



Flow is more Important than Temperature in Driving Patterns of Organic Matter Storage and Stoichiometry in Stream Ecosystems

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ABSTRACT

Understanding the connections between biological communities and elemental cycles is increasingly important given that alterations to both are occurring on a global scale. Biological control of elemental cycles is tied to patterns of biomass and the elemental stoichiometry of organisms and organic matter (OM) pools that comprise ecosystems. The structure and size of these ecosystem components are, in turn, shaped by key environmental factors that influence species composition, functional traits, and OM and element storage. In

stream and river ecosystems, temperature and flow regime have a strong influence on ecosystem structure and function, yet little is known about their relative importance in driving patterns of ecosystem OM and stoichiometry. We quantified ecosystem OM pools and elemental stoichiometry in 11 Icelandic streams across a wide gradient of temperature (~ 5 to 25 °C) and flow. Across these environmental gradients, we observed two orders of magnitude variation in ecosystem OM mass, as well as relatively large variation in certain ecosystem stoichiometries (that is, C:N, C:P). We found that flow regime was more important than temperature in driving variation in OM pools and stoichiometry because of large shifts in community structure, that is, from dominance by large-bodied macrophyte and bryophyte communities to epilithic and detrital OM pools. Although temperature is known to influence mass-specific rates of metabolic and chemical processes, our study suggests that the flow disturbance regime may be the dominant control on patterns of OM storage and may thus control ecosystem fluxes by constraining

Received 30 April 2020; accepted 30 October 2020

Electronic supplementary material: The online version of this article (<https://doi.org/10.1007/s10021-020-00585-6>) contains supplementary material, which is available to authorized users.

Author contributions: WFC, JPB, ADH, JMH, and JRJ conceived the study, all authors helped with study design, GMG and JSO provided field support and local arrangements, all authors contributed to data collection, JRJ performed analyses and wrote the first draft of the manuscript, and all authors provided input on further manuscript drafts.

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ecosystem OM pool mass, organism size structure, and stoichiometric traits.

Key words: Ecosystem biomass; Ecological stoichiometry; Temperature; Flow disturbance; Climate change; Species traits.

HIGHLIGHTS

- Flow was more important than temperature as a driver of BOM mass and stoichiometry.
- Mass, element composition, and stoichiometry of BOM were driven by species traits.
- Ecosystem N:P ratio was constrained despite a large range of mass and composition.

INTRODUCTION

Organisms influence the movement and storage of energy and elements within ecosystems through their collective metabolic processes. At the ecosystem level, energy and element fluxes are driven by two interconnected attributes: (1) the amount and composition of organic matter (OM), and (2) the metabolic activities of biomass components. Predicting the actual magnitude of fluxes consequently requires knowledge of OM pool sizes, elemental composition of these pools, and the size structure of constituent organisms (Allen and others 2005; Michaletz and others 2014; Padfield and others 2017). The controls on these factors are complex and are therefore difficult to predict. Yet, elucidating the environmental factors that control OM pool size and associated elemental content will be essential for understanding how energy and element fluxes may respond to global change.

Ecological responses to global change are mediated through species traits and how these traits are filtered by environmental variables such as temperature, disturbance, and the physiochemical environment (Norberg and others 2001; Enquist and others 2015). Many morphological and physiological traits influence organismal biomass and elemental composition (that is, organismal stoichiometry; Elser and others 1996; Woods and others 2004; Kerkhoff and Enquist 2006; Meunier and others 2017). A key trait in this regard is body size, which influences both the potential accrual of biomass and the relative balance of elements in tissue. Large-bodied organisms often maintain higher population biomass (Kerkhoff and Enquist

2006) and tend toward higher individual C:nutrient ratios than smaller organisms (Woods and others 2004; Kerkhoff and others 2005). As a consequence, the distribution of body sizes within the community has the potential to shape patterns in the accrual and stoichiometry of organic matter at the ecosystem level. Further, the accumulation and coupling of energy and elements is likely to depend on how environmental filters constrain organismal traits and the relative size of stoichiometrically distinct OM pools, both living and detrital (Keddy 1992; Grime 1998; Sistla and Schimel 2012; Cohen and others 2013).

Temperature acts as a principle environmental filter governing community assembly, community structure (Huey and Stevenson 1979), and individual metabolism (Gillooly and others 2001). Although temperature is known to have a strong influence on OM *fluxes* through its control of mass-specific rates of primary production and respiration (Allen and others 2005; Yvon-Durocher and others 2012), the effects of temperature on OM *pools* are less well understood. In general, the size of ecosystem OM pools should be a function of inputs (autochthonous production + allochthonous inputs) minus outputs (ecosystem respiration + export). Thus, if it is assumed that allochthonous inputs and export are held constant, the response of OM pool sizes to temperature should be determined by the balance of primary production and ecosystem respiration. From an ecosystem perspective, theory and empirical research suggests (Allen and others 2005; Michaletz and others 2014) that temperature should have minimal influence on the size of living autotroph pools because autotrophic respiration is constrained by photosynthesis and thus thermal effects on autotrophic gains and losses should be balanced. In contrast, warmer temperatures are predicted to reduce storage of detrital OM pools because of the steeper temperature dependence of microbial consumption (that is, detrital loss) relative to that of OM production and senescence by autotrophs (that is, detrital gains; Allen and others 2005). Other research has taken a more population-level perspective (Savage and others 2004; Bernhardt and others 2018) suggesting, in contrast, that population carrying capacities of both autotrophs and heterotrophs should decline with temperature as a result of increased per-capita metabolic demands on a fixed resource base. Clearly, given the contrasting nature of these studies, additional research—both theoretical and empirical—is needed to elucidate potential effects of temperature on ecosystem OM pools.

Such understanding, however, may be made more difficult if other environmental factors obscure or override the influence of temperature. One such factor is the disturbance regime, which has long been recognized as a strong determinant of ecosystem pattern and process (Pickett and White 1985). In stream and river ecosystems, patterns of stream flow (that is, the flow regime) can play a dominant role in influencing species composition and ecosystem characteristics (Poff 1997; Allan and Castillo 2007), as well as OM accumulation. Indeed, many stream organisms have evolved specific morphological, physiological, and life-history attributes in response to a system's flow regime (Resh and others 1988; Lytle and Poff 2004). As such, the flow regime likely structures patterns of ecosystem OM mass and stoichiometry, not only by increasing the downstream export of OM, but through shifts in species composition and traits. For example, high frequency floods can prevent the establishment of larger-sized primary producers such as bryophytes and macrophytes (Riis and Biggs 2003). In turn, this shift in average size may have large consequences for ecosystem biomass and stoichiometry. Thus, any potential influence of temperature on patterns of OM mass and stoichiometry must be considered in the context of other environmental filters—such as disturbance—that shape biological communities and species trait distributions (for example, organism size, organismal stoichiometry; Meunier and others 2017).

