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Variation in Detrital Resource Stoichiometry Signals Differential Carbon to Nutrient Limitation for Stream Consumers Across Biomes

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ABSTRACT

Stoichiometric ratios of resources and consumers have been used to predict nutrient limitation across diverse terrestrial and aquatic ecosystems. In forested headwater streams, coarse and fine benthic organic matter (CBOM, FBOM) are primary basal resources for the food web, and the distribution and quality of these organic matter resources may therefore influence patterns of secondary production and nutrient cycling within stream networks or among biomes. We measured carbon (C), nitrogen (N), and phosphorus (P) content of CBOM and FBOM and calculated their stoichiometric ratios (C/N, C/P, N/P) from first- to fourth-order streams from tropical montane, temperate deciduous, and boreal forests, and tallgrass prairie, to compare the magnitude and variability of these resource types among biomes. We then used the ratios to predict nutritional limitations for consumers of each resource type. Across biomes, CBOM had consistently higher %C and %N, and higher and more variable C/N and C/P than FBOM, suggesting that microbial processing results in more tightly constrained elemental composition in FBOM than in CBOM. Biome-specific differences were observed in %P and N/P between the two resource pools; CBOM was lower in %P but higher in N/P than FBOM in the tropical montane and temperate deciduous forest biomes, while CBOM was higher in %P but similar in N/P than FBOM in the grassland and boreal forest biomes. Stable ^{13}C isotopes suggest that FBOM likely derives from CBOM in tropical and temperate deciduous forest, but that additional non-detrital components may contribute to FBOM in boreal forests and grasslands. Comparisons of stoichiometric ratios of CBOM and FBOM to estimated needs of aquatic detritivores suggest that shredders feeding on

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CBOM are more likely to experience nutrient (N and/or P) than C limitation, whereas collector–gatherers consuming FBOM are more likely to experience C than N and/or P limitation. Our results suggest that differences in basal resource elemental content and stoichiometric ratios have the potential to affect consumer production and ecosystem rates of C, N, and P cycling in relatively consistent ways across diverse biomes.

Key words: nitrogen; phosphorus; benthic organic matter; elemental ratios; macroinvertebrate; lotic aquatic ecosystem; threshold elemental ratio.

INTRODUCTION

Ecological stoichiometry uses the balance of carbon (C) and other biologically essential macroelements (here nitrogen [N] and phosphorus [P]) to understand the mechanisms underlying nutrient dynamics (Sterner and Elser 2002) and has been used as a mechanistic framework to assess nutrient dynamics across diverse ecosystems (Elser and others 2007; Hessen and others 2013). A stoichiometric approach has been particularly useful in evaluating relationships between consumers and their food resources, as interactions between organisms and their environment are influenced by elemental demands relative to supplies (Elser and Urabe 1999). Indeed, elemental mass and stoichiometric imbalances between consumers and their resources can constrain consumer growth and in turn affect rates of nutrient cycling (Dodds and others 2004; Frost and others 2005; Cebrian and others 2009). For example, higher detrital carbon/nitrogen (C/N) ratios have been linked to lower litter breakdown rates due to nutritional imbalances for stream detritivores (Hladyz and others 2009) and may reduce N turnover rates in streams (Dodds and others 2004). Threshold elemental ratios (TERs; Sterner and Elser 2002), which estimate the resource ratio below which consumer growth is C limited and above which it is nutrient-limited (Frost and others 2006), predict effects of stoichiometric imbalances between consumers and their resources on ecosystem processes, including litter breakdown and N transformation. Combining basal resource stoichiometry with consumer TERs thus provides a framework with which to predict rates of nutrient cycling and constraints on organismal growth.

Whereas the stoichiometry of consumers and thus their TERs are generally constrained (Sterner and Elser 2002; Small and others 2009; but see Halvorson and others 2015), the elemental composition of basal resources varies widely within and across ecosystems. Synthesis efforts have assessed broad-scale differences between basal resources in terrestrial, marine, and lacustrine environments (Cebrian and others 1998, 2009; Elser and others 2000; McGroddy and others 2004; Cleveland and Liptzin 2007). A global synthesis of terrestrial green foliage and litter found that whereas the variability of C/N/P was tightly constrained within individual biomes, there were significant biome-level differences in resource stoichiometry; C/P and N/P were significantly higher in tropical than temperate forests, though C/N did not differ between the two biomes (McGroddy and others 2004). Also, in a cross-system comparison, Elser and others (2000) found that despite terrestrial foliage having much higher C/N and C/P ratios than lake seston, the N/P ratios of terrestrial and lacustrine autotrophs were nearly identical. Largely missing from these syntheses is an assessment of the range and variability of the stoichiometry of basal resources that fuel detritus-based lotic ecosystems (e.g., forested headwater streams), though stoichiometric ratios have been previously reported in site-specific stream studies (e.g., Cross and others 2003; Dodds and others 2004; Evans-White and others 2009; Cheever and others 2013).

The composition of benthic organic matter, the primary basal resources fueling food webs in forested headwater streams, may differ across biomes due to variation in inputs of source materials, the rate of decomposition, and the stoichiometry of consumers. Quantifying differences in C/nutrient ratios between coarse (CBOM; > 1 mm) and fine (FBOM; < 1 mm) benthic organic matter can provide insights into potential nutrient availability in detritus-based ecosystems, including many first- to fourth-order streams. Changes in the C/nutrient ratios of leaf detritus in streams due to microbial conditioning and breakdown are well documented, with both C/N and C/P decreasing with time in the stream as microorganisms colonize and process leaf material (e.g., Manning and others 2016). However, less is known about how the stoichiometry of detritus differs between C pools (coarse [e.g., leaf] and fine benthic C) and varies within and between stream networks (but see Cross and others 2005). In lotic environments, an understanding of variation in the elemental concentration and ratios of organic matter is needed to predict how basal resource nutrient content and stoichiometry may change under future climate and land use scenarios (Kominoski and Rosemond 2012).

Here, we present data on the stoichiometry of two compartments of detrital organic matter in streams: CBOM and FBOM, collected across four stream networks from different biomes. Our objectives in this study were twofold: (1) to assess differences in elemental content (%C, %N, %P) and stoichiometric ratios (C/N, C/P, N/P) between resources (CBOM, FBOM) and the role of biome in driving any differences, and (2) to evaluate potential C and nutrient (N and/or P) limitation of macroinvertebrate detritivores feeding on CBOM and FBOM, based on the stoichiometry of CBOM and FBOM and TERs of their respective consumers. We predicted that CBOM would consistently have higher C/N and C/P ratios than FBOM and that the variability of resource nutrient content and stoichiometry would be higher in CBOM than FBOM, but similar across biomes, due to cross-biome contrasts in terrestrial litter sources. We predicted consistent stoichiometry of FBOM across biomes, because microbial colonization and processing homogenizes detritus (Findlay and others 2002), resulting in less variable quality and higher relative nutrient content in FBOM than CBOM. Finally, we hypothesized that macroinvertebrate shredders feeding on CBOM may be more likely to experience N and/or P limitation, than collector–gatherers feeding on FBOM due to a relative lack of nutrients in CBOM compared to FBOM.

