Warming non-randomly speeds up food web fluxes in both an absolute and relative sense

James R. Junker[1,2,*] Wyatt F. Cross[1] James M. Hood[3]
Jonathan P. Benstead[4] Alex D. Huryn[4] Daniel Nelson[5] Jon S. Olafsson[6]
Gisli M. Gislason[7]

[1] Department of Ecology, Montana State University, Bozeman, MT USA
[2] Current `address:` Great Lakes Research Center, Michigan Technological University, Houghton, MI USA
[3] Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Translational Data Analytics Institute, The Aquatic Ecology Laboratory, Columbus, OH 43212, USA
[4] Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA
[5] National Aquatic Monitoring Center, Department of Watershed Sciences, Utah State University, Logan, UT 84322, USA
[6] Institute of Marine and Freshwater Fisheries, Reykjavik, Iceland
[7] Univeristy of Iceland, Institute of Life and Environmental Sciences, Reykjavik, Iceland
[*] Correspondence: James R. Junker <jrjunker@mtu.edu>

Abstract

Warming temperatures are altering communities and trophic networks globally. While the influence of warming in food webs is often context-dependent, increasing temperatures are predicted to alter food webs and ecosystems in a number of general and fundamental ways, among them, 1) decreasing organism body size and 2) increasing 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 webs 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 ~25°C 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) fluxes would skew towards smaller M and higher $P{:}B$ both across and within ecosystems and 2) fluxes would be more skewed 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. Lastly, in warmer ecosystems the relative distribution of organic matter fluxes appears to be increasingly 'non-random', evidence of potentially stronger selection for these traits with increasing temperature. The emerging picture is a warmer world that is both smaller and faster. Our study lends further support to this pattern and suggests that temperature will become an increasingly important environmental filter on warming communities in the future.

Introduction

Increasing global temperatures are altering the provisioning and maintenance of ecosystem services by modifying the network of interactions among species that underpin ecosystem functions (de Ruiter et al. 1995, Woodward et al. 2010, Brose et al. 2012, Thompson et al. 2012). Across global climate gradients, temperature mediates the dynamics and stability of food webs (Baiser et al. 2019) by altering the acquisition and allocation of resources among species (Zhang et al. 2017) and ultimately the magnitudes and relative distribution of biomass and fluxes among species and trophic levels (May 1972, McCann et al. 1998, Barnes et al. 2018, Gibert 2019). Temperature's effects 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), as an environmental niche filter of community assembly and indirectly through the distribution of species traits, such as body size, within and across species (Nelson et al. 2017a, Bideault et al. 2019).

In fact, reduced organismal body size with warming is considered a 'universal' response to climate change (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 (TSR) 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 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).

Organismal metabolic rate, in addition to being controlled by body size, is strongly influenced by temperature (Gillooly et al. 2001). Therefore, temperature may alter metabolic rate indirectly through reductions in body size, as well as directly through its effects on subcellular kinetics (Osmond et al. 2017, Bideault et al. 2019). The interactive effect of these processes has been shown to modulate ecosystem patterns through effects on population abundance (Bernhardt et al. 2018), consumer-resource interactions (Bideault et al. 2019), and food web structure (Gibert 2019). Importantly, the kinetic effects of temperatures 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). As such, the emerging picture suggests a smaller, faster world in which warming "speeds up" ecosystem processes through the compounded effects of smaller body size and higher turnover rates.*possibly simplify the paragraph and combined with above*

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). Therefore, food web processes may impart varying selective pressures on the distribution of body sizes and population turnover within communities. If strong, these pressures may leave distinct imprints on community structure and the distribution of energy fluxes within food webs with potential implications for the stability and functioning of ecosystems on a warming planet (Petchey et al. 1999, Fussmann et al. 2014).

