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ARTICLE

Environmental warming increases the importance of high-turnover energy channels in stream food webs

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Funding information

National Science Foundation, Grant/Award Numbers: DEB-0949726, DEB-0949774, DEB-1354624

Handling Editor: Hideyuki Doi**Abstract**

Warming temperatures are altering communities and trophic networks across Earth's ecosystems. While the overall influence of warming on food webs is often context-dependent, increasing temperatures are predicted to change communities in two fundamental ways: (1) by reducing average body size and (2) by increasing individual metabolic rates. These warming-induced changes have the potential to influence the distribution of food web fluxes, food web stability, and the relative importance of deterministic and stochastic ecological processes shaping community assembly. Here, we quantified patterns and the relative distribution of organic matter fluxes through stream food webs spanning a broad natural temperature gradient (5–27 °C). We then related these patterns to species and community trait distributions of mean body size and population biomass turnover ($P:B$) within and across streams. We predicted that (1) communities in warmer streams would exhibit smaller body size and higher $P:B$ and (2) organic matter fluxes within warmer communities would increasingly skew toward smaller, higher $P:B$ populations. Across the temperature gradient, warmer communities were characterized by smaller body size (~9% per °C) and higher $P:B$ (~7% faster turnover per °C) populations on average. Additionally, organic matter fluxes within warmer streams were increasingly skewed toward higher $P:B$ populations, demonstrating that warming can restructure organic matter fluxes in both an absolute and relative sense. With warming, the relative distribution of organic matter fluxes was decreasingly likely to arise through the random sorting of species, suggesting stronger selection for traits driving high turnover with increasing temperature. Our study suggests that a warming world will favor energy fluxes through “smaller and faster” populations, and that these changes may be more predictable than previously thought.

KEYWORDS

climate change, energy flux, environmental filtering, food webs, species traits, temperature

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INTRODUCTION

Increasing global temperatures influence the provision and maintenance of ecosystem services by modifying the network of species interactions that underpin ecosystem functions (Brose et al., 2012; de Ruiter et al., 1995; Thompson et al., 2012; Woodward et al., 2010). Warming effects permeate across multiple levels of biological organization, from control of individual metabolic rates (Brown et al., 2004; Gillooly et al., 2001) and biological activity (e.g., attack rate, handling time, growth rates; Dell et al., 2014), to broad-scale shifts in community assembly and structure (Gibert, 2019; Nelson et al., 2017b; Saito et al., 2021). Across global climate gradients, such temperature-induced changes have the potential to mediate food web stability (Baiser et al., 2019) by altering the acquisition and allocation of resources (Zhang et al., 2017) and the magnitude and relative distribution of energy fluxes in food webs (Barnes et al., 2018; Gilbert et al., 2014; McCann et al., 1998).

Understanding how warming alters energy flux in food webs requires information about how temperature modifies relationships between ecosystem structure and function. Such relationships depend upon how warming influences functional trait distributions and how functional traits translate to the magnitude and distribution of energy demands (Loreau et al., 2001; Norberg, 2004; Norberg et al., 2001). Additionally, warming can modify community assembly processes (Saito et al., 2021)—both deterministic (e.g., environmental/niche filtering; Whittaker, 1962) and stochastic (e.g., neutral theory; Hubbell, 2001)—leading to many possible relationships between warming, the relative abundance of species, and dominance of particular functional traits. For example, although temperature appears to have minimal control on species richness across taxonomic groups (e.g., Bastazini et al., 2021), warming can have profound effects on the dominance structure (i.e., evenness) of ecological communities, often by reducing community evenness and favoring a reduced set of warm-adapted species (Hillebrand et al., 2008). This strong environmental filtering is likely to skew trait distributions in natural communities (Therriault & Kolasa, 1999). However, the relative distribution of traits can be further modified by stochastic processes unrelated to environmental filtering (e.g., species interactions, Therriault & Kolasa, 1999; demographic stochasticity, Hubbell, 2001). The relative importance of these additional processes may increase with warming, as reduced population abundances (Bernhardt et al., 2018) and faster metabolic rates increase the possibility of local extirpation (Saito et al., 2021; Siqueira et al., 2020). The stochastic shifts in relative species abundances can either exaggerate or counter any skew in trait distributions

driven by environmental filtering and thereby modify the relationship between species' traits and the absolute and relative energy demands in food webs.

Body size is a fundamental trait that is influenced by temperature (for ectotherms see Atkinson, 1994; Daufresne et al., 2009; and Gardner et al., 2011, also see Riemer et al., 2018 for deviations across endotherms) and has great potential to influence energy flux. Reduced body size in response to warming can arise at multiple levels of organization, including increased relative abundance of smaller species in warmed communities (Bergmann, 1848), smaller individuals in warmer populations (James, 1970), or reduced absolute body size of warmed individuals (Atkinson, 1994). Thus, warmer communities are likely to contain both smaller species and individuals. These relationships can have important implications for energy and material flux in ecosystems because body size is a strong determinant of species life-history patterns (Altermatt, 2010; Nelson et al., 2020a; Peters, 1983; Zeuss et al., 2017), as well as developmental (Angilletta Jr. et al., 2004) and metabolic rates (Brown et al., 2004; Gillooly et al., 2001).

Metabolic rate, in addition to being controlled by body size, is another key trait that is influenced by temperature and tied to variation in energy flux through food webs (Barnes et al., 2018; Gillooly et al., 2001). Warming can influence metabolic rates indirectly through reductions in body size, as well as directly through its effects on subcellular kinetics (Bideault et al., 2019; Osmond et al., 2017). These processes can modify ecosystem patterns through changes in population carrying capacity (Bernhardt et al., 2018) and species relative abundances, with consequent effects on consumer-resource interactions or food web structure (Bideault et al., 2019; Gibert, 2019). Moreover, metabolic rates are also tied to many biological processes (Dell et al., 2014), including growth rate (Gillooly et al., 2001), developmental rate (Nelson et al., 2020a; Zuo et al., 2012), voltinism (Zeuss et al., 2017), and biomass turnover rate (Brown et al., 2004; Huryn & Benke, 2007). Taken together, these effects suggest that warming should lead to a smaller, faster world in which ecosystem processes accelerate through the effects of smaller body size and higher turnover rates, with a potentially strong imprint on food web structure and energy fluxes (Gibert, 2019).

