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

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# Abstract

Warming temperatures are altering communities and trophic networks globally. While the influence of warming on food webs is often context-dependent, increasing temperatures are predicted to influence communities in two fundamental ways: 1) by reducing average body size and 2) by increasing individual metabolic rates. Both body size and metabolic rate are important drivers of many ecological patterns. Therefore, warming-induced changes have the potential to propagate through countless ecosystem processes thereby altering the distribution of food web fluxes, food web stability, and potentially the importance of environmental and biological factors in community assembly. Here, we quantify the patterning and relative distribution of organic matter fluxes through stream food webs spanning a natural ~25C temperature gradient. We then related patterns in fluxes to species and community traits (body size, *M* and biomass turnover, *P:B*) within and across ecosystems. We predicted 1) warmer communities would skew towards smaller *M* and higher *P:B* across ecosystems and, 2) organic matter fluxes within communities would increasingly skew towards smaller, higher *P:B* populations at higher temperatures. Across the temperature gradient, communities in warmer streams were composed of smaller-bodied and higher-turnover populations on average. Additionally, material fluxes of warmer streams were increasingly skewed towards high-turnover populations *within* the community, showing higher temperatures restructured organic matter fluxes in both an absolute and relative sense. With warming, the relative distribution of organic matter fluxes also appeared to be increasingly ‘non-random’, suggesting the potential for stronger selection for these traits with increasing temperature. The emerging picture is a warmer world that is both smaller and faster. Our study provides clear empirical support for this pattern in natural communities and suggests that warming has the potential to shape pathways of energy and material flows in food webs in ways that may be predictable.

# Introduction

Increasing global temperatures can influence the provision and maintenance of ecosystem services by modifying the network of species interactions that underpin ecosystem functions (de Ruiter et al. 1995, Woodward et al. 2010, Brose et al. 2012, Thompson et al. 2012). The effects of warming permeate across levels of biological organization from its control on individual metabolic rates (Gillooly et al. 2001, Brown et al. 2004) and biological activity (e.g., attack rate, handling time, growth rates, etc.; Dell et al. (2014), to broad-scale shifts in community assembly and structure (Nelson et al. 2017b, Gibert 2019, Saito et al. 2021). Across global climate gradients, these temperature-induced changes have the potential to mediate food web stability (Baiser et al. 2019) by altering the acquisition and allocation of resources among species (Zhang et al. 2017) and the magnitudes and relative distribution of energy fluxes among species and trophic levels (May 1972, McCann et al. 1998, Barnes et al. 2018).

Understanding how warming alters energy fluxes in food webs requires information about how temperature modifies connections between ecosystem structure (i.e. biodiversity) and function (BEF). These connections hinge upon how warming influences functional trait distributions and how these functional traits translate to energy demands (Norberg et al. 2001, Loreau et al. 2001, Norberg 2004). Additionally, warming may modify both deterministic (e.g., environmental/niche filtering, Whittaker 1962) and stochastic (e.g., neutral theory, Hubbell 2001) community assembly processes (Saito et al. 2021), leading to many possible relationships between warming and species’ abundance and trait distributions. For example, although temperature appears to have minimal control on species richness across taxonomic groups (e.g., Bastazini et al. 2021), warming may have profound effects on the dominance structure (i.e. evenness) of ecological communities, often by reducing community evenness and favoring a few well-adapted species (Hillebrand et al. 2008). This strong environmental filtering is likely to skew trait distributions, to some extent, in natural communities (Therriault and Kolasa 1999). However, the relative distribution of traits can be modified by additional processes beyond environmental filtering that alter species relative abundance distributions [e.g., species interactions; Therriault and Kolasa (1999); demographic stochasticity; Hubbell (2001)]. These additional processes can exaggerate or counter any skew in trait distribution imparted through environmental filtering and may modify the relationship between species’ traits and the absolute and relative energy demands in food webs.

Body size is a fundamental trait that is strongly influenced by temperature and has great potential to influence energy flux (Atkinson 1994, Daufresne et al. 2009, Gardner et al. 2011). Body size reductions arise from multiple mechanisms acting at different levels of organization, such as the increased relative abundance of smaller species within warmer communities (Bergmann 1848), or smaller individuals in warmer populations (James 1970), or through reduced body size of warmer individuals (Atkinson 1994). Temperature-size relationships are likely to influence the distribution of body sizes both across and within ecosystems, such that warmer communities should contain smaller species and populations, on average, and smaller organisms should be more dominant within a community. These changes can have important implications for ecosystems pattern and processes that control energy and material fluxes in ecosystems because body size is a strong determinant of an organism’s biology (Peters 1983) influencing, life history patterns (Altermatt 2010, Zeuss et al. 2017, Nelson et al. 2020a), and developmental (Angilletta et al. 2004) and metabolic rates (Gillooly et al. 2001, Brown et al. 2004).

Metabolic rate, in addition to being controlled by body size, is a second key trait that is influence by temperature and tied to variation in energy flux through food webs (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 (Osmond et al. 2017, Bideault et al. 2019). These processes have been shown to modify ecosystem patterns through changes in population abundance (Bernhardt et al. 2018), consumer-resource interactions (Bideault et al. 2019), and food web structure (Gibert 2019). Importantly, the kinetic effects of temperature are tied to many biological processes (Dell et al. 2014), among them growth rate (Gillooly et al. 2001), developmental rate (Zuo et al. 2012, Nelson et al. 2020a), voltinism (Zeuss et al. 2017), and population turnover rate (Brown et al. 2004, Huryn and Benke 2007). Taken together, these changes suggest a smaller, faster world in which warming “speeds up” ecosystem processes through the compounded effects of smaller body size and higher turnover rates, with potentially lasting imprints on food web structure and energy fluxes (Gibert 2019).

We quantified patterns of organic matter flux in stream food webs across a natural temperature gradient (~5–28C) 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 within streams seasonally (O’Gorman et al. 2012, Hood et al. 2018). Invertebrates in these streams rely on autochthonous resources (O’Gorman et al. 2012, Nelson et al. 2020b), thus the dynamics of primary production have a strong control on consumer energy demand (Junker et al. 2020a). We, therefore, predicted that annual organic matter fluxes to consumers would increase with stream temperature mirroring patterns in resource availability and consumer energy demand. We also hypothesized that temperature would act as a principle environmental filter on community assembly and organic matter fluxes by favoring ‘fast’ life-history traits. Specifically, we predicted that warming temperatures among streams would lead to a decrease in average body size and an increase in average biomass turnover (i.e., *P:B* ratio) of populations, channeling the majority of energy flux through these taxa among stream communities. We also predicted that *within* communities, organic matter fluxes would be driven by small-bodied and high *P:B* taxa, and that these would not arise by random change (i.e., a ‘selection effect’ *sensu* Huston 1997). Our results should help refine general predictions about how warming, and its influence on key traits, is likely to shape energy flux through animal food webs.

# Methods

We studied six streams within the Hengill geothermal field of southwestern Iceland (64 03’N 021 18’W) that varied in mean annual temperature. Hengill is characterized by indirect geothermal heating of groundwater (Arnason 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 (O’Gorman et al. 2014, Nelson et al. 2017b). We selected streams to maximize the temperature range, while minimizing differences in the structural aspects of the primary producer community (Junker et al. 2020b). 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). Light availability in the watershed was measured every 15 min from atmospheric stations (HOBO pendant temperature/light UA-002-64, 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 2010–2011 were part of a separate warming manipulation during the reference (i.e., non-manipulated) year (Nelson et al. 2017a, 2017b). Inter-annual comparisons of primary and secondary production in previous studies showed minimal differences among years in unmanipulated streams, suggesting that combining data from different years would not significantly bias our results (Nelson et al. 2017a, Hood et al. 2018). We collected five Surber samples (0.023 m2, 250 m mesh) from randomly selected locations within each stream. Within the sampler, inorganic substrates were disturbed to ~10 cm depth and invertebrates and organic matter 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 m – <1 mm) fractions using nested sieves and then removed invertebrates from each fraction under a dissecting microscope (10–15 x magnification). For particularly large samples, fine fractions were sub-sampled (1/2–1/16th) using a modified Folsom plankton splitter prior to removal of invertebrates. Subsamples were scaled to the rest of the sample assuming similar abundance and body size distributions. Macroinvertebrates were identified to the lowest practical taxonomic level (usually genus) with taxonomic keys (Peterson 1977, Merritt et al. 2008, Andersen et al. 2013). 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 and Huryn 2017). Growth rates were determined using taxon-appropriate approaches described in Junker and others (2020a). Briefly, growth rates of common taxa (e.g., Chironomidae spp., *Radix balthica*, etc.) were determined using *in situ* chambers ( *sensu* Huryn and 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 pre-conditioned 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 (mg ash-free dry mass [AFDM]) using published length-mass regressions (Benke et al. 1999, O’Gorman et al. 2012, Hannesdóttir et al. 2013). Growth rates (*g*, d-1) were calculated by the changes in mean body size (*M*) over a given time interval (*t*) with the following equation:

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 regression cited above, and size-frequency histograms were visually inspected for directional changes in body size through 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 > . If this condition was not met after 1e4 resamplings, a minimum growth rate of 0.001 was used. 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 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 interval, size classes were summed for each taxon to calculate total population-level production. Intervals were summed to estimate annual secondary production (g AFDM m-2 y-1).