Here, we measured the patterning and distribution of energy fluxes within invertebrate food webs across a natural stream temperature gradient (~5–28°C). Previous research in these streams has shown a strong positive effect of temperature 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). Consumers rely largely on autochthonous resources (O'Gorman et al. 2012, Nelson et al. 2020b) and therefore the dynamics of primary production have a strong control on consumer energy demand (Junker et al. 2020). As such, we predicted annual energy fluxes of consumers to scale with among-stream patterns in resource availability and consumer energy demand and increase with temperature across streams. We hypothesized

temperature to be a strong environmental filter of community assembly and the distribution of energy and organic matter fluxes, especially at the extremes. From this we made a number of predictions regarding the patterning of energy fluxes within and across communities of different temperature, with particular focus on two species traits: body size and population biomass turnover (production:biomass ratios, *P:B*). First, we predict warmer temperatures should favor smaller and faster turnover species leading to a decrease in body sizes and increase in *P:B* on average across communities. Second, within communities energy fluxes should be dominated by smaller, higher turnover species at warmer temperatures. 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.

Methods

Invertebrate sampling

We sampled macroinvertebrate communities approximately monthly from July 2011 to August 2012 in four streams and from October 2010 to October 2011 in two streams used in a previous study (n = 6 streams). The two streams were part of an experiment beginning October 2011, therefore overlapping years were not used to exclude the impact of experimental manipulation (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 m^2, 250 μm 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 (<1 mm but >250 μm) 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 et al. 2020). Briefly, growth rates of common taxa (e.g., Chironomidae spp., *Radix balthica*, etc.) were determined using *in situ* chambers (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 into the stream within pre-conditioned chambers for 7–15 days, after which they were again 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 (W) over a given time interval (t) with the following equation:

$$g = log_e(W_{t+\Delta t}/W_t)/\Delta t$$

Variability in growth rates was estimated by bootstrapping through repeated resampling of individual lengths with replacement (n = 1000). For taxa which 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 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 $W_{t+\Delta t} > W_t$. 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 data against body size and temperature within each stream. 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.

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 μm 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,$\overrightarrow{y_{ij}}$, of

$$\overrightarrow{y_{ij}} \sim Multinomial(\overrightarrow{p_{ij}}, n_{ij})$$

$$\overrightarrow{p_i} \sim Dirichlet(\overrightarrow{q_i} \times \alpha)$$

where, $\overrightarrow{p_i}$, is a vector of consumer diet proportions, $\overrightarrow{q_i}$ is a vector of the population's diet proportions and α is a concentration parameter of the Dirichlet process. We used uniform priors for $\overrightarrow{q_i}$ and α,

$$\overrightarrow{q_i} \sim Dirichlet(\overrightarrow{\mathbf{1}})$$

$$\alpha \sim Uniform(0, c)$$

where, $\overrightarrow{\mathbf{1}}$ is a vector of ones the same length of basal resource types and c 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:

$$PS = 1 - 0.5 \sum_{j=1}^{S} |p_{x,i} - p_{y,i}|$$

where, $p_{x,i}$ is the proportion of food resource i in the diet of taxon x, $p_{y,i}$ 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.

Organic Matter Consumption Estimates

Consumption fluxes (g m^{-2} t^{-1}) were calculated using the trophic basis of production method (TBP, Benke and Wallace 1980). Taxon-specific secondary production estimates were combined with diet proportions, diet-specific assimilation efficiencies, AE_i, and assumed net production efficiencies, NPE, to estimate consumption of organic matter. For each food category, i, diet proportions were multiplied by the gross growth efficiency ($GGE_i = AE_i * NPE$) 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 consumption of organic matter from each food category by a consumer (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* above), diet-specific assimilation efficiencies, and net production efficiency. Variability in AE_i 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 consumers

To visualize and quantify how evenly OM fluxes were distributed among consumers within a stream, we constructed Lorenz curves (Lorenz 1905) on ordered relative consumption fluxes, such that in a community with S species and the relative consumption of species i, p_i, is ordered $p_1 \leq p_2 \leq ...p_S$. The Lorenz curve plots how a value, in this case OM flux, accumulates with increasing cumulative proportion of species. In a community with perfectly equal distribution of OM consumption among species, 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 S among streams, G^* (Solomon 1975, Chao and Ricotta 2019):

$$G^* = (2 \sum_{i=1}^{S} ip_i - 2)/(S - 1)$$

where G^* represents an index of relative evenness of OM fluxes bounded between zero and one–one representing a community with exactly equal proportion of total community OM flux for all species ($1/S$), and a value of zero where total community flux is attributed to a single species.

