











RESEARCH ARTICLE

Warming reduces trophic diversity in high-latitude food webs

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Abstract

The physical effects of climate warming have been well documented, but the biological responses are far less well known, especially at the ecosystem level and at large (intercontinental) scales. Global warming over the next century is generally predicted to reduce food web complexity, but this is rarely tested empirically due to the dearth of studies isolating the effects of temperature on complex natural food webs. To overcome this obstacle, we used 'natural experiments' across 14 streams in Iceland and Russia, with natural warming of up to 20°C above the coldest stream in each high-latitude region, where anthropogenic warming is predicted to be especially rapid. Using biomass-weighted stable isotope data, we found that community isotopic divergence (a universal, taxon-free measure of trophic diversity) was consistently lower in warmer streams. We also found a clear shift towards greater assimilation of autochthonous carbon, which was driven by increasing dominance of herbivores but without a concomitant increase in algal stocks. Overall, our results support the prediction that higher temperatures will simplify high-latitude freshwater ecosystems and provide the first mechanistic glimpses of how warming alters energy transfer through food webs at intercontinental scales.

KEYWORDS

Arctic, climate change, freshwater, invertebrate community, stable isotope

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1 | INTRODUCTION

Our planet is warming at an accelerating rate, with average surface temperatures rising by more than 1°C in the last 80 years and an increase of 1.5–4°C forecast for the end of this century (IPCC, 2023; NASA, 2024). Even small changes in temperature can dramatically alter natural systems, and biological responses to warming can manifest anywhere from the individual to the ecosystem level (Walther, 2010; Woodward, Perkins, & Brown, 2010). The >1°C warming that our planet has experienced within the past century has already been implicated in reduced insect abundances (Hallmann et al., 2017; Leather, 2018), body size declines within and across taxa (Sheridan & Bickford, 2011; van Buskirk et al., 2010), and widespread local extinctions of hundreds of aquatic and terrestrial species (Wiens, 2016). Whole-community responses are less well-described, partly because natural ecosystems commonly consist of many hundreds of species and thousands of interactions and documenting such phenomena is logistically challenging. However, even in these seemingly complex food webs, each species is often only two links removed from any other (Woodward et al., 2008), so the system as a whole can be very sensitive to perturbations and may respond in ways that cannot be simply extrapolated from studying individual populations. Characterising how natural food webs respond to changes in temperature is therefore essential if we are to understand wider ecosystem responses to warming. Here we employ an isotopic approach to food web characterisation which offers a common currency that is both logistically tractable and transferable across ecosystems and through space and time. This allows us to compare how temperature shapes ecosystems from contrasting biogeographical histories and with negligible taxonomic overlap.

The carbon and nitrogen stable isotope values of a consumer's body tissue reflect that of their diet, and they are, therefore, useful indicators of feeding interactions. Carbon isotopes reflect diet source (allochthonous vs. autochthonous), while nitrogen isotopes indicate trophic position (Jackson et al., 2012). These feeding interactions are expected to be temperature dependent; therefore, this should be reflected in consumers carbon and nitrogen stable isotope values. For instance, diet can be affected by warming directly through elevating the metabolic rates of consumers (Brown et al., 2004; Yvon-Durocher et al., 2010), thereby increasing their feeding activity and forcing diet switching to keep up with rising metabolic demands (O'Gorman et al., 2016). Diet might also change due to the indirect effects of warming. For instance, high temperatures might alter resource quality or abundance (Tseng et al., 2021). In freshwaters warming is generally expected to increase the abundance of primary producers by promoting faster algal growth which can promote herbivory (the 'green' pathway; Delgado et al., 2017). These changes, both within individuals of the same species and between species, could ultimately lead to rewiring within the food web. Additionally, higher temperatures will put local cold-adapted taxa at a disadvantage, and these may be replaced by more eurythermal taxa with further implications for trophic diversity. We also expect food chains to shorten if warming reduces trophic transfer efficiency and

favours smaller species, which tend to be herbivorous (Barneche & Allen, 2018; Brown et al., 2004; Yvon-Durocher et al., 2010).