METHODS

Study Sites

We sampled basal resources in four relatively undisturbed stream networks that represented distinct biomes: tropical montane forest, temperate deciduous forest, tallgrass prairie, and boreal forest (Table 1; Figure 1). The four stream networks are affiliated with the Luquillo, Coweeta, Konza Prairie, and Bonanza Creek Long Term Ecological Research (LTER) sites, respectively. The upper Río Mameyes (LUQ) is a fifth-order network in northeastern Puerto Rico that drains 17.80 km^2 of tropical montane forest, where streams are heavily shaded by a canopy dominated by tabonuco (*Dacryodes excelsa*) and sierra palm (*Prestoea montana*; Benstead and others 2010). Coweeta Creek (CWT) is a fifth-order network draining 15.32 km^2 in the southern Appalachian Mountains in North Carolina with streams heavily shaded by an overstory of temperate mixed hardwood species (primarily oak [*Quercus* spp.], tulip poplar [*Liriodendron tulipifera*], and red maple [*Acer rubrum*]) and a dense understory of *Rhododendron maximum* (Swank and Crossley 1988). Kings Creek (KNZ) is a fourth-order network draining 16.23 km^2 of tallgrass prairie in the Flint Hills of Kansas where stream flow is intermittent and floods occur seasonally. Riparian vegetation throughout the prairie watershed consists of gallery forests of oak (*Quercus macrocarpa*, *Q. muehlenbergii*), hackberry (*Celtis occidentalis*), and elm (*Ulmus americana*), and C$_4$ prairie grasses (e.g., *Andropogon gerardii*, *A. scoparius*, *Sorghastrum nutans*; Gray 1997; Veach and others 2014). Caribou Poker Creek (CPC) is a third-order network draining 104.00 km^2 of boreal forest in interior Alaska. The boreal stream network drains watersheds underlain by discontinuous permafrost, and riparian vegetation is dominated by dwarf shrubs (birch [*Betula glandulosa*], cranberry [*Vaccinium vitis-idaea* and *V. oxycoccus*], and blueberry [*Vaccinium uliginosum*]) and tussock-forming grasses and sedges (*Eriophorum* spp. and *Calamagrostis canadensis*; Haugen and others 1982).

Sampling occurred between February 2013 and March 2014 as part of the Scale, Consumers, and Lotic Ecosystem Rates (SCALER) project, and included 3–4 replicate samples each of CBOM and FBOM per reach, collected from up to 15 stream reaches across each stream network (Table 1). Sampled stream reaches within each network represented a range of stream sizes to capture gradients in discharge, elevation, and upstream drainage area (Table 1). Streams were sampled during baseflow (Rüegg and others 2015), and discharge was either measured by dilution gauging of salt slugs (Kilpatrick and Cobb 1985) or obtained from co-located USGS gauging stations. Dissolved inorganic N (DIN: nitrate [NO_3^-] and ammonium [NH_4^+]) and soluble reactive P (SRP) were analyzed using standard colorimetric methods (APHA 2005) or ion chromatography (NO_3^-) on water samples that were filtered (0.7 μm glass fiber) and frozen until analysis. Upstream drainage area, streambed slope, and elevation of study streams were calculated from a high-resolution digital elevation model of each drainage basin. Coordinates of the downstream end of each study reach were combined with a flow accumulation grid to calculate upstream drainage area (K. Sheehan, unpublished data).

Organic Matter Elemental Mass, Stoichiometry, and Isotopic Composition

Samples of coarse (> 1 mm, CBOM) and fine (< 1 mm, FBOM) benthic organic matter were collected from up to four transects distributed

Table 1. Physical and Chemical Characteristics of Stream Networks Sampled for Coarse (CBOM) and Fine (FBOM) Benthic Organic Matter Quality and Stoichiometry

Network	Biome	Sampling period(s)	Reaches (#)	Sample number (CBOM, FBOM)	Q (L s^{-1})	Elev. (m)	Upstream area (km^2)	DIN (μg L^{-1})	SRP (μg L^{-1})	DIN/SRP
Luquillo (LUQ)	Tropical montane forest	February–March 2013, March 2014	9[1]	60, 52	1.78–1472	77–673	0.09–17.80	92 ± 7	11 ± 1	20 ± 2
Coweeta (CWT)	Temperate deciduous forest	July–August 2013	15	45, 45	0.95–881	704–1025	0.09–15.32	72 ± 11	4 ± 1	63 ± 7
Konza (KNZ)	Tallgrass prairie	May–June 2013	4	15, 15	0.53–0.97	323–362	1.27–16.23	10 ± 1	8 ± 1	4 ± 1
Caribou Poker Creek (CPC)	Boreal forest	July–August 2013	8	29, 26	16.4–451	218–330	5.96–104.00	343 ± 31	1 ± 1	591 ± 70

Sampling periods indicate the months during which samples were collected. Reaches (#) indicates the number of total stream reaches sampled within each network; sample number indicates total CBOM and FBOM samples per biome, respectively. Dissolved inorganic nitrogen (DIN: nitrate [NO_3^-] and ammonium [NH_4^+]) and soluble reactive phosphorus (SRP) were measured at least once in each sampled reach. Values show the range encompassed by sampled streams, except DIN, SRP, and DIN/SRP, which report mean ± 1 SE for each network.

[1] *5 reaches sampled in both 2013 and 2014, 4 additional reaches (9 total) sampled in 2014.*

within each sampled stream reach. CBOM, which was a composite sample of terrestrially derived material (e.g., leaves, twigs, and small wood conditioned by microbial biofilms), was collected from the benthic surface by hand and stored in a polyethylene bag. FBOM was collected from the benthic surface using a 50-mL bulb syringe, or was subsampled after agitating surface sediments enclosed in an open-bottom bucket and stored in a 250-mL polyethylene bottle. All samples were stored on ice after collection and frozen (− 20°C) upon return to the laboratory.

All organic matter samples were processed at the University of Georgia Analytical Chemistry Lab (Athens, GA). Samples of both CBOM and FBOM were freeze-dried and then ground to a fine powder using a ball mill (SPEX SamplePrep, Metuchen, New Jersey, USA). Subsamples of each resource type (CBOM, FBOM) were analyzed for total C and N, as well as isotopic C and N ratios ($\delta^{13}C$, $\delta^{15}N$), with a CHN elemental analyzer (Carlo Erba NA-1500, Milan, Italy) coupled to a Thermo Delta V isotope ratio mass spectrometer via a Thermo Conflo III interface (Thermo Fisher Scientific, Bremen, Germany). Phosphorus concentrations of subsamples were analyzed colorimetrically following acid digestion (APHA 2005) using a spectrophotometer (Shimadzu UV-1800, Shimadzu Corporation, Kyoto, Japan) at 640 μm wavelength. Percent elemental content (%C, %N, %P) was calculated based on sample dry mass (CBOM: 100 mg, FBOM: ~ 25 mg). All elemental ratios are presented in molar units. Stable isotope signatures of CBOM and FBOM were calculated based on deviation from a standard ($\delta^{13}C$: Pee Dee Belemnite; $\delta^{15}N$: atmospheric N_2) using the following equation:

$$\delta X(‰) = \left(\frac{\delta X_{\text{sample}} - \delta X_{\text{standard}}}{\delta X_{\text{standard}}}\right) \times 1000,$$

where X is ^{13}C or ^{15}N (Peterson 1999). Repeatability was ± 0.08‰ for $\delta^{13}C$ and ± 0.10‰ for $\delta^{15}N$.