Distribution of OM fluxes in relation to species' traits

We predicted that warming would favor species 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. Across communities, we assessed the relationships between mean annual temperature (°C) and mean population M and *P:B* of each community with bootstrapped linear regressions. Here, values of population M or *P:B* were resampled with replacement for each species within each stream. The mean of all populations within a stream was calculated and a linear model was fit between log_e-transformed M or *P:B* and mean annual temperature. Response variables M and *P:B* were transformed to meet the assumption of normally distributed residual variation.

To quantify the distribution of energy fluxes ***within*** a community, we assessed if relative OM flux was skewed towards populations with lower or higher relative M or *P:B*. To do this, we ordered species based on within-stream ranking 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 species traits as:

$$Sk_{flux} = f_{Q0.75} - 2f_{Q0.5} + f_{Q0.25}/f_{Q0.75} - f_{Q0.25}$$

where, f_{Qx}, is the cumulative flux at some quantile, Qx, of the community trait distribution. We repeated this analysis for all bootstrapped estimates of OM flux in all communities. Skewness coefficients exist in the range [-1, 1], where -1 indicates OM fluxes are skewed perfectly away from a trait and 1 indicates higher relative flux is perfectly associated with higher trait values. To determine if Sk_{flux} with population 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, $(Sk_{flux} + 1)/2$, thereby standardizing values between 0 and 1. Model coefficients were back-transformed to estimate effect sizes.

To assess the strength of environmental filtering of species' traits within a community, we quantified how likely it was to observe such a skewed distribution in OM fluxes by random chance. Here, we predicted that communities with strong filtering for traits would exhibit highly skewed OM distributions that would be unlikely due to chance (i.e., 'non-random ordering'). In contrast, weak environmental filtering would produce OM fluxes with skew values that are likely due to random chance ('random ordering'). 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., $S!$, 10 species ~$3.6e^6$ unique orderings). Therefore, we chose to permute a random subset of each stream community's feasible set by randomly ordering species and calculating the skewness in the cumulative distribution of annual OM fluxes 100,000 times in each stream. The number of random orderings was chosen as a balance between characterizing the distribution of skewness values within each feasible set and computational and time constrains. This permuted set allowed us to calculate the probability of observing the empirical skewness, Sk_{flux}, in each stream compared to a random ordering given the distribution of relative OM flux. To assess the relationship between the probability of 'non-random ordering' and temperature, we again used beta regression on estimates of the probability of seeing the empirical Sk_{flux} 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 Sk_{flux} was associated with mean annual temperature across streams. We predicted increasingly 'non-random' distributions in OM fluxes with increasing temperature.

Results

Community OM fluxes

Evenness of OM fluxes within streams

OM fluxes along species trait distributions among sites and taxa

Discussion

Acknowledgements

We are grateful to..

References

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B: Biological Sciences 277:1281–1287.

Andersen, T., P. S. Cranston, and J. H. Epler. 2013. Chironomidae of the Holarctic region: Keys and diagnoses, Part 1. Media Tryck, Lund, Sweden.

Angilletta, M. J., Jr., T. D. Steury, and M. W. Sears. 2004. Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle. Integrative and Comparative Biology 44:498–509.

Atkinson, D. 1994. Temperature and organism size: A biological law for ectotherms? Advances in ecological research 25:1–58.