Here, we address two overarching and open questions focused on temperature effects on food web dynamics. First, how does ecosystem temperature shape the relationship between organic matter (OM) fluxes and community-level trait distributions, specifically body size and biomass turnover, across ecosystems? Second, how does temperature shape the role of deterministic vs. stochastic sorting processes in driving relative fluxes

of OM through consumer communities? We quantified patterns of OM flux in stream food webs across a natural temperature gradient (~5–27 °C) in southwestern Iceland. Previous research in these streams has shown a strong positive effect of warming on primary production both among streams (Demars et al., 2011; Padfield et al., 2017) and seasonally within streams (Hood et al., 2018; O’Gorman et al., 2012). Due to high light levels and minimal OM inputs from surrounding terrestrial habitat, invertebrates in these streams rely on autochthonous production (Nelson et al., 2020b; O’Gorman et al., 2012); thus, the dynamics of in-stream primary production act as a strong control on energy flow through consumers (Junker et al., 2020). Due to the positive relationship of primary production with temperature, we predicted that annual OM fluxes to consumers would increase with stream temperature, mirroring patterns in resource availability. We also hypothesized that temperature would act as a principal environmental filter on community assembly and OM fluxes by favoring “fast” life-history traits associated with small-bodied organisms. Specifically, we predicted that warming temperatures would lead to reduced average body size and increased average biomass turnover (i.e., *Production:Biomass* or *P:B* ratio) of populations among streams. We also predicted that within communities, OM fluxes would be skewed toward small-bodied and high *P:B* taxa at higher temperatures, and that these patterns would not arise by random sorting, but instead through nonrandom ordering, suggesting deterministic filtering of species traits. Our results should help refine general predictions about how ongoing climate warming, and its influence on key traits, is likely to shape energy flux through food webs dominated by ectotherms.

METHODS

We studied six streams within the Hengill geothermal field of southwestern Iceland (64°03' N, 21°18' W) that varied in mean annual temperature from ~5–27 °C. Hengill is characterized by indirect geothermal heating of groundwater (Árnason et al., 1969), leading to natural variability in stream temperatures (4.5–54.0 °C), but similar solute chemistries (Friberg et al., 2009). These conditions create a “natural laboratory” for isolating the effects of temperature on ecosystem processes (Nelson et al., 2017b; O’Gorman et al., 2014). We selected streams to maximize the temperature range, while minimizing differences in the structural aspects of the primary producer community (Junker et al., 2021). However, this led to an unequal distribution of streams along the temperature gradient with three streams concentrated in the cooler temperature ranges. In each stream, we measured

temperature and water depth every 15 min from July 2010 through August 2012 (U20-001-01 water-level logger, Onset Computer Corp., Pocasset, MA, USA).

Invertebrate sampling

We sampled macroinvertebrate communities approximately monthly in six streams, four from July 2011 to August 2012 and two from October 2010 to October 2011 ($n = 6$ streams). The two streams sampled from 2010 to 2011 were part of a separate warming manipulation but data for this study were collected during the un-manipulated reference period (Nelson et al., 2017a, 2017b). Interannual comparisons of primary and secondary production in previous studies showed minimal differences among years in un-manipulated streams, suggesting that combining data from different years would not significantly bias our results (Hood et al., 2018; Nelson et al., 2017a). We collected five Surber samples (0.023 m², 250-μm mesh) from randomly selected locations within each stream encompassing all habitat types. Within the sampler, inorganic substrates were disturbed to ~10 cm depth and invertebrates and OM were removed from stones with a brush. Samples were then preserved with 5% formaldehyde until laboratory analysis. In the laboratory, we split samples into coarse (>1 mm) and fine (>250 μm to <1 mm) fractions using nested sieves and then removed invertebrates from each fraction under a dissecting microscope (×10–15 magnification). For particularly large samples, fine fractions were subsampled (1/2–1/16th) using a modified Folsom plankton splitter prior to the removal of invertebrates. Macroinvertebrates were identified to the lowest practical taxonomic level (usually genus) with taxonomic keys (Andersen et al., 2013; Merritt et al., 2008; Peterson, 1977). Taxon-specific abundance and biomass were scaled to a per-meter basis by dividing by the Surber sampler area.

Secondary production

Daily secondary production of invertebrate taxa was calculated using the instantaneous growth rate method (IGR; Benke & Huryn, 2017). Growth rates were determined using taxon-appropriate approaches described by Junker et al. (2020). Briefly, growth rates of common taxa (e.g., Chironomidae spp., *Radix balthica*, etc.) were measured using in situ chambers (Huryn & Wallace, 1986). Multiple individuals ($n = 5–15$) within small size categories (~1-mm length range) were photographed next to a field micrometer, placed in the stream within preconditioned chambers for 7–15 days, and removed and photographed.

Individual lengths were measured from field pictures using image analysis software (Schindelin et al., 2012), and body lengths were converted to mass (in milligrams of ash-free dry mass [AFDM]) using published length-mass regressions (Benke et al., 1999; Hannesdottir et al., 2013; O’Gorman et al., 2012). Growth rates (g , d^{-1}) were calculated from changes in mean body size (M) over a given time interval (t) with the following equation:

$$g = \frac{\log_e \frac{M_{t+\Delta t}}{M_t}}{\Delta t}. \quad (1)$$

Variability in growth rates was estimated by bootstrapping through repeated resampling of individual lengths with replacement ($n = 1000$). For taxa that exhibit synchronous growth and development (e.g., Simuliidae spp., some Chironomidae spp., etc.), we examined temporal changes in length-frequency distributions and calculated growth rates and uncertainty using a bootstrap technique similar to that described in Benke and Huryn (2017). Individual lengths were converted to mass (mg AFDM) using published length-mass regressions cited above, and size-frequency histograms were visually inspected for directional changes in body size over time. For each date, size-frequency distributions were resampled with replacement and growth rates estimated from Equation 1. We prevented the calculation of negative growth rates by requiring $M_{t+\Delta t} > M_t$. If this condition was not met after 10,000 resamplings, a minimum growth rate of 0.001 was used (<5% of total instances). To estimate growth rates of taxa for which growth could not be estimated empirically, we developed stream-specific growth rate models by constructing multivariate linear regressions of empirical growth rates against body size and temperature. To estimate uncertainty in the production of each taxon, we used a bootstrapping technique that resampled measured growth rates, in addition to abundance and size distributions from individual samples. For each iteration, size-specific growth rates were multiplied by mean interval biomass for each size class and the number of days between sample dates to estimate size class-specific production. For each time interval, size classes were summed for each taxon to calculate total population-level interval production. Intervals were summed to estimate annual secondary production (g AFDM $m^{-2} y^{-1}$).