Consumer Threshold Elemental Ratios

We compared resource nutrient content to the nutritional requirements of macroinvertebrate shredders, which consume CBOM, and collector–gatherers, which consume FBOM, using estimated detritivore C/N and C/P threshold elemental ratios (TERs). TER estimates assumed an assimilation efficiency of 0.8 for both N and P, and a gross growth efficiency of 0.2 (sensu Tant and others 2013). We estimated a range of TERs for each detritivore functional feeding group (shredder,

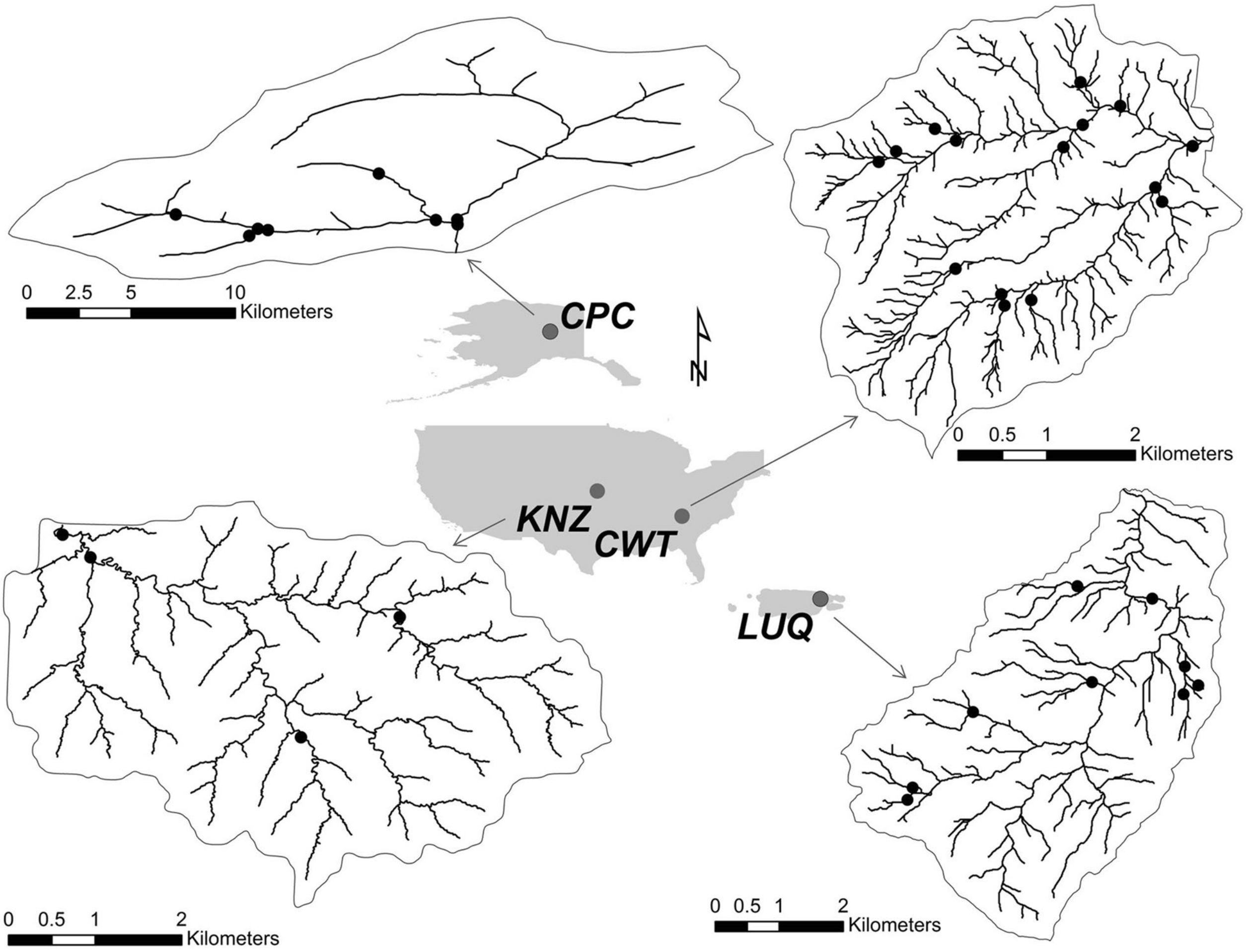

Figure 1. Sampled headwater stream networks in four biomes: tropical montane forest (Luquillo; LUQ), temperate deciduous forest (Coweeta; CWT), temperate tallgrass prairie (Konza Prairie; KNZ), and boreal forest (Caribou Poker Creek; CPC). Points indicate sites of basal resources collection within each network. Map of Puerto Rico is enlarged relative to contiguous United States and Alaska to show detail of network location. Note that scale bars vary by network. See text and Table 1 for site descriptions.

collector–gatherer) using the mean ± 1 SE of consumer body stoichiometry values reported by Cross and others (2003). Shredder body stoichiometry estimates were based on whole-body samples of Diptera (*Tipula* spp.), Plecoptera (*Leuctra* and *Tallaperla* spp.), and Trichoptera (*Fattigia*, *Lepidostoma*, *Pycnopsyche* spp.; Cross and others 2003). Collector–gatherers included Diptera (non-Tanypodinae Chironomidae, *Dixa*, and *Simulium* spp.), Ephemeroptera (*Stenonema* spp.), and Trichoptera (*Diplectrona* and *Parapsyche* spp.; Cross and others 2003). Although this approach is limited in that TERs were estimated based on macroinvertebrate taxa collected from a single location (CWT, Tant and others 2013), few published measurements of macroinvertebrate body stoichiometry for both C/N and C/P are available. In addition, there may be limited regional variation in the body stoichiometry of macroinvertebrates within taxonomic and functional groups (Evans-White and others 2005). We compared C/N and C/P TERs to the stoichiometric ratios of CBOM and FBOM to estimate whether stream detritivores in each biome were likely limited by C or nutrients (e.g., CBOM $\text{ratio}_{[\text{C/N or C/P}]} > \text{TER}_{\text{shredder C/N or C/P}}$ = N or P limitation; FBOM $\text{ratio}_{[\text{C/N or C/P}]} < \text{TER}_{\text{collector–gatherer C/N or C/P}}$ = C limitation). TER estimates provide an approximation of potential nutritional limitations for stream macroinvertebrates based on resource nutrient content.

Statistical Analyses

We used linear mixed effects models (lme4 package; Bates and others 2015) to test for differences in nutrient content (%C, %N, %P), stoichiometry (C/

N, C/P, N/P), and isotopic composition between CBOM and FBOM within and among biomes. For each model of nutrient content, stoichiometric ratio, or isotope, we included an interaction between categorical fixed effects of resource type (CBOM, FBOM) and biome, and a nested random effect of stream within biome to account for non-independence of replicate samples of resources within each stream. Degrees of freedom and *p* values were estimated using Satterthwaite's approximations in the 'lmerTest' package (Kuznetsova and others 2016). Post hoc comparisons of each resource type among biomes, and between resource types within a biome, were conducted based on least-squares means using the 'lsmeans' package (Lenth 2016).

To quantify the change in nutrient content (%C, %N, %P) and stoichiometry (C/N, C/P, N/P) between CBOM and FBOM among biomes, we first calculated the mean nutrient content and stoichiometry of each resource pool in each sampled stream. We then used the stream-level means to estimate the proportional change in nutrient content and stoichiometry between CBOM and FBOM (i.e., CBOM/FBOM), and compared the changes among biomes using one-way analysis of variance of the proportional change as a function of biome. Post hoc comparisons among biomes were conducted using 'lsmeans.'

To assess whether variability in nutrient content and stoichiometry differed between resource pools and among biomes, we calculated a coefficient of variation (CV) for CBOM and FBOM for each nutrient (%C, %N, %P) and ratio (C/N, C/P, N/P). CVs were calculated separately for CBOM and FBOM ($n = 3$–4 replicates each) within each sampled reach. Differences in the variability of each nutrient and ratio were assessed using linear mixed effects models with additive categorical fixed effects of resource (CBOM, FBOM) and biome, and a nested random effect of site within biome. *p* value estimation and post hoc testing were performed as described for the mixed effects models above. All analyses were conducted using R 3.4.3 and the 'tidyverse' package (R Core Team 2018; Wickham 2017).