Baiser, B., D. Gravel, A. R. Cirtwill, J. A. Dunne, A. K. Fahimipour, L. J. Gilarranz, J. A. Grochow, D. Li, N. D. Martinez, A. McGrew, T. Poisot, T. N. Romanuk, D. B. Stouffer, L. B. Trotta, F. S. Valdovinos, R. J. Williams, S. A. Wood, and J. D. Yeakel. 2019. Ecogeographical rules and the macroecology of food webs. Global Ecology and Biogeography 28:1204–1218.

Barnes, A. D., M. Jochum, J. S. Lefcheck, N. Eisenhauer, C. Scherber, M. I. O'Connor, P. de Ruiter, and U. Brose. 2018. Energy Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning. Trends in Ecology & Evolution 33:186–197.

Belgorodski, N., M. Greiner, K. Tolksdorf, and K. Schueller. 2017. rriskDistributions: Fitting Distributions to Given Data or Known Quantiles.

Benke, A. C., and A. D. Huryn. 2017. Secondary production and quantitative food webs. Pages 235–254 Methods in Stream Ecology. Elsevier.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Benke, A. C., and J. B. Wallace. 1980. Trophic Basis of Production Among Net-Spinning Caddisflies in a Southern Appalachian Stream. Ecology 61:108–118.

Benke, A. C., and J. B. Wallace. 1997. Trophic Basis of Production Among Riverine Caddisflies: Implications for Food Web Analysis. Ecology 78:1132–1145.

Bergmann, C. 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.

Bernhardt, J. R., J. M. Sunday, and M. I. O'Connor. 2018. Metabolic Theory and the Temperature-Size Rule Explain the Temperature Dependence of Population Carrying Capacity. The American Naturalist:000–000.

Bideault, A., M. Loreau, and D. Gravel. 2019. Temperature Modifies Consumer-Resource Interaction Strength Through Its Effects on Biological Rates and Body Mass. Frontiers in Ecology and Evolution 7.

Brose, U., J. A. Dunne, Montoya José M., O. L. Petchey, F. D. Schneider, and U. Jacob. 2012. Climate change in size-structured ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 367:2903–2912.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a Metabolic Theory of Ecology. Ecology 85:1771–1789.

Bürkner, P.-C. 2017. Brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software 80:1–28.

Chao, A., and C. Ricotta. 2019. Quantifying evenness and linking it to diversity, beta diversity, and similarity. Ecology 100:e02852.

Coblentz, K. E., A. E. Rosenblatt, and M. Novak. 2017. The application of Bayesian hierarchical models to quantify individual diet specialization. Ecology 98:1535–1547.

Cross, W. F., C. V. Baxter, K. C. Donner, E. J. Rosi-Marshall, T. A. Kennedy, R. O. Hall, H. A. W. Kelly, and R. S. Rogers. 2011. Ecosystem ecology meets adaptive management: Food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications 21:2016–2033.

Cross, W. F., J. B. Wallace, and A. D. Rosemond. 2007. Nutrient Enrichment Reduces Constraints on Material Flows in a Detritus-Based Food Web. Ecology 88:2563–2575.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences 106:12788–12793.

de Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. Science 269:1257–1260.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

DeLong, J. P. 2012. Experimental demonstration of a "rate–size" trade-off governing body size optimization:10.

DeLong, J. P., T. C. Hanley, and D. A. Vasseur. 2014. Predator–prey dynamics and the plasticity of predator body size. Functional Ecology 28:487–493.

Demars, B. O. L., J. R. Manson, J. S. Ólafsson, G. M. Gíslason, R. Gudmundsdóttir, G. Woodward, J. Reiss, D. E. Pichler, J. J. Rasmussen, and N. Friberg. 2011. Temperature and the metabolic balance of streams. Freshwater Biology 56:1106–1121.

Diaz, R. M., H. Ye, and S. K. M. Ernest. 2021. Empirical abundance distributions are more uneven than expected given their statistical baseline. Ecology Letters n/a.

Fordyce, J. A., Z. Gompert, M. L. Forister, and C. C. Nice. 2011. A Hierarchical Bayesian Approach to Ecological Count Data: A Flexible Tool for Ecologists. PLOS ONE 6:e26785.