Here, we test whether temperature has these predicted effects in stream food webs using a natural experiment spanning biogeographically independent high-latitude catchments in Hengill (Iceland) and Kamchatka (Russia). Within each region, streams vary naturally in temperature due to indirect heating of groundwater. For many years, research in geothermal regions has focused on extremophiles (e.g. in Yellowstone National Park) adapted to very high temperatures and these study systems are often associated with (and conflated with) high acidity, so they are poorly suited to studying the more subtle effects of global warming and in disentangling these from other physicochemical covariables. However, our study streams differ fundamentally from these extreme environments because they are all heated via gentle warming of the bedrock, hydrologically stable, and with no significant confounding effects of water chemistry across the temperature gradient (see [Supporting Information](#)), therefore providing an ideal 'natural experiment' where temperature can be isolated as a 'master variable' (O'Gorman et al., 2014). Our previous work in Hengill has shown that temperature causes a shift in community structure (Friberg et al., 2009; O'Gorman et al., 2017; Woodward, Dybkjaer, et al., 2010), but here we test the transferability of these findings by expanding to a second naturally heated suite of streams in Kamchatka (Jackson et al., 2024). We also use a novel approach to detect further food web trends: stable isotope-derived—and biomass weighted—community metrics, which allow us to compare trophic structures over contrasting biogeographical regions by using common currencies that apply even in the face of 100% species turnover.

Since the carbon isotopic values of a consumer reflect the origin of their assimilated food (autochthonous vs. allochthonous), while nitrogen isotopes describe trophic status, the distribution of organisms in isotopic space (the 'IsoWeb') relative to one another captures the overall food web structure (Cucherousset & Villéger, 2015; Jackson et al., 2012). Typically, most such studies have given equal weighting to abundant and rare species due to the challenges of measuring population abundance or biomass, but our measures are weighted by the latter to map more meaningfully onto associated ecosystem processes (following Cucherousset & Villéger, 2015). We hypothesise that under warming we will see reduced (H1) trophic diversity (i.e. simpler food webs) and (H2) average trophic level (i.e. shorter food chains) with (H3) consumers shifting increasingly from 'brown' to the 'green' trophic pathways.

2 | METHODS

Sampling took place in July 2016 (Hengill, Iceland) and August 2017 (Kamchatka, Russia, [Figure S1](#)). At each location, we sampled 7 streams across a comparable range of ambient (i.e., the coldest stream) and elevated temperatures for stable isotope analysis (mean summer stream temperature: Iceland, 4.2–20.2°C; Kamchatka, 5.2–21.6°C). At each site, we measured temperature every minute for

at least 1 week (MiniDot DO Loggers). Conductivity and pH were measured every minute for at least 24 h (using a Manta+, Eureka). Total nitrogen (TN) was measured from one water sample as the sum of organic and inorganic nitrogen using a TOC-L CPH/CPN analyser with a chemiluminescence detector (Shimadzu).

2.1 | Consumer sampling

We collected benthic invertebrates using a 25×25 cm Surber sampler (mesh size 250 μm) at 3 locations in each stream. The samples were preserved in 80% ethanol and taken back to the laboratory. Individuals were identified to the highest possible taxonomic resolution (i.e. species where possible), counted and measured using a Nikon SMZ800 at a magnification of 10–63×. We then calculated rarefied invertebrate richness for each stream based on the lowest number of invertebrates sampled ($n=116$) using the *vegan* package in R (Oksanen et al., 2019; R Core Team, 2022). Next, we quantified the total invertebrate biomass in each stream by first estimating average invertebrate species body masses. Here, a single linear dimension (head width or body length) was measured for an average of 24 individuals (range: 1–161; 5966 individuals measured in total) of each species in each stream, and individual biomass was estimated using published length-mass equations (see O'Gorman et al., 2019). Biomass of each species was then calculated by multiplying the average species body mass of each taxon in the community by the population abundance.