## Organic Matter Consumption Estimates

Organic matter fluxes through the community were calculated using the trophic basis of production method (TBP, Benke and Wallace 1980). Taxon-specific secondary production estimates were combined with diet proportions (see Supplemental Materials), diet-specific assimilation efficiencies, *AEi*, and net production efficiencies, *NPE* (e.g., McCullough 1975), to estimate consumption of organic matter. For each food category, *i*, diet proportions were multiplied by the gross growth efficiency () 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 to estimate consumption of organic matter from each food category by each taxon (Benke and Wallace 1980). Consumption was calculated for each taxon across sampling intervals (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, wherein bootstrapped vectors of secondary production for each taxon (see *Secondary production* methods above) were resampled and consumption estimated with the TBP method using modeled diet proportions (see *Diet analysis* in Supplemental Materials), diet-specific assimilation efficiencies, and net production efficiency. Variability in *AEi* was incorporated by resampling values from beta distributions fit to 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 non-vascular plants (bryophytes) = 0.1 (95% PI: 0.08-0.12), and animal material = 0.7 (95% PI: 0.56-0.84)(Welch 1968, Benke and Wallace 1980, 1997, Cross et al. 2007, 2011). Variability in *NPE* was incorporated by resampling values from an assumed beta distribution with median *NPE* = 0.45 (95% PI = 0.4-0.5). Beta distributions were fit 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 among taxa within each stream, we constructed Lorenz curves (Lorenz 1905) on rank-ordered OM fluxes, such that in a community with species and the relative OM flux of species *i*, , is ordered . The Lorenz curve shows how a value, in this case OM flux, accumulates with increasing cumulative proportion of taxa. In a community with perfectly equal distribution of OM flux among taxa, the Lorenz curve is simply a straight diagonal line. Deviation from perfect equality was calculated as the Gini coefficient (Gini 1921), normalized for differences in among streams, (Solomon 1975, Chao and Ricotta 2019):

where 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 (), and a value of zero represents a community in which the total OM flux is attributed to a single taxa.

### Distribution of OM fluxes in relation to taxa traits

We predicted that warming would favor taxa with smaller body size and higher population turnover and therefore OM fluxes would be skewed towards small body size (*M*) and higher *P:B* across and within communities. To assess the potential effects of environmental filtering across communities, we used bootstrapped linear regressions to quantify the relationship between mean annual temperature (C) and mean population body size () and biomass turnover () of each stream community. Here, 1000 values of population *M* or *P:B* were resampled with replacement from population secondary production vectors (see *Secondary Production* above) for each taxa within each stream. The mean of all populations within a stream was calculated and a linear model was fit between *loge*-transformed or and mean annual temperature. Response variables were transformed to meet the assumption of normally distributed residual variation.

To quantify how the distribution of organic matter fluxes were modified *within* a community and whether this modification was related to temperature, we assessed the extent to which the relative OM fluxes among taxa were skewed towards 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, , based on quartiles of the distribution of OM fluxes in relation to taxa traits as:

where, , is the cumulative flux at some quantile, , of the community trait distribution. We repeated this analysis for all bootstrapped estimates of OM flux in each stream community. Skewness coefficients exist in the range [-1, 1], where -1 indicates that OM fluxes are skewed perfectly away from a trait and 1 indicates that higher relative fluxes are perfectly associated with higher trait values. To determine if the skewness of fluxes with *M* and *P:B* was related to mean annual stream temperature, we use bootstrapped beta regression with a simple transformation, , 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 whether and how temperature influences 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’ and 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., ‘non-random 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 govern the distribution of OM fluxes within communities. To accomplish this, we first had to account for statistical constraints that restrict the range of possible outcomes (i.e., feasible set, Haegeman and Loreau 2008, Diaz et al. 2021), given the number of species and the relative distribution of OM fluxes within a community. The number of unique orderings of species increases to computationally intractable numbers very quickly (e.g., , 10 species ~3.6e6 unique orderings). Therefore, we chose to permute 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, , compared to a random ordering given the distribution of relative OM flux.

# Results

## Community organic matter fluxes

Annual community OM fluxes mirrored patterns of secondary production reported previously (Junker et al. 2020a). Organic matter flux to invertebrates varied ~45-fold among streams (mean [95% percentile interval (PI)]: 3.9[2.1 – 6.2 to 177.1 [126 – 236.4] g AFDM ) and was positively related to temperature (Figure 1A).

Differences in OM flux among streams was driven by variation in total energy demand rather than composition of consumed resources, as consumer diets were highly similar among streams (Figure S1). Diets were dominated by diatoms (44%; 0–75.7; 95% PI), amorphous detritus (17.3%; 0–32.3; 95% PI), and green algae (13.3%; 0–42.8; 95% PI). Within streams, diet overlap ranged from 68% (65 – 71%) to 0.75% (70 – 79%) among invertebrate taxa. Among streams, diet overlap was similarly high with a mean overlap of 89% (84 – 92%; 95% PI). Diet similarities based on pairwise comparisons among streams showed little difference and no clear relationship with temperature.

## Evenness of organic matter 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 95% PI; Table S1] and were dominated by insects in the families Simuliidae and Chironomidae, pulmonated snails (*Radix balthica*), and oligochaete worms (Figure 2A & B; Figure S2). In an absolute sense,~85% of total OM flux was contributed by 2 and 10 taxa, which comprised only 3% to 29% of total taxon richness. Although differences in evenness among streams were partially attributed to variation in taxon richness (range: 14 to 35), fluxes were still highly uneven after accounting for differences in richness (i.e., similar ‘Normalized’ Gini coefficients, 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. In the warmest stream, where maximum temperatures approach ~40C, taxon richness was lowest and OM fluxes were dominated by oligochaete worms in the family Naididae, the chironomid *Cricotpous sylvestris*, and *R. balthica*. Among-stream differences in evenness and dominance of OM fluxes were not related to temperature (Appendix II Table S1).