Fussmann, K. E., F. Schwarzmüller, U. Brose, A. Jousset, and B. C. Rall. 2014. Ecological stability in response to warming. Nature Climate Change 4:206–210.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: A third universal response to warming? Trends in Ecology & Evolution 26:285–291.

Gibert, J. P. 2019. Temperature directly and indirectly influences food web structure. Scientific Reports 9:5312.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science (New York, N.Y.) 293:2248–2251.

Gini, C. 1921. Measurement of Inequality of Incomes. The Economic Journal 31:124–126.

Greyson-Gaito, C. J., G. Gellner, and K. S. McCann. 2022. Slower organisms exhibit sudden population disappearances in a reddened world. Preprint, Ecology.

Haegeman, B., and M. Loreau. 2008. Limitations of entropy maximization in ecology. Oikos 117:1700–1710.

Hannesdóttir, E. R., G. M. Gíslason, J. S. Ólafsson, Ó. P. Ólafsson, and E. J. O'Gorman. 2013. Increased Stream Productivity with Warming Supports Higher Trophic Levels. Advances in Ecological Research 48:285–342.

Hood, J. M., J. P. Benstead, W. F. Cross, A. D. Huryn, P. W. Johnson, G. M. Gíslason, J. R. Junker, D. Nelson, J. S. Ólafsson, and C. Tran. 2018. Increased resource use efficiency amplifies positive response of aquatic primary production to experimental warming. Global Change Biology 24:1069–1084.

Huryn, A. D., and A. C. Benke. 2007. Relationship between biomass turnover and body size for stream communities. Body size: the structure and function of aquatic ecosystems. Cambridge University Press, Cambridge, UK:55–76.

Huryn, A. D., and J. B. Wallace. 1986. A method for obtaining in situ growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. Limnology and Oceanography 31:216–221.

James, F. C. 1970. Geographic Size Variation in Birds and Its Relationship to Climate. Ecology 51:365–390.

Junker, J. R., W. F. Cross, J. P. Benstead, A. D. Huryn, J. M. Hood, D. Nelson, G. M. Gíslason, and J. S.

Ólafsson. 2020. Resource supply governs the apparent temperature dependence of animal production in stream ecosystems. Ecology Letters 23:1809–1819.

Kozłowski, J., M. Czarnołęski, and M. Dańko. 2004. Can Optimal Resource Allocation Models Explain Why Ectotherms Grow Larger in Cold?1. Integrative and Comparative Biology 44:480–493.

Lorenz, M. O. 1905. Methods of Measuring the Concentration of Wealth. Publications of the American Statistical Association 9:209.

May, R. M. 1972. Will a Large Complex System be Stable? Nature 238:413–414.

McCann, K. S. 2011. Food Webs (MPB-50). Princeton University Press.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An Introduction to the Aquatic Insects of North America. Fourth. Kendall/Hunt Publishing Co., Dubuque, IA.

Nelson, D., J. P. Benstead, A. D. Huryn, W. F. Cross, J. M. Hood, P. W. Johnson, J. R. Junker, G. M. Gíslason, and J. S. Ólafsson. 2017a. Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. Ecology 98:1797–1806.

Nelson, D., J. P. Benstead, A. D. Huryn, W. F. Cross, J. M. Hood, P. W. Johnson, J. R. Junker, G. M. Gíslason, and J. S. Ólafsson. 2017b. Experimental whole-stream warming alters community size structure. Global Change Biology 23:2618–2628.

Nelson, D., J. P. Benstead, A. D. Huryn, W. F. Cross, J. M. Hood, P. W. Johnson, J. R. Junker, G. M. Gíslason, and J. S. Ólafsson. 2020b. Thermal niche diversity and trophic redundancy drive neutral effects of warming on energy flux through a stream food web. Ecology.