Organic matter consumption estimates

Organic matter fluxes (g AFDM $m^{-2} y^{-1}$) through stream communities were calculated using the trophic basis of

production method (TBP; Benke & Wallace, 1980). Taxon-specific secondary production estimates were combined with diet proportions, diet-specific assimilation efficiencies, AE_i , and net production efficiencies, NPE (e.g., McCullough, 1975), to estimate consumption of OM. Consumer diets of numerically dominant taxa were quantified through direct inspection of gut contents from multiple individuals throughout the year. Removal and preparation of gut tracts followed the methods outlined by Rosi-Marshall and coauthors (Rosi-Marshall et al., 2016). To estimate variability in diet compositions and to impute missing values for nondominant taxa, we modeled the diet proportions within each stream using a hierarchical multivariate model (Coblentz et al., 2017; Fordyce et al., 2011). Here, diet proportions for food categories were modeled following a Dirichlet distribution with expected proportions in diet and a concentration parameter to estimate variability around this expectation. We accounted for the hierarchical data structure by fitting stream-specific random intercepts, as well as random intercept offsets for taxa nested within each stream. All models were specified in the Stan language (Stan Development Team, 2019) using the *brms* package in R (Bürkner, 2017). Further model details can be found in supporting information (Appendix S1). We estimated diet overlap within and across-stream food webs by calculating diet overlap from 1000 independent draws from the posterior distributions of modeled diet estimates. Overlap was calculated with the “overlap()” function in the *RInSp* package (Zaccarelli et al., 2013).

For each food category, i , diet proportions were multiplied by the gross growth efficiency ($GGE_i = AE_i \times NPE$) to calculate the relative production attributable to each food category. The relative production from each food type was then multiplied by the interval-level production and finally divided by GGE_i to estimate the consumption of OM from each food category by each taxon (Benke & Wallace, 1980). Consumption was calculated for each taxon during each sampling interval (typically ~1 month). Total interval consumption was calculated by summing across all taxa, while annual consumption was calculated by summing across all taxa and intervals. Variability in consumption estimates was estimated through a Monte Carlo approach, where bootstrapped vectors of secondary production for each taxon (see [Secondary production](#) methods above) were resampled and consumption was estimated with the TBP method using modeled diet proportions, diet-specific assimilation efficiencies, and net production efficiency. Variability in AE_i was incorporated by resampling values from beta distributions fitted to the median and 2.5% and 97.5% percentiles for each diet item: diatoms = 0.30 (95% percentile interval [PI]: 0.24–0.36), filamentous and green algae = 0.30 (95% PI: 0.24–0.36),

cyanobacteria = 0.10 (95% PI: 0.08–0.12), amorphous detritus = 0.10 (95% PI: 0.08–0.12), vascular and nonvascular plants (bryophytes) = 0.10 (95% PI: 0.08–0.12), and animal material = 0.70 (95% PI: 0.56–0.84; Benke & Wallace, 1980, 1997; Cross et al., 2007, 2011; Welch, 1968). Variability in NPE was incorporated by resampling values from an assumed beta distribution with median NPE = 0.45 (95% PI = 0.40–0.50). Further details can be found in supporting materials (Appendix S2: Section S1: Trophic basis of production workflow and assumptions). Beta distributions were fit in R (R Core Team, 2022) using the “get.beta.par()” function within the *rriskDistributions* package (Belgorodski et al., 2017).

Quantifying the distribution of food web fluxes

Evenness among taxa

To visualize and quantify the evenness of OM fluxes, p , among taxa within each stream, we constructed Lorenz curves (Lorenz, 1905) on rank-ordered OM fluxes, such that in a community with S species the relative OM flux of species j , p_j , is ordered $p_1 \leq p_2 \leq \dots p_S$. The Lorenz curve shows how a value, in this case OM flux, accumulates with an increasing cumulative proportion of taxa. In a community with an equal distribution of OM flux among taxa, the Lorenz curve is a straight diagonal line. Deviation from equality was calculated as the Gini coefficient (Gini, 1921), normalized for differences in S among streams, G (Chao & Ricotta, 2019; Solomon, 1975):

$$G = \frac{2 \sum_{j=1}^S p_j \left(\sum_{k=1}^j p_k - \frac{j}{S} \right)}{(S-1)}, \quad (2)$$

where G represents an index of relative evenness of OM fluxes bounded between zero and one; a value of one represents a community with equal proportion of total community OM flux for all species ($1/S$), and a value of zero represents a community in which the total OM flux is attributed to a single taxon.

Distribution of OM fluxes in relation to taxa traits

We predicted that warming would favor taxa with smaller body size and higher biomass turnover rates and that OM fluxes would therefore be skewed toward small body size (M) and higher $P:B$ at higher temperatures

across and within communities. To assess the change in the average population trait values and potential for environmental filtering across communities, we used bootstrapped linear regressions between either mean population body size ($\bar{M}$) or biomass turnover ($\bar{P:B}$) of each stream community and mean annual temperature (in degrees Celsius). Here, 1000 values of population M or $P:B$ were resampled with replacement from population secondary production vectors (see *Secondary production* above) for each taxon within each stream. We calculated the mean body size or $P:B$ of the populations within each stream by first calculating the mean annual body size or annual $P:B$ for each taxon and then taking the median across all taxa. We then calculated the least squares estimate between $\log_e$ -transformed $\bar{M}$ or $\bar{P:B}$ and mean annual temperature. Response variables were $\log_e$ -transformed to conform to assumptions of linearity and normally distributed residual variation and the ordinary least squares estimate was calculated using the “lm()” function in R.