2.2 | Basal resource sampling

We removed and dried all coarse particulate organic matter (CPOM, particles >2 mm) in each Surber sample as a measure of energy available via the 'brown' trophic pathway—representing decaying organic material, which is often terrestrial in origin. We scrubbed uniform areas (8.28 cm²) of biofilm from rocks using a toothbrush as an estimate (Jackson et al., 2014). This was resuspended in stream water before we used a Fluoroprobe (bbe Moldaenke GmbH) to calculate total chlorophyll for different taxonomic groups in each sample. We considered the palatable groups which are important as food resources (diatoms and green algae, of which most species are edible for aquatic invertebrates) but not cyanobacteria or cryptophytes in our analysis (see [Supporting Information](#) for full methods).

2.3 | Stable isotope analyses

The same invertebrate samples collected above and stored in ethanol were used for stable isotope analyses (see below) following (González-Bergonzoni et al., 2015). Ethanol preservation has been shown to have less of an effect on isotopic signatures than other preservation techniques (Ruiz-Cooley et al., 2011) and is becoming increasingly common in stable isotope ecology, particularly in

aquatic studies. For instance, studies have effectively used ethanol preserved samples to quantify the diet of fish (González-Bergonzoni et al., 2015; Kische-Machumu et al., 2017) penguins (Cherel & Hobson, 2007) and collembolans (Ferlian et al., 2015), and to study whole food webs (Feunteun et al., 2015; Hempson et al., 2017). We also froze some of the most abundant invertebrates for comparison of preservation techniques. This showed consistent differences between frozen and ethanol-preserved samples (see [Supporting Information](#)), allowing comparison of our results to other studies using frozen samples. For each stream, we ran three samples of each species for stable isotope analysis, following Jackson et al. (2020). To gain sufficient material for robust isotopic analysis, we grouped 2–20 individuals of a similar size for each invertebrate species. We removed them from ethanol and washed them in distilled water. We used whole primary consumers and omnivores without guts removed because several papers have shown that the removal of guts (or gut clearance) does not alter results because the biomass of gut contents is so small as to be effectively negligible, especially for smaller individuals lower in the food web (Jardine et al., 2005; Woodward et al., 2005). However, we removed the guts of larger invertebrate predators. Samples were then dried for 48 h at 60°C before being ground up and 0.5–1 mg weighed into ultra-clean tin cups (6×4 mm, Elemental Microanalysis). Carbon and nitrogen stable isotope analysis was performed on a Sercon Integra II combined elemental analyser and mass spectrometer following Barneche et al. (2021). We collected taxa representing on average 94% of the total biomass of each stream (range: 76%–100%), thus we are confident our isotopic metrics are a good representation of the entire animal community (Perkins et al., 2018). We also collected potential basal resources (biofilm, aquatic weeds, terrestrial leaves, moss and grass) to determine what consumer isotopic shifts mean for actual diet composition ([Supporting Information](#)).

We scaled nitrogen and carbon values in each region from 0 to 1 to standardise isotopic baselines following Cucherousset and Villéger (2015). Next, we calculated biomass-weighted metrics of food web structure for each stream using the mean scaled isotope signature of each consumer species. This uses the relative spread of populations in ordination space and is, therefore, unaffected by the sample preservation technique since all samples are affected similarly. We calculated *isotopic diversity* (also called *isotopic divergence*; I_{div}) as a measure of whole food-web trophic diversity (see full equations in Cucherousset & Villéger, 2015). Values close to 0 indicate that most of the community biomass is distributed at the centre of the isotopic web, suggesting low trophic variation between species and that dietary generalism dominates. Values close to 1 indicate that most of the biomass is near the borders of the isotopic web and the food web has high trophic diversity and specialists are common. We calculated *carbon position* (C_{pos}) as biomass-weighted $\delta^{13}C$ (Cucherousset & Villéger, 2015). This is scaled from 0 to 1, with lower values indicating that more of the biomass is reliant on the 'brown' trophic pathway and allochthonous input ([Figure S4](#)). Higher values indicate that most of the biomass is reliant on the 'green' trophic pathway and autochthonous input ([Figure S4](#)). We also calculated

nitrogen position (Npos) as biomass-weighted and scaled $\delta^{15}\text{N}$, which is indicative of trophic level (Cucherousset & Villéger, 2015). Higher values indicate that a higher biomass of predators (Cucherousset & Villéger, 2015).

