



RESEARCH ARTICLE

Experimental N and P additions relieve stoichiometric constraints on organic matter flows through five stream food webs

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Handling Editor: Natalie Clay**Abstract**

1. Human activities have dramatically altered global patterns of nitrogen (N) and phosphorus (P) availability. This pervasive nutrient pollution is changing basal resource quality in food webs, thereby affecting rates of biological productivity and the pathways of energy and material flow to higher trophic levels.
2. Here, we investigate how the stoichiometric quality of basal resources modulates patterns of material flow through food webs by characterizing the effects of experimental N and P enrichment on the trophic basis of macroinvertebrate production and flows of dominant food resources to consumers in five detritus-based stream food webs.
3. After a pre-treatment year, each stream received N and P at different concentrations for 2 years, resulting in a unique dissolved N:P ratio (target range from 128:1 to 2:1) for each stream. We combined estimates of secondary production and gut contents analysis to calculate rates of material flow from basal resources to macroinvertebrate consumers in all five streams, during all 3 years of study.
4. Nutrient enrichment resulted in a 1.5× increase in basal resource flows to primary consumers, with the greatest increases from biofilms and wood. Flows of most basal resources were negatively related to resource C:P, indicating widespread P limitation in these detritus-based food webs. Nutrient enrichment resulted in a greater proportion of leaf litter, the dominant resource flow-pathway, being consumed by macroinvertebrates, with that proportion increasing with decreasing leaf litter C:P. However, the increase in efficiency with which basal resources were channelled into metazoan food webs was not propagated to macroinvertebrate predators, as flows of prey did not systematically increase following enrichment and were unrelated to basal resource flows.
5. This study suggests that ongoing global increases in N and P supply will increase organic matter flows to metazoan food webs in detritus-based ecosystems by reducing stoichiometric constraints at basal trophic levels. However, the extent to which those flows are propagated to the highest trophic levels likely depends on responses of individual prey taxa and their relative susceptibility to predation.

KEYWORDS

detritus, ecological stoichiometry, food webs, nitrogen, nutrient pollution, phosphorus, secondary production, streams

1 | INTRODUCTION

Human activities have altered the physical and chemical properties of ecosystems world-wide, with numerous consequences for ecosystem structure and function (Cramer et al., 2001; Elser et al., 2007; Halpern et al., 2008). Shifts in nitrogen (N) and phosphorus (P) availability are important due to the roles these elements play in limiting biological productivity in terrestrial (LeBauer & Treseder, 2008) and aquatic habitats (Elser et al., 2007). Although increased N and P availability often stimulates activity at the base of food webs, the extent to which those changes alter food web properties at higher trophic levels is less predictable and likely mediated by the effect of nutrient concentrations on the composition, quantity and quality of basal resource pools (Boersma et al., 2008; Cebrian, 2004; Cebrian et al., 2009). Such nutrient-induced changes to basal resources have been shown to alter the taxonomic composition (Demi, Benstead, Rosemond, & Maerz, 2019; Evans-White, Dodds, Huggins, & Baker, 2009; Moe et al., 2005), productivity (Cross, Wallace, Rosemond, & Eggert, 2006; Ott et al., 2014) and trophic structure of consumer communities (Davis, Rosemond, Eggert, Cross, & Wallace, 2010a; Worm, Lotze, & Sommer, 2000). Understanding how basal resource pools respond to variation in nutrient supply, particularly the relative availability of N and P (i.e. N:P ratios), is a major challenge in predicting the effect of nutrient enrichment on food web dynamics (Elser et al., 2000).

Flows of basal resources to consumers are likely mediated by both resource quality and quantity, which may respond differently to altered nutrient availability (Cebrian et al., 2009). For example, stoichiometric quality of basal resources, expressed as the ratio of carbon (C) to N and P (C:N:P) relative to consumer requirements, typically increases as a result of nutrient enrichment in both detritus-based and autotroph-based food webs (Bracken et al., 2015; Cross, Benstead, Rosemond, & Wallace, 2003; Singer & Battin, 2007). However, nutrient enrichment typically increases autotroph standing stocks (Elser et al., 2007; LeBauer & Treseder, 2008), but reduces detrital standing stocks due to nutrient-stimulated microbial decomposition (Ferreira et al., 2014; Sistla & Schimel, 2012). As such, predicting how flows of individual resources will respond to altered nutrient availability requires consideration of (a) the quantity of available food resources, (b) the relative change in nutrient content of those resources driven by the dominant microbial composition of resources (i.e. algal, bacterial or fungal), and (c) consumer stoichiometric demand relative to supply.

Ecological stoichiometry theory (hereafter EST; Sterner & Elser, 2002) provides a key framework for making such predictions by applying an elemental mass-balance approach to biological interactions at scales ranging from molecular to ecosystem-level. However, ecosystem-level manipulations of N and P supply ratios that would facilitate tests of EST across multiple organizational levels are currently lacking, particularly in detritus-based ecosystems. In this paper, we investigate the effects of variation in N:P supply ratio on consumer-mediated organic matter dynamics in five detritus-based streams that were continuously enriched with N and P for 2 years. Each stream received N and P at different concentrations, resulting in a unique dissolved N:P ratio (target range from 2:1 to 128:1) for each stream. The streams were studied for 1 year prior to enrichment, allowing us to examine the

potential for increased nutrient availability to alter consumer-resource dynamics. Our large-scale experiment in detritus-dominated systems provides a novel test of the effects of nutrient availability on patterns of energy flow from basal resources to consumers, which is critical to our understanding of ecosystem responses to altered N and P supply.

We expected an increase in total material flows to primary consumers following enrichment given that higher rates of annual secondary production during the 2 years of enrichment have been previously reported for the study streams (Demi, Benstead, Rosemond, & Maerz, 2018). We predicted that the response of individual resource flows would vary in proportion to the stoichiometric disparities between the various resource pools and consumer requirements (Frainer et al., 2015; Hladyz, Gessner, Giller, Pozo, & Woodward, 2009). Specifically, we predicted the greatest response for flows of leaf detritus and wood because consumers of leaves and wood suffer characteristically large imbalances between elemental supply and demand ratios relative to other common resources (Cross et al., 2003; Evans-White, Stelzer, & Lamberti, 2005; Lauridsen et al., 2012). As such, we predicted that increased flows would largely be channelled through leaf-shredding macroinvertebrates rather than other primary consumer functional groups, such as biofilm scrapers and fine-particle collectors (i.e. collector-gatherers), which are less stoichiometrically imbalanced with their preferred resources (Cross et al., 2003; Lauridsen et al., 2012). Additionally, we expected that flows of fine particulate organic matter (<1 mm, hereafter FPOM), and thereby material flows to collector-gatherers, would experience the smallest response to nutrient enrichment given that FPOM stoichiometry is less responsive to nutrient enrichment than other resources (Tant, Rosemond, & First, 2013) and tends to be more stoichiometrically balanced with consumer requirements than other resources (Cross et al., 2003; Lauridsen et al., 2014).

We further predicted that total organic matter flows to primary consumers, which are largely driven by patterns of secondary production, would be positively related to the flow of animal prey to macroinvertebrate predators, providing evidence that the effects of nutrient-induced shifts in basal resource stoichiometry propagate upward to multiple trophic levels (Boersma et al., 2008). Lastly, we compared leaf litter consumption by the macroinvertebrate community to reach-scale leaf litter mass loss rates (Rosemond et al., 2015) to test the hypothesis that consumption of leaf detritus by macroinvertebrates is an important driver of reach-scale organic matter dynamics. Furthermore, we predicted that nutrient-induced shifts in leaf litter C:P would drive increases in the proportion of total leaf litter mass loss via macroinvertebrate consumption (Cebrian, 2004).

