Received: 5 July 2021 | Revised: 25 September 2021 | Accepted: 9 October 2021

DOI: 10.1111/gcb.15956

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities

Samuel R. P.-J. Ross[1] | Jorge García Molinos[2,3] | Atsushi Okuda[4] | Jackson Johnstone[5] | Keisuke Atsumi[6] | Ryo Futamura[4,7] | Maureen A. Williams[1,8,9] | Yuichi Matsuoka[4] | Jiro Uchida[4] | Shoji Kumikawa[4] | Hiroshi Sugiyama[4] | Osamu Kishida[4] | Ian Donohue[1]

[1]Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[2]Arctic Research Center, Hokkaido University, Sapporo, Japan

[3]Global Station for Arctic Research, Global Institution for Collaborative Research and Education, Hokkaido University, Sapporo, Japan

[4]Tomakomai Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Tomakomai, Hokkaido, Japan

[5]Graduate School of Environmental Science, Hokkaido University, Hakodate, Hokkaido, Japan

[6]Graduate School of Environmental Science, Hokkaido University, Sapporo, Hokkaido, Japan

[7]Graduate School of Environmental Science, Hokkaido University, Takaoka, Hokkaido, Japan

[8]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

[9]Biology Department, McDaniel College, Westminster, Maryland, USA

Correspondence
Samuel R. P.-J. Ross, Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.
Email: s.ross.res@outlook.com

Funding information
National Geographic Society, Grant/Award Number: EC-51224R-18; Japan Society for the Promotion of Science, Grant/Award Number: 17H03725, 18J10096, 19H04314 and SP19005/Y; Irish Research Council, Grant/Award Number: GOIPG/2018/3023

Abstract

Amidst the global extinction crisis, climate change will expose ecosystems to more frequent and intense extreme climatic events, such as heatwaves. Yet, whether predator species loss—a prevailing characteristic of the extinction crisis—will exacerbate the ecological consequences of extreme climatic events remains largely unknown. Here, we show that the loss of predator species can interact with heatwaves to moderate the compositional stability of ecosystems. We exposed multitrophic stream communities, with and without a dominant predator species, to realistic current and future heatwaves and found that heatwaves destabilised algal communities by homogenising them in space. However, this happened only when the predator was absent. Additional heatwave impacts on multiple aspects of stream communities, including changes to the structure of algal and macroinvertebrate communities, as well as total algal biomass and its temporal variability, were not apparent during heatwaves and emerged only after the heatwaves had passed. Taken together, our results suggest that the ecological consequences of heatwaves can amplify over time as their impacts propagate through biological interaction networks, but the presence of predators can help to buffer such impacts. These findings underscore the importance of conserving trophic structure, and highlight the potential for species extinctions to amplify the effects of climate change and extreme events.

KEYWORDS
biodiversity, climate change, ecological stability, extreme events, food web, heatwaves, Horonai stream, spatial variability, temporal variability

[Correction added on 6 November, 2021, after first online publication: The copyright line was changed.]

1 | INTRODUCTION

Increases in the frequency and intensity of extreme climatic events are reshaping ecological communities globally (Harris et al., 2018; Kreyling et al., 2011; Parmesan et al., 2000; Smale et al., 2019; Wernberg et al., 2013), a trend that is predicted to become even more acute as the century progresses (Easterling et al., 2000; Fischer et al., 2021; Oliver et al., 2018). The problem is particularly pertinent to freshwater ecosystems because of the narrower thermal safety margins of aquatic ectotherms relative to their terrestrial counterparts (Comte & Olden, 2017; Pinsky et al., 2019; Sunday et al., 2012). For example, more than 30% of 463 European freshwater species already exceed their preferred thermal temperatures within their current distribution ranges (Kärcher et al., 2019). Consequently, as the climate warms, aquatic ecosystems are increasingly likely to experience temperature-driven biodiversity change, including species redistributions and extinctions (Comte & Olden, 2017; Fussmann et al., 2014; García Molinos et al., 2016; Inagaki et al., 2020; Waldock et al., 2018; Wernberg et al., 2013). Such biodiversity change is highly likely to disrupt the capacity of aquatic ecosystems to provide many vital ecosystem processes, functions and services (Bernhardt & O'Connor, 2021; Chen et al., 2020; Oliver et al., 2015; Pecl et al., 2017; Smale et al., 2019; Worm et al., 2006).