RESULTS

Organic Matter Elemental Mass, Stoichiometry, and Isotopic Composition

CBOM had consistently higher C/nutrient ratios than FBOM, though significant interactions for all metrics indicated that there were biome-specific differences in the degree of change in nutrient content and stoichiometry between CBOM and FBOM (biome × resource type: %C: $F_{3,235.0} = 54.0$, $p < 0.001$; %N: $F_{3,237.4} = 20.0$, $p < 0.001$; %P: $F_{3,237.2} = 40.3$, $p < 0.001$; C/N: $F_{3,232.9} = 21.0$, $p < 0.001$; C/P: $F_{3,248.4} = 21.8$, $p < 0.001$; N/P: $F_{3,240.3} = 36.3$, $p < 0.001$). Across all biomes, CBOM had 5–9 times higher %C than FBOM ($F_{3,29} = 7.54$, $p = 0.001$; Figure 2A; Table 2), with larger differences between CBOM and FBOM at LUQ (tropical montane forest) than in other biomes (Figure 3A). Percent N was 1.5–2.5 times higher in CBOM than in FBOM ($F_{3,29} = 2.9$, $p = 0.052$; Figures 2B, 3B). There were biome-specific differences in %P between CBOM and FBOM ($F_{3,29} = 23.2$, $p < 0.001$; Figures 2C, 3C; Table 2); in KNZ (tallgrass prairie) and CPC (boreal forest), %P was 2–3 times higher in CBOM than FBOM, whereas in LUQ and CWT (temperate deciduous forest), %P was higher in FBOM than in CBOM (Figure 3C).

Differences in %C and %N between CBOM and FBOM resulted in significantly higher C/N and C/P ratios in CBOM than in FBOM (Figure 2D–E). Across all biomes, mean CBOM C/N was 2.5–4 times greater than FBOM C/N ($F_{3,29} = 4.25$, $p = 0.013$; Figure 3D), and mean CBOM C/P was 4–13 times greater than FBOM ($F_{3,29} = 10.6$, $p < 0.001$; Figure 3E). However, C/P in KNZ did not significantly differ between resources (Figure 2E). Samples from LUQ exhibited the highest degree of C/P reduction (~ 13 times) between CBOM and FBOM (Figure 3E) compared to the other three biomes. Differences in N/P between CBOM and FBOM were only significant in LUQ and CWT ($F_{3,29} = 19.5$, $p < 0.001$; Figure 2F), where CBOM N/P was 2–3 times higher than FBOM N/P (Figure 3F).

Isotopic signatures of both ^{13}C and ^{15}N were distinct between CBOM and FBOM, with site-specific differences in the degree of change between the resource pools. For ^{13}C, there was an interaction between sample type (CBOM, FBOM) and biome ($F_{3,196.4} = 196.36$, $p < 0.001$), and within each biome, CBOM was significantly depleted in ^{13}C relative to FBOM (Figure 4A). In both LUQ and CWT, CBOM ^{13}C signatures were similar to FBOM, with FBOM enriched an average of 2.13 and 0.76‰, respectively, relative to CBOM (Figure 4A). Differences in the ^{13}C signature between CBOM and FBOM were larger at CPC and KNZ, with FBOM at those sites enriched on average 4.22 and 11.34‰, respectively, relative to CBOM (Figure 4A). There was also a sample by biome interaction for ^{15}N ($F_{3,194.6} = 4.34$, $p = 0.005$). In all four biomes, FBOM was significantly enriched in ^{15}N relative to CBOM (Figure 4B), and the amount of enrichment was similar across biomes. Within biomes, average FBOM ^{15}N enrichment relative to CBOM ranged from 1.93‰ in KNZ to 3.29‰ in CPC, with intermediate enrichment in LUQ (2.54‰) and CWT (2.63‰; Figure 4B).

Variability in Elemental Mass and Stoichiometry of CBOM and FBOM

Variability, estimated by the coefficient of variation, of nutrient content and stoichiometric ratios of basal resources at the reach scale was generally higher for CBOM than FBOM (Figure 5A), though %C was more variable for FBOM than for CBOM ($F_{1,66} = 44.6$, $p < 0.001$). In contrast, CBOM was more variable than FBOM in %P ($F_{1,66} = 16.4$, $p < 0.001$), C/N ($F_{1,66} = 32.0$, $p < 0.001$), and C/P ($F_{1,66} = 13.0$, $p = 0.001$). Although variability between CBOM and FBOM was not different for %N ($F_{1,66} = 0.58$, $p = 0.45$) or N/P ($F_{1,66} = 0.86$, $p = 0.36$), there were significant differences among biomes in resource CV (Figure 5B). For both CBOM and FBOM, CVs for %N were higher at CWT than in other biomes ($F_{3,66} = 9.2$, $p < 0.001$), while N/P CVs at CWT were lower than at LUQ and CPC ($F_{3,66} = 4.7$, $p = 0.005$). In addition, C/P variability for both CBOM and FBOM was higher at CPC than in other biomes ($F_{3,66} = 6.2$, $p = 0.001$).

Organic Matter Stoichiometry and Consumer Threshold Elemental Ratios

Measured CBOM C/N and C/P were often above estimated TERs for aquatic detritivores that feed on CBOM (Figure 6A). Across biomes, 90% of CBOM samples had C/N values that exceeded the estimated mean shredder $\mathrm{TER}_{C/N}$ of 26.8 (Tant and others 2013). Within each biome, the proportion of CBOM samples that exceeded the $\mathrm{TER}_{C/N}$ ranged from 70% in CPC to 100% in CWT. CBOM C/P was not as strongly skewed above the estimated mean $\mathrm{TER}_{C/P}$ of 1992 (Tant and others 2013), though 59% of samples across biomes had higher C/P than the estimated $\mathrm{TER}_{C/P}$. The proportion of CBOM samples exceeding the $\mathrm{TER}_{C/P}$ ranged from 0% in KNZ to 80% in CWT. This suggests that if the estimated TERs are generally representative of shredding macroinvertebrates that feed on CBOM, many food resources from streams across our sampled biomes would result in nutrient (N and/or P) limitation, with 58% of CBOM samples indicating co-limitation of both N and P (Figure 6A).

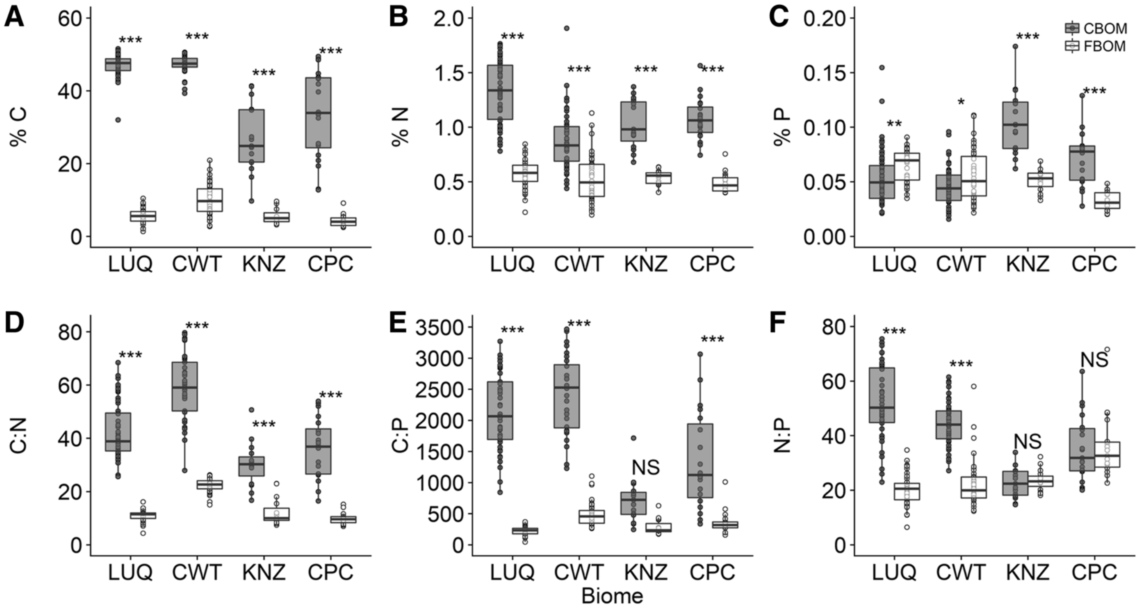

Figure 2. Percent elemental mass (**A** percent carbon [%C], **B** nitrogen [%N], and **C** phosphorus [%P]) and stoichiometric molar ratios (**D** carbon/nitrogen [C/N], **E** carbon/phosphorus [C/P], **F** nitrogen/phosphorus [N/P]) for coarse (CBOM; gray) and fine (FBOM; white) benthic organic matter within stream networks from four biomes (LUQ, CWT, KNZ, CPC). Boxes indicate 25th and 75th percentile, whereas whiskers indicate 10th and 90th percentile; points show individual samples. Asterisks indicate significant differences between CBOM and FBOM within each biome based on pairwise comparisons of least-squares means. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. *NS* not significant.