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental nutrient additions

Five headwater streams located within the Dryman Fork watershed at the Coweeta Hydrologic Laboratory (CHL; Macon County, North Carolina, USA) were selected for N and P enrichment. The streams

drained adjacent watersheds situated along the same hillside and shared similar physical characteristics (elevation, slope, aspect and temperature) and ambient water chemistry (dissolved inorganic N: 18–189 $\mu\text{g/L}$; soluble reactive P: 2.5–3.1 $\mu\text{g/L}$). Forest vegetation at the CHL consists primarily of mixed hardwood species (oak, maple and poplar) with a dense understorey of *Rhododendron maximum*, which provides year-round shading of headwater streams. As such, CHL streams are strongly heterotrophic, with >90% of secondary production derived from terrestrial detritus (Cross, Wallace, & Rosemond, 2007; Hall, Wallace, & Eggert, 2000).

Nutrient addition and sample collection were constrained to 70-m experimental reaches within each stream. Sampling began during July 2010 and continued at monthly intervals until June 2013. Whole-reach, continuous N and P enrichment began in July 2011, following 1 year of pre-enrichment monitoring, and continued through July 2013. Aqueous N (21% ammonium nitrate) and P (85% phosphoric acid) were continuously added to each stream at different concentrations, where the highest N concentration (dissolved inorganic N [DIN] target range: 81–650 $\mu\text{g/L}$) was paired with the lowest P concentration (and vice versa; soluble reactive P [SRP] target range: 90–11 $\mu\text{g/L}$), thus creating a gradient in dissolved N:P ratio (target molar N:P ratios: 2:1, 8:1, 16:1, 32:1, 128:1; see Bumpers, Maerz, Rosemond, & Benstead, 2015 for a detailed description of the nutrient addition apparatus and the target and measured N and P concentrations). Briefly, N and P were added to each stream via a discharge-proportional delivery system in which metering pumps, calibrated to estimates of instantaneous discharge, delivered the nutrient mixture to gravity-fed irrigation lines. Drip spouts were installed approximately every 5 m to ensure uniform delivery throughout the 70-m experimental reaches.

2.2 | Trophic basis of production and organic matter flows

We used the trophic basis of production approach (Benke & Wallace, 1980, 1997) to calculate material flows from basal resources to macroinvertebrate consumers in all five streams during the 2 years of nutrient enrichment (YR1 = July 2011–June 2013; YR2 = July 2012–June 2013) and during 1 year prior to nutrient enrichment (PRE = July 2010–June 2011). We constrained our analysis to the 20 most productive taxa (including primary consumers and predators) in each stream during each year, which accounted for $\geq 90\%$ of total annual macroinvertebrate production for any given stream or year. Annual secondary production was estimated from benthic core samples collected monthly from July 2010 to June 2013. Detailed protocols and methods of estimating secondary production are described in Demi et al. (2018). A list of the 20 taxa used for each stream during each year, along with secondary production estimates for each taxon can be found in Appendix S1, Table S1.

Estimating the trophic basis of production requires quantifying the relative proportion of different food resources in consumer diets combined with knowledge of bioenergetic efficiencies (i.e. assimilation and production efficiencies) of each food type (Benke & Wallace, 1980).

For primary consumer taxa, gut contents were analysed from five individuals of each taxon from each stream during the pre-enrichment year, and during one of the enrichment years (typically YR2). We assumed that consumer diets were similar during YR1 and YR2 of enrichment based on results from a similar fertilization of a CHL stream (Cross et al., 2007). Individuals used for gut contents analysis were typically collected from each stream during late April of each year of the study and preserved in Kahle's solution (Stehr, 1987) until processing. We acknowledge that this approach does not account for potential seasonal differences in consumer diets. However, seasonal diet shifts have been shown to be negligible among Coweeta's stream invertebrate taxa (Cross et al., 2007). When an insufficient number of individuals (i.e. fewer than five) for a given taxon were collected during an April sampling trip, additional individuals were retrieved from monthly benthic samples to achieve a minimum number of five individuals for gut contents analysis. In several instances, we were unable to collect enough individuals to perform gut analysis for some taxa in a given stream. In such cases we used the average diet of that taxon (from a minimum of five individuals), or for a closely related taxon from the other four streams during the same year. Predator diets were assumed to be composed entirely of animal prey, as reported by Cross et al. (2007) for another CHL stream, and thus were not analysed.

Processing of gut contents was based upon Cross et al. (2007). Briefly, gut contents were removed from individual consumers under $\geq 10\times$ magnification into distilled water, transferred to a 60-ml syringe, sonicated for ~ 60 s and filtered onto a 0.45- μm cellulose membrane filter (Millipore). Filters were then placed on glass microscope slides, air-dried, cleared with immersion oil and topped with a glass coverslip. Quantification of diets was done under $400\times$ magnification on a compound microscope equipped with a digital camera. We estimated proportional contribution of each food type by measuring the area of approximately 50 food particles from each slide using ImageJ (Schneider, Rasband, & Eliceiri, 2012). Food particles were identified as one of the following six dominant food types: leaf detritus, wood, diatoms, fungi, amorphous detritus and animals. Diatoms were the only major algal group observed in guts. Bacteria are assumed to dominate microbial biomass on amorphous detritus (Hall & Meyer, 1998; Tant et al., 2013). As such, we assumed that production attributed to amorphous detritus was largely supported by assimilation of bacteria and bacterial exopolymers (Cross et al., 2007). A summary of consumer gut contents analysis for all primary consumer taxa is presented in Table S2 of Appendix S1.

Assimilation efficiencies of the dominant food types were based on literature values (Benke & Wallace, 1980, 1997; Cross et al., 2007) with a value of 10% being used for amorphous detritus, 30% for diatoms, 70% for fungi and 80% for animal tissue. Because fungal hyphae embedded within leaf detritus and wood are difficult to quantify microscopically, we estimated the contribution of fungi to consumers, via consumption of leaves and wood, by multiplying the total area of leaf detritus and wood in the guts by the percent fungal biomass in each of these substrates, averaged across each year in each stream (V. Gulis, unpubl. data). As such, we used an assimilation efficiency of 5% for leaf detritus and wood rather than the common

value of 10%, as the latter value does not distinguish between production derived from the substrate and the associated fungal hyphae (Cross et al., 2007).

Nutrient enrichment has the potential to alter consumer assimilation efficiencies via shifts in resource elemental composition (Halvorson, Sperfield, & Evans-White, 2017; Pandian & Marian, 1986; Urabe, Shimizu, & Yamaguchi, 2018), thereby altering patterns of material consumption and flows. Given that experimental whole-stream N and P additions altered the C:N:P stoichiometry of basal resources in our study systems (Demi et al., 2018), we acknowledge that any resulting shifts in consumer assimilation efficiencies have the potential to change the results and interpretation of our material flow calculations. To assess this potential, and to compare the relative effects of realistic shifts in consumer assimilation efficiency to those of uncertainty around secondary production estimates (based on bootstrapped 95% CIs) on material flow calculations, we conducted a sensitivity analysis whereby each of these parameters was systematically varied in isolation to assess its impact on material flow calculations (Appendix S2). Based in part on the results of our sensitivity analysis, we did not account for potential nutrient-induced shifts in assimilation efficiencies in our material flow calculations. However, we acknowledge the possibility of such effects and discuss their potential implications for material flow calculations, as well as some of the complications with estimating variable assimilation efficiencies, below (see Section 4).