To better understand the role of temperature and disturbance regime in shaping ecosystem-level OM mass, its distribution among living and non-living compartments, and its elemental stoichiometry, we leveraged a 'natural geothermal laboratory' in Iceland that contains many small streams along a steep gradient of both temperature and flow characteristics (O'Gorman and others 2014). Although these streams vary considerably in these two factors, they have relatively similar chemical composition, as well as minimal allochthonous OM inputs. As such, this set of streams provides a unique opportunity to examine the relative influence of temperature and flow regime on autochthonously derived OM pools. Previous empirical measurements in this study system provide a basis for predicting the effects of temperature on biologically mediated OM production and consumption. Demars and others (2011, 2016) showed that gross primary production (GPP) and whole-ecosystem respiration (ER) measured over short time periods exhibit similar temperature dependences. Thus, if temperature is the dominant control on OM storage, we predicted that gains and

losses of OM should balance, leading to a null effect of temperature on equilibrium OM pool sizes. With respect to OM stoichiometry, we predicted that warmer temperatures would favor tissue or taxa with reduced nutrient content, reflecting population or community shifts toward individuals or taxa with increased nutrient use efficiency (Rhee and Gotham 1981; Woods and others 2003; Cross and others 2015). In addition, if flow regime is the dominant control on OM accumulation, export, and community composition, we expected that flow could modify, or even override, expectations based on temperature alone, leading to wide variation in OM pool sizes and ecosystem stoichiometry. In this case, greater flow-mediated disturbance is expected to reduce the size of dominant primary producers and thus total OM mass, as well as reduce the C:nutrient ratios of OM pools.

METHODS

Study Area

Our study was conducted in 11 first- or second-order grassland streams near the Hengill geothermal field of southwestern Iceland (64° 03' N 021° 18' W; Figure S1), a region with high spatial heterogeneity in geothermal activity. Ten streams were located within the Hengladalsá river valley, and one was located in the Hveragerði watershed about 6 km to the southeast. Geothermal heating of groundwater in this area is indirect (Árnason and others 1969), resulting in large variation in stream temperature (mean annual stream temperature range: 4.5–54.0 °C) but similar water solute chemistries (Friberg and others 2009). These streams also vary in watershed size, position, and the magnitude of surface water influx during precipitation events and snowmelt, leading to variation in stream flow regime and disturbance (see below and Figure S2).

Physicochemical Measurements

In each stream, we measured a suite of stream physicochemical variables. We measured water temperature and stage height every 15 min beginning in July 2010 through July 2016 using Onset U20-001-01 water-level loggers (Onset Computer Corp. Pocasset, MA, U.S.A). To quantify stream flow characteristics, we first estimated stream discharge using depth-discharge relationships based on salt dilution gauging ($n = 7\text{--}13$ salt releases per stream). These predictive equations were used to construct time series of hourly discharge (Gore 2006), and to derive important characteristics of

the annual flow regime, including: median discharge, maximum discharge, and the coefficient of variation of stream discharge (CV_Q). In addition, we measured wetted width, stream slope, and sediment size distributions to characterize how stream flow may interact with the stream bed. Wetted width (m) was measured with a meter stick at stream transects every meter along the length of each stream. Wolman pebble counts (Wolman 1954) were used to calculate sediment size distributions from 100 particles in each stream. The intermediate axis of each particle was measured (± 1 mm). For particles that were too large to remove, the shortest axis accessible was measured.

Water surface slope (cm/m) was measured along the full length of each stream reach (~ 30 – 120 m) once using a meter stick and line level. Stream slope was combined with discharge to create a time series of estimated stream power (Ω), a measure of the rate of energy dissipation against the streambed and a proxy for energy available to move sediment (Gordon and others 2004):

$$\Omega = 1000 \cdot 9.8 \cdot Q \cdot S \quad (1)$$

here Ω is stream power in Watts, 1000 (kg/m^3) is the density of water, 9.8 (m/s^2) is the acceleration due to gravity, Q is stream discharge (m^3/s), and S is mean channel slope.

Water samples were collected in July 2011, passed through $0.45\text{-}\mu\text{m}$ glass-fiber filters, and analyzed for dissolved inorganic nitrogen (DIN: ammonium-N and nitrate-N), and soluble reactive phosphorus (SRP) concentrations. Ammonium concentrations were measured using the orthophthalaldehyde fluorometric method (Holmes and others 1999; as modified by Taylor and others 2007). Nitrate concentrations were measured using ion chromatography (Dionex ICS 2000; Dionex Corp. Sunnydale, CA, USA), and SRP concentrations were measured using the ascorbic acid method (Murphy and Riley 1962). Mean nutrient concentrations, daily discharge, and area stream bed measurements were used to estimate daily mean areal nutrient flux as a measure of nutrient supply ($\text{mol m}^{-2} \text{d}^{-1}$; King and others 2014).

Benthic Organic Matter

In these grassland streams, there are minimal allochthonous OM inputs and benthic organic matter (BOM) consists of macrophytes, epilithic and colonial algae and cyanobacteria, along with coarse and fine particulate organic matter (that is, CBOM, FBOM; Gudmundsdottir and others 2011). We comprehensively sampled BOM pools in each

stream in August 2012 to capture peak biomass and maximum potential temperature effects. We sampled both attached (epilithic and rooted) and interstitial BOM with a modified core sampler (area = 0.09 m^2 , $n = 5$ per stream). We characterized attached BOM as the ‘green’ fraction and interstitial BOM as the ‘brown’ fraction because these components were dominated by either living or detrital material, respectively. The ‘green’ fraction was sampled by removing biomass from rock and benthic surfaces with shears and/or a wire brush. The loose ‘brown’ fraction was sampled by disturbing the water and top about 10 cm of sediment within the core sampler to suspend and homogenize BOM; a subsample of known volume was then quickly removed from the slurry. For both fractions, samples were rinsed into a 1-mm sieve to separate coarse (> 1 mm) and fine (< 1 mm) fractions. Samples were frozen until laboratory analysis, during which invertebrates were removed and the coarse BOM was further split into species or functional group using appropriate identification keys (Stefansson 1948; Jóhannsson 2003). Large coarse samples were subsampled (1/2–1/8) and the relative mass of each species or functional group was scaled to the total mass of each sample. Total water volume in the sampler was determined by measuring the water depth in three locations within the core sampler and calculating the total volume based on the core sampler dimensions. When subsamples were taken, the ratio of total sample volume to subsample volume was used to estimate total sample BOM from the subsample.