Biodiversity change across the globe is a non-random process (Chen et al., 2020; Estes et al., 2011; Gerhard et al., 2020; Gross & Cardinale, 2005; Purvis et al., 2000). Of particular concern is trophic downgrading, whereby species extinctions follow a pattern of systematic community disassembly starting from the highest trophic levels, as a result of the larger body sizes, metabolic demands and resource requirements of apex predators (Estes et al., 2011; Tanentzap et al., 2020). Loss of predator species, in turn, often triggers trophic cascades and a wave of secondary extinctions (Donohue et al., 2017; Nakano et al., 1999), further modifying ecosystem structure and function (Chen et al., 2020), increasing the vulnerability of key ecosystem processes (Ross, Arnoldi, et al., 2021) and undermining the overall stability of the system (Donohue et al., 2013; White et al., 2018). A defining characteristic of global environmental change is that ecological communities are exposed to multiple anthropogenic stressors simultaneously (Birk et al., 2020), forming a complex backdrop against which species extinctions occur. A particularly important research question is the extent to which biotic and abiotic drivers of biodiversity change interact (Kordas et al., 2017; O'Connor & Donohue, 2013; O'Connor et al., 2015; Rasher et al., 2020; White et al., 2018; Zarnetske et al., 2012). Within this question, the capacity of individual species to confer resistance to future climate change remains understudied, particularly for aquatic systems (Goldenberg et al., 2018; Kordas et al., 2017; Nagelkerken et al., 2020; Rasher et al., 2020). While the ecological consequences of climate change and species extinctions have primarily been considered independently, species extinctions clearly have the potential to compound the effects of climate change on ecosystems (Isbell et al., 2015; Kishi et al., 2005; Kordas et al., 2017; Post & Pedersen, 2008; Rasher et al., 2020).

To date, manipulative experiments exploring the effects of future climate change on ecological communities have relied largely on Global Circulation Model projections that do not represent adequately the climatic conditions at the local scales of relevance to the manipulated systems (Korell et al., 2020). The consequent scale mismatch limits the representativeness of predictions of ecological responses to climate change. Here, we use contemporary and projected local temperatures, extracted from a local weather station and a highly resolved (5-km) regional climate model, respectively, to test experimentally whether trophic downgrading moderates the response of a well-resolved multitrophic cold temperate stream community (Fausch et al., 2002; Marcarelli et al., 2020) to simulated heatwaves in Tomakomai, northern Japan. Using flow-through mesocosms connected to a nearby stream, thus enabling continuous dispersal of microbes, algae and invertebrates both into and out of the experimental system, we tested whether and how the functional and compositional responses of benthic algal and macroinvertebrate communities to simulated heatwaves were modified in the presence and absence of *Cottus nozawae*—a freshwater sculpin and dominant predator in the system (Kishi et al., 2005; Konishi et al., 2001; Marcarelli et al., 2020; Miyasaka et al., 2003). Our experimental heatwaves were comprised of two levels: a lower intensity (+2.76°C mean water temperature increase) heatwave representative of a current local heatwave, and a higher intensity (+6.06°C) heatwave representing future extreme events as inferred from the local temperatures projected by the regional climate model towards the end of the 21st century. For both heatwave treatments, we simulated realistic temperature dynamics before, during and after the heatwaves based on local long-term records and future projections. We tested for treatment effects both during and after the heatwaves to separate their immediate impacts from their longer lasting effects and reveal legacy impacts of heatwaves on multiple aspects of our experimental stream communities (Fugère et al., 2020; Jacquet & Altermatt, 2020; Miller et al., 2021).

2 | METHODS

2.1 | Study location and experimental system

Our experiment (Figure 1) ran for 50 days (10 July–29 August 2019), using streamside mesocosms (Piggott et al., 2015) installed adjacent to a section of the Horonai stream, a forested headwater stream that runs past the Tomakomai Experimental Forest field station in Hokkaido, Japan (42°43′N, 141°36′E). The experimental system was comprised of 48 flow-through mesocosms (volume 3.5 L), allowing near-natural immigration and emigration of algae, microorganisms, and invertebrates from and to the stream. A Kawamoto GS3-C pump fed three header tanks with stream water, each of which gravity-fed 16 mesocosms. After flowing through the mesocosms, water drained back into the stream downstream of the pump intake. One of the main advantages of this system is its potential to support natural community dynamics (e.g. colonisation, predation), with conditions