We calculated the relative amount of production attributed to each food type (F_i) in the diet using the following equation derived from Benke and Wallace (1980, 1997): $F_i = (G_i \times AE_i \times NPE)$, where G_i is the proportion of food type i in the guts, AE_i is the assimilation efficiency of food type i and NPE is the net production efficiency (proportion of assimilated C that is allocated to production), which was assumed to be 40% for each food type (Benke & Wallace, 1997). To calculate the actual amount of production attributed to each food type, we converted the relative amount of production from each food type to the proportion of total production attributed to each food type (PF_i) using the following equation: $PF_i = F_i \div (F_i + F_j + \dots + F_n)$. We then multiplied total production by PF_i to determine the actual production derived from each food type. Material flows were estimated for each food type using the following equation from Cross et al. (2007): $FC_i = (PF_i \times P) / (AE_i \times NPE)$, where FC_i is the amount of food type i that is consumed by a given taxon and P is the total annual production of that taxon. Flows are reported as gram ash-free dry mass (hereafter, AFDM) $m^{-2} year^{-1}$ and presented by macroinvertebrate functional feeding groups (FFGs). Functional feeding group classifications, which describe the mode of feeding, for individual taxa were based upon Merritt, Cummins, and Berg (2008) and our knowledge of consumer diets based on gut contents analysis. Material flow estimates are reported for each of the primary consumer taxa analysed in this study in Appendix S1, Table S3.

2.3 | Statistical analysis

We tested for nutrient effects on the trophic basis of production and material flows by calculating natural log response ratios

(hereafter InRRs) between each year of nutrient enrichment and the pre-enrichment year (i.e. $\ln[YR1/PRE]$ or $\ln[YR2/PRE]$) for all material flow pathways to primary consumers (including animal tissue). Because fungal biomass was 2.8× greater on leaves than wood (leaves: 3.95% of dry mass; wood: 1.42% of dry mass; V. Gulis, unpubl. data) and consumption of leaf litter was 6.7× greater than wood (on average, gut contents were 33.7% leaves and 5.1% wood) in these streams, we assumed flows of fungi were primarily driven by consumption of fungi-colonized leaf litter. As such, we combined flows of leaf litter and fungi for our material flow analyses. We calculated average InRRs by averaging response ratios for both YR1/PRE and YR2/PRE, across all five streams. We used a two-sided t test to determine whether average InRRs were significantly different from zero, which represents no change in the response variable. Additionally, we performed a one-way analysis of variance to test for differences in the magnitude of response to nutrient enrichment among flows from the different resources, excluding animals. Comparisons between individual resource pairs were performed using Tukey's HSD test. We used linear regression to test for relationships between flows of each food type, excepting animals, to primary consumers and resource C:N, C:P and biomass, expressed as AFDM. Flows of diatoms were evaluated using biofilm stoichiometry and AFDM, and FPOM was used to represent changes in the stoichiometry and biomass of amorphous detritus. We assume that diatom consumption is primarily an indicator of biofilm grazing, with the understanding that diatoms represent only a portion of epilithic biofilm biomass. The elemental content of FPOM, leaf litter, biofilm and wood were determined in each stream at least quarterly with annual values used in analyses; see Rosemond et al. (2015) and Manning, Rosemond, Gulis, Benstead, and Kominoski (2018) for sampling methods of leaf litter, FPOM and wood. Carbon, N, and P were analysed using methods described in Manning et al. (2016). We used linear regression to test for relationships between DIN, SRP and the ratio of DIN:SRP to total organic matter flows and flows of animal prey to primary consumers and to predators. We analysed the effect of nutrient enrichment on the efficiency with which basal resource flows were channelled to production of predator biomass by using a single-factor ANOVA on the ratio of annual predator production (Demi et al., 2018) to total basal resource flows. Additionally, we used linear regression to test for relationships between this ratio and stream water nutrient concentrations.

We calculated the proportion of leaf mass lost from each reach that was consumed by the macroinvertebrate community by dividing the total annual flow of leaf litter to macroinvertebrates (see Section 2.2 above) by the difference between the maximum and minimum monthly leaf litter biomass estimates for each stream, in each year of the experiment (Rosemond et al., 2015). This approach likely overestimates the proportion of leaf litter mass that was consumed by macroinvertebrates by using maximum monthly leaf litter biomass rather than estimates of annual leaf litter inputs to these systems, as the former does not account for inputs during months of non-peak litter biomass. However, highly seasonal litter inputs and the close spatial proximity and similar watershed

characteristics of these systems suggest that the streams should experience similar pulses of inputs throughout the year. Thus, we believe the data represent realistic, relative differences in the contribution of macroinvertebrates to reach-scale litter dynamics among the streams. We used a single-factor ANOVA to determine whether nutrient enrichment affected the contribution of macroinvertebrates to total leaf mass loss. We used linear regression to test the effects of leaf litter C:N and C:P on the contribution of macroinvertebrates to reach-scale leaf litter dynamics, and to determine whether there was a positive relationship between reach-scale litter decay rates (k) and the amount of leaf litter consumed by macroinvertebrates. Briefly, k indicates the negative slope of the regression of the natural log of percent of initial leaf mass remaining plotted against time (in cumulative days) over multiple sampling intervals. All data on reach-scale leaf litter dynamics, including total leaf mass loss and k are from Rosemond et al. (2015; see that paper for a more detailed description of associated methods). We used natural log-transformed data as necessary to conform to model assumptions of normality and homogeneity of variance across all analyses. We used conventions of $\alpha = 0.05$ for determining adequate statistical support of inferences. All statistical analyses were performed using the R statistical environment (version 3.10; R Core Team, 2016).

3 | RESULTS

3.1 | Consumer diets and trophic basis of production

Leaf detritus constituted 65% percent of total gut contents averaged among streams and all years of this study (Figure 1a; range ~52% to ~75%). Wood and amorphous detritus each accounted for ~13% of total gut contents (Figure 1a; ranges: wood ~5% to ~21%; amorphous detritus ~9% to ~20%), thus bringing total average flows from detritus to ~90%. The average contribution of fungi, animals and diatoms to total primary consumer diets was <5% for each food type (Figure 1a; mean contribution: fungi 4.5%; animals ~4%; diatoms 0.9%), with diatoms being the least common food source for the primary consumer communities in these detritus-based ecosystems.

Leaf detritus and fungi each accounted for an average of ~34% of annual primary consumer production among the five streams over the duration of the study (Figure 1b; range: ~31% to ~38% for fungi; ~25% to ~40% for leaf detritus). Among individual taxa the proportion of production derived from these two sources ranged from ~2% to ~60% of production for fungi and from ~2% to ~56% for leaf detritus (Appendix S1, Table S1). Nutrient enrichment did not affect the proportion of primary consumer production derived from leaf detritus (Figure 2; t test: $t_9 = 0.42$, $p = 0.69$), but increased the proportion derived from fungi by 4% (Figure 2; t test: $t_9 = 3.03$, $p = 0.01$). The average proportion of primary consumer production attributed to amorphous detritus was ~19% (Figure 1b;