To quantify how the distribution of organic matter fluxes was modified within communities and whether this modification was related to temperature, we assessed the extent to which the relative OM fluxes among taxa were skewed toward populations with lower or higher relative M or $P:B$. To do this, we ordered taxa based on within-stream rankings of annual population traits (i.e., M , $P:B$) and then calculated a measure of skewness, Sk_{flux} , based on quartiles of the distribution of OM fluxes in relation to taxon traits as:

$$Sk_{flux} = f_{Q0.75} - 2f_{Q0.5} + \frac{f_{Q0.25}}{f_{Q0.75}} - f_{Q0.25}, \quad (3)$$

where f_{Qx} is the cumulative flux at some quantile, Qx , of the community trait distribution. We chose this quantile-based formula over other parametric or moments-based approaches because it is well defined and requires no assumptions of the moments of the distribution (Groeneveld & Meeden, 1984). We repeated this analysis for all estimates of OM flux used to calculate M and $P:B$ in each stream community. Skewness coefficients range from -1 to 1 , where -1 indicates that OM fluxes are skewed perfectly away from a trait while 1 indicates that higher relative fluxes are perfectly associated with higher trait values. To determine whether the skewness of fluxes with M and $P:B$ was related to mean annual stream temperature, we used bootstrapped beta regression with a simple transformation, $(Sk_{flux} + 1)/2$, to meet the assumptions of the model and standardize values between 0 and 1 . Model coefficients were back-transformed to estimate effect sizes.

To examine the extent to which temperature influenced the skew of OM flux among populations within each community, we quantified the probability of observing the skewed distributions in OM fluxes by random chance. The feasible range of skewness values within a community is inherently tied to the evenness of OM fluxes. This dependence on evenness can make it difficult to determine the importance of random versus ecological processes on the distribution of OM fluxes by comparison of raw skewness measures alone. We predicted that species M and $P:B$ would be increasingly important traits structuring OM fluxes within a community and therefore warmer streams would exhibit highly skewed OM distributions that would be unlikely due to chance (i.e., nonrandom ordering). In contrast, cooler streams would exhibit OM fluxes with skew values that are more likely due to random chance (“random ordering”), regardless of raw skewness values, suggesting other traits or processes govern the distribution of OM fluxes within their communities. To accomplish this, we first had to account for statistical constraints that restrict the range of possible outcomes (i.e., feasible set; Diaz et al., 2021; Haegeman & Loreau, 2008), given the number of species and the relative distribution of OM fluxes within a community. We permuted a random subset of each stream community’s feasible set by randomly ordering species and calculating skewness in the cumulative distribution of annual OM fluxes 100,000 times in each stream. This permuted set allowed us to calculate the probability of observing the empirical skewness value, Sk_{flux} , compared to a random ordering given the distribution of relative OM flux. We assessed the likelihood of nonrandom ordering as the distance from the central mass of the random skew distributions within each stream. Therefore, communities in which OM fluxes are likely organized nonrandomly are indicated by observed skew values near the tails of these random distributions.

RESULTS

Community OM fluxes

Annual community OM fluxes mirrored patterns of secondary production reported previously (Junker et al., 2020). Organic matter flux to invertebrates varied ~45-fold among streams, from 3.9 (2.1–6.4; mean [95% PI]) to 176.7 (124.1–236.5) g AFDM $m^{-2}y^{-1}$ and was positively related to temperature (Figure 1a).

Differences in OM flux among streams were driven by the variation in total energy demand rather than the composition of consumed resources, as consumer diets were highly similar among streams (Appendix S1: Figure S1).

Across all streams, community-level diets were dominated by diatoms (43.9%; 0%–75.8%), amorphous detritus (17.2%; 0%–32.2%), and green algae (13.3%; 0%–43%). Within streams, diet overlap ranged from 68% (65%–71%) to 75% (69%–79%) among invertebrate taxa. Among streams, diets were also highly similar with a mean overlap of 89% (85%–92%). Diet overlap based on pairwise comparisons among streams showed little difference and no clear relationship with temperature.

Evenness of OM fluxes

In general, OM fluxes were unevenly distributed among taxa (Gini inequality coefficients ranged from 0.09 [0.07–0.11, 95% PI] to 0.29 [0.25–0.32]; Appendix S3: Table S1) and were dominated by insects in the families Simuliidae and Chironomidae, pulmonate snails (*Radix balthica*), and oligochaete worms (Figure 2a,b; Appendix S3: Figure S2). In absolute terms, ~85% of total OM flux was contributed by 2–10 taxa, which comprised only 3%–29% of total taxon richness among streams. Although differences in the evenness among streams were partially attributed to variation in taxon richness (range: 14–35), fluxes were still highly uneven after accounting for differences in richness (i.e., similar “Normalized” Gini coefficients, Appendix S3: Table S1). As average stream temperature increased, OM fluxes shifted from dominance by Simuliidae in the coolest stream to Chironomidae and *R. balthica* at moderate temperatures (Figure 2a). In the warmest stream, where maximum temperatures can often approach ~40 C, taxon richness was lowest and OM fluxes were dominated by oligochaete worms in the family Naididae, the chironomid *Cricotopus sylvestris*, and *R. balthica* (Figure 2a). Among-stream differences in evenness of OM fluxes were not clearly related to temperature (Appendix S3: Table S1).

Organic matter fluxes in relation to body size and biomass turnover rate

Across-stream communities, the average population body size ($\bar{M}$; mg AFDM individual $^{-1}$) decreased and the average population biomass turnover rate ($\bar{P:B}$; y^{-1}) increased with increasing temperature (Figure 1b,c). $\bar{M}$ decreased from 2.75 mg AFDM ind $^{-1}$ (1.03–5.08; 95% PI) in the coldest stream to 0.10 mg AFDM ind $^{-1}$ (0.08–0.13) in the warmest stream, corresponding to an -8.7% (-11.1 to -6.4) change in mean body size for every 1 C increase in temperature (Figure 1b). $\bar{P:B}$ ratio increased from 4.4 y^{-1} (3.6–5.1) in the coldest stream to 35.5 y^{-1} (29.6–43.3) in