2.4 | Statistical analysis

First, we tested for a relationship between temperature and the availability of resources via the 'green' (algal standing stock) and 'brown' (CPOM biomass) trophic pathways using simple linear models in R. Next, variation in invertebrate taxonomic community structure was explored using Detrended Correspondence Analysis (DCA) in the *vegan* package (Oksanen et al., 2019). We used square root transformed relative biomass data to dampen the influence of outliers and passively overlaid associations with environmental variables (temperature, pH, total nitrogen, flow). We also assigned each species as either a herbivore, omnivore or predator using functional feeding groups (following Merritt & Cummins, 2008) for analysing biomass trends.

Finally, for each response metric (Idiv, Cpos, Npos, rarefied richness and biomass of different groups) we tested for an effect of temperature and location (and their interaction) using an ANCOVA in R. This allowed us to test if response-temperature relationships vary between Hengill and Kamchatka. We plotted a single trend line if the location was not significant (to represent a significant temperature-response relationship) and separate trend lines for each location where there was a significant difference (and therefore, a significant temperature-response relationship within each region). We also explored both linear and exponential relationships with temperature, selecting a simple linear model unless the AIC values for the exponential model were >2 AIC units lower, indicating a significantly better fit (using the 'AIC' function in R; Table S2). All our selected models satisfied tests for normality of the residuals (using Shapiro-Wilk tests) in the 'olsrr' package in R. All results are for simple linear models unless stated (see model comparison in Table S2). All data is provided in FigShare (Jackson, 2024).

3 | RESULTS

3.1 | Resource availability

There was no effect of temperature on resource standing stock via the 'green' ($F_{1,10}=0.963$, $p=.350$; Figure S5a) or 'brown' ($F_{1,10}=1.008$, $p=.339$; Figure S5b) pathways.

3.2 | Stable isotope metrics

As predicted in H1, biomass-weighted isotopic divergence declined with temperature ($F_{1,10}=9.112$, $p=.013$) and was significantly higher in Iceland ($F_{1,10}=11.192$, $p=.007$, Figure 1a,b). There was no

significant interactive effect of temperature and location (Table S2). Community carbon position significantly increased with warming ($F_{1,10}=6.728$, $p=.027$, Figure 1c; Table S2), indicating a consistent trend in both locations towards greater consumption of biomass from the green trophic pathway and autochthonous material as predicted in H3 (see Figure S4 for resource isotopes). In contrast to our prediction (H2), however, community nitrogen position was not significantly altered by temperature ($F_{1,10}=2.363$, $p=.155$, Figure 1d; Table S2).

3.3 | Taxonomy metrics

Warming caused a shift in the invertebrate community, but the other environmental variables were also important (Figure 2a,b). Invertebrate richness declined exponentially with warming in each location (Figure 2c) ($F_{1,10}=4.03$, $p=.072$; Table S2), supporting H1. Warming also significantly increased herbivore biomass in both locations ($F_{1,10}=7.71$, $p=.02$; Table S2; Figure 2d), supporting H3. There were no significant effects on generalist or predator biomass (Table S2).

4 | DISCUSSION

Our results show a decline in trophic diversity and an increase in carbon position with warming, suggesting lower trophic variation between species and convergence on the 'green' trophic pathway, despite no change in the standing stock of this resource. This is supported by the taxonomic results, revealing an overall decline in invertebrate richness at high temperatures, but an increase in herbivore biomass.