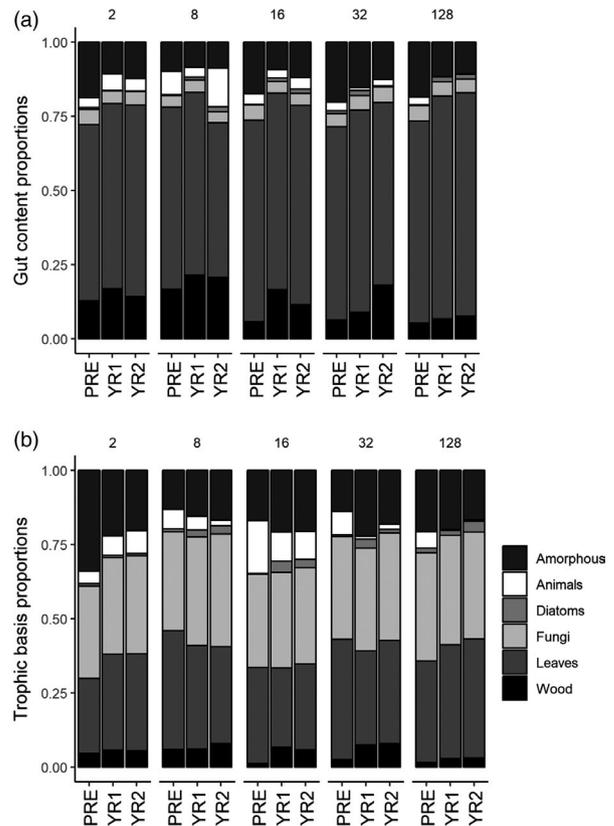


FIGURE 1 Summary of primary consumer gut contents (a) and the trophic basis of primary consumer production (b) for each of the five streams during each of the 3 years of study. Stacked bars represent the fraction of total gut contents and of primary consumer production attributed to each food type in panels a and b respectively. Bars are grouped by stream (indicated by target N:P ratio above groups)

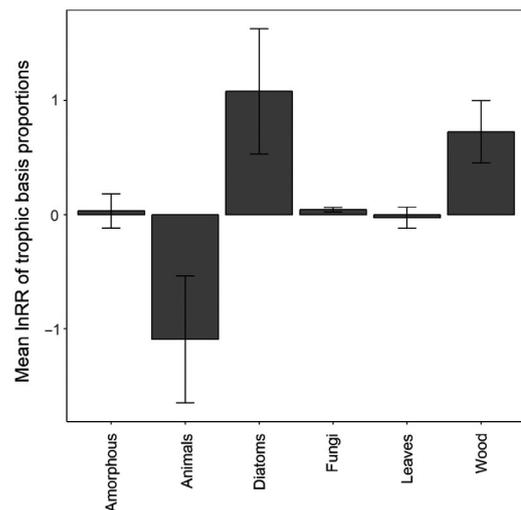


FIGURE 2 Mean response ratios of the proportion of production attributed to each food type for primary consumer taxa. Each bar represents the average lnRR of each food type for both years of nutrient enrichment (i.e. YR1/PRE and YR2/PRE) across all five streams. A value of 0 indicates no change, positive values indicate an increase and negative values indicate a decrease in the proportion of production derived from each food type following nutrient enrichment. Error bars represent standard error

range ~13% to ~34%) and was unaffected by nutrient enrichment (Figure 2; t test: $t_9 = 0.34$, $p = 0.74$). Among individual taxa the proportion of production attributed to amorphous detritus ranged from <1% to ~64% (Appendix S1, Table S1). The proportion of primary consumer production supported by the consumption of animal material was highly variable among streams (mean ~6%, range <1% to ~18%), and was greatest for the crayfish *Cambarus bartonii* and two genera of caddisflies (i.e. *Parapsyche* and *Psilotreta*). The proportion of primary consumer production derived from animal prey decreased by 67% during 2 years of nutrient enrichment compared to the pre-enrichment year (Figure 2; t test: $t_9 = -2.86$, $p = 0.02$). Though relatively small, the contribution of both wood and diatoms to primary consumer production was approximately double during the 2 years of nutrient enrichment (wood ~6%; diatoms ~2%) compared to the pre-enrichment year (Figure 2; wood ~3%, t test: $t_9 = 3.98$, $p < 0.01$; diatoms <1%, t test: $t_9 = -2.86$, $p < 0.05$). Increases in the contribution of wood to primary consumer production were mostly observed among several common leaf-shredding insects (i.e. *Tallaperla*, *Pycnopsyche*; Appendix S1, Table S1). An increase in the relative contribution of diatoms to primary consumer production was largely observed among the mayfly *Maccaffertium*, which accounted for an average of ~31% of total production from diatoms following nutrient enrichment compared to ~10% prior to enrichment (Appendix S1, Table S1).

3.2 | Organic matter flows

Total organic matter flow to primary consumers increased by 52% from an average of 97 to 147 g AFDM $m^{-2} year^{-1}$ following nutrient enrichment (Figures 3 and 4; t test: $t_9 = 3.52$, $p = 0.02$) and was significantly positively related to stream water SRP, but not DIN or DIN:SRP (Table 1; Figure 5). Total organic matter flows were largely channelled through collector-gatherer (primarily Non-Tanypodinae members of Chironomidae) and leaf-shredding macroinvertebrates, which respectively accounted for an average of 63% and 27% of total flows during the pre-enrichment year and 57% and 38% during the 2 years of enrichment. Flows of all resources, except animal tissue, increased following enrichment though the magnitude of those responses varied among resource types (Figure 4; ANOVA: $F_{5,54} = 4.74$; $p = 0.01$). Reduced flows of animal prey were indicative of decreased omnivory among primary consumers following nutrient enrichment (t test: $t_9 = -1.91$, $p = 0.09$). Flows of animal prey to primary consumers were unrelated to either DIN or SRP but were significantly negatively correlated to the stream water DIN:SRP ratio (Table 1; Figure 5). Flows of diatoms were small compared to other resources (Figure 3), never exceeding 1.5% of total flows, but showed the largest relative increase during nutrient enrichment (Figure 4; t test: $t_9 = 3.52$, $p = 0.001$). Flows of diatoms during the pre-enrichment year were dominated by collector-gatherer and leaf-shredding macroinvertebrates (59% and 32% of flows on average, respectively), but shifted during the 2 years of nutrient enrichment towards a greater contribution by biofilm scrapers

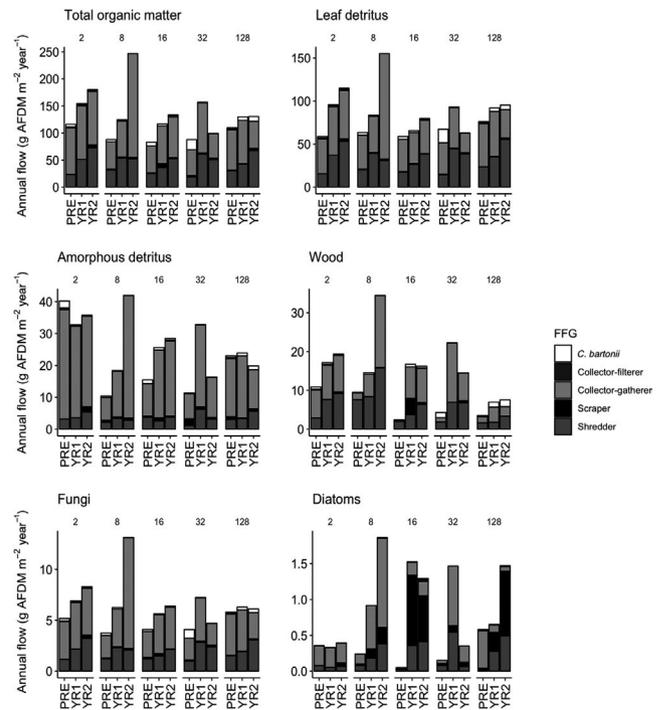


FIGURE 3 Flows of individual food types and total organic matter to primary consumers. Bars are grouped by stream (indicated by N:P ratio above groups) where different colours indicate flows attributed to different functional feeding groups (FFGs) and the crayfish *Cambarus bartonii*. Flows of animal prey to primary consumers are not shown