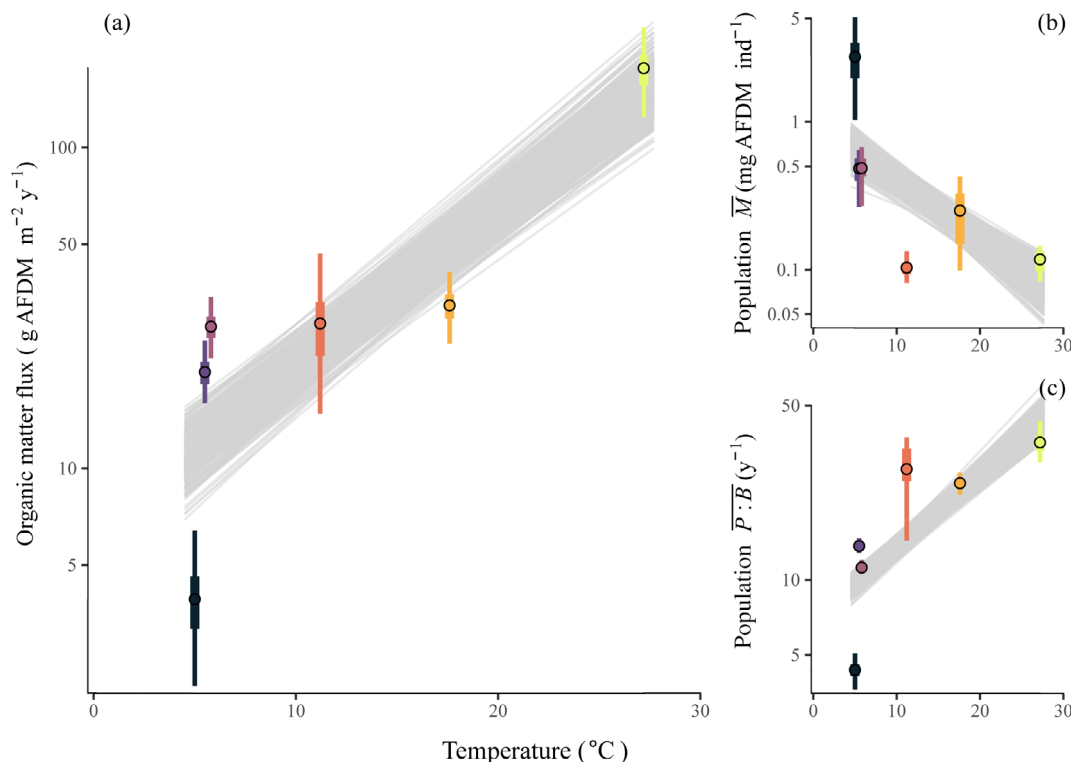


FIGURE 1 (a) Total organic matter flux (g AFDM m⁻² y⁻¹) increased with mean annual temperature. Higher stream temperatures also led to (b) a decrease in mean population body size ($\bar{M}$, mg individual⁻¹) and (c) an increase in mean population biomass turnover rate ($\bar{P}:\bar{B}$, y⁻¹). For all panels, points represent the mean value, wide bars represent the 25 and 75th percentile bounds, narrow bars represent the 2.5 and 97.5th percentile bounds, and gray lines show a random sample of bootstrapped linear models ($n = 400$).

the warmest stream corresponding to a 6.9% (6.1–7.9) increase in $\bar{P}:\bar{B}$ ratio for every 1 °C increase (Figure 1c).

Within stream communities, there were diverse body size–OM flux relationships, with some streams showing greater relative OM flux through larger-bodied taxa (positive skew), others showing greater OM flux through smaller-bodied taxa (negative skew), and some that showed no size-related trend in OM flux (skew range: –1 to 0.56; Figure 3a,b). Skew estimates of OM fluxes in relation to body size showed little association with stream temperature except in the warmest stream, where fluxes were heavily skewed toward small-bodied taxa (Figure 3b). Similarly, skew in OM fluxes in relation to $P:B$ ratios varied among streams, ranging from –0.4 to 1. In this case, OM fluxes to consumers skewed increasingly toward higher turnover ($P:B$) taxa with increasing temperature (Figure 4a,b).

We compared our skew estimates (i.e., Sk_{flux}) of OM flux based on ordered data (i.e., ordered from small to large M or low to high $P:B$ ratios; Figures 3b and 4b) to skew estimates based on randomly sorted data to detect whether OM fluxes through smaller and higher $P:B$ taxa could be attributed to these traits instead of random community assembly processes. The probability of

observing a similar or more extreme skew of OM fluxes in relation to body size was variable among streams and ranged from 0.34 (0.19–0.55; 95% PI) to 0.79 (0.07–0.96); there was little association between this probability and temperature (Figure 3c). In contrast, the probability of a similar or more extreme skew in relation to $P:B$ ratios ranged from 0.06 (0–0.75) to 0.62 (0.23–0.81; Figure 4c) and, in this case, there was a clear trend toward a more structured OM flux distribution; that is, fluxes through high $P:B$ taxa were favored at higher temperatures. The likelihood of higher relative fluxes among high $P:B$ taxa became much higher with warming, and the probability of random ordering decreased by –4.6% (–5.1% to 4.2%) for every 1 °C increase in temperature (Figure 4c).

DISCUSSION

While a growing body of theoretical and empirical research has enhanced our knowledge of temperature-mediated changes to ecosystems (e.g., O'Connor et al., 2009), general patterns remain elusive and empirical studies often show idiosyncratic outcomes (Nelson et al., 2017a;