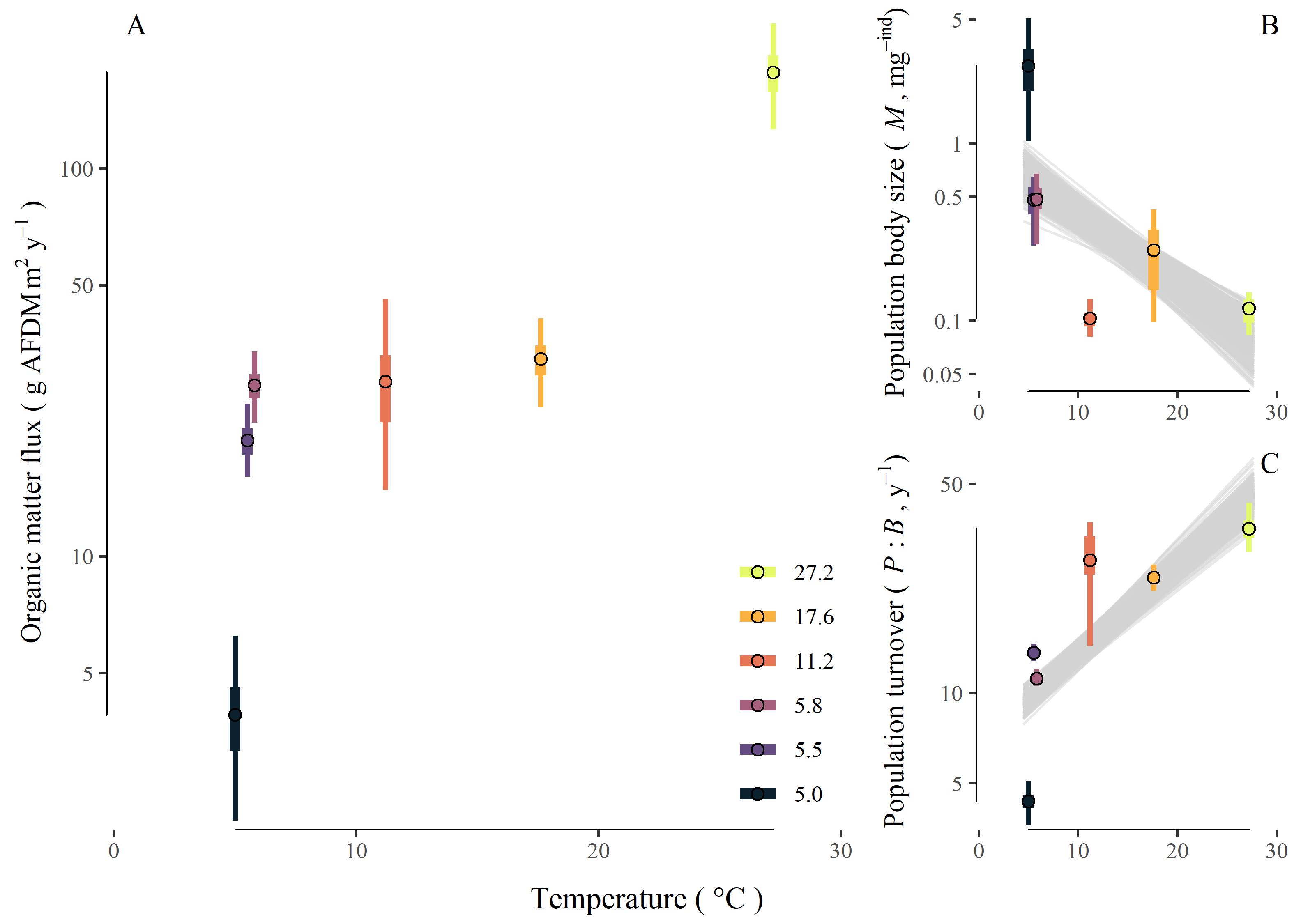


Figure 1. (A) Total organic matter flux (g AFDM m-2 y-1) increased with increasing mean annual temperature. Warming stream temperatures also led to (B) a decrease in mean population body size (*M*, mg ind-1) and (C) an increase in mean population biomass turnover rate (*P:B*, y-1). For all panels, points represent the mean value, wide bars represent the 25th and 75th percentile bounds, and narrow bars represent the 2.5th and 97.5th percentile bounds.

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

Across stream communities, average population body size (*M* [mg AFDM ind-1]) decreased and average population biomass turnover rate (*P:B* [y-1]), increased with increasing temperature (Figure 1B, C). Average *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; 95% PI) in the warmest stream, corresponding to an -8.7% (-11.1 – -6.4; 95% PI) decrease in mean body size for every 1C increase in temperature (Figure 1B). Average population *P:B* ratio increased from 4.36 y-1 (3.63 – 5.09; 95% PI) in the coldest stream to 35.51 y-1 (29.59 – 0.14; 95% PI) in the warmest stream corresponding to a 6.94% (6.15–7.85; 95% PI) increase in *P:B* ratio for every 1C increase (Figure 1C).

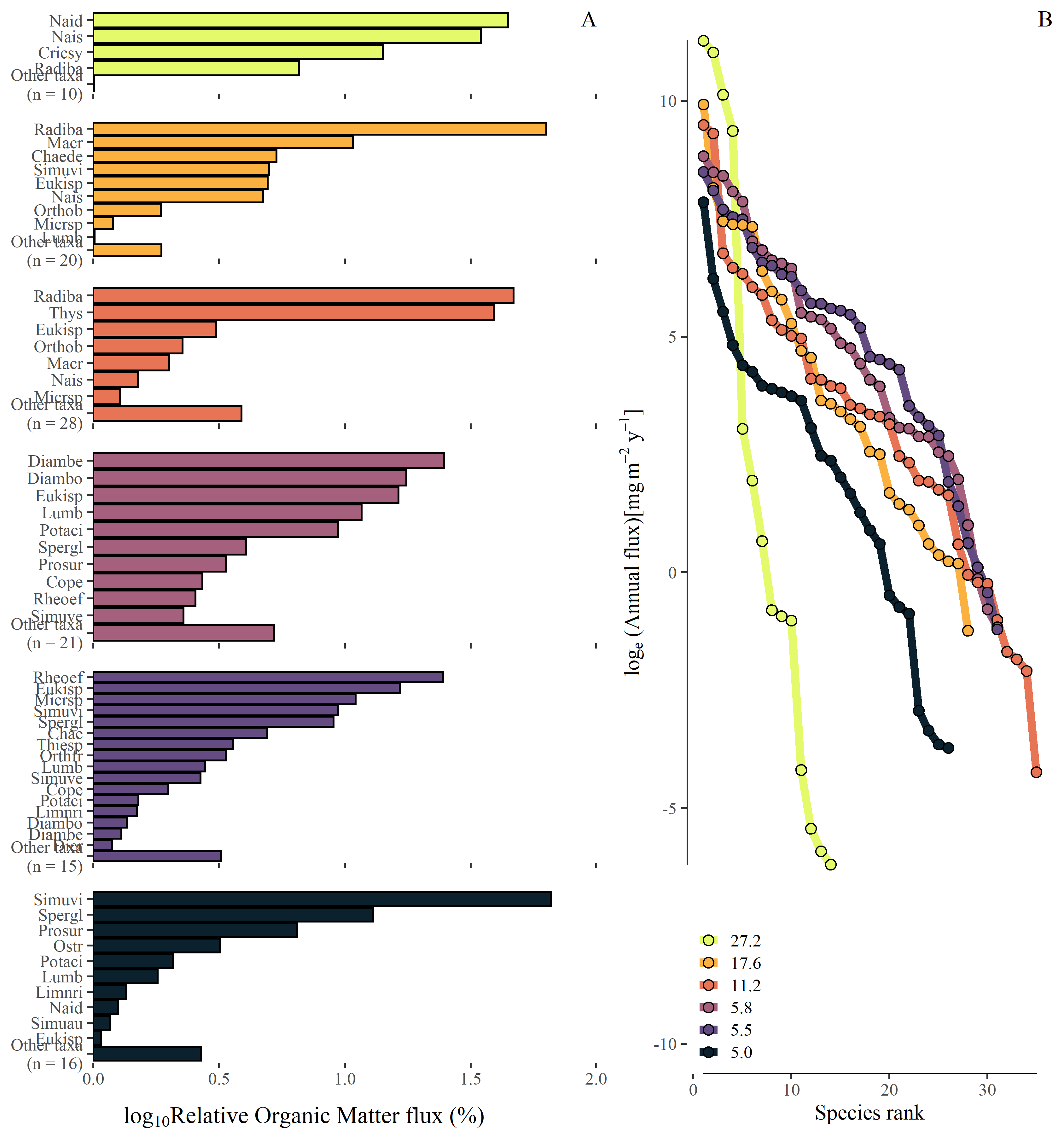


Figure 2. (A) Relative contribution (log10%) of different taxa to OM flux in each stream; colors correspond to mean annual temperature shown in the legend; (B) rank ordered organic matter flux (loge(mg AFDM m-2 y-1) by taxon. See supporting materials for the full key of taxonomic abbreviations.

Within stream communities, OM fluxes exhibited diverse relationships with regard to body size, showing skew toward taxa with larger body sizes (positive skew), toward smaller body sizes (negative skew), and neutrally with respect to body size (Figure 3A). Skew estimates with body size (skew range: -1 to 0.56; Figure 3B). 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. Similarly, skew in OM fluxes in relations 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).