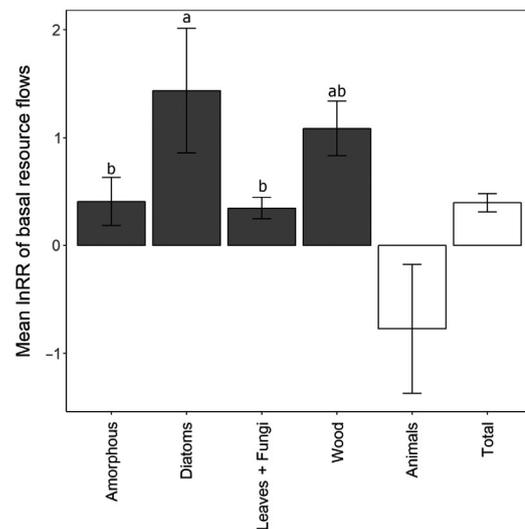


FIGURE 4 Mean response ratios of flows of each food type to primary consumers. Each bar represents the average lnRR of each food type for both years of nutrient enrichment (i.e. YR1/PRE and YR2/PRE) across all five streams. A value of 0 indicates no change, positive values indicate an increase and negative values indicate a decrease in the proportion of production derived from each food type following nutrient enrichment. Error bars represent standard error. Lower case scripts indicate significant differences (Tukey's HSD). Total flows and those of animals were excluded from the ANOVA and all individual pair-wise comparisons. Individual Student's t tests were used for each resource to test for a PRE and YR1/YR2 difference in average flows and are summarized in the text

TABLE 1 Summary of linear regression results examining relationships between organic matter flows to primary consumers from each food type and either resource stoichiometry and biomass (C:N, C:P and AFDM for flows of amorphous detritus, diatoms, leaf detritus and fungi and wood) or dissolved nutrient concentrations (DIN, SRP, DIN:SRP for flows of animal prey and total organic matter). Error is standard error of the slope estimate

Resource type	Predictor	F-stat	Error	R ²	p-value	Slope	Intercept
Amorphous detritus	FPOM C:N	1.44	3.49	0.10	0.25	4.195	-61.53
	FPOM C:P	0.12	0.02	0.01	0.74	0.00563	22.46
	FPOM AFDM	0.50	0.019	0.04	0.49	0.014	19.90
Diatoms	Biofilm C:N	2.18	0.12	0.14	0.16	-0.173	2.31
	Biofilm C:P	7.03	0.001	0.35	0.020	-0.00256	1.66*
	Biofilm AFDM	3.91	42.567	0.23	0.070	84.133	-0.050
Leaf detritus + fungi	Leaf C:N	0.13	1.73	0.01	0.72	0.631	51.74
	Leaf C:P	5.46	0.013	0.30	0.036	-0.0307	172.67*
	Leaf AFDM	3.81	0.040	0.23	0.073	-0.0787	121.07
Wood	Wood C:N	1.61	0.18	0.18	0.23	-0.229	47.10
	Wood C:P	8.01	0.001	0.38	0.014	-0.00204	33.15*
	Wood AFDM	1.43	0.037	0.10	0.25	0.044	5.30
Animals	DIN	2.09	0.001	0.14	0.17	-0.002	1.18
	ln(DIN:SRP)	6.94	0.150	0.35	0.021*	-0.394	2.26**
	ln(SRP)	0.22	0.143	0.02	0.65	0.067	0.67
Total flows	DIN	0.09	0.082	0.01	0.77	0.025	124.53
	ln(DIN:SRP)	1.73	11.17	0.12	0.21	-14.17	183.45
	ln(SRP)	7.33	7.382	0.36	0.018*	19.989	80.14**

Note: Bold font indicates statistical significance ($\alpha = 0.05$).

Abbreviations: AFDM, ash-free dry mass; DIN, dissolved inorganic N; FPOM, fine particulate organic matter; SRP, soluble reactive P.

** and * indicate relationships that are graphically represented in Figures 5 and 6 respectively. ln indicates a natural log transformation of the predictor variable.

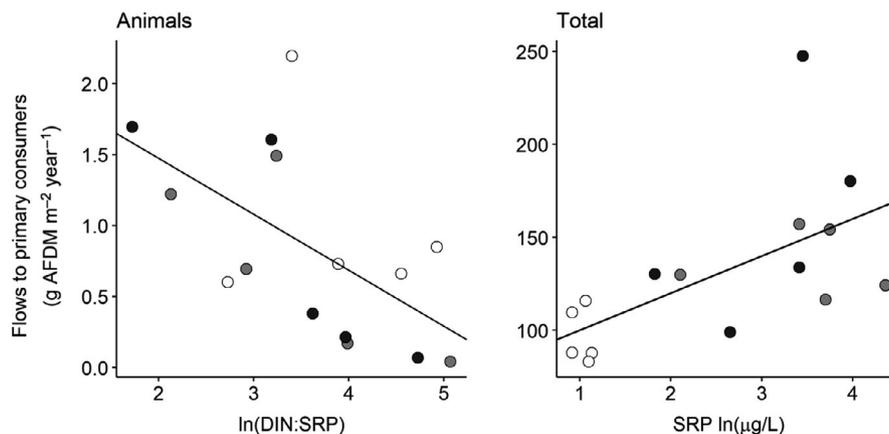


FIGURE 5 Relationships between flows of animal prey to primary consumers and stream water dissolved inorganic N:soluble reactive P (DIN:SRP) ratios and between total organic matter flows to primary consumers and stream water SRP. Open circles indicate pre-enrichment flows, while grey and black circles represent flows from enrichment YR1 and YR2 respectively. Summary statistics of the linear regression models for each of these relationships, including model coefficients (slopes and intercepts), are presented in Table 1

(average of 9% of flows during pre-enrichment and 31% during enrichment). The increase in the flow of diatoms was negatively correlated with biofilm C:P (Figure 6) but not biofilm C:N or AFDM (Table 1). Wood consumption accounted for an average of ~11% of material flows during the study (range ~3% to ~15%), and the flow of wood increased by 283% from 6 g AFDM m⁻² year⁻¹ during the

pre-enrichment year to 17 g AFDM m⁻² year⁻¹ during the 2 years of enrichment (Figure 4; *t* test: $t_9 = 5.86$, $p = 0.0002$). Collector-gatherer and leaf-shredding macroinvertebrates were the primary consumers of wood in the study streams, together accounting for an average of 88% and 90% of wood flows during the pre-enrichment year and two years of enrichment respectively. The flow of wood