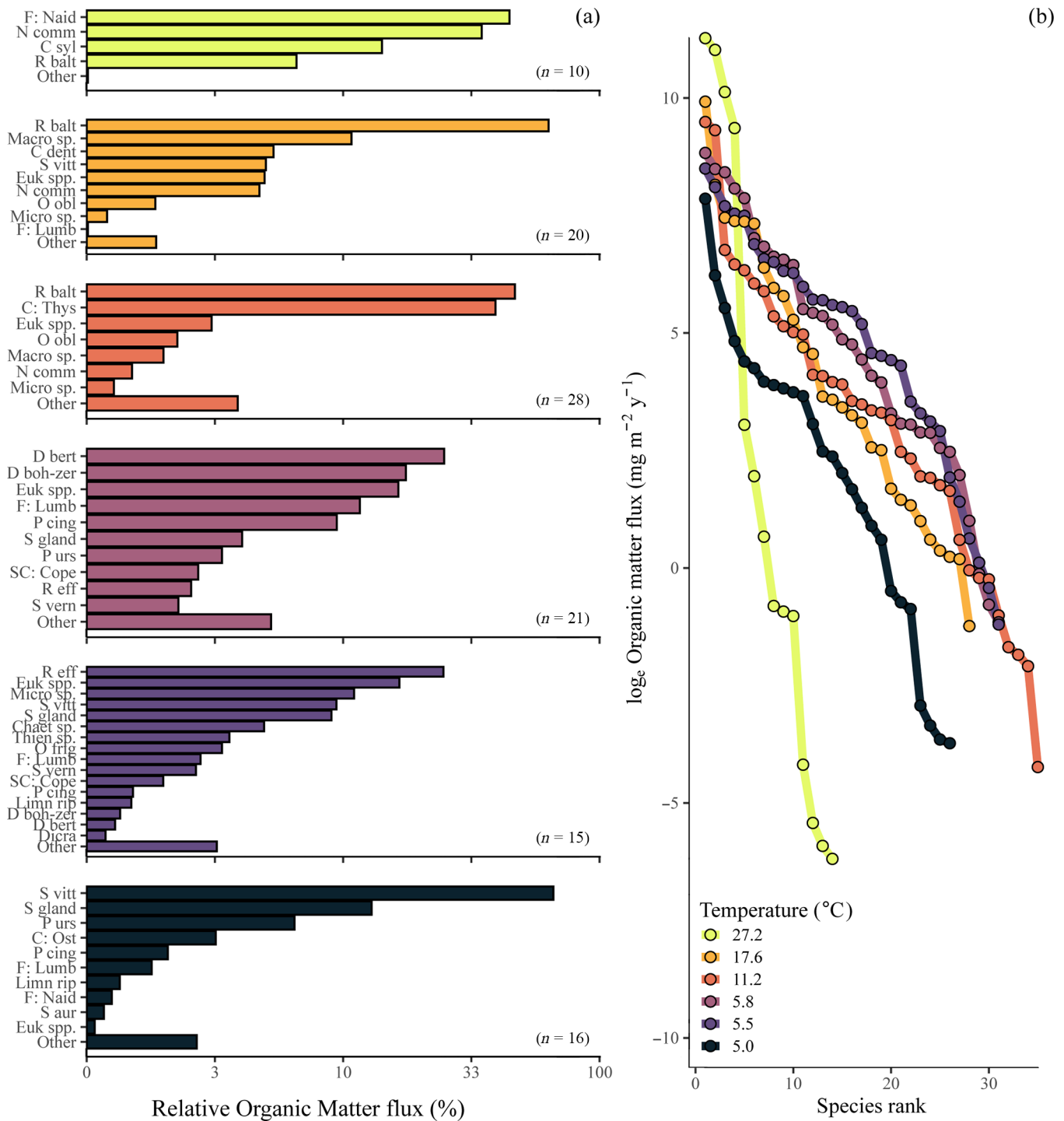


FIGURE 2 (a) Percent contribution of taxa to OM flux ($\log_e[\text{mg AFDM m}^{-2} \text{ y}^{-1}]$) in each stream; colors correspond to mean annual temperature shown in the legend; (b) rank-ordered organic matter flux ($\log_e[\text{mg AFDM m}^{-2} \text{ y}^{-1}]$) by taxon. Taxon: F: Naid, Family Naididae; N comm, *Nais communis*; C syl, *Cricotopus sylvestris*; R balt, *Radix balthica*; Macro sp., *Macropelopia* sp.; C dent, *Chaetocladius dentiforceps*; S vitt, *Simulium vittatum*; Euk spp., *Eukiefferiella* spp.; O obl, *Orthocladus oblidenis*; Micro sp. *Micropsectra* sp.; D bert, *Diamesa bertrami*; D boh-zer, *Diamesa bohemani-zernyi*; F: Lumb, Family Lumbricidae; P cing, *Potamophylax cingulatus*; S gland, *Sperchon glandulosus*; P urs, *Prosimulium ursinum*; SC: Cope, Subclass Copepoda; R eff, *Rheocricotopus effusus*; S vern, *Simulium vernum*; Chaet sp., *Chaetocladius* sp.; Thien sp., *Thienemanniella* sp.; O frig, *Orthocladus frigidus*; Limn rip, *Limnophora riparia*; Dicra, *Dicranota* sp.; C: Ost, Class Ostracoda; S aur, *Simulium aureum*. The number of taxa represented in the "Other" category for each stream is shown in the lower right corner of each panel.