Table 2. Mean Values ± 1 SE for Coarse (CBOM) and Fine (FBOM) Benthic Organic Matter Nutrient Content (Percent Carbon [%C], Nitrogen [%N], and Phosphorus [%P]) and Molar Stoichiometric Ratios (C/N, C/P, N/P) from Sampled Streams in Four Stream Networks

	LUQ	CWT	KNZ	CPC
CBOM				
%C	47.0 ± 0.4 (32.0–51.5)^{a}	47.2 ± 0.4 (39.3–50.6)^{a}	26.9 ± 2.5 (9.7–41.3)^{b}	33.8 ± 2.7 (12.8–49.4)^{b}
%N	1.36 ± 0.04 (0.78–2.01)^{a}	0.88 ± 0.04 (0.44–1.91)^{b}	1.03 ± 0.06 (0.68–1.37)^{b}	1.07 ± 0.04 (0.74–1.56)^{b}
%P	0.05 ± 0.00 (0.02–0.15)^{b}	0.05 ± 0.00 (0.02–0.10)^{b}	0.10 ± 0.01 (0.06–0.17)^{a}	0.07 ± 0.01 (0.03–0.13)^{ab}
C/N	42.6 ± 1.3 (25.6–68.4)^{b}	68.6 ± 3.0 (27.9–121.6)^{a}	30.3 ± 2.2 (16.7–50.7)^{b}	36.3 ± 2.5 (16.5–53.9)^{b}
C/P	2657 ± 141 (843–5941)^{a}	3111 ± 203 (1228–7475)^{a}	721 ± 93 (246–1717)^{b}	1508 ± 237 (336–4603)^{b}
N/P	63.9 ± 3.5 (23.0–156.2)^{a}	44.4 ± 1.2 (27.2–61.5)^{b}	22.7 ± 1.5 (14.7–33.9)^{c}	37.7 ± 3.6 (20.1–85.4)^{bc}
FBOM				
%C	5.5 ± 0.3 (1.3–10.4)^{b}	10.1 ± 0.7 (2.7–20.9)^{a}	5.6 ± 0.6 (3.2–9.6)^{b}	4.0 ± 0.4 (2.5–9.1)^{b}
%N	0.57 ± 0.02 (0.22–0.85)^{a}	0.52 ± 0.03 (0.20–1.13)^{a}	0.54 ± 0.02 (0.40–0.64)^{a}	0.48 ± 0.02 (0.40–0.75)^{a}
%P	0.07 ± 0.00 (0.03–0.09)^{a}	0.05 ± 0.00 (0.02–0.11)^{a}	0.05 ± 0.00 (0.03–0.07)^{ab}	0.03 ± 0.00 (0.02–0.05)^{b}
C/N	11.06 ± 0.27 (4.4–16.1)^{b}	22.36 ± 0.37 (15.0–26.3)^{a}	12.27 ± 1.34 (7.4–23.0)^{b}	9.16 ± 0.49 (6.9–15.2)^{b}
C/P	223 ± 10 (45–370)^{b}	493 ± 29 (263–1103)^{a}	288 ± 33 (171–627)^{ab}	336 ± 35 (157–1010)^{ab}
N/P	20.1 ± 0.8 (6.4–34.7)^{b}	22.0 ± 1.3 (12.3–58.1)^{b}	23.7 ± 1.0 (18.1–32.3)^{ab}	35.4 ± 2.2 (22.6–71.6)^{a}

Values in parentheses indicate range of each constituent. Superscript letters indicate pairwise comparisons for nutrient content and stoichiometry of each resource type among biomes; different letters indicate significant ($p < 0.05$) differences.
LUQ = Luquillo; CWT = Coweeta; KNZ = Konza; CPC = Caribou Poker Creek.

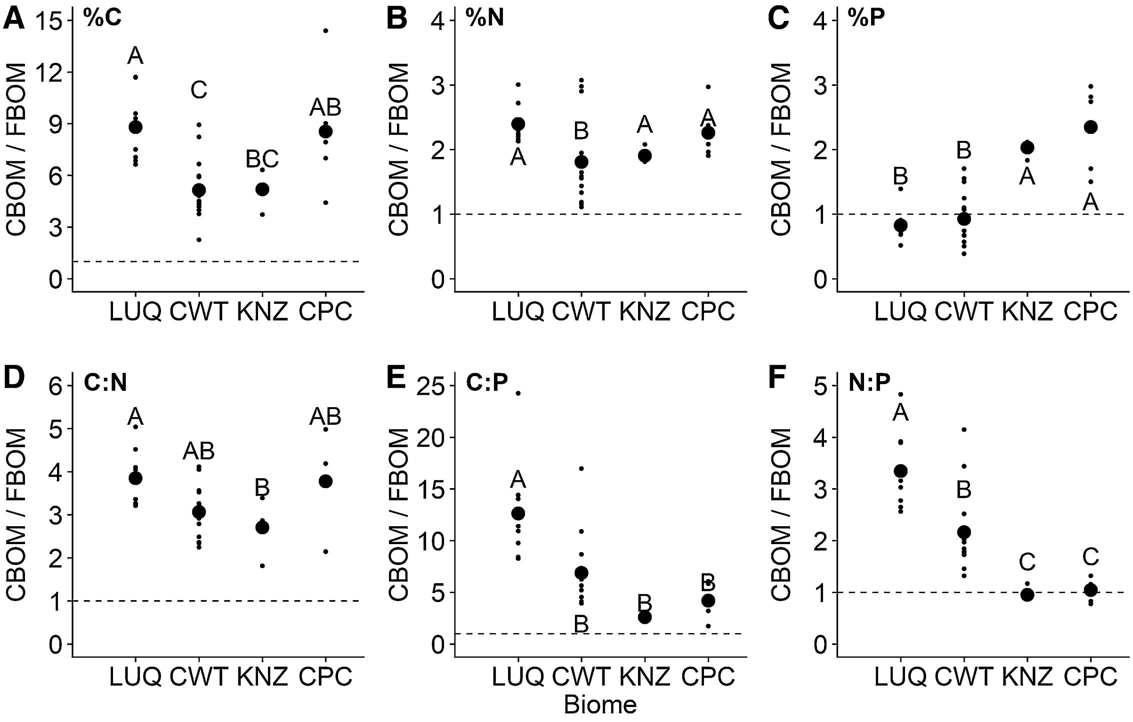

Figure 3. Proportional differences in nutrient content (**A** percent carbon [%C], **B** nitrogen [%N], and **C** phosphorus [%P]) and stoichiometric molar ratios (**D** carbon/nitrogen [C/N], **E** carbon/phosphorus [C/P], **F** nitrogen/phosphorus [N/P]) between CBOM and FBOM in four sampled biomes. Values represent CBOM/FBOM for each nutrient or ratio; small dots indicate stream means within a biome, and large dots indicate biome mean. Values above the dashed line (= 1) indicate higher nutrient content or ratios in CBOM than in FBOM; values below the dashed line indicate higher content or ratio in FBOM. Letters indicate significant differences ($p < 0.05$) between biomes based on pairwise comparisons of least-squares means. Note that extent of y-axis differs between panels.