Following separation into compartments, BOM samples were dried in an oven at 50°C to a constant mass (> 48 h) and weighed to estimate dry mass (g). Ash-free dry mass (g AFDM) was quantified by weighing a dried subsample, combusting the sample in a muffle furnace at 500°C for 4 h, and reweighing. The OM content was calculated as the difference between dry mass and post-combustion mass as a percentage of total initial dry mass. All BOM estimates were reported on a per-square-meter basis.

Elemental Concentration and Stoichiometry of BOM

In each stream, we measured carbon (C), nitrogen (N), and phosphorus (P) content of each species or functional group as well as other BOM compartments (for example, fine BOM). Subsamples of dried BOM were weighed into tin capsules for analysis of %C and %N using a Costech elemental

analyzer (Costech Analytical Tech. Inc. Valencia, CA, U.S.A). Acetanilide standards were used as an external standard for C and N analyses (average recovery was 98% and 99% for %C and %N, respectively). Phosphorus content was quantified using persulfate digestion and the ascorbic acid method (APHA [American Public Health Association] 1992). Bovine muscle was used as an external standard for P analysis (average recovery was 97%). Total C, N, and P for each BOM compartment was quantified by multiplying the nutrient content of each compartment by the compartment dry mass. Because of the large contribution of inorganic mass in fine fractions, nutrient content was adjusted to organic matter content (for example, g C AFDM⁻¹ versus g C bulk dry mass⁻¹) to allow comparison of nutrient content of fine BOM fractions among streams. Compartment C, N, and P mass was summed across all compartments and standardized to a per-square-meter basis to estimate ecosystem-level BOM C, N, and P pools. We described BOM pools in units of g C m⁻² for compartment- and ecosystem-level BOM. Elemental ratios were calculated on a molar basis for BOM compartments and ecosystem-level BOM.

Statistical Analyses

The influence of stream flow on BOM is complex because it includes direct effects of flow as well as indirect effects of flow on sediment movement and size distribution. We therefore selected a set of variables that capture both basic characteristics of the flow environment and proxies of flow-sediment interactions. Some of these variables were correlated with one another, but together these helped to capture the complex ways that flow may influence BOM. To account for correlation among flow variables, we used a principal components analysis (PCA) to consolidate stream flow variables into fewer, orthogonal axes. PCA axes were then used as a proxy of the stream flow environment to assess the influence of stream flow on patterns of BOM mass, composition, and stoichiometry. Variables included in the PCA were: median discharge, median velocity, discharge coefficient of variation (CV_Q), channel slope, maximum power, and median substrate size. For statistical analyses, we included only PCA axes with eigenvalues greater than one.

We used an information-theoretic framework based upon Akaike's Information Criterion adjusted for small data sets (AICc; Burnham and Anderson 2002) to select among competing hypotheses regarding the individual and interactive

effects of temperature and flow on BOM characteristics (see Supplemental Materials). In these models, temperature was represented by mean annual stream temperature and flow was characterized by selected principal component axes. We compared five models that included assessment of the influence of temperature and flow individually, an additive model, an interactive model, and an intercept-only model. When necessary, ecosystem BOM and elemental mass were log₁₀-transformed to meet model assumptions of normality. Exploratory plots and residual variation of linear models were examined to identify potential non-linear relationships between explanatory and response variables. Residual analysis and added-variable plots were used to assess and visualize the effects of individual variables in multivariate models.

To characterize and compare the BOM pool composition among streams, we conducted non-metric multidimensional scaling (NMDS) analysis on Bray–Curtis distance matrices of OM component C mass using the *vegan* package (Oksanen and others 2019) in R (R Core Team 2016). Differences in BOM composition were then assessed with a permutational multivariate analysis of variance (PERMANOVA) using the 'adonis' function in the *vegan* package. We fitted environmental vectors onto the NMDS ordination using the 'envfit' function in *vegan* to examine environmental variables associated with variation in BOM composition.

Differences in elemental content and stoichiometry among BOM compartments (for example, *Fontinalis antipyretica*, biofilm, CBOM, FBOM) were assessed with multivariate analysis of variance (MANOVA) and subsequent analysis of variance (ANOVA). Relationships between ecosystem BOM C, N, and P pools were assessed using reduced major axis regression with the *lmodel2* package in R (Legendre 2018). Reduced major axis regression accounts for variability in both explanatory and response variables rather than the response variables alone.

RESULTS

Stream Physicochemical Variables

The study streams exhibited wide variation in mean annual temperature, ranging from 4.8 to 27.4 °C (Table 1). Streams also varied with respect to multiple hydrologic and geomorphologic variables (Table 1; Figure S3). Dissolved nutrient concentrations were relatively low, ranging from 3.0 to

Table 1. Physical and Chemical Characteristics of the Study Streams.

Stream	Temperature (°C)	Median Discharge (L/s)	CV _Q	Substrate (D ₅₀)	Slope (cm/m)	DIN (NO ₃ ⁻ + NH ₄ ⁺ μg L ⁻¹)	SRP (SRP μg L ⁻¹)	DIN:SRP (molar)
hver	27.4	21.0	0.99	11.6	1.0	6.8 ± 0.5	21.9 ± 4.3	0.7
st8	20.5	23.1	0.12	40.3	14.5	5.8 ± 3.4	29.6 ± 2.2	0.4
st6	17.5	13.7	0.44	47.0	6.9	26.4 ± 1.2	29.2 ± 2.0	2.0
st5	15.9	22.7	0.17	21.0	3.0	9.3 ± 1.0	28.5 ± 5.3	0.7
st9	11.0	3.0	1.06	30.0	14.7	3.0 ± 1.7	32.7 ± 2.7	0.2
st1	10.7	36.4	0.40	4.0	1.8	6.5 ± 1.0	7.3 ± 3.9	2.0
st11U	7.4	6.6	0.98	18.0	5.5	4.3 ± 1.0	15.9 ± 6.5	0.6
st13	5.7	14.6	0.11	5.0	2.9	5.9 ± 4.0	12.3 ± 1.9	1.1
st11L	5.2	16.8	1.41	45.0	5.7	3.9 ± 0.54	21.1 ± 5.4	0.4
st14	4.8	12.5	2.31	39.5	4.2	25.1 ± 0.9	12.7 ± 1.6	4.4
st17	4.8	117.8	1.21	22.0	0.6	5.8 ± 0.3	9.5 ± 1.1	1.3

Temperature and discharge represent the mean annual values. CV_Q is the coefficient of variation in stream discharge. Dissolved nutrient values represent the mean ± 1 standard deviation from replicate samples taken in July.

