecological strategies of animals in annual temporary pools.

Wissinger SA, Bohonak AJ, Whiteman HH, Brown WS. 1999a. Subalpine wetlands in Colorado: habitat permanence, salamander predation and invertebrate communities. Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York: 757–790.

Wissinger SA, Oertli B, Rosset V. 2016. Invertebrate Communities of Alpine Ponds. Invertebrates in Freshwater Wetlands, p55–103.

Wissinger SA, Whissel JC, Eldermire C, Brown WS. 2006. Predator defense along a permanence gradient: roles of case structure, behavior and developmental phenology in caddisflies. Oecologia 147:667–678.

Wissinger SA, Whiteman HH, Sparks GB, Rouse GL, Brown WS. 1999b. Foraging trade-offs along a predator–permanence gradient in subalpine wetlands. Ecology 80:2102–2116.