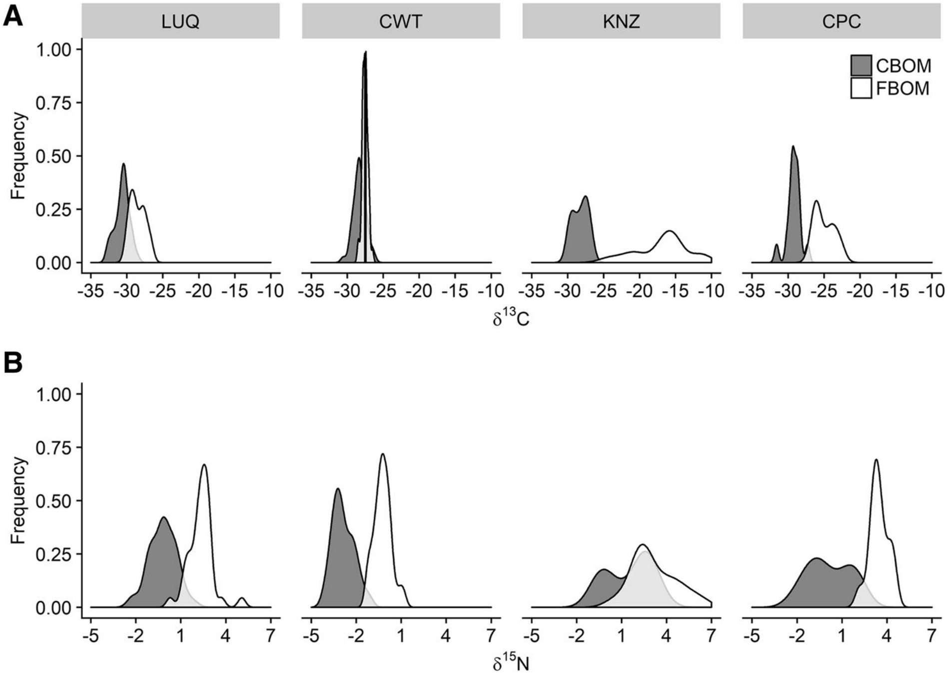

Figure 4. Smoothed density estimates of **A** carbon (δ^{13}C) and **B** nitrogen (δ^{15}N) stable isotopes in coarse (CBOM; gray) and fine (FBOM; white) benthic organic matter from streams in four biomes: tropical montane forest (Luquillo; LUQ), temperate deciduous forest (Coweeta; CWT), temperate tallgrass prairie (Konza Prairie; KNZ), and boreal forest (Caribou Poker Creek; CPC). Density estimates were computed and visualized using the 'tidyverse' package in R (R Core Team 2018; Wickham 2017).

In contrast, measured FBOM C/N and C/P were generally below TERs for collector–gatherers that feed on FBOM (Figure 6B). Among FBOM samples, only 3.9% had C/N that exceeded the estimated mean collector–gatherer $\mathrm{TER}_{\mathrm{C/N}}$ of 25.6 (Tant and others 2013), and all of those samples were from within the CWT network. No sampled FBOM had C/P above the estimated mean $\mathrm{TER}_{\mathrm{C/P}}$ of 1108 (Tant and others 2013).

DISCUSSION

Large-Scale Patterns in Detrital Stoichiometry

Among stream networks spanning a continental-scale extent, including tropical montane forest (LUQ), temperate deciduous forest (CWT), tallgrass prairie (KNZ), and boreal forest (CPC), we found relatively consistent patterns in the nutrient content, stoichiometry, and isotopic signatures between CBOM and FBOM basal resource pools. Although CBOM was higher in C and N relative to FBOM in all four biomes, CBOM tended to be lower quality than FBOM, with higher C/N in all four biomes and higher C/P in three biomes. CBOM also varied widely in its nutrient content, both within and among biomes. This variability in CBOM nutrient content was likely representative of the varying quality of allochthonous inputs to streams across biomes, which persisted despite likely microbial colonization and conditioning of litter inputs, both on the floodplain and in the streams. Variability in CBOM may also reflect the range of particle sizes that constituted the resource pool encompassing materials ranging from 1-mm leaf fragments to sticks. While FBOM was generally lower in nutrient content than CBOM (in %C, %N, and in two biomes, %P), it was lower in C/N and C/P and stoichiometric ratios were less variable (lower CVs) than in CBOM. This consistent pattern across biomes emphasizes the role of in-stream homogenization during the breakdown of CBOM with variable composition into FBOM that is less variable, through the combined actions of leaching, microbial and potentially algal colonization, macroinvertebrate breakdown, and other factors.

The observed enrichment in isotopic ^{13}C signatures of FBOM relative to CBOM across biomes is consistent with microbially driven enrichment of basal resources, as respiration of ^{12}C is favored during decomposition of organic matter in both terrestrial (Natelhoffer and Fry 1988) and aquatic (Finlay 2001) systems. FBOM was also enriched in

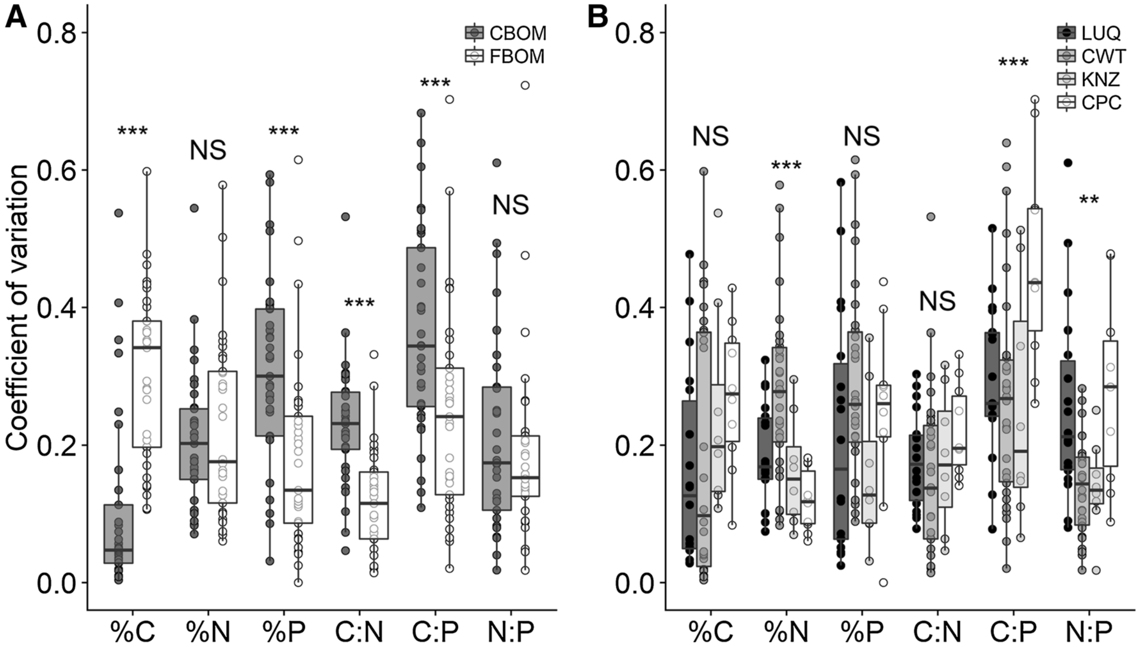

Figure 5. Coefficient of variation (CV) for percent elemental mass (%C, %N, %P) and molar ratios (C/N, C/P, and N/P) as a function of **A** resource type (coarse [CBOM] and fine [FBOM] benthic organic matter) and **B** sample biome. CVs were calculated separately for CBOM and FBOM (n = 3–4 replicates each) within each sampled stream reach. Boxes indicate 25th and 75th percentile, whereas whiskers indicate 10th and 90th percentile. Asterisks indicate significant differences between **A** CBOM and FBOM or **B** biome based on pairwise comparisons of least-squares means. ***p < 0.001; **p < 0.01; *p < 0.05. *NS* not significant.