We found that *isotopic divergence* (trophic diversity) declined with warming in both Kamchatka and Iceland, suggesting climate change could simplify food webs, as suggested in recent studies using more traditional metrics, such as network connectance (O'Gorman et al., 2012). Our results indicate species taxonomic richness is also lost at high temperatures, but the decline in *isotopic divergence* suggests that this is not fully functionally compensated by expanding trophic niches in the remaining heat tolerant species. Low *isotopic divergence* indicates that more of the community biomass is clustered close to the centre of the isotopic web, suggesting low trophic variation between species and a dominance of generalism, as we predicted. In general, streams are usually dominated by generalists, suggesting this phenomenon might intensify further still with warming. Other studies have found an increase in generalism and a loss of specialist species with global change (measured indirectly using trait-based approaches), leading to biotic homogenisation (Clavel et al., 2011). For instance, long-term studies spanning decades on both terrestrial ectotherms (Valtonen et al., 2017) and endotherms (Bowler et al., 2019) have found similar declines in dietary specialists over time which could be linked to climate change. Such biotic homogenisation can lead to a loss of ecosystem functions, due to a

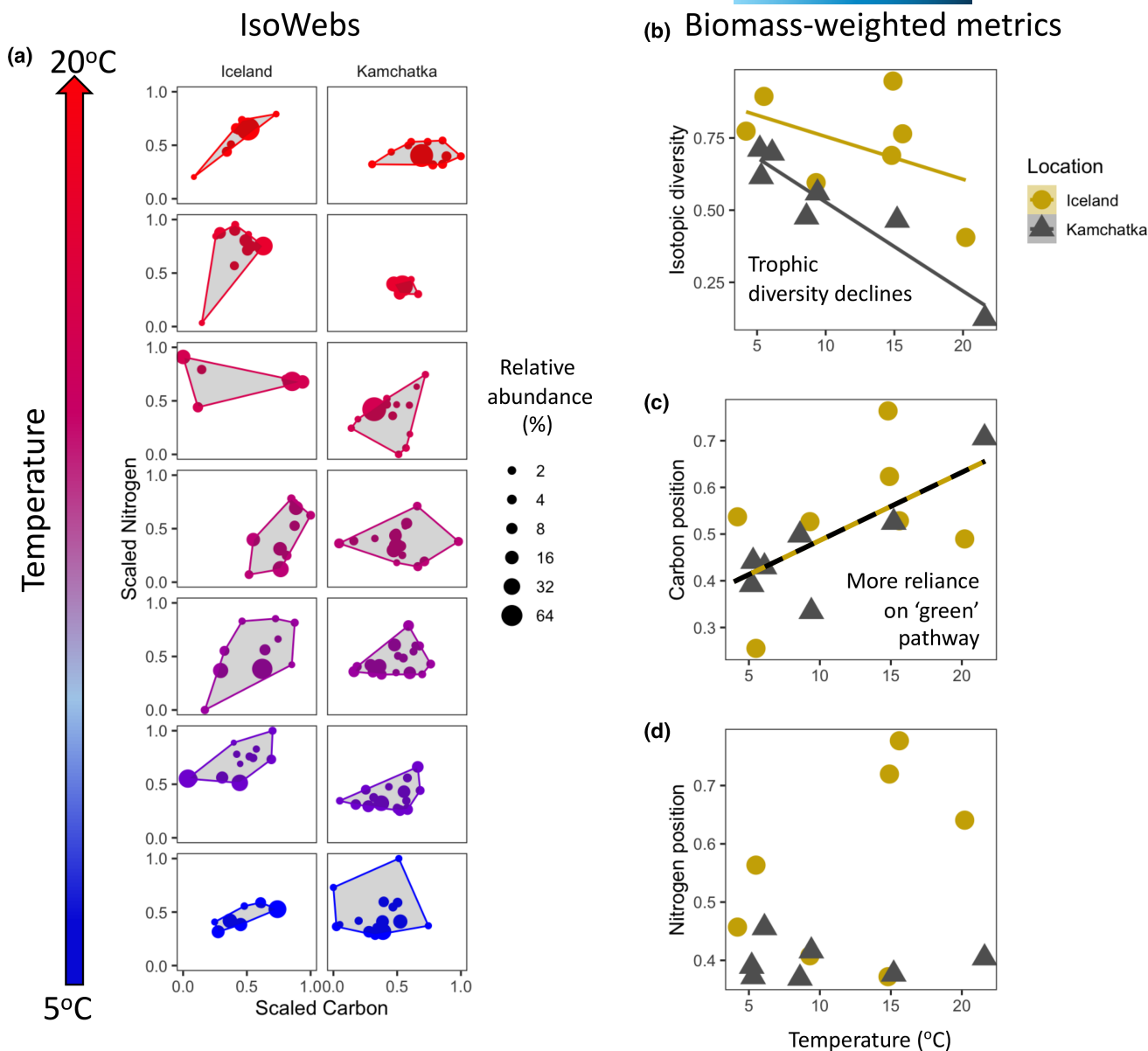


FIGURE 1 Isotopic changes with temperature. (a) Each plot shows a polygon to illustrate each stream's 'IsoWeb' coloured by temperature. Each data point represents the average carbon and nitrogen scaled stable isotope value of a species, with the symbol size representing relative biomass (%) of that species. Biomass-weighted functional diversity metrics were then calculated from this data to test how they change across the temperature gradient: (b) isotopic diversity (as a measure of food web complexity), (c) carbon position (as an indicator of reliance on 'green' vs. 