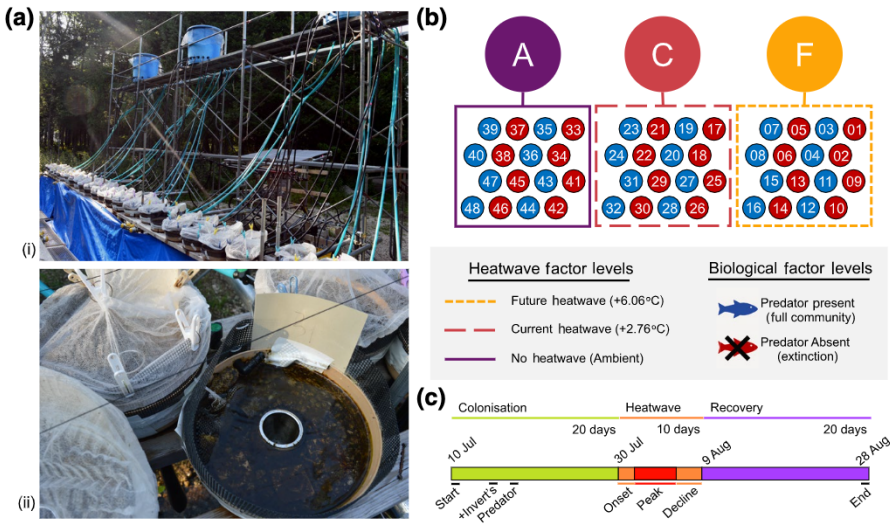

FIGURE 1 Experimental design and timeline. (a) Photographs of (i) our experimental set-up consisting of 48 flow-through aquatic mesocosms, and (ii) an individual mesocosm, post-colonisation of algae and macroinvertebrates. (b) Treatment design for our biological and heatwave factors and their levels. Mesocosms are numbered 1–48 and comprise either the full community including a predatory sculpin (*Cottus nozawae*) [24 blue circles] or the community minus *C. nozawae* [24 red circles]. Mesocosms were either heated to reflect future [F] climate conditions (mean = +6.06°C), current [C] climate conditions (mean = +2.76°C) or were kept at ambient temperatures [A]. See Table S1 for further details of the heatwave conditions. (c) Timeline for the experiment beginning 10 July when water began flowing and ending 28 August when water flow was terminated. The experiment comprised 20 days of colonisation, 10 days of heating including 5 days at peak heat intensity and 20 days of ambient conditions following the heating period. Our predation treatments were applied from 17 July [Predator]. Heatwave onset began on 30 July when leaf packs were also added to the mesocosms. Heatwave peak intensity ran 1–6 August [Peak] and was reduced to ambient by 9 August [Decline]. On Day 5, macroinvertebrate colonisation was supplemented with a kick-sample [+Invert's]. Daily algal measurements began on 18 July, immediately after predator addition [Predator], and continued until flow stopped and all samples were removed on 28 August [End]. Photographs: S.R.P.-J.R.

such as temperature, light and water chemistry similar to those in the nearby stream (Piggott et al., 2015). The total flow rate into the mesocosms throughout the duration of the experiment was maintained at 2.09 ± 0.05 L min^{-1} (mean ± SE).

2.2 | Experimental design

Our experimental design was comprised of two factors—predation and heatwave intensity—with, respectively, two (presence/absence of fish predators) and three (ambient temperatures, current and future heatwaves) levels (Figure 1). Each of the resulting six experimental treatments was replicated eight times. Each 3.5 L mesocosm (25 cm external diameter and 6 cm inner outflow ring; see Piggott et al., 2015) contained 1 L volume of substrate taken from the shallow riverbed downstream, and we allowed representative algal and macroinvertebrate communities to establish for 20 days before implementing experimental heatwaves. On Day 5, we supplemented natural colonisation of each mesocosm with invertebrates collected from the stream with a standardised 2-min kick sample with a 1 mm mesh pond net. This was done to facilitate colonisation of poorly dispersing taxa that might be underrepresented in natural drift through the inflow pipe (e.g. annelids, *Tipula* crane fly larvae) and to ensure that all mesocosms had an invertebrate community that was, as far as possible, representative of the natural stream community (Marcarelli et al., 2020).

Our predation treatments began on Day 7 with the addition of a single freshwater sculpin (*C. nozawae*) to half of the mesocosms (Figure 1c). *C. nozawae* (ハナカジカ in Japanese) is a temperature-sensitive (Kishi et al., 2005; Yagami & Goto, 2000), dominant, predatory benthic fish in the Horonai stream (Goto & Nakano, 1993), accounting for ~30% of total fish abundance (R. Futamura, unpublished data). *C. nozawae* forages on exposed benthic prey on the streambed (Yamamoto et al., 1988), consuming primarily amphipods (e.g. *Sternomoera yezoensis*) but also Ephemeroptera, Oligochaeta, and others (Marcarelli et al., 2020). Single individuals of *C. nozawae* were allocated randomly to mesocosms and varied in length from 54 to 79 mm (mean ± SE: 66.71 ± 16.4 mm).