^{15}N compared to CBOM across all four biomes, which is consistent with patterns of ^{15}N enrichment during soil decomposition (Natelhoffer and Fry 1988), and suggests that continued microbial colonization and processing of CBOM is contributing to changes in the isotopic signatures of stream basal resources. However, biome-specific differences in ^{13}C fractionation between CBOM and FBOM suggest that the relative contributions of different source materials to FBOM may differ among stream networks. In LUQ and CWT, mean FBOM ^{13}C signatures were within about 2‰ of CBOM signatures, indicating that FBOM in those streams aligned with CBOM signatures and that changes in isotopic signatures were driven by microbial decomposition of CBOM. In contrast, CPC and KNZ FBOM ^{13}C signatures were between about 4–11‰ more enriched than in CBOM, which may indicate that FBOM in those biomes is comprised of other components (e.g., algae, protozoans) not derived from CBOM. At KNZ specifically, the substantial ^{13}C enrichment of FBOM relative to CBOM suggests that FBOM may be derived from C4 prairie grasses and soil organic matter rather than C3 plant litters, as mean FBOM ^{13}C and C/N were similar to soil cores from tallgrass prairie that had major contributions of C4 roots (Still and others 2003). Future comparisons that include potential sources of terrestrial carbon (e.g., different litter or wood species) could help resolve the degree to which observed differences in ^{13}C and ^{15}N were driven by differences in source material for CBOM and FBOM, versus microbial processing of CBOM to FBOM in each biome.

The magnitude of differences in CBOM and FBOM stoichiometry varied among biomes. Both C/P and N/P changed more between CBOM and FBOM in LUQ than in other biomes. This may reflect a legacy of terrestrial detrital quality, as tropical forest species tend to have high rates of P resorption prior to litterfall (Vitousek 1984), resulting in particularly P-poor litter entering streams (Boyero and others 2017). In addition, tropical litters tend to have higher rates of P than N leaching (Schreeg and others 2013), which could contribute to higher C/P and N/P in LUQ CBOM than in CBOM from other biomes. The higher N/P in LUQ may also reflect higher %N in tropical than temperate leaf litter (Ardón and others 2009), and/or higher rates of biological N fixation in tropical forests (Cusack and others 2009). Interestingly, the N/P of CBOM and FBOM did not significantly differ in either KNZ or CPC (both %N and %P decreased in FBOM) and was similar to the N/P of FBOM in

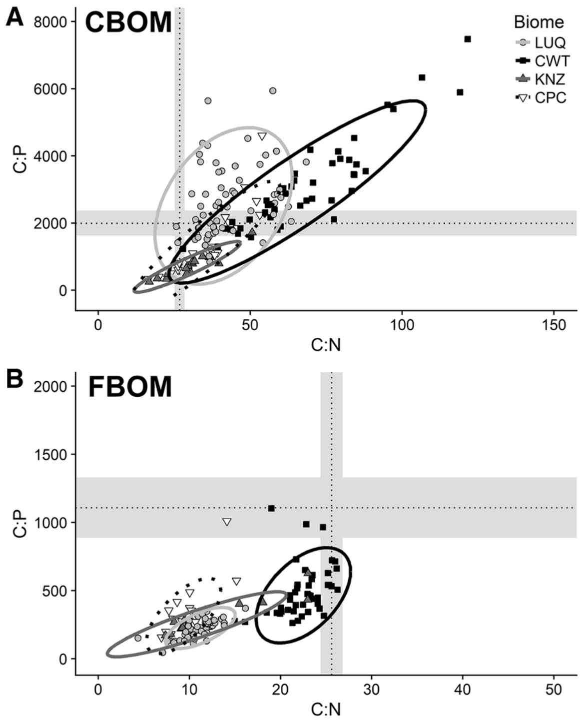

Figure 6. Carbon/phosphorus (C/P) ratios in relation to carbon/nitrogen (C/N) ratios for **A** coarse and **B** fine benthic organic matter in headwater stream networks in four biomes (*LUQ* light gray circle, *CWT* black square, *KNZ* dark gray triangle, *CPC* white upside down triangle). Ellipses indicate 95% confidence levels of sample points for each biome (*LUQ* light gray, *CWT* black, *KNZ* dark gray, *CPC* dotted black). Thin dotted black lines indicate mean threshold elemental ratios (TERs) of C/N (vertical) and C/P (horizontal) for macroinvertebrate **A** CBOM shredders and **B** FBOM collector–gatherers. Gray shaded areas correspond to the range of TERs estimated using ± 1 SE of body stoichiometry. Values below (C/P) or to the left (C/N) of the TER line indicate areas of potential consumer C limitation, whereas values above (C/P) and to the right (C/N) of the TER line indicate areas of P and N limitation, respectively. Note that axis limits differ between **A** and **B**.

LUQ and CWT. Although this pattern may reflect differences between streams in heavily forested biomes (LUQ, CWT) compared to biomes with a mixture of forest and herbaceous understory, it also suggests there may be a universal constraint on nutrient use during decomposition, based on microbial stoichiometries (Danger and others 2016).

Although we detected differences in CBOM and FBOM elemental mass, stoichiometry, and isotopic composition across space, our one-time sampling represents a snapshot of a temporally variable resource base. Streams in temperate forests, such as those at CWT, experience annual pulses of organic matter with autumn leaf fall (Benfield and others 2000). Conditioning by aquatic microbes changes the chemical composition of litter over time (Tant and others 2015; Manning and others 2016) and changes feeding rates by macroinvertebrates (Golladay and others 1983). In general, we collected benthic organic matter resources during summer, when litterfall and CBOM standing stocks in boreal and temperate streams are low relative to peak inputs in fall due to flushing from late spring snowmelt (Petrone and others 2006) and winter/spring processing by microbial and invertebrate consumers (Gray 1997; Benfield and others 2000). Although we sampled streams in Puerto Rico during winter, this coincided with the months of annual litterfall minima (Zou and others 1995; Silver and others 2014). At KNZ, sampling occurred during a period of prolonged drought (~ 1.5 years; Trentman 2015), and low flushing rates of organic matter may have allowed for increased microbial conditioning of organic matter, along with the potential for accumulations of algal material and other non-detrital FBOM components. Because our current analysis assumed that the standing stocks of sampled resource pools were similar in each network with respect to the duration of conditioning, some variability in resource stoichiometry across biomes could be due to differences in time since deposition or rate of decomposition in the stream.

Previous syntheses of terrestrial and lacustrine basal resources have found that despite some biome-specific differences, basal resource stoichiometry is similar within terrestrial and aquatic ecosystems (Elser and others 2000; McGroddy and others 2004; Cleveland and Liptzin 2007). In terrestrial ecosystems, litter C/N tends to be globally constant, despite biome-level differences in foliage stoichiometry, which reflects similar mechanisms of resorption across diverse species (McGroddy and others 2004). Ratios of CBOM C/N in this study were more similar to previously compiled ratios of green foliage than terrestrial litter (foliage: 43.6 ± 3.5; litter: 66.2 ± 6.3, McGroddy and others 2004), and mean C/P of CBOM fell between the values reported for foliage (1334 ± 138) and litter (3144 ± 342, McGroddy and others 2004). This may be due to counteracting processes of resorption of foliar nutrients and microbial conditioning of CBOM, as resorption of foliar nutrients prior to leaf senescence results in significantly higher C/N and C/P in litter than in foliage (McGroddy and others 2004), but in-stream colonization of CBOM by fungi and bacteria decrease litter C/N and C/P by increasing loss rates of C and immobilizing nutrients from the water column (Findlay and others

2002; Danger and others 2016). In our study, FBOM was similar to mean C/N and C/P ratios previously reported for lake seston (C/N 10.2 ± 0.2; C/P 307 ± 13, Elser and others 2000) and soils (C/N 14.3 ± 0.5; C/P 186.0 ± 12.9, Cleveland and Liptzin 2007), indicating that these composite pools of fine detritus and microorganisms are nutritionally similar across diverse ecosystem types. Although N/P ratios did not significantly differ between the terrestrial and lake resources compiled by Elser and others (2000), N/P of CBOM in our streams was significantly higher than terrestrial samples, and N/P of FBOM was intermediate between lake seston and soils. This indicates that stream resources tend to be enriched in N, relative to P, compared to patterns previously seen in lake and terrestrial data (Elser and others 2000), and may be the result of low water column SRP availability in our streams relative to DIN, particularly in CPC (Table 1). Differences in the N and P content of CBOM and FBOM may also be a function of relative colonization of fungi (which dominate on CBOM) and bacteria (which dominate on FBOM; Findlay and others 2002). Fungi can store P to a greater degree than N when it is available (Gulis and others 2017), which may help explain the variable %P we observed in CBOM across biomes.