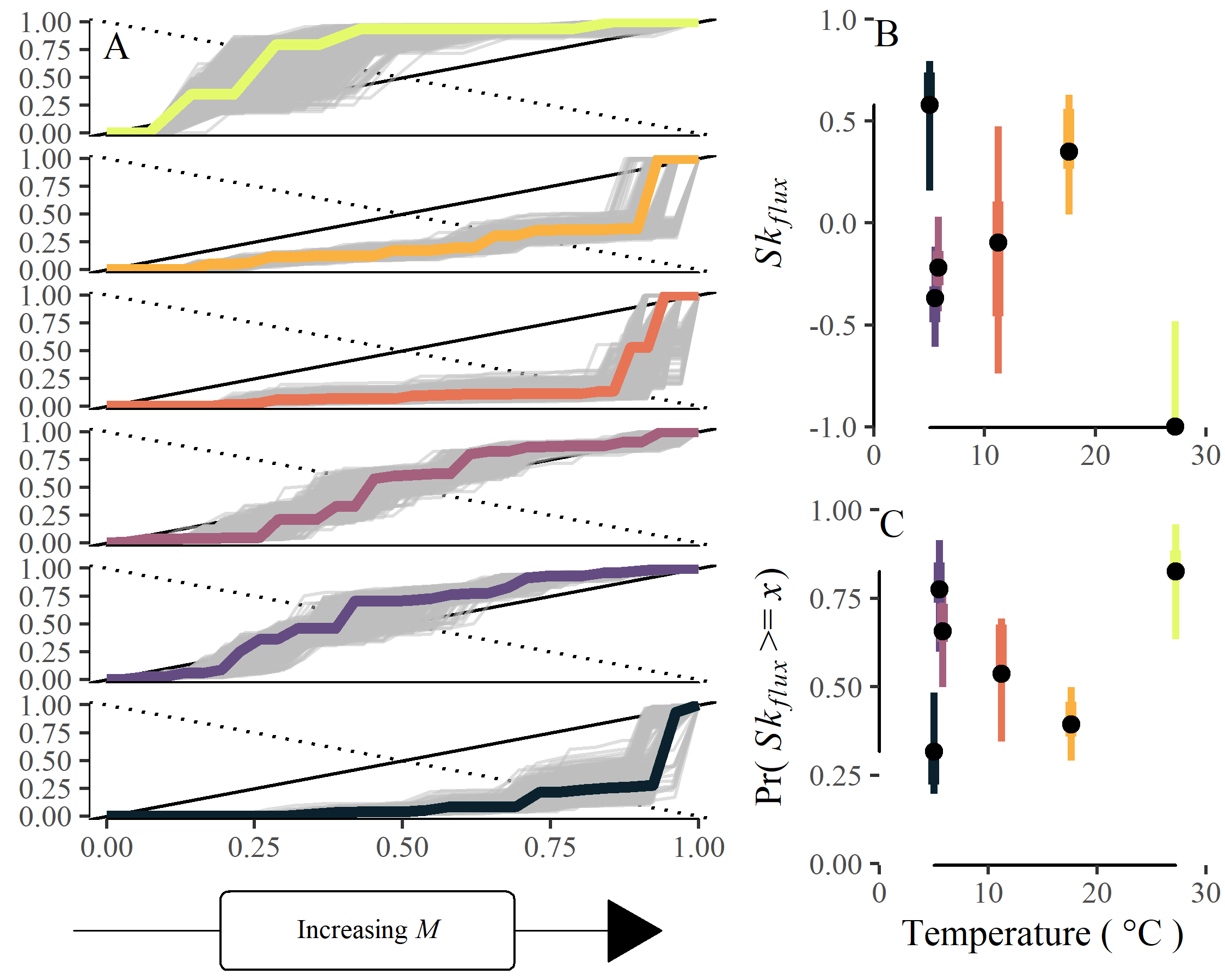


Figure 3. (A) Lorenz curves showing cumulative relative organic matter flux among taxa with increasing body size (from left to right; *M*, mg AFDM ind-1). The solid line 1:1 line from the origin represents the line of perfect equality. Distributions near this line suggest minimal structuring of OM fluxes 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 (i.e. s) ordering.For panels B and C, points represent the mean value, wide bars represent the 25th and 75th percentile bounds, and narrow bars represent the 2.5th and 97.5th percentile bounds.

We compared our empirical skew estimates (i.e., ) absed on ordered data (i.e., ordered from small to large *M* or low to high *P:B* ratios; Figure 3B and Figure 4B) to skew estimates based on randomly sorted data to detect whether OM fluxes through smaller and higher *P:B* taxa were based on random selection (i.e., stochastic) or were truly based on these traits. 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 (0.07–0.95; 95% PI); there was a very weak positive association between this probability and temperature (Figure 3C). In contrast, the probability of a similarly or more extreme skew in relation to *P:B* ratios ranged from 0.06 (0 – 0.75; 95% PI) to 0.62 (0.22 – 0.82; 95% PI, Figure 4C) and in this case there was a clear trend towards a more structured OM flux distribution–i.e., favoring fluxes through high *P:B* taxa–at warmer temperatures. The likelihood of elevated fluxes among high *P:B* taxa became much more likely with warming, and the probability of random ordering decreased -4.6% (-5.1% – -4.2%; 95% PI) for every 1C increase in temperature (Figure 4C).

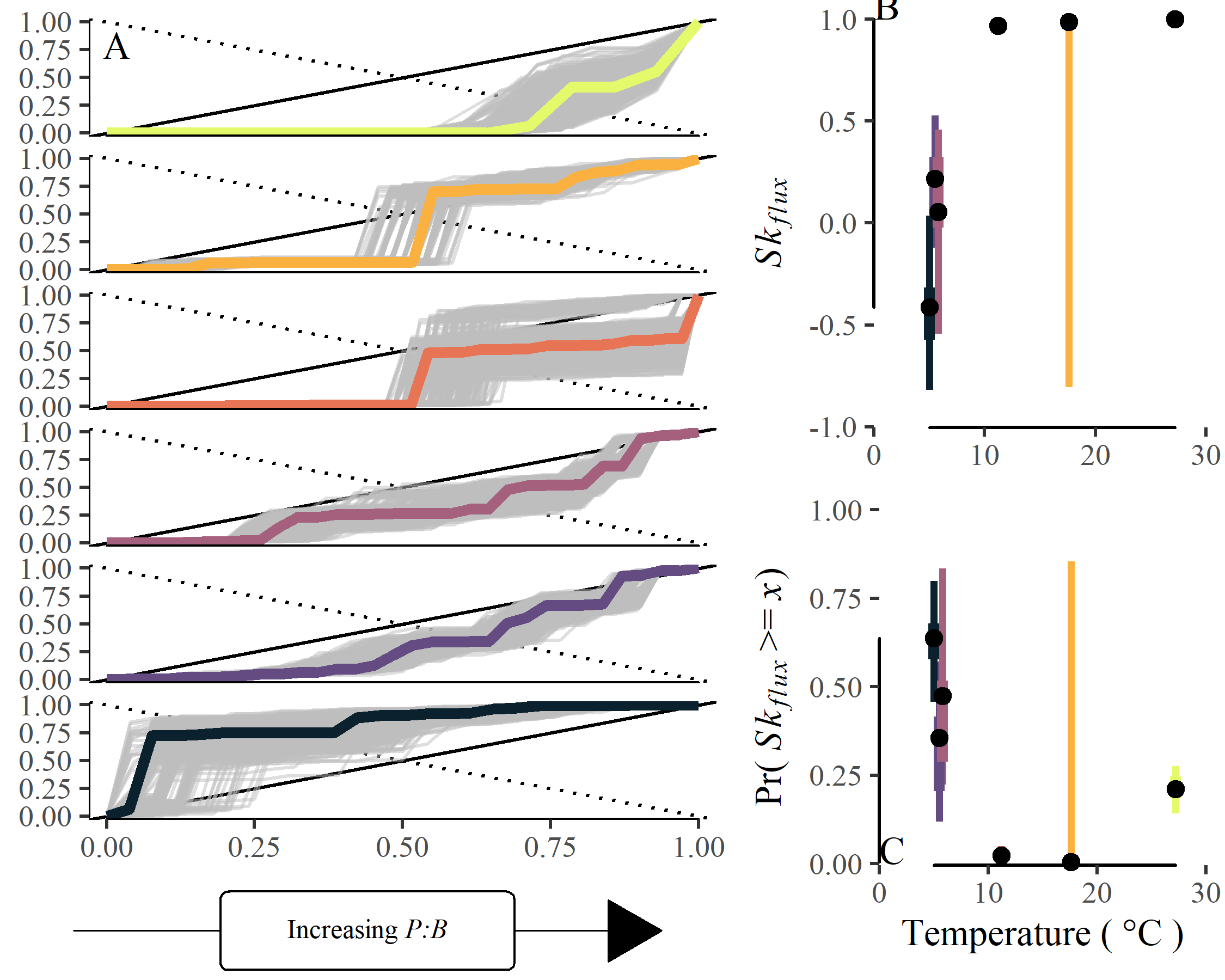


Figure 4. (A) Lorenz curves showing cumulative relative organic matter flux among taxa with increasing *P:B* ratio (from left to right; y-1). The solid line 1:1 line from the origin represents the line of perfect equality. Distributions near this line suggest minimal structuring of OM fluxes in relation to *P:B* ratio. The dotted line allows for visualization of skewness in OM fluxes based on its intersection with the empirical lorenz curve. (B) Empirical 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 mean value, wide bars represent the 25th and 75th percentile bounds, and narrow bars represent the 2.5th and 97.5th percentile bounds.