Nelson, D., J. P. Benstead, A. D. Huryn, W. F. Cross, J. M. Hood, P. W. Johnson, J. R. Junker, G. M. Gíslason, and J. S. Ólafsson. 2020a. Contrasting responses of black fly species (Diptera: Simuliidae) to experimental whole-stream warming. Freshwater Biology 65:1793–1805.

O'Gorman, E. J., D. E. Pichler, G. Adams, J. P. Benstead, H. Cohen, N. Craig, W. F. Cross, B. O. L. Demars, N. Friberg, G. M. Gíslason, R. Gudmundsdóttir, A. Hawczak, J. M. Hood, L. N. Hudson, L. Johansson, M. P. Johansson, J. R. Junker, A. Laurila, J. R. Manson, E. Mavromati, D. Nelson, J. S. Ólafsson, D. M. Perkins, O. L. Petchey, M. Plebani, D. C. Reuman, B. C. Rall, R. Stewart, M. S. A. Thompson, and G. Woodward. 2012. Impacts of Warming on the Structure and Functioning of Aquatic Communities. Pages 81–176 Advances in Ecological Research. Elsevier.

Ohlberger, J. 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. Functional Ecology 27:991–1001.

Osmond, M. M., M. A. Barbour, J. R. Bernhardt, M. W. Pennell, J. M. Sunday, and M. I. O'Connor. 2017. Warming-Induced Changes to Body Size Stabilize Consumer-Resource Dynamics. The American Naturalist 189:718–725.

Padfield, D., C. Lowe, A. Buckling, R. Ffrench-Constant, S. Jennings, F. Shelley, J. S. Ólafsson, and G. Yvon-Durocher. 2017. Metabolic compensation constrains the temperature dependence of gross primary production. Ecology Letters 20:1250–1260.

Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Peterson, B. V. 1977. Black flies of Iceland (Diptera-Simuliidae). Canadian Entomologist 109:449–472.

Rosi-Marshall, E. J., H. A. Wellard Kelly, R. O. Hall, and K. A. Vallis. 2016. Methods for quantifying aquatic macroinvertebrate diets. Freshwater Science 35:229–236.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J.-Y. Tinevez, D. J. White, V. Hartenstein, K. Eliceiri, P. Tomancak, and A. Cardona. 2012. Fiji: An open-source platform for biological-image analysis. Nature Methods 9:676–682.

Solomon, D. L. 1975. A comparative approach to species diversity:7.

Thompson, R. M., U. Brose, J. A. Dunne, R. O. Hall, S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer, and J. M. Tylianakis. 2012. Food webs: Reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27:689–697.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Welch, H. E. 1968. Relationships between Assimiliation Efficiencies and Growth Efficiencies for Aquatic

Consumers. Ecology 49:755–759.
Whittaker, R. H. 1952. A Study of Summer Foliage Insect Communities in the Great Smoky Mountains. Ecological Monographs 22:1–44.
Woodward, G., J. P. Benstead, O. S. Beveridge, J. Blanchard, T. Brey, L. E. Brown, W. F. Cross, N. Friberg, T. C. Ings, U. Jacob, S. Jennings, M. E. Ledger, A. M. Milner, J. M. Montoya, E. O'Gorman, J. M. Olesen, O. L. Petchey, D. E. Pichler, D. C. Reuman, M. S. A. Thompson, F. J. F. Van Veen, and G. Yvon-Durocher. 2010. Ecological Networks in a Changing Climate. Pages 71–138 Advances in Ecological Research. Elsevier.
Zeuss, D., S. Brunzel, and R. Brandl. 2017. Environmental drivers of voltinism and body size in insect assemblages across Europe. Global Ecology and Biogeography 26:154–165.
Zhang, L., D. Takahashi, M. Hartvig, and K. H. Andersen. 2017. Food-web dynamics under climate change. Proceedings of the Royal Society B: Biological Sciences 284:20171772.
Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2012. A general model for effects of temperature on ectotherm ontogenetic growth and development. Proceedings of the Royal Society B: Biological Sciences 279:1840–1846.

Appendix

Spare(d) words