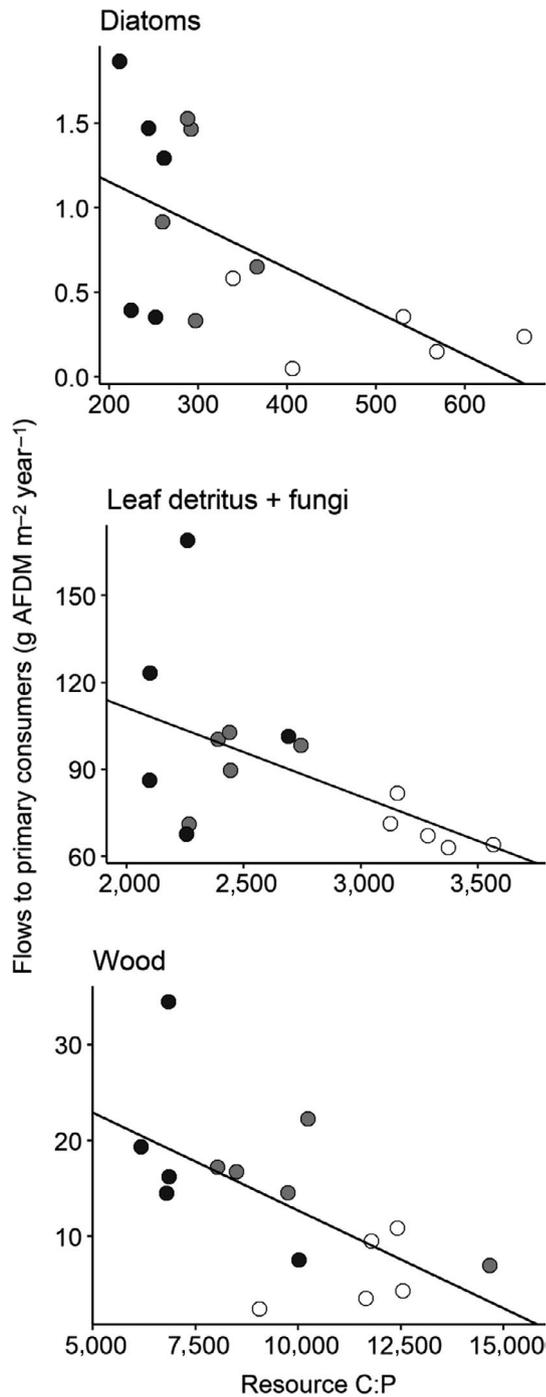


FIGURE 6 Relationships between individual basal resource flows and resource C:P where resource C:P indicates that of biofilm, leaf detritus and wood in the top, middle and bottom panels respectively. Open circles indicate pre-enrichment flows, while grey and black circles represent flows from enrichment YR1 and YR2 respectively. Summary statistics of the linear regression models for each of these relationships, including model coefficients (slopes and intercepts), are presented in Table 1

was negatively correlated to its C:P ratio (Figure 6) but not to its C:N or AFDM (Table 1).

Leaf litter and fungi accounted for an average of ~70% (range ~55% to 81%) of total flows to primary consumers. Flow of leaf litter and fungi increased 58% during enrichment from an average of 69 to

TABLE 2 Summary of linear regression results examining potential relationships between material flows to predators and dissolved nutrient concentrations and basal resource flows (BR flows) to primary consumers (i.e. potential prey taxa). Error is standard error of the slope estimate

Response	Predictor	F-stat	Error	R ²	p-value
Flows to predators	DIN	2.17	0.005	0.14	0.16
	ln(DIN:SRP)	0.79	0.777	0.06	0.39
	ln(SRP)	2.12	0.577	0.14	0.17
	BR Flows	0.04	0.019	0.00	0.84
Predator production:basal resource flows to primary consumers	DIN	0.66	0.000	0.05	0.43
	ln(DIN:SRP)	0.00	0.002	0.00	0.95
	ln(SRP)	0.01	0.002	0.00	0.92

Note: ln indicates a natural log transformation of the predictor variable. Abbreviations: DIN, dissolved inorganic N; SRP, soluble reactive P.

101 g AFDM m⁻² year⁻¹ during the 2 years of enrichment (Figures 3 and 4; *t* test: *t*₉ = 3.52, *p* = 0.02), and was negatively correlated to leaf litter C:P (Table 1; Figure 6). Additionally, leaf litter AFDM (Table 1) explained ~23% of the variation in flows of leaf litter and fungi, though this negative relationship was not statistically supported at a significance level of 0.05. Increased flows of leaf litter and fungi during the 2 years of enrichment were largely driven by leaf-shredding macroinvertebrates, which accounted for 45% of leaf litter flows, on average, during nutrient enrichment compared to only 28% prior to enrichment. Amorphous detritus accounted for an average of ~19% (range ~12% to 35%) of total organic matter flows and increased by 40% in response to nutrient enrichment from 20 to 28 g AFDM m⁻² year⁻¹ (Figures 3 and 4; *t* test: *t*₉ = 2.40, *p* = 0.04). Flows of amorphous detritus were dominated by collector-gatherer taxa, such as members of the family Chironomidae, which collectively accounted for an average of 74% and 80% of flows prior to and during nutrient enrichment respectively. The flow of amorphous detritus was unrelated to the quality (C:N or C:P) or quantity of FPOM (Table 1).

The flow of animal prey to macroinvertebrate predators ranged from 3.8 to 8.2 g AFDM m⁻² year⁻¹ among streams during the pre-enrichment year and from 3.1 to 14.2 g AFDM m⁻² year⁻¹ among streams during the 2 years of enrichment. These flows were unrelated to basal resource flows and streamwater nutrient concentrations (Table 2). On average, ~1.8% of basal resource flows were converted to predator production during all 3 years of study (range = ~0.1% to ~3.9%). This percentage did not vary predictably across the 3 years of study (ANOVA: *F*_{2,12} = 0.64; *p* = 0.54). The ratio of predator production to basal resource flows was unrelated to stream water N and P concentrations or dissolved N:P ratio (Table 2).

3.3 | Role of macroinvertebrates in organic matter processing

The proportion of reach-scale leaf litter loss that was attributed to consumption by macroinvertebrates increased 101% during the

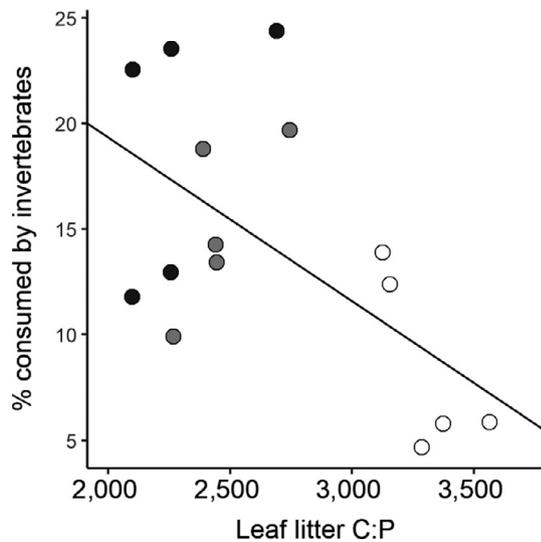


FIGURE 7 The relationship between the proportion of leaf mass loss that was consumed by macroinvertebrates and leaf litter C:P. Open circles indicate pre-enrichment values, while grey and black circles represent enrichment YR1 and YR2 respectively. Linear equation: $y = -0.0075x + 34.24$; $R^2 = 0.34$, $p = 0.024$

2 years of nutrient enrichment (pre-enrichment: 8.5%; during enrichment = 17.1%; ANOVA: $F_{2,12} = 5.912$; $p < 0.05$). The proportion of leaf mass loss attributed to consumption by macroinvertebrates was negatively correlated with leaf litter C:P (Figure 7; linear regression: $F_{1,13} = 6.57$; Error = 0.003; $R^2 = 0.34$; $p = 0.024$) but was not related to leaf litter C:N ($F_{1,13} = 0.32$; $R^2 = 0.02$; $p = 0.58$). The total amount of leaf detritus consumed by macroinvertebrates was not a significant predictor of reach-scale litter decay rates (k ; $F_{1,13} = 1.66$; $R^2 = 0.11$; $p = 0.22$).

4 | DISCUSSION

Total organic matter flows to primary consumers increased following nutrient enrichment due to higher rates of secondary production, which were primarily driven by greater P availability rather than N availability across our experimental dissolved N:P gradient (Demi et al., 2018). These results suggest that the response of food webs in nutrient-poor detritus-based stream ecosystems may exhibit minimal response to anthropogenic N increases in the absence of concurrent increases in P (i.e. when N:P enrichment ratio is high). However, elevated concentrations as low as 7 $\mu\text{g/L}$ SRP triggered changes in resource nutrient content in our study (which was the 2-year average SRP concentration in the target 11 $\mu\text{g/L}$ SRP stream; Manning et al., 2016), indicating very little P, combined with N enrichment, can result in changes in food resource nutrient content. Increases in total organic matter flows to primary consumers were largely driven by leaf-shredding macroinvertebrates, which exhibited the greatest response to nutrient enrichment among macroinvertebrate FFGs (Demi et al., 2019). Nutrient enrichment produced clear but modest shifts in the trophic basis of primary consumer production relative

to pre-enrichment conditions but did not alter the contribution of dominant food types (leaf detritus and fungi) to production. As we predicted, flows of individual resources were often best explained by resource C:P (except for amorphous detritus), suggesting widespread P limitation across macroinvertebrate primary-consumer FFGs. However, counter to our predictions, increased material flows to primary consumers were not propagated to macroinvertebrate predators in this study (however, see growth responses of predatory salamanders in Bumpers et al., 2015). Lastly, nutrient enrichment increased the role of macroinvertebrates in the processing of leaf detritus, as consumption of leaf litter accounted for a greater proportion of total leaf mass lost from the experimental reaches following N and P fertilization, a pattern best explained by reductions in leaf litter C:P.