# Discussion

While a growing body of theoretical and empirical study has enhanced our knowledge of temperature-mediated changes to ecosystems (e.g., O’Connor et al. 2009), general patterns are elusive and empirical studies often idiosyncratic (Nelson et al. 2017a, Zhang et al. 2017), especially at higher levels of organization such as communities and food webs (Walther et al. 2002, Woodward et al. 2010). We documented shifts in the pathways of material flows across a wide natural temperature gradient and found that increasing temperatures were associated with reductions in mean population body size and increases in mean population biomass turnover across stream invertebrate communities. In addition, we found that warming systematically skewed OM fluxes *within* communities such that, OM flows were increasingly skewed towards rapid life-cycle taxa. Lastly, we discovered that the distribution of fluxes *within* communities was non-randomly organized, especially with respect to *P:B* ratios at moderate to high temperatures, suggesting that environmental filtering is especially important in the community assembly of warm communities. These patterns suggest that the acceleration of energy and material fluxes through ecosystems in both an absolute and relative sense may be a general effect of environmental warming. Further, environmental filtering that is driven by warming is likely governed by both the traits of species present and the ways in which energy and material fluxes are distributed among taxa.

Warming increased rates of materials flux in an absolute sense largely through shifts in community body-size structure. At the community level, we observed a ~7% increase in the mean biomass turnover rate (*P:B*; y-1) of populations for each 1 of warming. Although this effect among communities may be 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 and 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. 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 were, may in large part, be attributed to reduced organism body sizes (Figure 1B & C). Organism body size is 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 exists across ecosystems (Thresher et al. 2007, O’Gorman et al. 2012, Ohlberger 2013). We observed a clear decrease in the average individual body size of populations from cool to warm communities (Figure 1B), corresponding to ~-9% decline in the mass of individuals for every 1C increase in temperature. While this change is based on community-level shifts (i.e., different sets of taxa), the magnitude of decline is consistent with intra-taxon patterns measured across broad phylogenetic groups (Deutsch et al. 2022). Interestingly, our results contrast with a previous warming experiment in one of our study streams showing a 3C increase in temperature shifted community biomass and productivity from smaller to larger organisms (Nelson et al. 2017a, 2017b). Moreover, a study of diatom communities across the same temperature gradient in Iceland that reported no consistent change in body size at either the population- or community-level (O’Gorman et al. 2012, Adams et al. 2013). 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 certainly a strong propensity for reduced body size with warming, clearly other processes can modify the direction and magnitude of body size shifts and how they play out from individual to ecosystem scales.

In addition to community-level responses, temperature was also an important modifier of the relative performance of species *within* communities, causing an increase in the rates of material flux in a *relative* sense with warming. Generally speaking, OM fluxes were unevenly distributed among consumers. Given the systematic unevenness in the distribution of individuals among species (Diaz et al. 2021), it may not be surprising that this pattern carries over into energy and material fluxes. Interestingly, however, we found important structure in the unevenness of OM fluxes with increasing temperature. In particular, we found that OM fluxes, to some degree, showed non-random patterning along multiple trait axes. Firstly with respect to body size, the results were equivocal. In the coldest and warmest streams, we saw a strong skew in material fluxes towards larger and smaller species, respectively, but this pattern was not apparent at moderate temperatures (~6–17C). A much clearer pattern was the increased skewness of OM fluxes towards taxa with high biomass turnover rates at warmer temperatures. This pattern also appeared to be increasingly non-random with warming (Figure 4B & C). That the relative distribution of OM fluxes was unlikely due to chance reduces the likelihood this pattern could be attributable to demographic stochasticity (e.g., Hubbell 2001) and suggests temperature may be a strong environmental filter at even at high temperature (e.g., Saito et al. 2021). Further, warming may filter for taxa with high *P:B* and associated life history traits ( i.e., multi-voltinism: Zeuss et al. 2017, Nelson et al. 2020a, short lifespan: Munch and Salinas 2009, high growth rate, Donhauser et al. 2020), especially at temperature “extremes” (Donhauser et al. 2020).

A growing body of theoretical and empirical research is beginning to explore the implications of warming for the stability of ecosystems (Fussmann et al. 2014). “Natural laboratories”, such as the geothermal watershed studied here, offer a unique opportunity to isolate the effects of warming and the dominant processes by which it may modulate ecosystem structure and dynamics (O’Gorman et al. 2014). Particularly relevant in our study is the stability and functioning of light-driven ecosystems in response to present and future warming. One aspect of climate change that is especially pronounced in high-latitude ecosystems is the decoupling of light regimes—and thereby energy supply regimes—and the timing of temperature-driven metabolic demands (McMeans et al. 2015, Huryn and Benstead 2019). Here, our within-community contrast in how warming skewed fluxes through *P:B* vs. body size taxa lends potential insight into the proximate ways in which temperature alters ecosystem structure and function. Temperature-size responses vary with a number of ecological factors (Ohlberger 2013), however, warming-induced body size reductions act as a stabilizing process in consumer-resource interactions by reducing consumer:resource biomass ratios (Gilbert et al. 2014, Sentis et al. 2017, Osmond et al. 2017) and consumer energy demand relative to resource supply (Kozłowski et al. 2004, McCann 2011, DeLong 2012). This gives credence to alternative models of organism body size optimization influenced by, for example, the balance of resource supply and energy demand (e.g., Kozłowski et al. 2004, DeLong 2012). Crucially, these alternative models highlight the trade-off between asymptotic body size and metabolic demand (DeLong 2012), a trade-off that may be particularly important in seasonally variable energetic regimes. In the absence of other limiting factors, increasing temperatures are likely to make seasonal “boom and bust” cycles of primary production more extreme because of the interactive effects of light and temperature limitation on photosynthetic rates (e.g., Rae and Vincent 1998). This process may increase the autocorrelation, as well as, the magnitude (i.e., enrichment) of resource supply, thereby, exaggerating the selection for reduced body sizes because larger and/or slower consumers destabilize consumer-resource dynamics in the face of increasingly extreme seasonal autocorrelation of resource growth (Greyson-Gaito et al. 2022). This suggesting a connection between warming responses and a more general food web dynamic of increased relative rates of resource supply and consumer demand (e.g., paradox of enrichment, McCann 2011). Therefore, the general response of reduced body size with warming or latitudinal temperature gradients may reflect, in part, constraints imparted by food web dynamics, in addition to, physiological mechanisms (e.g., oxygen, Deutsch et al. 2022, differential responses of biological process rates, Forster et al. 2011). The importance of this dynamic may be especially under-appreciated in high-latitude ecosystems (McMeans et al. 2020).

Here, we documented the important structuring role of temperature in community assembly and the relative distribution of material fluxes across and within streams of a natural 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 was an increasingly important structuring trait at warmer temperatures, more so than organism body size. Yet, our results give support 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.

# Acknowledgements

We are grateful to Sigurður Guðjonsson, Guðni Guðbergsson, and the staff at the Veiðimlastofnun for providing laboratory space and logistical support. We are also grateful to Sveinbj€orn 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, Friðþjófur Árnason, Liliana García, Ragnahildur Magnúsdottír, 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. This study was supported by the National Science Foundation (DEB-0949774 and DEB-1354624 to JPB and ADH and DEB-0949726 to WFC).