'brown' trophic pathways), and (d) nitrogen position (as an indicator of average trophic level). Fitted lines are shown where significant: For isotopic diversity there was a significant effect of temperature and location, with trend lines shown in gold for Iceland and grey for Kamchatka. For carbon position, there was only a significant main effect of temperature, so a single best-fit line is shown in both colours.

loss of species with unique functional roles and an overall decline in community resilience (Petsch & Os-Grduas, 2016).

The increase in generalism occurred simultaneously with greater reliance on the 'green' trophic pathway, suggesting warming is making consumers more reliant on autochthonous carbon, versus the 'brown' detrital-based pathways. The standing stock of algal biofilms did not increase with temperature, but past evidence suggests primary productivity does, with this matched by an increase in herbivory (O'Gorman et al., 2017). Our results support this, with a marked increase in keystone herbivore biomass (primarily grazing snails,

Radix sp.) under warming (O'Gorman et al., 2017). Overall, this suggests that food webs under warming will become increasingly simpler and dominated by herbivory. Similarly, O'Gorman et al. (2019) found a decline in food web complexity (measured as linkage density or connectance in trophic networks) and mean trophic level in the same system in Iceland using traditional gut content analysis (which captures only recent ingestion, rather than assimilation over time—a major advantage of isotopes). Our results provide another key piece of evidence by demonstrating the same pattern of declines in food web complexity is repeated not only using a complementary isotopic