26.4 μg L⁻¹ inorganic nitrogen (DIN; NO₃⁻ + NH₄⁺) and 7.3 to 32.7 μg L⁻¹ soluble reactive phosphorus (SRP; Table 1). Dissolved molar N:P ratios ranged from 0.2:1 to 4.4:1 (Table 1). Physicochemical variables showed relatively little association with temperature, except for SRP which was positively associated with temperature (Table S1).

Principal components analysis of flow characteristics captured 73% of the variation among streams in the first two component axes (Figure S3). Principal component axes one (flow PC1) and two (flow PC2) showed little to modest association with temperature (Spearman's $\rho = 0.43$ and -0.05 , respectively; Table S1), but variability around these correlation coefficients overlapped with zero. Flow PC1 showed moderate association with specific stream flow variables, including discharge variability (CV_Q) and maximum stream power, while flow PC2 showed moderate association with stream slope, median substrate size, velocity, median discharge (Table S1).

Patterns of BOM Mass and Their Relationship to Environmental Variables

In contrast to our predictions based on temperature alone (that is, no effect of temperature on BOM), ecosystem-level BOM varied two orders of magnitude among streams (from 2.0 to 209.5 g C m⁻²; Figure 1A). BOM mass showed univariate associations with both temperature (Spearman's $\rho = 0.34$; Figure 2A) and flow characteristics (Spearman's $\rho = 0.45$ & 0.61 for flow PC1 and flow PC2; Figure 2B, C). However, the model selection analysis

of competing hypothetical models found that the flow-only model had the most support in explaining BOM mass (flow PC1 + flow PC2; Figure 2E, F), while the temperature-only and more complex additive and interactive models had considerably less support ($\Delta\text{AICc} > 2$; Table 2) relative to the top model. Residual analysis further confirmed that unexplained variation was relatively small and mean annual stream temperature was not associated with total BOM mass after accounting for the effects of flow ($r^2 = 0.04$, Figure 2D) supporting our prediction that BOM mass does not vary with temperature.

BOM Composition and Relationship to Environmental Variables

The composition of ecosystem BOM varied widely among streams (PERMANOVA; $P = < 0.001$; $r^2 = 0.59$) but was generally characterized by two broad categories: (1) streams with relatively large-sized primary producers (for example, macrophytes, bryophytes, and colonial microbial autotrophs), and (2) streams dominated by biofilms and detrital pools (that is, CBOM, FBOM) and lacking large-sized taxa (Figure 1A; Figure S4). Of the streams with large-sized taxa, the bryophyte *Fontinalis antipyretica* was the most common (Figure 1A). Other larger and colonial microbial compartments included the liverwort *Jungermannia exsertifolia*, macrophytes of the genus *Callitriche* spp., *Veronica* sp., a few emergent plant species such as *Equisetum* sp., filamentous green algae, and the cyanobacteria group *Nostoc* spp. Non-metric multi-dimensional scaling showed the two relatively