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# Appendix

## Appendix 1

### Diet analysis

Macroinvertebrate diets were quantified for dominant taxa in each stream. We focused on numerically abundant taxa and/or taxa with relatively high annual production. A minimum of five individuals were selected from samples, and, when possible included individuals of different size classes to account for ontogenetic shifts in diet. We included individuals from different seasons to capture concurrent ontogenetic and seasonal changes. For small-bodied taxa, we combined multiple individuals (*n* = 3–5) to ensure samples contained enough material for quantification. We used methods outlined in Rosi-Marshall (2016) to remove gut tracts and prepare gut contents for quantification. Briefly, we removed the foregut from each individual or collection of individuals and sonicated contents in water for 30 seconds. Gut content slurries were filtered onto gridded nitrocellulose membrane filters (Metricel GN-6, 25 mm, 0.45 m pore size; Gelman Sciences, Ann Arbor, MI, USA), dried at 60 C for 15 min, placed on a microscope slide, cleared with Type B immersion oil, and covered with a cover slip. We took 5–10 random photographs under 200–400x magnification, depending on the density of particles, using a digital camera mounted on a compound microscope. From these photographs we identified all particles within each field and measured the relative area of particles using image analysis software (Schindelin et al. 2012). We classified particles into six categories: diatoms, green and filamentous algae, cyanobacteria, amorphous detritus, vascular and non-vascular plants (e.g., bryophytes), and animal material and then calculated the proportion of each food category in the gut by dividing their summed area by the total area of all particles. Gut contents of many predators were empty or contained unidentifiable, macerated prey. For these taxa, we assumed 100% animal material.

To estimate variability in diet compositions and to impute missing values for non-dominant, yet present, taxa, we modeled the diet proportions within each stream using a hierarchical multivariate model (Fordyce et al. 2011, Coblentz et al. 2017). Here, the diet of a consumer population, *i*, in stream, *j*, is a multinomial vector,, of

where, , is a vector of consumer diet proportions, is a vector of the population’s diet proportions and is a concentration parameter of the Dirichlet process. We used uniform priors for and ,

where, is a vector of ones the same length of basal resource types and is the assumed concentration value. Models were fit in Stan with the ‘brms’ package in R (Bürkner 2017). For non-dominant taxa, diet proportions were imputed from the hierarchical model by resampling from posterior distributions. Importantly, this process allowed to maintain the hierarchical structure of the data when imputing missing values.

From modeled diet compositions, we estimated trophic redundancy within and across stream food webs by calculating proportional similarities ( *PS*, Whittaker 1952) among modeled diet estimates. Proportional similarities were calculated as:

where, *px,i* is the proportion of food resource *i* in the diet of taxon *x*, *py,i* is the proportion of food resource *i* in the diet of taxon *y*, and there are *S* food categories. Proportional similarity was calculated across all taxa within a stream based on modeled diet contributions from each taxon. To calculate *PS* among streams we sampled 1000 estimates of the mean stream-level diet proportions for each stream and calculated *PS* for each.

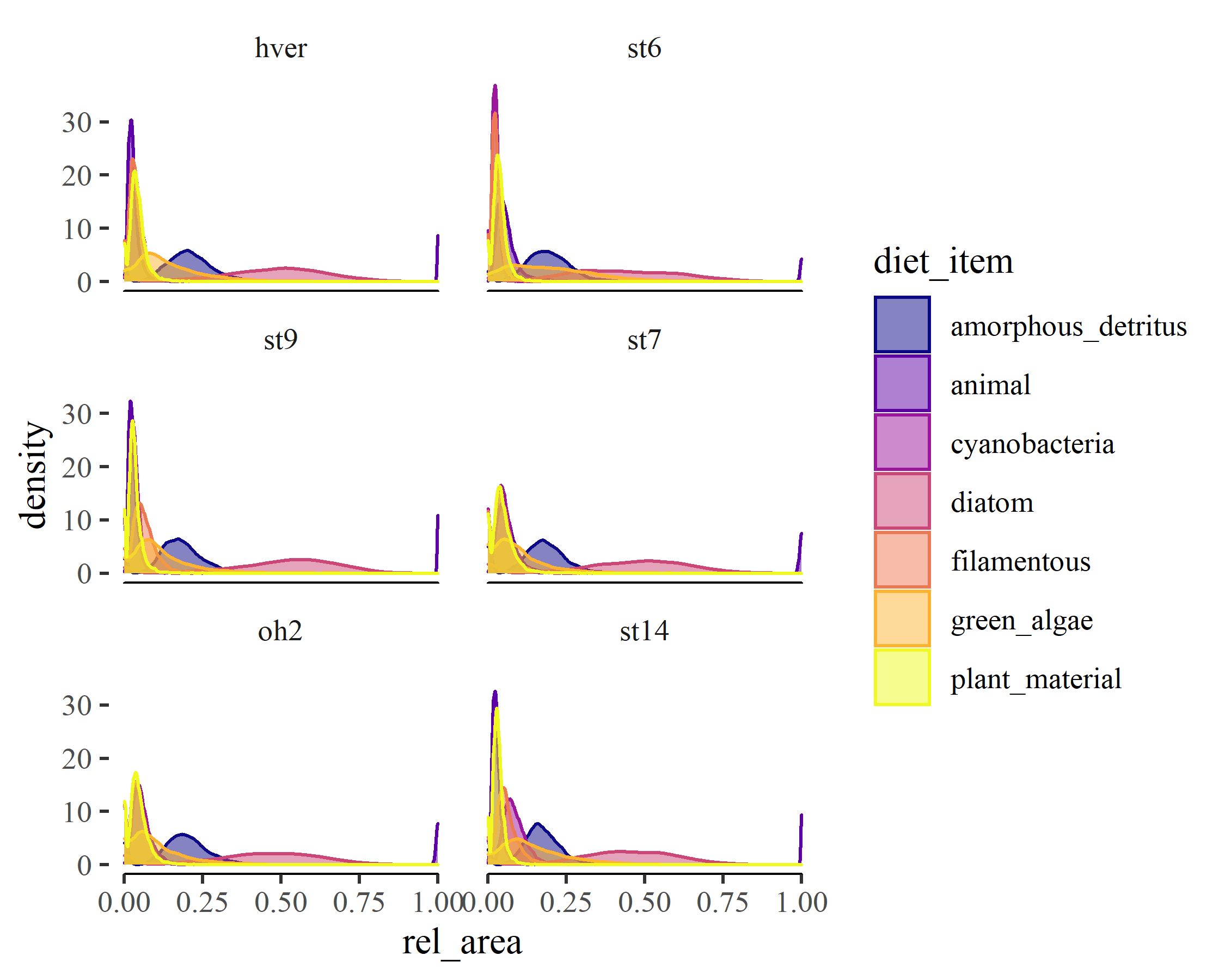


Figure S1. Modeled diet proportions of consumer communities across the temperature gradient.

## Appendix 2

Table 1. Evenness of organic matter fluxes among consumers within a stream community measured by the Gini index, both raw ('non-normalized') and 'normalized' for consumer richness

| site | Non-normalized Gini | Normalized Gini |
| --- | --- | --- |
| hver | 0.22 ( 0.18 - 0.27 ) | 0.15 ( 0.11 - 0.19 ) |
| oh2 | 0.29 ( 0.25 - 0.32 ) | 0.26 ( 0.23 - 0.3 ) |
| st14 | 0.14 ( 0.098 - 0.2 ) | 0.1 ( 0.059 - 0.17 ) |
| st6 | 0.13 ( 0.11 - 0.16 ) | 0.1 ( 0.079 - 0.13 ) |
| st7 | 0.23 ( 0.2 - 0.26 ) | 0.2 ( 0.18 - 0.23 ) |
| st9 | 0.092 ( 0.073 - 0.11 ) | 0.064 ( 0.045 - 0.082 ) |