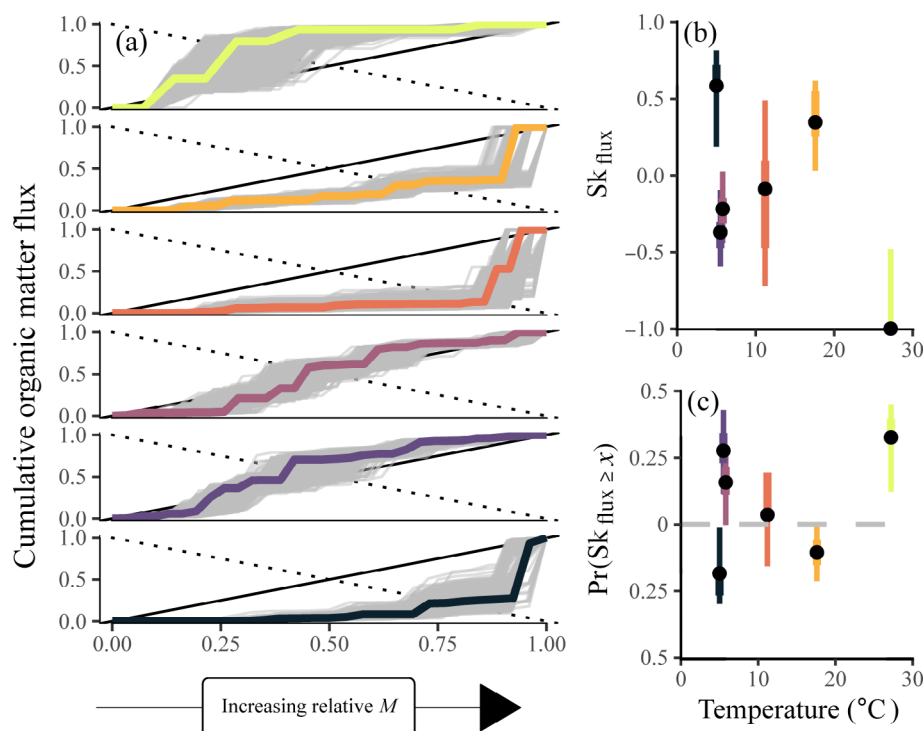


FIGURE 3 (a) Lorenz curves showing cumulative relative organic matter flux among taxa with increasing body size (from left to right; M , mg AFDM individual⁻¹). The solid line 1:1 line from the origin represents the line of equality. Distributions near this line suggest minimal structuring of OM fluxes in relation to body size. The dotted line allows for visualization of skewness in OM fluxes based on its intersection with the empirical Lorenz curve. (b) Empirical estimates of body size-related OM flux skewness in relation to stream temperature. (c) The probability of observing these skewness values when compared to a random ordering. For panels B and C, points represent the median value, wide bars represent the 25 and 75th percentile bounds, and narrow bars represent the 2.5 and 97.5th percentile bounds.

Zhang et al., 2017), especially at higher levels of biological organization (Walther et al., 2002; Woodward et al., 2010). Here, we demonstrate that warming acts as a strong environmental filter of species traits along a wide natural gradient of ecosystem temperatures. In particular, we found that increasing temperatures were associated with reduced population body size and increased population biomass turnover among stream invertebrate communities, leading to higher OM fluxes through these populations. In addition, we found that higher temperatures systematically skewed OM fluxes within communities, such that OM flows were increasingly dominated by taxa with rapid life cycles. Last, we discovered that the distribution of fluxes within communities was nonrandom, especially with respect to $P:B$ ratios at moderate to high temperatures, suggesting that temperature was especially important in structuring relative performance and resource acquisition within warm communities. These patterns show that the acceleration of energy and material fluxes through ecosystems in both an absolute (among ecosystems) and relative (within ecosystems) sense may be a general effect of environmental warming.

Across-stream trends in community $\overline{P:B}$ and $\overline{M}$

Warming-induced shifts in community body size distributions were associated with a community-level increase in the absolute rates of material flux. At the community level, we observed an ~7% increase in the mean biomass turnover rate ($P:B$; y^{-1}) of populations for each 1 °C of warming. Although this effect among communities may be partially attributed to the thermodynamic influence of temperature (Gillooly et al., 2001), biomass turnover rate is also closely related to organism body size (Brown et al., 2004; Huryn & Benke, 2007). Thus, warming may influence the distributions of $P:B$ ratios directly through its effects on metabolic rate and indirectly through reductions in organism body size and associated life-history traits. The increase in $P:B$ we observed across communities was similar in magnitude to the reduction in body size (i.e., +7% vs. -9%, respectively), reinforcing the fundamental connection between organism body size and $P:B$, but also suggesting increases in mean population $P:B$ across communities may, in part, be attributed to reduced organism body sizes (Figure 1b,c). Organism body size is

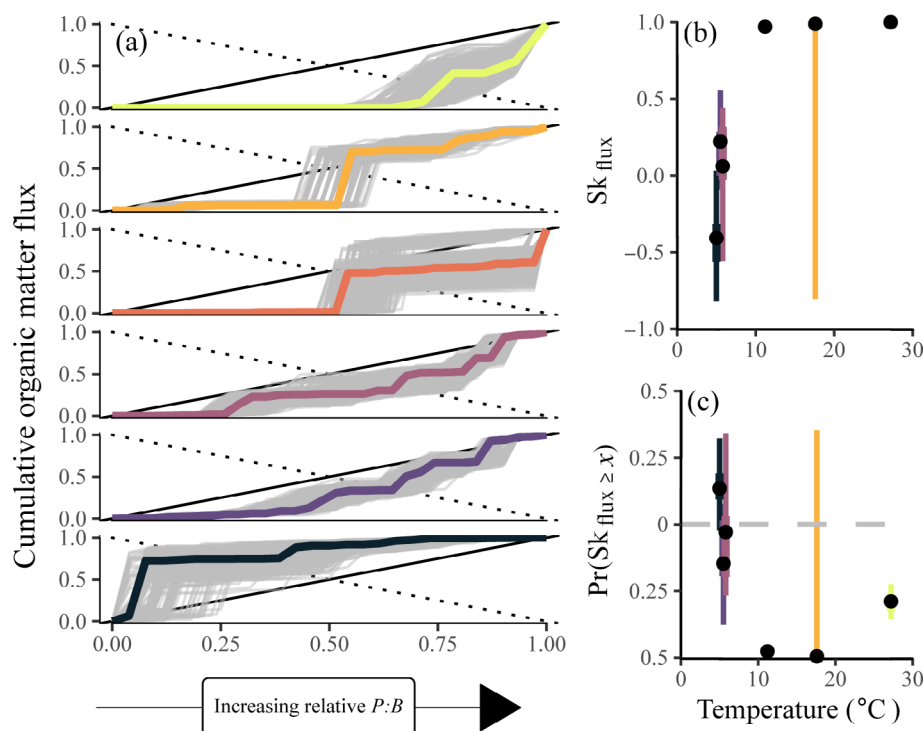


FIGURE 4 (a) Lorenz curves showing cumulative relative organic matter flux among taxa with increasing $P:B$ ratio (from left to right; y^{-1}). The solid 1:1 line from the origin represents the line of equality. Distributions near this line suggest minimal structuring of OM fluxes in relation to $P:B$ ratio. The dotted line allows for visualization of skewness in OM fluxes based on its intersection with the Lorenz curve. (b) Estimates of $P:B$ -related OM flux skewness in relation to stream temperature. (c) The probability of observing these skewness values when compared to a random (i.e., stochastic) ordering. For panels b and c, points represent the median value, wide bars represent the 25 and 75th percentile bounds, and narrow bars represent the 2.5 and 97.5th percentile bounds.

related to a number of other ecological attributes (Peters, 1983) and changes in body size with increasing temperatures are likely to have broad implications for ecosystems in a changing climate (Gibert, 2019).