4.1 | Trophic basis of production and material flows to primary consumers

Nutrient availability is an important driver of basal resource dynamics as it may constrain rates of primary production (Elser et al., 2007) and decomposition (Cebrian & Lartigue, 2004; Ferreira et al., 2015), while also being an important determinant of basal resource quality in food webs (Bowman, Chambers, & Schindler, 2005; Scott et al., 2013). In this study, N and P fertilization led to increased material flows from each of the four major basal resource pools (wood, leaf litter, fungi, amorphous detritus and diatoms) as predicted. However, our prediction that the greatest relative increases would occur for flows of wood and leaf litter (and associated fungi) was not supported. Rather, the greatest average increases were observed for flows from diatoms (~276%) and wood (~176%), respectively, although due to high variance, the average increase in flows of wood was not significantly different from that of leaf (~45%) or amorphous detritus (~33%).

Increased flows of diatoms and wood were facilitated, in part, by increased consumption of those resources following nutrient enrichment, although the fraction of production attributed to each of these two food types remained small throughout the study. The greater relative response of diatom flows to nutrient enrichment was driven in large part by the facultative biofilm-scraper mayfly *Maccaffertium*, which not only shifted its diet towards a greater proportion of diatoms (Appendix S1, Table S2), but also increased in production (Appendix S1, Table S1). This response could be a result of a combination of greater primary production, increases in algal components of biofilms and increased nutrient content of biofilms in response to enrichment. Indeed, biofilm experienced the greatest shift in C:P (~52% decrease, on average) among basal resources following nutrient enrichment (leaves and wood: ~28% and ~24% decrease, respectively; FPOM: ~34% increase; A.D. Rosemond, unpubl. data). These effects occurred despite relatively constrained effects on biofilm biomass in this and a previous N+P fertilization study at CHL (Greenwood & Rosemond, 2005). Increased wood consumption was driven primarily by leaf-shredding taxa and may reflect a shift towards a more

abundant, albeit lower-quality, resource (Eggert & Wallace, 2007; Hall et al., 2000) in response to the reduced availability of leaf detritus following nutrient enrichment (Demi et al., 2018; Rosemond et al., 2015). By comparison, the smaller relative increases in flows of leaf litter and amorphous detritus were driven not by modified consumption of those resources per se, but rather by increases in consumer production, as the proportion of those resources in consumer diets was relatively unaffected by nutrient enrichment.

Interestingly, we observed reduced flows of animal prey to taxa that we have identified as primary consumers (i.e. *Psilotreta* and *Parapsyche*, Appendix S1, Table S3) following nutrient enrichment. Increased animal prey consumption by omnivores has previously been proposed as a strategy for acquiring limiting nutrients such as N or P by taxa that otherwise consume nutrient-poor resources (Denno & Fagan, 2003; Diehl, 2003). The patterns of reduced omnivory following nutrient enrichment presented in this study may therefore be a product of reduced stoichiometric constraints between primary consumers and basal resources. Indeed, several studies have reported similar patterns in which the degree of animal predation in omnivores decreased with increasing nutrient content of other resources, such as plant material or phytoplankton (Siuda & Dam, 2010; Zhang, van der Berg, van Leeuwen, Blonk, & Bakker, 2018). As such, modification of important food web properties, such as the relative strength of top-down and bottom-up forces, via changes to predator-prey interactions among omnivores may be widespread considering the global alteration of N and P dynamics (Peñuelas et al., 2013).

Our study in detritus-based systems, allows us to attribute the effects of resource quality (stoichiometry) versus resource quantity on consumer material flows since the quantity of food resources typically decreased with nutrient enrichment. We found that total organic matter flows in these detritus-based systems are largely governed by the effects of P-availability on the C:P stoichiometry of multiple resource pools. While %P of wood and biofilm experienced a mostly uniform increase across the dissolved N:P (and thus SRP) gradient following enrichment (A.D. Rosemond, unpubl. data), leaf litter %P experienced a greater response in the high SRP (low DIN and N:P) treatments (Demi et al., 2018). The N content of leaf litter, wood and biofilm also tended to increase following enrichment, but typically experienced a smaller magnitude increase than that of %P and did not exhibit systematic variation across the dissolved N:P gradient (A.D. Rosemond, unpubl. data). The increased P content of leaf litter and wood was likely driven by both increased fungal biomass and luxury P storage by fungal decomposers (Beever & Burns, 1981; Gulis et al., 2017; Gulis, Suberkropp, & Rosemond, 2008), whereas N content likely reflects increased fungal biomass only, given that aquatic fungi are relatively homeostatic with regards to N content (Danger, Gessner, & Bärlocher, 2016; Gulis et al., 2017; Persson et al., 2010). The relative roles of these processes were previously corroborated using a structural equation approach to studying the effects of stream water N and P on leaf litter nutrient content in our study sites (Manning et al., 2015). Biofilm N and P content each increased with increasing DIN and SRP in the study streams (P.M. Bumpers,

in prep) suggesting potential co-limitation by N and P of the autotrophic food web pathway in our study systems.

Negative relationships between resource flows and C:P, but not C:N, for leaf litter and fungi, wood and biofilm support our prediction that flows of those resources would be P limited based on previous analyses of consumer and resource stoichiometry in streams (Cross et al., 2003; Lauridsen et al., 2012). However, the flow of amorphous detritus, despite increasing on average, was not related to either FPOM C:P or C:N following nutrient enrichment. This is consistent with the prediction that consumers of FPOM (i.e. collector-gatherers) are less likely to be P or N limited than consumers from other functional groups (i.e. shredders; Lauridsen et al., 2014; Tant et al., 2013).

We should note that the material flow estimates presented in this manuscript do not account for potential variability in assimilation efficiencies that may arise as a result of shifts in resource stoichiometry (Halvorson, Scott, Sanders, & Evans-White, 2015; Pandian & Marian, 1986). Reduced stoichiometric constraints are likely to result in increases in consumer AE, meaning that material flow calculations that do not account for such shifts may overestimate material flows, thereby mischaracterizing the response of individual food web compartments to altered nutrient availability. Indeed, our sensitivity analysis of material flow calculations revealed that increases in consumer AE can substantially reduce estimates of material flows to consumers in our study systems (Appendix S2, Figure S1). However, we found that our material flow estimates were, on average, at least as sensitive to uncertainty around our estimates of secondary production, on average, than to uncertainty around consumer AEs predicted by either resource N or P content. Furthermore, we argue that predicting consumer AEs based on bulk resource stoichiometry remains a difficult challenge given the lack of published data on variation in AE along gradients of resource N or P content, the potential for selective feeding to minimize elemental imbalances inferred from bulk stoichiometry (as in Hood, McNeely, Finlay, & Sterner, 2014) and the potential for AE to vary as a function of resource supply rates in addition to resource stoichiometry (Halvorson et al., 2017).