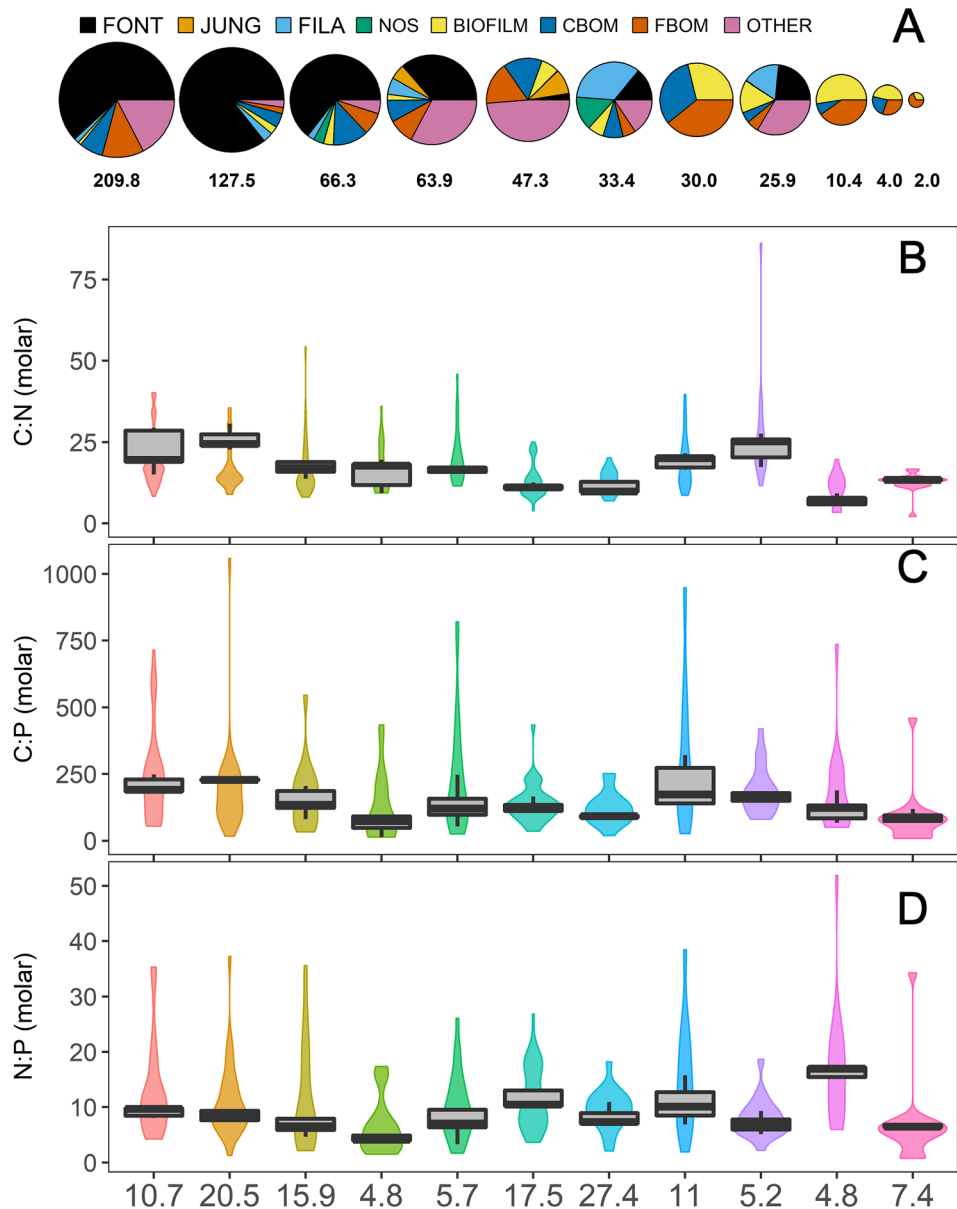


Figure 1. Stream ecosystem patterns of total benthic organic matter mass (BOM; **A**) and composition. The size of each pie is scaled to the ecosystem BOM mass in g C m^{-2} (printed below each pie). Organic matter compartment abbreviations are: “FONT” = *Fontinalis antipyretica*, “JUNG” = *Jungermannia exsertifolia*, “FILA” = Filamentous algae, “NOS” = *Nostoc* spp., “BIOFILM” = epilithic biofilm, “CBOM” = coarse benthic organic matter, “FBOM” = fine benthic organic matter, and “OTHER” = other macrophyte and bryophyte species. The stoichiometry of aggregate ecosystem BOM (boxplots) and individual biomass compartments (violin plots) are shown in panels **B–D**. Stoichiometry is presented in molar ratios of C:N (**B**), C:P (**C**), and N:P (**D**). Mean annual temperature ($^{\circ}\text{C}$) of each stream is printed on the *x*-axis.

distinct community types (that is, with or without large-sized taxa) generally aligned along flow PC1 (Figure S4). This axis was positively associated with the dominant bryophyte, *Fontinalis antipyretica*, and negatively associated with CV_Q (Table S1, Figure S4). Temperature was positively associated with the relative abundance of filamentous algae and the cyanobacteria group,

Nostoc spp., but these categories were only prominent in two of the 11 streams. In addition, SRP concentration was associated with a higher relative abundance of filamentous algae and *Nostoc* spp. (Figure S4).

Ecosystem-level BOM mass was associated with the relative proportions of ‘green’ and ‘brown’ BOM pools (Figure S5, Figure S6). Generally,

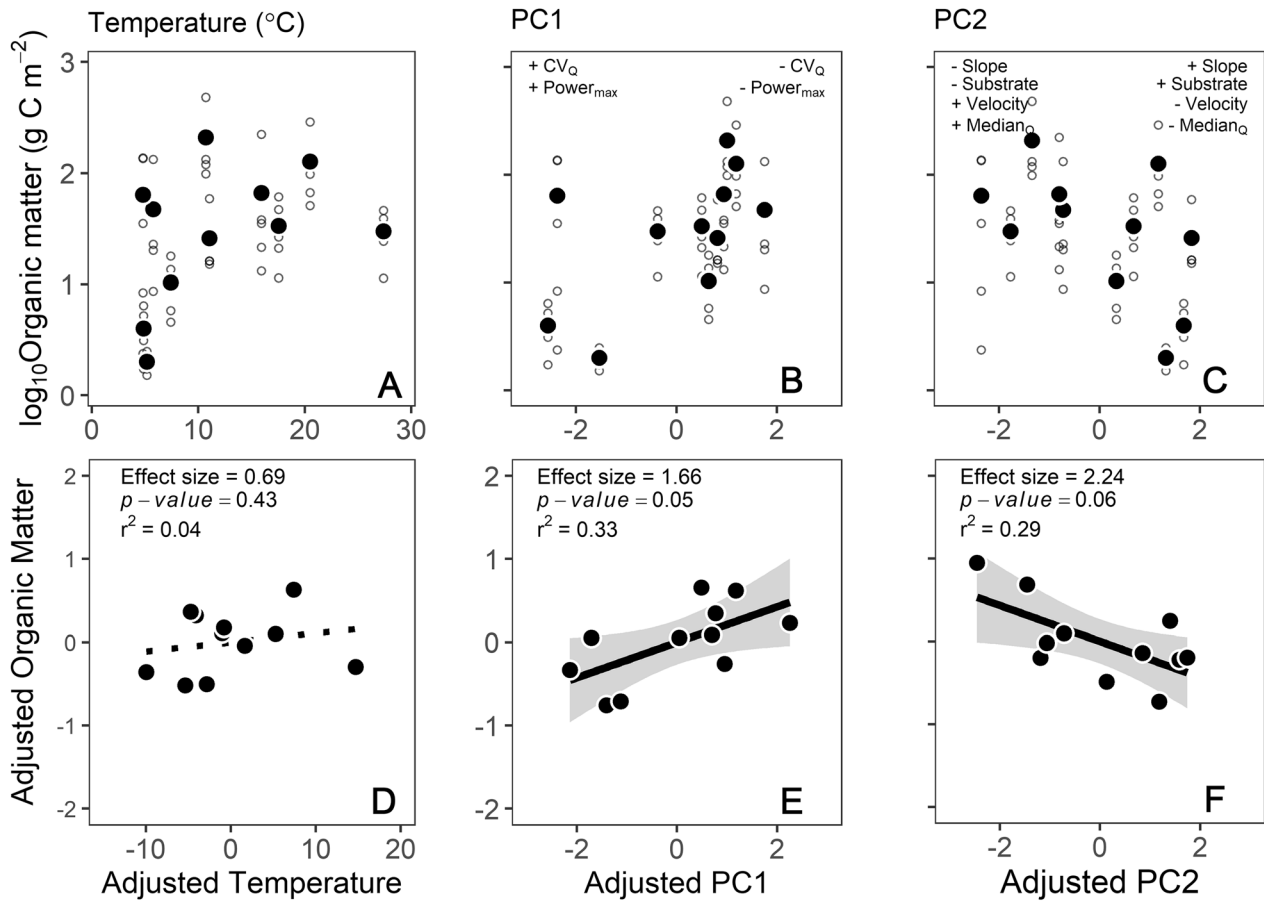


Figure 2. Bivariate relationships between annual mean temperature ($^{\circ}\text{C}$; **A**), principal component one (flow PC1; **B**), principal component two (flow PC2; **C**), and \log_{10} -transformed benthic organic matter (BOM; g C m^{-2}). Large filled symbols represent the mean BOM mass for each stream, while individual samples are shown with small open symbols. Variables most strongly associated with principal component axes ($|r| > 0.40$) are listed on raw principal plots (**B** & **C**). Added variable plots (**D–F**) of each variable were constructed based on the additive multivariate linear regression model: $\log_{10}(\text{BOM}) \sim \text{flow PC1} + \text{flow PC2} + \text{Temperature}$. Added variable plots show the relationship between each explanatory variable (**D** temperature, **E** flow PC1, **F** flow PC2) and \log_{10} -transformed BOM mass while holding the other variables constant.