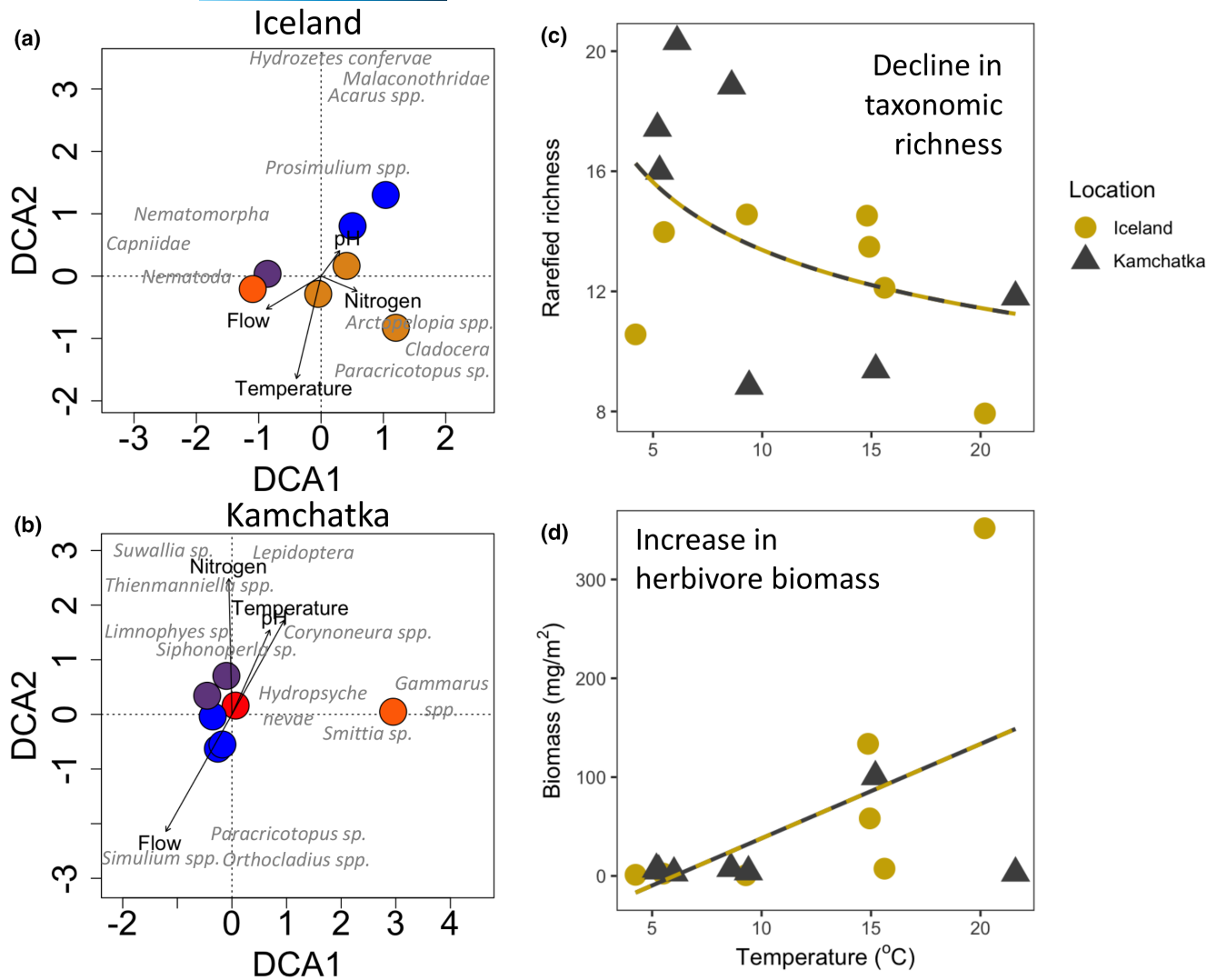


FIGURE 2 Taxonomic changes with temperature. (a, b) Ordinations (DCA) where each point is a stream coloured by temperature along a gradient from blue (cold) to red (warm). The top 10% of species driving the differences between streams are included on the plots, and environmental variables are overlaid. Changes in rarefied richness (c) and the biomass of herbivores (d) were best explained by an exponential and linear model, respectively. In (c) and (d) there was only a significant main effect of temperature, so a single best-fit line is shown in gold and grey for both locations.

approach but that it also applies in a biographically independent suite of sites, suggesting the potential universal transferability of these findings. Despite our study sites being >6500km apart, the food webs responded in the same way to temperature—indicating a fundamental response to warming (despite different species pools) and shows how isotope metrics can be used as a common global currency.