A general reduction in body size has been deemed a “universal” response to warming (Daufresne et al., 2009; Gardner et al., 2011; Uszko et al., 2022), but notable deviations exist across ecosystems (O’Gorman et al., 2012; Ohlberger, 2013; Thresher et al., 2007). Based on our monthly sampling over a full annual cycle, we observed a clear decrease in the average body size of populations from cool to warm communities (Figure 1b), corresponding to an ~9% decline in the mass of individuals for every 1 °C increase in temperature. While this change is based on community-level shifts (i.e., different sets of taxa), the magnitude of the decline is consistent with intra-taxon patterns measured across broad phylogenetic groups (Deutsch et al., 2022). Interestingly, our results contrast with a warming experiment conducted in one of our study streams showing that a relatively small increase in temperature (3 °C) shifted invertebrate community biomass and productivity from smaller to larger organisms

(Nelson et al., 2017a, 2017b). Moreover, an additional study at Hengill that examined community size spectra across a much broader range of body sizes and taxonomic groups (i.e., diatoms to fish), but with limited temporal sampling (i.e., August only), reported an unexpected shallowing of mass-abundance slopes, suggesting warming may favor larger-bodied individuals (Adams et al., 2013; O’Gorman et al., 2017). Other studies have reported similar deviations from the “universal” response for other taxonomic groups (e.g., invertebrates: Zeuss et al., 2017, birds: Geist, 1987; Riemer et al., 2018, fish: Rypel, 2014). While there is a strong propensity for reduced body size with warming, clearly many processes can modify the direction and magnitude of body size shifts and how they play out from individual to ecosystem levels (e.g., growth and developmental rates, resource supply, competition, predation; Ohlberger, 2013). In addition, it is evident that the range of temperatures and body sizes considered, as well as the temporal scale of sampling, is likely to influence our understanding of how temperature influences patterns of body size in ecosystems (Jennings et al., 2007).

Relative OM fluxes in relation to species trait distributions

In addition to the cross-ecosystem effects of temperature on patterns of species traits and organic matter flux, we found that temperature had strong effects on the relative performance of species within communities, leading to an increase in OM fluxes through populations with high biomass turnover rates. Generally speaking, OM fluxes were unevenly distributed among populations within communities, which may be expected given the systematic unevenness in the distribution of individuals among species (Diaz et al., 2021). However, we found an important residual structure in the unevenness of OM fluxes that appeared to be related to functional trait axes. With respect to body size, the results were somewhat equivocal. In the coldest and warmest streams, we saw a strong skew in material fluxes toward larger and smaller species, respectively, but this pattern was not apparent at moderate temperatures (~6–17 C). In contrast, we found a much clearer pattern with respect to biomass turnover rates, in which OM fluxes were increasingly skewed toward taxa with high turnover within warmer streams. We also found that this pattern was clearly nonrandom, suggesting that it is not likely to have arisen from stochastic, neutral processes alone (e.g., Hubbell, 2001; Shoemaker et al., 2020). These results suggest that temperature may be a strong environmental filter—and therefore natural selection agent—for taxa with high turnover rates and associated life-history traits (e.g., multivoltinism: Nelson et al., 2020a; Zeuss et al., 2017, short lifespan: Munch & Salinas, 2009; Stoks et al., 2014, high growth rate: Donhauser et al., 2020), especially at relatively high temperatures.

Warming and food-resource interactions

The ecological and evolutionary effects of warming are likely mediated by their interaction with food resource availability and dynamics (Cross et al., 2015; McMeans et al., 2015). In high-latitude ecosystems where light plays a dominant role in driving resource dynamics, consumer energy demands may be affected by resources more than by temperature *per se* (Huryn & Benstead, 2019; Junker et al., 2020). This may be particularly apparent in open-canopied streams where primary production is highly synchronous with seasonal light regimes. Under such conditions, simplified resource dynamics may create a strong selection for high growth and turnover rates (and associated *r*-selected life-history traits, such as small body size) because consumers cannot compensate for periods of resource scarcity through diet shifts (e.g., consumptive “portfolio” effects,

Gutgesell et al., 2022). Future warming may exaggerate these effects because ectotherms may experience increased temperature-driven energy demands that are increasingly decoupled from resource availability (Huryn & Benstead, 2019). Acknowledging these dynamics may lead to a more general framework for understanding different responses to warming across organisms (Greyson-Gaito et al., 2023), latitudes (Gibert, 2019), and ecosystem types (Gutgesell et al., 2022; McMeans et al., 2015).

CONCLUSIONS

We documented the important role of temperature in structuring key functional traits and the relative distribution of material fluxes across a natural stream temperature gradient. Higher temperatures were associated with increased total flux through the food web, as well as reductions in average population body size and increases in population biomass turnover. Further, biomass turnover rate—but less so body size—was increasingly important for structuring OM fluxes at warmer temperatures. Our results support the idea that warming may reduce organism size and also “speed up” ecosystem dynamics in both an absolute and relative sense. These changes have important implications for the maintenance of biodiversity, as well as for the connections between biodiversity and the magnitude and stability of ecosystem energy and material cycles in a warming world.

ACKNOWLEDGMENTS

We are grateful to Sigurður Guðjonsson, Guðni Guðbergsson, and the staff at the Veiðimalastofnun for providing laboratory space and logistical support. We are also grateful to Sveinbjörn Steinþorsson at the University of Iceland for super-jeep transport to our field sites during the winter. We thank Lauren David, David Hernandez, Amanda Keasberry, Elena Nava, Camille Perrett, Jackie Pitts, Friðþjofur Árnason, Liliana García, Ragnahildur Magnúsdóttir, Ryan McClure, Vija Pelekis, Adam Toomey, Chau Tran, Brooke Weigel, Tanner Williamson and many undergraduate workers for field and laboratory help. Jeff Wesner and Abe Kanz generously provided R code and discussions on modeling diet proportions. We thank Dr. Victor Saito and two anonymous reviewers for constructive comments that improved the paper. This study was supported by the National Science Foundation (DEB-0949774 and DEB-1354624 to Jonathan P. Benstead and Alexander D. Huryn and DEB-0949726 to Wyatt F. Cross).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Junker, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10455905>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Junker, James R., Wyatt F. Cross, James M. Hood, Jonathan P. Benstead, Alexander D. Huryn, Daniel Nelson, Jon S. Ólafsson, and Gísli M. Gíslason. 2024. “Environmental Warming Increases the Importance of High-Turnover Energy Channels in Stream Food Webs.” *Ecology* 105(6): e4314. <https://doi.org/10.1002/ecy.4314>