Table 2. Model Selection Results Examining the Drivers of Ecosystem BOM Mass Using Akaike’s Information Criterion Corrected for Small Sample Sizes (AICc).

Model	<i>K</i>	AICc	ΔAICc	ModelLik	AICc wt	LL	Cum. wt
Flow	4	23.4	0.00	1.00	0.82	– 4.38	0.82
Temp	3	26.8	3.35	0.19	0.15	– 8.68	0.97
Flow + Temp	5	30.3	6.89	0.03	0.03	– 4.16	1.00
Intercept	2	43.6	20.18	0.00	0.00	– 20.59	1.00
Flow*Temp	7	47.8	24.38	0.00	0.00	1.76	1.00

K is the number of model terms in each model. ΔAICc represents the change in model AICc from the top model. LL represents the model log-likelihood.

streams with high BOM mass were dominated by larger-sized producers (for example, macrophytes and bryophytes) and attached living biomass. In

contrast, streams with low BOM mass were dominated by detrital pools and epilithic biofilms (Figure 1A).

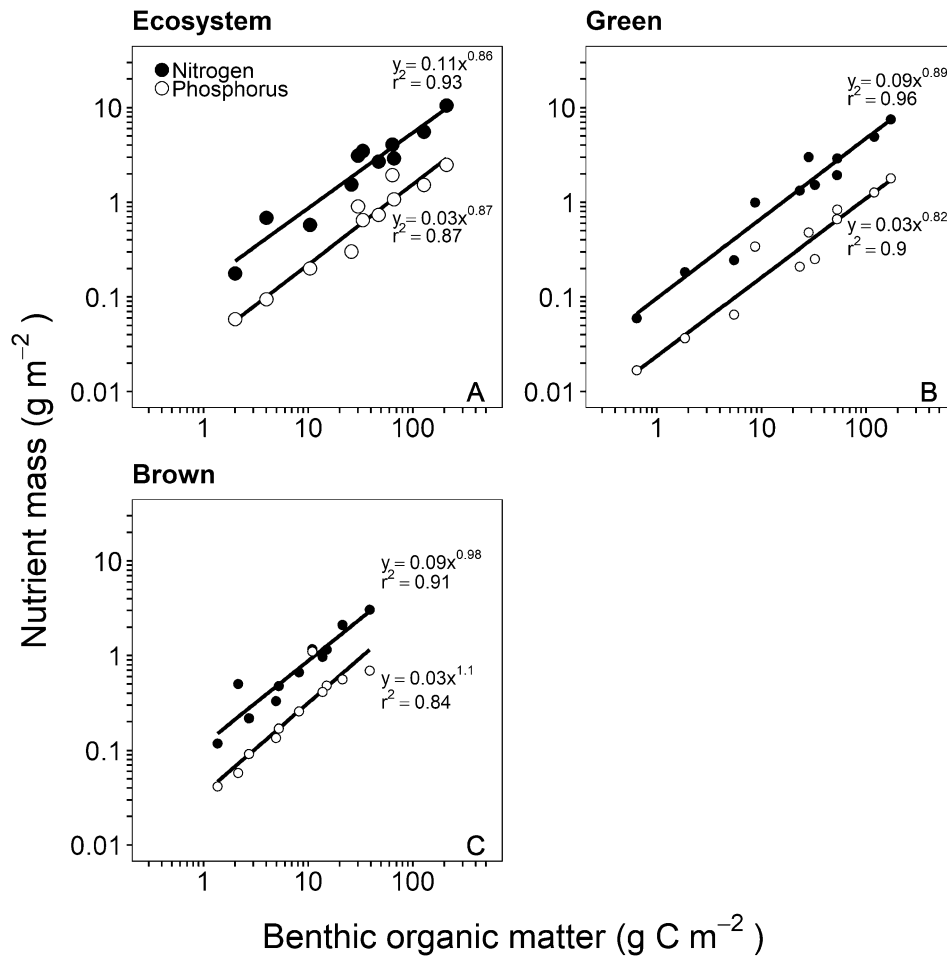


Figure 3. The scaling of nitrogen (filled symbols) and phosphorus (open symbols) in aggregate ecosystem benthic organic matter (A) and in 'Green' BOM (B) and 'Brown' (C) BOM. All scaling relationships were fit with reduced major axis regression on log₁₀-transformed nutrient mass (g m⁻²) and ecosystem BOM (g C m⁻²).

Compartment and Ecosystem-Level Elemental Content and Stoichiometry

Among streams, C, N, and P content, as well as C:N:P stoichiometry of individual BOM compartments, varied widely, and there were differences among compartments with respect to all elemental and stoichiometric measures (MANOVA $P < 0.001$, all ANOVA corrected $P < 0.001$; Figure S7). Stoichiometric variation among BOM compartments was greatest for C:P (0.91 CV), followed by N:P (0.69 CV) and C:N (0.46 CV; Figure S6). Across streams, variability of ecosystem-level OM stoichiometry was markedly lower than variation among BOM compartments (Figures 1B–D and S7), and the CV of ecosystem-level stoichiometry ranged from 0.25 to 0.37 (0.35, 0.37, and 0.36 for C:N, C:P, N:P in all streams; with a single outlier removed, CV of N:P = 0.25).

Generally, C:nutrient stoichiometry of ecosystem-level BOM was related to multiple flow characteristics (flow PC1; Tables S2 and S3), but temperature was not an important driver of ecosystem-level C:N or C:P ratios (Tables S2 and S3). Ecosystem-level BOM C:N had nearly equal support between the flow-only and DIN concentration (Table S2) and C:P ratios were more strongly associated with flow characteristics than with SRP (Table S3).

With increasing mass of ecosystem-level BOM, the relative concentrations of both N and P showed similar dilution, reflected in log–log scaling exponents that were less than one, indicating that ecosystem-level nutrient content declined with the ecosystem BOM pool size (Figure 3A). However, when ecosystem-level BOM was divided into 'green' and 'brown' compartments nutrient dilution was only evident in 'green' biomass (C:N

scaling exponent = 0.89 [0.84–0.94], mean [95%CI lower–95%CI upper]; C:P scaling exponent = 0.82 [0.75–0.90]; Figure 3B), while nutrient concentrations in ‘brown’ pools scaled isometrically with C (C:N scaling exponent = 0.98 [0.90–1.07]; C:P scaling exponent = 1.1 [0.97–1.24]; Figure 3C). Thus, dilution of nutrients in ecosystem BOM was driven by ‘green’ components of BOM; streams with a larger proportion of ‘green’ mass had elevated ecosystem C:N and C:P, but not N:P, ratios (BOM C:N $r^2 = 0.37$, $P = 0.03$; BOM C:P $r^2 = 0.65$, $P = 0.002$; BOM N:P $r^2 = 0.02$, $P = 0.67$, Figure S8).