The changes in food web complexity we observed can be linked to convergence on the ‘green’ trophic pathway despite no increase in algal standing stock, suggesting an increase in algal growth (and overall productivity) leading to increased herbivory. Generally, these ‘green’ resources are a higher quality food resource than those from the ‘brown’ trophic pathway (Evans-White & Halvorson, 2017). Therefore, the increased reliance on the ‘green’ pathway may be an energy efficient response to keep up with the greater metabolic demands of living in a warmer environment (Allen et al., 2005;

Barneche & Allen, 2018). However, in a mesocosm experiment Gossiaux et al. (2020) found that increases in invertebrate growth rates with 2°C of warming was not linked to any improvement in basal resource quality. Furthermore, Leal et al. (2023) showed no relationship between climate factors and the relative contribution of ‘green’ resources in a meta-analysis of lotic systems. The clear shift to a higher reliance on ‘green’ resources could, therefore, also be due to a shift in the community (Jackson et al., 2024) to more efficient grazer species, which is supported by our ordination results. Although stocks did not differ with temperature, net primary production (NPP) commonly increases with warming (Yvon-Durocher et al., 2015), and this could also be contributing to the increased consumption of ‘green’ energy by invertebrates. Indeed, previous field experiments and bioassays in the same Icelandic systems have shown that both the brown and green pathways run ‘faster’ under warming, with algal growth and NPP (a resource flux) in the latter rising with

temperature and increased herbivore biomass (Junker et al., 2020; O'Gorman et al., 2012; Woodward, Dybkjaer, et al., 2010). Other research in the same system in Iceland has found that microbial decomposition increases with temperature, which may reduce the availability of leaf litter and, therefore, force consumers to switch from the brown to the green pathway (Friberg et al., 2009).

By using biomass-weighted isotope metrics, we can say that the food web shifts are driven by community-level changes in consumption by abundant species. Isotopic metrics of food web structure are becoming an increasingly important tool for understanding how networks of interacting species are affected by global change because they are transferable across huge biogeographical gradients (Cucherousset et al., 2012; Jackson et al., 2020; Layman et al., 2012; McCue et al., 2020). Here, we demonstrate the successful application of these tools to show how temperature can shift food web diversity and pathways of energy transfer. Importantly, our metric of isotopic complexity is strongly associated with linkage density, a measure of complexity calculated using classical food web approaches based on gut content analysis, calculated in the same streams (O'Gorman et al., 2019; see correlation in Figure S6). This is the first time (as far as we are aware) that isotopic complexity has been shown to match classical measures of food web complexity. This has important implications for these two largely separate fields of study—food web theory and stable isotope ecology. By working together researchers from these two disciplines have the potential to provide more robust large-scale predictions about how food webs will respond to global change.

AUTHOR CONTRIBUTIONS

Michelle C. Jackson: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; visualization; writing – original draft; writing – review and editing. **Eoin J. O'Gorman:** Data curation; formal analysis; investigation; validation; writing – review and editing. **Bruno Gallo:** Data curation; investigation; writing – review and editing. **Sarah F. Harpenslager:** Data curation; investigation; writing – review and editing. **Kate Randall:** Data curation; investigation; writing – review and editing. **Danielle N. Harris:** Data curation; investigation; writing – review and editing. **Hannah Prentice:** Data curation; investigation; writing – review and editing. **Ian Sanders:** Data curation; writing – review and editing. **Tom C. Cameron:** Data curation; investigation; writing – review and editing. **Alex J. Dumbrell:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing. **Mark Trimmer:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing. **Katrin Layer:** Data curation; writing – review and editing. **Yulia Bespalaya:** Data curation; writing – review and editing. **Olga Aksenova:** Data curation; writing – review and editing. **Nikolai Friberg:** Conceptualization; data curation; investigation; writing – review and editing. **Luis Moliner Cachazo:** Data curation; investigation; writing – review and editing. **Stephen J. Brooks:** Data curation; methodology; writing – review and editing.

Guy Woodward: Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and associated code are published in FigShare: <https://doi.org/10.6084/m9.figshare.26356276>.

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