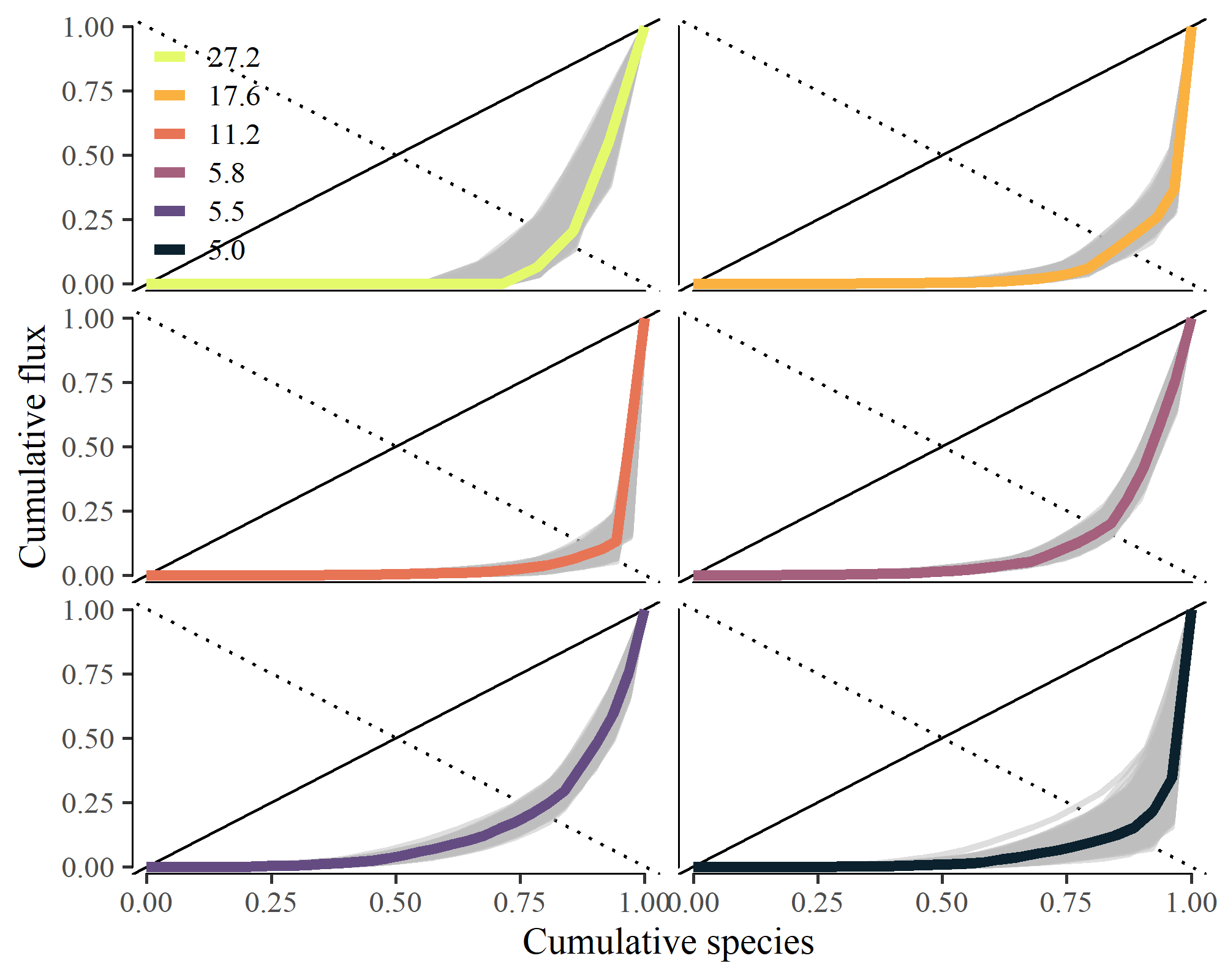


Figure S2. Lorenz plot of relative community flux by species in ascending order of annual population organic matter flux (mg AFDM m-2 y-1)

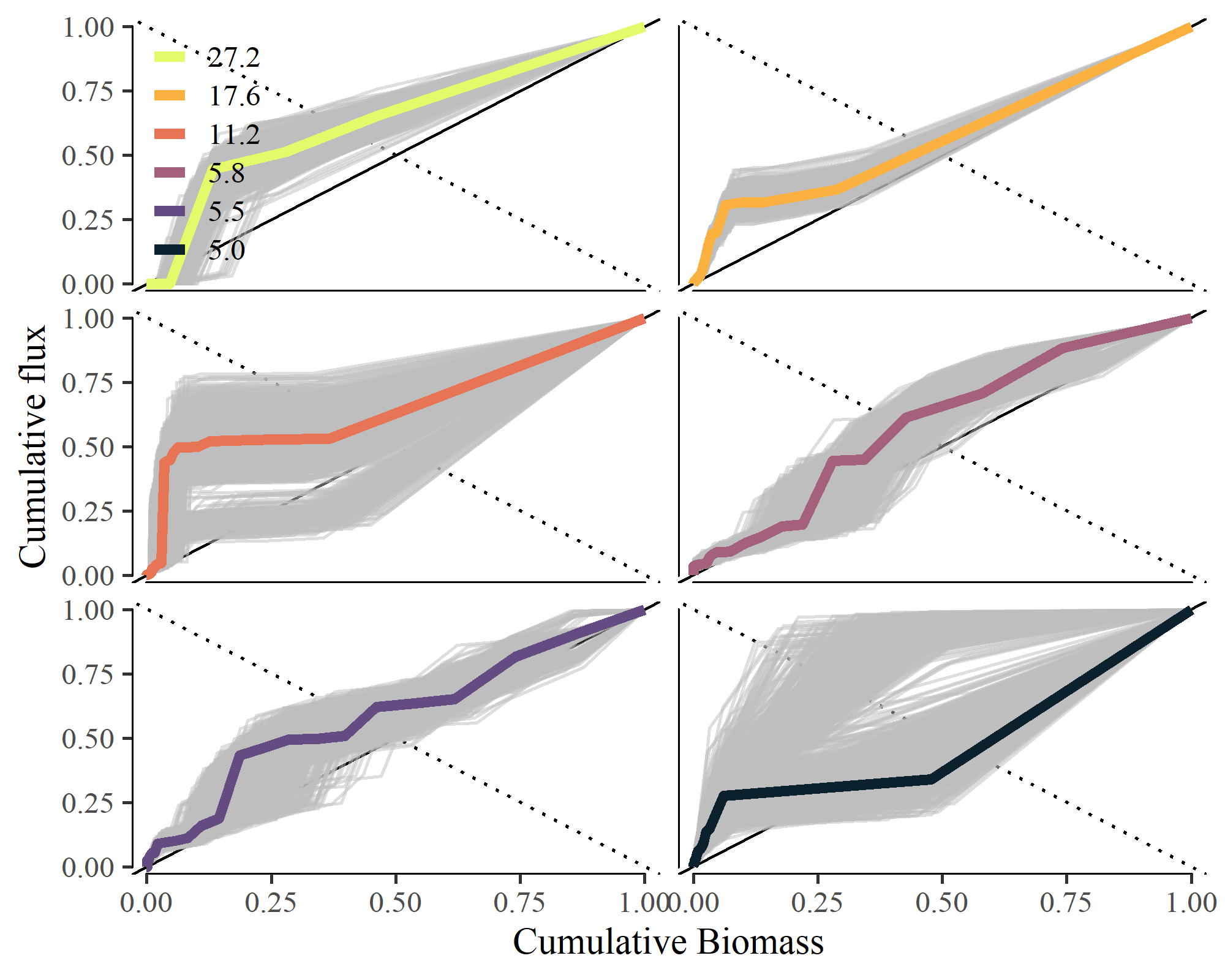


Figure S3. Cumulative plot of relative community flux by species in relation to mean annual population biomass (mg m-2).

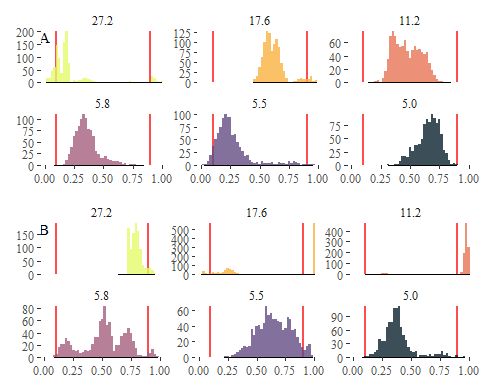


Figure S4. Probability distribution of empirical Skflux measurements in relation to (a) mean body size and (b) annual P:B compared to random species ordering. The red lines represent the 2.5% and 97.5% percentiles of the Skflux values from random ordering distributions in each stream community.