Relationships Between N:P Supply and Ecosystem BOM N:P

The most likely model of ecosystem-scale BOM N:P contained a term for stream water DIN:SRP and indicated that temperature and flow regime were not important determinates of BOM N:P at the ecosystem scale. To explore this phenomenon further, we examined the coupling of N and P in both ecosystem BOM and stream water dissolved nutri-

ent supply (expressed as stream water DIN and SRP flux; Figure 4). Although stream water dissolved N and P supply were not strongly coupled, ecosystem-scale BOM N and P scaled isometrically indicating that at the ecosystem-scale BOM N:P was tightly constrained (N:P scaling exponent = 0.91 ± 0.09 SE; testing slope against 1.0, $P = 0.16$), not influenced by variation in stream water N:P supply, and was enriched in N:P compared to dissolved N:P supply (imbalances ranging from 2.5 to 11.9; 7.6 ± 2.5 , mean ± 1 SD; Figure 4) and composition (Figure S8C). This conclusion was also supported by the relationship between ecosystem-scale BOM N:P and stream water N:P supply after a single outlier stream was removed (without the outlier: $r^2 = -0.08$, $P = 0.62$, slope = 0.62, 95% CI: -2.1 – 3.3 ; Figure 4 inset).

DISCUSSION

We quantified patterns of organic matter storage, composition, and stoichiometry across large gradients of stream temperature and flow regimes. We found that flow regime was much more important than temperature in explaining characteristics of BOM, and we attribute this finding to the influence of disturbance regime on the presence or absence of large-sized primary producers (that is, macrophytes and large colonial groups). Although we found systematic increases in ecosystem C:N and C:P ratios at higher levels of BOM mass, variation in N:P was more constrained. We also found that streams consistently accumulated more N than P relative to the availability of these elements in the environment despite large inter-stream differences in total BOM mass and environmental conditions. Our study provides a rare assessment of ecosystem-level biomass and stoichiometry and highlights the importance of environmental context in shaping responses to warming temperatures. Here, apparent responses to temperature could only be understood after accounting for the influence of disturbance regime on ecosystem-level BOM pools and stoichiometry.

Temperature has long been recognized as a fundamental driver of ecosystem patterns and processes, influencing metabolic rates (Gillooly and others 2001), species composition (Vannote and Sweeney 1980), and the distribution of species traits (for example, nutrient content; Rhee and Gotham 1981). However, the influence of temperature at the ecosystem-level can be constrained by energetic and mass-balance limitations leading to minimal effects on aggregate patterns and pro-

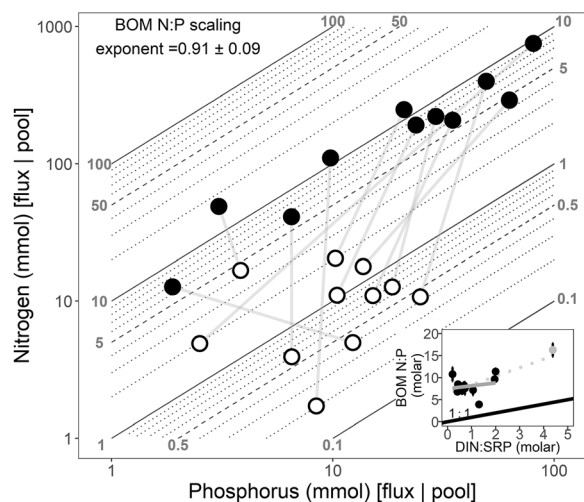


Figure 4. Median molar flux of dissolved inorganic nitrogen and phosphorus ($\text{mmol m}^{-2} \text{d}^{-1}$; open circles) and standing stocks of benthic nitrogen and phosphorus (mmol m^{-2} ; closed circles) in all study streams. Gray lines in the large panel connect the dissolved element flux and the BOM element standing stock within a stream. Thin black and dashed lines represent stoichiometric isoclines. The inset displays the relationship between molar dissolved DIN:SRP ratios and BOM N:P ratios (mean \pm SE). The lower black line is a 1:1, and the dotted gray line represents the linear relationship with all streams included: When we removed the single outlier, the relationship between dissolved N:P and BOM N:P (solid gray line) was indistinguishable from zero.

cesses (Allen and others 2002, 2005). We found that temperature had no detectable effect on BOM mass or stoichiometry once the effects of flow were taken into account (Figure 2D, Table 2), and the null effect of temperature on BOM mass was consistent with expectations based on previous ecosystem-level flux measurements (Demars and others 2011, 2016). This result is also consistent with other studies of autotroph-dominated communities (Allen and others 2005; Stegen and others 2011) and ecosystems lacking large external inputs of OM, such as open-canopied streams. In such ecosystems, respiration is likely constrained by photosynthesis at the individual (Dewar and others 1999; Allen and others 2005) and ecosystem level (Yvon-Durocher and others 2012).

The fact that we could not detect an effect of temperature on OM storage is inconsistent with results from a number of warming experiments that have shown increased OM with warming, at least in the short term. A recent ecosystem-level warming experiment at our study site showed a near tripling of OM mass with 3 °C warming (Hood and others 2018) associated with increased dominance by a single species of filamentous algae. Similarly, positive short-term increases in OM pools were observed in warmed plots of montane plant communities following a shift in community structure and plant functional form (Harte and Shaw 1995). In each of these cases, the positive effects of warming were associated with changes in the community that altered the size distribution of organisms. Thus, the total size of ecosystem OM storage may be controlled by environmental factors that alter the distribution of organism size, whether it's temperature (Šímová and others 2019) or other factors, such as disturbance.