Consumer–Resource Elemental Imbalances

Comparison of basal resource stoichiometry with TERs suggests that consumer–resource mismatches could be widespread in headwater streams across biomes yet differ among functional feeding groups. Our estimates of consumer nutrient limitation are constrained by the availability of calculated C/N and C/P TERs, but suggest that shredding macroinvertebrates that consume CBOM may be consistently limited by N and/or P. In contrast, collector–gatherers consuming FBOM may more often experience limitation by C than by N or P. If this is the case, we would expect shredders to contribute to C use and cycling in forested headwater streams, while collector–gatherers in those streams would play a larger role in mobilizing nutrients in order to obtain sufficient C (Sterner and Elser 2002; Cross and others 2005).

Detritivores tend to have low growth efficiencies due to consumption of low-quality (high C/nutrient) foods (Elser and others 2000), although resources that are rich in nutrients relative to C may also reduce consumer growth (Boersma and Elser 2006). Biome-specific differences in resource quality could affect the degree of nutrient limitation experienced by local consumers, as aquatic detritivore phylogeny is predicted to be a stronger driver of body stoichiometry, and thus nutrient limitation, than the local environment (Cross and others 2005 and references therein; Evans-White and others 2005). Higher-quality (low C/nutrient) CBOM, as was collected from KNZ and CPC, may reduce nutrient limitation for shredding detritivores in those streams, which could result in increased growth rates and survival of those organisms (Danger and others 2013). In contrast, shredders at LUQ and CWT may exhibit increased feeding rates through compensatory feeding on low-quality CBOM (Jochum and others 2017), though this may be less pronounced in LUQ as neotropical taxa may exhibit more generalist feeding behaviors than their temperate congeners (e.g., Tomanova and others 2006).

At the tallgrass prairie site (KNZ), potential C3 versus C4 sources for CBOM and FBOM, respectively, highlight limitations to predicting carbon or nutrient limitation based on bulk resources. Previous research has found that aquatic macroinvertebrate detritivores as well as other invertebrates and fishes tend to preferentially consume and assimilate C3 over C4 food resources, despite higher C/N ratios in C3 detritus that would suggest lower nutritional value (Hamilton and others 1992; Thorp and others 1998; Clapcott and Bunn 2003). This may be due in part to structural and nutrient availability differences in C4 detritus compared to C3 sources (Clapcott and Bunn 2003 and references therein). A full understanding of potential C and nutrient limitation in food webs thus requires further refinement of TERs to include variation in preference and assimilation of a wide variety of detrital carbon resources, particularly in regard to carbon quality.

Previous research has found that organisms experience unimodal growth responses to increasing food nutrient content (Boersma and Elser 2006 and references therein), which suggests that low C/P food resources could also reduce detritivore growth rates. This response to high-quality food is predicted to be particularly strong in detritivores that have evolved in chronically nutrient-stressed environments (Boersma and Elser 2006), which would include many minimally disturbed streams with low nutrient availability. Although shredder responses to high-quality foods may be biome specific, collector–gatherers feeding on relatively low C/nutrient FBOM may experience C limitation rather than nutrient limitation across all sampled biomes. An important caveat to our findings is that bulk resources are not necessarily indicative of consumer feeding, as selective feeding by macroinvertebrates may constrain the degree of nutrient limitation experienced compared to observed patterns of resource stoichiometry assessed from bulk samples (Hood and others 2014). Preferential assimilation of active versus refractory nutrients from basal resources may lead to mismatches between predicted and actual consumer limitation based on bulk resource stoichiometry (Dodds and others 2014), and both shredders and collector–gatherers are known to preferentially feed on non-detrital algal and microbial components of CBOM and FBOM, even in small headwater streams (e.g., Hall 1995; Mulholland and others 2000; Brett and others 2017). In addition, functional feeding groups (e.g., shredders, collector–gatherers) are broad categories that each include taxa representing a range of feeding specificity versus generality. Thus, our specific estimates of likely C or nutrient limitation may vary for specific taxa within a group, or among biomes due to differences in taxonomic composition of local functional feeding groups. Despite these limitations, our preliminary estimates of detritivore C and nutrient limitation indicate that consumer–resource imbalances may be widespread and that future studies that assess organism-specific gross assimilation and growth efficiencies will facilitate more specific estimates of consumer C or nutrient limitations (Halvorson and others 2015), and in turn, effects of these imbalances on C and nutrient cycling.

Potential Changes to Detrital Resources with Nutrient Enrichment

Headwater streams tend to be hotspots of nutrient retention (e.g., Peterson and others 2001), and understanding the magnitude and variability of resource stoichiometry in headwater networks from multiple biomes provides an important baseline for estimating the potential for nutrient uptake and retention in these systems. Specifically, documenting the magnitude and variability of basal resource stoichiometry can provide insights into coupled C and nutrient cycling and retention in streams. For example, nitrate availability is inversely correlated with organic carbon concentration across diverse ecosystems, including streams, due to constraints of microbial stoichiometry and thermodynamics (Taylor and Townsend 2010; Helton and others 2015). In streams, detritus is high in C relative to N and P, leading to low rates of N turnover (Dodds and others 2004) and high rates of P retention (Aldridge and others 2009). As N and P availability in streamwater increases through anthropogenic eutrophication, resource C/N and C/P are expected to decrease (e.g., Rosemond and others 2010; Manning and others 2015), and eventually reach a breakpoint beyond which biotic demand is fulfilled and N and P retention in streams decreases (e.g., Dodds and others 2004; Taylor and Townsend 2010). Even at low-to-moderate concentrations of nutrient enrichment in streams, reduced CBOM C/N and C/P ratios are associated with accelerated breakdown rates through microbial, fungal, and macroinvertebrate pathways (Woodward and others 2012; Kominoski and others 2015; Manning and others 2015). In addition, nutrient enrichment could affect the diversity of stream detritivores, as shredder and collector–gatherer richness tends to decrease with increasing streamwater P concentrations (Evans-White and others 2009). Because our samples were collected from relatively undisturbed headwater networks, information on their nutrient content and stoichiometry can provide a baseline against which to compare resources from nutrient enriched streams.

Our data provide a unique comparison of broad-scale variability in the stoichiometry of two basal resource pools and suggest potential implications of those ratios for consumers. This cross-biome assessment indicated despite %C, %N and sometimes %P being higher in CBOM than FBOM, that FBOM is consistently lower in C/N and C/P. This gives rise to the pattern that consumers of FBOM may broadly experience less nutrient (N and/or P) limitation than CBOM consumers. While further assessments of the variability of detrital resource quality over seasons and across additional geographic regions will advance our understanding of ecological stoichiometry in headwater streams, this study provides a first cross-site comparison to which future studies can add to enhance our understanding of the role of basal resource stoichiometry in stream biogeochemical processes.

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