4.2 | Role of macroinvertebrates in organic matter processing

Primary consumers are central to energy transformations and the turnover of basal C resources in most ecosystems (Cebrian, 2004). In forested headwater streams, macroinvertebrates are key to the processing of leaf detritus, which, in part, results in its conversion and export as FPOM (Cummins, Wilzbach, Gates, Perry, & Taliaferro, 1989; Graça, 2001; Wallace, Ross, & Myer, 1982). As such, processing of coarse detritus by macroinvertebrate consumers plays an important role in reach-scale C and nutrient dynamics in these systems (Covich, Palmer, & Crowl, 1999; Cross, Rosemond, Benstead, Eggert, & Wallace, 2005). For example, Graça et al. (2015) demonstrated that shredders consume as much as 64% of leaf litter biomass in

low-order streams and Cross et al. (2007) reported that macroinvertebrates consume ~15% of annual leaf litter inputs under ambient (i.e. low N and P availability) nutrient conditions in one CHL stream. Consumption of leaf litter inputs increased to ~35% during 2 years of moderate N and P fertilization (at molar N:P ratio of 16:1), presumably in response to reduced stoichiometric constraints on macroinvertebrate consumers under elevated nutrient concentrations (Cross et al., 2007). The lower values reported in the current study (8.5%, PRE to 17.1%, YR1/YR2) are likely a function of greater hydrologic export resulting from higher discharge among the streams used in the present study (mean discharge: 5–20 L/s) than those studied by Cross et al. (2007; mean discharge: ~1 L/s). Nevertheless, our results generally support a similar conclusion but provide a more nuanced understanding of how macroinvertebrates contribute to reach-scale organic matter dynamics under elevated N and P regimes. Specifically, we have demonstrated that leaf litter P-, but not N content is a significant driver of leaf litter consumption by the macroinvertebrate community in these systems and that the efficiency with which available leaf litter is channelled into metazoan food web increases due to reduced stoichiometric imbalances between leaf-shredding macroinvertebrates and leaf detritus.

Consumers in both terrestrial and aquatic habitats tend to process a greater proportion of primary production and detritus as N and P content of basal resources increases (Cebrian & Lartigue, 2004). However, the question remains as to whether increased material processing is primarily due to metazoan consumers or heterotrophic microorganisms in most systems (Cebrian & Lartigue, 2004; Enríquez, Duarte, & Sand-Jensen, 1993), which has important implications for the fate of carbon in food webs. In our study, material flows to shredders roughly doubled following nutrient enrichment, while Manning et al. (2016) similarly reported that leaf litter mass loss attributed to shredders versus microbial processing (via litter breakdown studies) increased with nutrient enrichment in these study streams. The relative effects of altered N and P availability on carbon flows to shredders versus microbial decomposers likely depend on the relative strength of N versus P limitation among these groups. For example, laboratory experiments have revealed greater N than P limitation of production and biomass of aquatic hyphomycetes (the predominant microbial decomposers of leaf detritus in streams) across a similar range of N and P concentrations and ratios to that used in this study (Gulis et al., 2017), while secondary production of macroinvertebrates in these streams has been linked to leaf litter P, but not N content (Demi et al., 2018). Thus, the proportion of total leaf litter inputs processed by microbial decomposers, thereby bypassing metazoan food webs, may be more susceptible to variation in supply of N than of P. However, evidence from both whole-stream and laboratory experiments suggest the potential for luxury P uptake in aquatic hyphomycetes (Beever & Burns, 1981; Danger et al., 2016; Gulis et al., 2017). As such, low levels of P fertilization, in the absence of increased N, may result in reduced detrital C:P without increasing fungal biomass, thereby increasing the efficiency with which leaf litter is channelled to primary consumers.

The flow of animal prey to predators did not systematically change following nutrient enrichment and was unrelated to total flows of

organic matter to primary consumers, which were dominated by leaf litter. The lack of a systematic response in flows to predatory macroinvertebrates may reflect shifts in the potential prey assemblage towards a greater prevalence of large-bodied, predator-resistant taxa (Davis et al., 2010a; Davis, Rosemond, Eggert, Cross, & Wallace, 2010b; Demi et al., 2019). For example, an earlier analysis of macroinvertebrate community composition in the study streams revealed that the communities shifted towards greater biomass of the common, large-bodied shredders *Pycnopsyche* (Trichoptera), *Tallaperla* (Plecoptera) and *Tipula* (Diptera; Demi et al., 2019). The patterns of material flow reported in this study are consistent with this observation, as the proportion of leaf litter flows, which represent the dominant pathway, attributed to these taxa increased from 14% during the pre-enrichment year to 19% and 25% during enrichment year one and two respectively. This is despite the fact that there was no apparent increase in the relative amount of leaf detritus in diets of those taxa (Appendix S1, Table S2). Thus, if increased material flows occur along food web pathways that are less available to predators, we might not expect prey consumption by predators to track community-level estimates of basal resource flows.

Though predatory macroinvertebrates did not exhibit a consistent positive response to nutrient enrichment, Bumpers et al. (2015) reported increased growth rates of larval salamanders, which are the top predators in the study streams, during the 2 years of enrichment. This pattern was attributed to increased consumption of algal grazing taxa (i.e. *Maccafertium*; Bumpers et al., 2015; Bumpers, Rosemond, Maerz, & Benstead, 2017), which is consistent with our finding of increased grazer biomass (Demi et al., 2019), as well as diatom consumption and flows during the 2 years of enrichment. These results highlight the importance of shifts in individual material flow pathways for higher-level consumers. Furthermore, we suggest that propagation of reduced stoichiometric constraints on primary consumers to higher trophic levels is likely dependent, in part, upon relative responses among prey taxa in combination with their susceptibility to predation.

Studies exploring the effects of excess nutrients on stream and river ecosystems have lagged behind those in lakes and coastal zones (Wurtsbaugh, Pearl, & Doods, 2019). Further, previous studies have focused on nutrient effects on changes in mass and activity of primary producers and detrital resources (Dodds & Smith, 2016), whereas our study shows how changes in basal resource stoichiometry changed energy flow pathways. Our findings likely apply broadly to other ecosystems in which anthropogenic nutrient mobilization has the potential to influence the nutrient content of detritus and biofilms. This would occur in any ecosystem in which other factors such as altered hydrology or excess contaminants did not otherwise suppress microbial uptake and sequestration of nutrients. Such patterns have been shown to be robust in studies determining nutrient-resource stoichiometry relationships for both biofilms and wood across moderate land-use gradients (O'Brien & Wehr, 2010; Usher, Wood, Bumpers, Wenger, & Rosemond, 2020).

The global reach of human influence has resulted in altered nutrient dynamics in many of Earth's ecosystems, with both N and

P affected (Dodds & Smith, 2016; Peñuelas et al., 2013; Stoddard et al., 2016). Ecological stoichiometry theory has emerged as a framework for understanding how variation in the relative supply of N and P can influence biological processes across multiple ecological scales. We have used this framework to investigate how variation in dissolved N and P ratios influences organic matter flows and patterns of resource consumption by macroinvertebrates in detritus-based stream food webs. In our study systems, flows of most basal resources to primary consumers were driven by resource C:P (which is largely a function of dissolved P availability), a pattern consistent with our predictions for these systems based on fundamental principles of EST. Thus, our analysis provides strong support for EST as an effective tool for predicting the consequences of altered N and P availability for food web dynamics wherever there is a priori knowledge of stoichiometric imbalances among trophic levels.

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AUTHORS' CONTRIBUTIONS

A.D.R., J.P.B. and J.C.M. conceived the ideas, designed the methodology and acquired funding for this project; L.M.D. collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n02v6vwwt4> (Demi, Benstead, Rosemond, & Maerz, 2020).

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SUPPORTING INFORMATION

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

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