Flow regime is a leading driver of pattern and process in streams, and most organisms in these ecosystems exhibit behavioral, morphological, and life-history adaptations in response to variation in flow (for example, Lytle and Poff 2004). Previous studies suggest that variability in flow can influence the size of BOM pools through several processes. First, high flows can simply move material downstream, thereby limiting local accrual of OM. Second, a higher frequency and magnitude of stream flooding can inhibit the establishment of larger-bodied macrophyte and bryophyte species (Riis and Biggs 2003). Our results support these ideas, as flow PCA axes were generally related to BOM composition and storage among streams (Figure S4). Discharge variability (CV_Q) also influenced BOM composition and showed negative associations with ecosystem-level BOM mass (Fig-

ure 2) and the relative abundance of the dominant bryophyte, *Fontinalis antipyretica* (Figure S4). Other, less dominant macrophyte and bryophyte species showed similar, but weaker, negative associations with CV_Q , suggesting that the negative effect of flow disturbance on large-sized primary producers may be general. It is important to note, however, that the effects of flow disturbance on organism body size and OM pool sizes may operate differently in open-canopied grassland streams than in forested streams that receive large annual inputs of OM from riparian vegetation. In forested streams, OM pool sizes are donor-controlled and influenced by the magnitude of annual litter inputs and the subsequent removal of OM through biological processing and physical export (Benstead and others 2009). Nonetheless, in both of these ecosystem types, flow disturbance may be more important than temperature in setting constraints on detrital BOM storage, as well as mediating fluxes of energy and materials in stream ecosystems (Valett and others 2008).

We initially anticipated that warmer temperatures would alter the relative balance of carbon and nutrients in BOM, leading to increased C:nutrient ratios as demonstrated in previous experiments in these Icelandic streams (Hood and others 2018) and elsewhere (De Senerpont Domis and others 2014). According to this hypothesis, warmer temperatures and higher fluxes of C per unit nutrient (O'Gorman and others 2012; Demars and others 2016) should increase C:nutrient ratios given no change in inorganic nutrient supply (that is, increased nutrient use efficiency; Vitousek 1982; Hood and others 2018). Alternatively, if warming favors nitrogen-fixing primary producers, as reported from previous mesocosm experiments in Iceland (Welter and others 2015; Williamson and others 2016), warming could increase N acquisition in biomass, leading to no effect of temperature on BOM C:N ratios. Based on our results, we could neither confirm nor refute either of these outcomes, as models including temperature had little support and explanatory power for predicting ecosystem nutrient stoichiometries (Supplemental Materials Tables S2–S4). In general, we found that any potential warming-induced change in C:nutrient ratios was masked by large flow-mediated shifts in the composition of benthic communities (that is, relative contribution of macrophytes and bryophytes to total organic matter pools). Greater variation in flow prevented the establishment of large-sized macrophytes, which tend to have increased investment in structural tissues with high and relatively constrained C:nutrient ratios (Demars and

Edwards 2007), leading to ecosystems with greatly reduced standing biomass (that is, diatoms, filamentous algae, cyanobacteria) and lower biomass-weighted C:nutrient ratios. These patterns mirror those in terrestrial ecosystems globally, where ecosystem-level N and P concentrations become more diluted at higher ecosystem biomass (Kerckhoff and Enquist 2006). In addition, these patterns underscore the potential importance of stream flow as a primary moderator of stream biomass and stoichiometry and suggest that flow regime may also drive broad-scale inter-stream patterns of nutrient cycling. As the Earth's climate continues to warm, it will be crucial to understand how predicted changes in precipitation and flow regimes interact with temperature to influence how streams store and process energy and materials.

Despite large among-stream differences in temperature, flow regime, and BOM mass and composition, BOM N and P mass scaled approximately isometrically, and streams consistently accumulated N relative to P when compared to nutrient delivery fluxes (mean N:P imbalance: 7.6, Figure 4). In addition, after removing a single outlier, BOM N:P ratio was independent of supply N:P ratios across the full range of dissolved N:P (range: 0.2–4.4 N:P). Although other studies have shown similarly conserved scaling of N:P across a range of organisms, ecosystems, and environmental conditions (Redfield 1958; McGroddy and others 2004; Reich and Oleksyn 2004; Cleveland and Liptzin 2007; Sinsabaugh and others 2009), few have explored these patterns in benthic systems (but see Farrell and others 2018) and even fewer have extended these patterns beyond a few OM compartments (Schade and others 2005; Cohen and others 2013). Although organisms vary in the extent to which their stoichiometry can respond to variation in nutrient delivery (Persson and others 2010), aggregate ecosystem OM, with its diverse living and non-living biomass compartments which vary widely in C:N:P stoichiometry (Elser and others 2000; Cross and others 2005; Townsend and others 2008), may exhibit much larger flexibility in balancing nutrient supply and demand across wide environmental gradients (Schade and others 2005). Nonetheless, many questions remain about the balance of nutrient supply and demand in ecosystems, the conditions that cause supply and demand to deviate, and how such patterns influence other ecosystem processes (Cardinale and others 2009).

Models of global change predict large changes to future temperature and precipitation regimes (IPCC

2014), with likely consequences for the thermal and flow environments of lotic ecosystems globally (van Vliet and others 2013). Here, we show that flow disturbance regime had primacy in determining ecosystem OM mass and stoichiometric patterns despite a large gradient in stream temperatures. These patterns were mediated through shifts in community structure and trait distributions (for example, organism body size), highlighting the complex controls of environmental drivers on OM and elemental storage, as well as coupled biogeochemical cycles within ecosystems. Future efforts to predict how stream ecosystems may respond to changes in temperature and flow will need to consider the relative importance of multiple environmental drivers and organismal traits on the accumulation, removal, and composition of organic matter pools.

ACKNOWLEDGEMENTS

We would like to thank a number of individuals who contributed to this work: A. Toomey, B. Weigel, S. Layton, and R. McClure provided indispensable help in the field and laboratory. E. J. N. Brookshire, G. C. Poole and B. O. L. Demars contributed input on earlier versions and two anonymous reviewers provided feedback that greatly improved the clarity of the manuscript. We are grateful to Sigurður Guðjonsson, Guðni Guðbergsson, and the staff at the Veiðimálastofnun for laboratory space and logistical support. We are also grateful to Sveinbjörn Steinórsson of the University of Iceland for winter transport to our field sites. This work was supported in part by a Grant-In-Aid-of-Research to JRJ from Sigma-Xi (Grant ID #G20120315162084) and from the National Science Foundation (DEB-0949726 to WFC and DEB-0949774 and DEB-1354624 to JPB and ADH).

AUTHOR CONTRIBUTIONS

WFC, JPB, ADH, JMH, and JRJ conceived the study, all authors helped with study design, GMG and JSO provided field support and local arrangements, all authors contributed to data collection, JRJ performed analyses and wrote the first draft of the manuscript, and all authors provided input on further manuscript drafts.

DATA AVAILABILITY

Code and data for reconstructing the results and figures are available at: https://github.com/jimjunker1/Junker_OMstoic and Zenodo: <https://doi.org/10.5281/zenodo.3756279>.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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