### Construction zone

Possible other themes to layer in:

effects of temperature on species evenness, evenness of fluxes, and the statistical and ecological constraints on the organization of energy fluxes in communities (e.g., (Diaz et al. 2021) SAD are more uneven than their statistical background and energy fluxes are also but there is important structure in this unevenness). This relates to the random vs non-random patterning questions…pull in the concepts of niche filtering and neutral processes in community assembly. Pull a little thinking from Saito et al. (2021).

Below is more of a set-up for the next paper but a little foreshadowing and hand waving may find a place in here:

These maximize energy intake when resources are available (Atkinson and Sibly 1997)

* Seasonal systems have unique constraints
* These seasonal constraints are greater at higher temps

This creates a situation where body sizes are selected for that 1) stabilize c-r dynamics (Osmond et al. 2017), ecological stability response to warming (Fussmann et al. 2014),… 2) optimize for energy availability and demand, 3) and this selection is stronger at extreme temperatures.

### Spare(d) words from previous versions. Keeping around for now.

directly kinetic effects and indirectly through the distribution of species traits, such as body size, within and across species (Nelson et al. 2017a, Bideault et al. 2019).

environmental filtering of compared the observed distributions of material fluxes among consumer populations to random distributions to quantify the likelihood the patterning of organic matter fluxes arise through random ordering of species or measure the potential strength of environmental filtering on the relative distribution of organic matter we tested the potential strength of environmental filtering to determine the distribution of within stream energy fluxes by comparing the how likely it was Third, we hypothesized that the selective pressure from environmental temperature on body sizes and population turnover would be greatest at temperature extremes, therefore, the patterning of energy fluxes will be ‘non-random’ at coldest and warmest temperatures.

Yet, considerable uncertainty remains in the predicted short- and long-term effects of climate warming, especially at higher levels of organization such as communities and food webs (Walther et al. 2002, Woodward et al. 2010). For example, species interactions in food webs may modulate species’ TSRs (DeLong et al. 2014), leading to varied responses among species and trophic levels (Ohlberger 2013). Additionally, warming-induced body size reductions may act as a stabilizing process in some consumer-resource interactions through reduced consumer:resource biomass ratios (Osmond et al. 2017) and reductions in consumer growth rates relative to resource supply (Kozłowski et al. 2004, McCann 2011, DeLong 2012, Greyson-Gaito et al. 2022).

For example, we lack a complete understanding of TSRs to explain deviations that exist across taxonomic groups (e.g., diatoms, Adams et al. (2013); invertebrates Zeuss et al. (2017); birds Geist (1987); and fish Rypel (2014)). Explanations for these deviations vary (Ohlberger 2013), some highlight additional processes such as competition and predation (DeLong et al. 2014), while others propose alternative models of organism body size optimization, such as the balance of resource supply and energy demand (e.g., Kozłowski et al. 2004, DeLong 2012). Crucially, these alternative models highlight the trade-off between asymptotic body size and metabolic demand (DeLong 2012) that can shape life history patterns (i.e., voltinism, Zeuss et al. (2017); Nelson et al. (2020a)). and community structure across ecosystems…

Recent, models have proposed However, - both bottom-up (e.g. resource supply) and top-down (e.g., predation) proceesses - competition and predation (DeLong et al. 2014), stabilize c-r dynamics (Osmond et al. 2017), optimization, such as the balance of resource supply and energy demand (e.g., Kozłowski et al. 2004, DeLong 2012)

To assess the relationship between the probability of ‘non-random ordering’ and temperature, we used beta regression on estimates of the probability of seeing the empirical value or one more extreme based on random ordering of species in the permuted feasible set. Here, values can take the range between 0 and 1 so no transformation was necessary. As necessary when we observed many values near 0 and 1, we implemented a zero-one inflated beta regressions in brms (Bürkner 2017) to test if the probability of observing the empirical was associated with mean annual temperature across streams. We predicted increasingly ‘non-random’ distributions in OM fluxes with increasing temperature.

Warmer streams had communities with smaller mean body sizes and faster turnover rates on average (Figure 2). Both among and within streams, OM fluxes were distributed differently across body sizes and turnover rates (*P:B*). Among streams, mean population body size ranged from 0.1 to 2.66 mg ind-1 and mean population annual P:B ranged from 4.23 to 31.67 (Figure 2).Both, *M* and *P:B* showed associations with mean annual stream temperature that were negative and positive, respectively. Generally, mean *M* of the community decreased -8.7% (95% PI, -11.1% – -6.4%) for each increase in 1C. In contrast, mean population *P:B* of the community increased 6.9% (95% PI, 6.1% – 7.9%) for each 1C in mean annual stream temperature.

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 exists across ecosystems (Thresher et al. 2007, O’Gorman et al. 2012, Ohlberger 2013). We observed a clear decrease in the average individual body size of populations from cool to warm communities (Figure 1B), corresponding to ~-9% decline in the mass of individuals for every 1C increase in temperature. While this change is based on community-level shifts (i.e., different sets of taxa), the magnitude of decline is consistent with intra-taxon patterns measured across broad phylogenetic groups (Deutsch et al. 2022). Interestingly, our results contrast with a previous warming experiment in one of our study streams showing a 3C increase in temperature shifted community biomass and productivity from smaller to larger organisms (Nelson et al. 2017a, 2017b). Moreover, a study of diatom communities across the same temperature gradient in Iceland that reported no consistent change in body size at either the population- or community-level (O’Gorman et al. 2012, Adams et al. 2013). 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). Although explanations for these deviations vary (Ohlberger 2013), some highlight additional factors that influence body size distributions such as competition and predation (DeLong et al. 2014), while others have proposed alternative models of organism body size optimization influenced by, for example, the balance of resource supply and energy demand (e.g., Kozłowski et al. 2004, DeLong 2012). Crucially, these alternative models highlight the trade-off between asymptotic body size and metabolic demand (DeLong 2012) that can shape life history patterns ( i.e., voltinism: Zeuss et al. 2017, Nelson et al. 2020a, lifespan: Munch and Salinas 2009). Considering the connections between organism body size and many other ecological attributes (Peters 1983), changes in body size with increasing temperatures—whether positive or negative—are likely to have broad implications for ecosystems in a changing climate (Gibert 2019).

Although this effect among communities may be partly attributed to the thermodynamic effects of temperature (Gillooly et al. 2001), biomass turnover rate is also closely related to organism body size (Brown et al. 2004, Huryn and Benke 2007). Thus, warming may influence the distribution of *P:B* ratios directly through its effects on metabolic rate and indirectly through reductions in organism body size. 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 be largely attributed to reduced organism body sizes. providing equivocal evidence for the presence and/or importance of an interaction between body size and temperature from this broad view. Despite this, the influence of this interaction between the direct and indirect effect of temperature on ecological patterns in increasingly recognized. For example, the effects of temperature on population carrying capacity appear to deviate from metabolic scaling predictions until the effects of concurrent changes to organism body size are taken into account (Bernhardt et al. 2018).

Further, there is growing evidence that the interactive effects warming-induced changes to metabolic rates and body size distributions have important implications for the structure and functioning of food webs at higher temperatures (Sentis et al. 2017, Bideault et al. 2019, Gibert 2019) and may reflect shifting selection for species traits.

Temperature was not clearly associated with the broad biodiversity metrics of species richness or evenness/dominance of OM fluxes, yet . We observed no clear decrease in species richness with increasing temperature found in other works (Petchey et al. 1999) beyond the warmest stream having the fewest species. However, variability in the taxonomic resolution among groups precludes a more robust analysis of any richness effects. Still, generally OM fluxes were unevenly distributed among consumers. Given the systematic unevenness in the distribution of individuals among species (Diaz et al. 2021), it may not be surprising that this pattern carries over into energy and material fluxes. Interestingly, however, we found important structure in the unevenness of OM fluxes with increasing temperature. As That the relative distribution was of OM fluxes was unlikely due to chance reduces that likelihood this pattern could be attributable to demographic stochasticity of consumers. This counters recent hypotheses integrating the metabolic theory of ecology (Brown et al. 2004) and neutral theory (Hubbell 2001) that suggest neutral processes should be more important at higher temperatures (Saito et al. 2021). The extent to which the patterns we observe here–i.e., the apparent increased importance of environmental/niche filtering at higher temperature–represent general patterns or results from the specific context of this “natural laboratory” (O’Gorman et al. 2014) remains an open question.