2.3 | Heatwave implementation

On Day 20, we started the heatwave treatment, which was comprised of three levels: a higher intensity (mean = +6.06°C) heatwave based on future climate conditions; a lower intensity (mean = +2.76°C) heatwave based on current climate conditions; and an ambient (control) temperature treatment (Figure S1). We regulated water temperature in two header tanks by mixing stream water heated at 37°C using a Rinnai RUX-A2400W-E series gas boiler and 140 V series controller with unheated stream water via valve-regulated intakes. We monitored temperatures manually and adjusted intake ratios every hour to maintain the desired temperatures for each treatment (Table S1).

To produce locally relevant heatwaves for the region, we used daily mean contemporary (1995–2017) and projected (2076–2096) temperature series. Contemporary temperatures were extracted from the Tomakomai weather station (42.62°N, 141.55°E; ~6 km from the experimental site). Future projections were extracted from the 5-km grid cell containing the experimental site (cell centroid 42.68°N, 141.11°E) from the dynamical downscaling non-hydrostatic regional climate model NHRCM05 (Sasaki et al., 2011), corresponding to the simulation experiment Global Warming Projection V9 performed by the Japan Meteorological Agency for the IPCC RCP8.5 high-emissions scenario (Moss et al., 2010). Heatwaves for each period were then estimated using the approach recommended by Hobday et al. (2016) and implemented by the *RMarineHeatwaves R* package (ver 0.16.1; Smit et al., 2018). Briefly, heatwaves, defined as a discrete prolonged anomalously warm event in a given location, were characterised as events with at least five consecutive days with mean daily temperatures above the 10% of temperatures recorded during that time of the year for the whole series (Hobday et al., 2016). The definition of a heatwave is therefore contextual to the time of the year as the intensity threshold is seasonally adjusted (we used the default recommended 5 day duration before and after each focal day in the series). From the set of all detected heatwaves, we extracted those for the summer season (June–September) coincident with our experimental period and used their properties (Table S1) to inform the heatwaves implemented in our experiment. Detected heatwaves differed in their intensity as well as onset and decline rates between current and future periods, but not in their duration properties (Current median = 7.5 days, Future = 5.5 days, Mann–Whitney test: $U = 134.5$, $p = .245$; Table S1). Accordingly, we set the same total duration for our current and future experimental heatwaves, with a consistent 2-day onset followed by 5 days at peak intensity and a 3-day decline, resulting in a total duration of 10 days of heating (during experimental days 20–30 inclusive; Figure S1). We thus achieved the intended experimental realism (Korell et al., 2020) by reproducing the current and future local conditions associated with the observed and projected heatwaves at the Tomakomai experimental site.

2.4 | Algae biomass and composition

We placed three identical terracotta tiles (45 × 45 mm) in each mesocosm on Day 1 to allow for natural colonisation and continued accrual of algae during the 20-day establishment phase of the experiment. We measured benthic algal biomass and composition from the surface of each tile in situ daily using a BenthoTorch fluorometer (BBE Moldänke Gmbh) to quantify the total periphytic chlorophyll *a* concentration as a proxy for algal community biomass (Cardinale, 2011; Steinman et al., 2007), as well as that of diatoms, cyanobacteria and green algae separately (Kahlert & McKie, 2014). Due to breakage, only a single tile was measured in two mesocosms where predators were present (one under future heatwaves and one under current heatwaves). Before assessing algal community composition, we Hellinger-transformed the matrix of chlorophyll *a* concentrations of each algal group, because this transformation is insensitive to abundance (it does not give high weights to rare taxa; Legendre & Gallagher, 2001), and then generated dissimilarity matrices using the Bray–Curtis dissimilarity index.

2.5 | Macroinvertebrate communities and ecosystem processing

On Day 20, just before experimental heating began, we added a leaf litter decomposition pack (Benfield, 2007) to each mesocosm to measure leaf litter processing by microbes and macroinvertebrates. Leaf packs were constructed from polyethylene nets (mesh size 3 mm) and contained ~3.5 g (mean ± SE: 3.45 ± 0.01 g) of dried oak leaves (*Quercus crispula*), a dominant tree along the Horonai stream. To estimate background rates of microbial decomposition, we also placed bags of smaller mesh size (~0.1 mm) in each mesocosm to prevent access by macroinvertebrates. Each of these bags contained ~0.5 g (mean ± SE: 0.5 ± 0.01 g) dried *Q. crispula* leaves. Leaf packs were in place for a total of 29 days (i.e. until the end of the experiment; Figure 1), incorporating both the heatwave and subsequent recovery period. We then calculated macroinvertebrate leaf shredding rates as the change in the dry mass of the leaf pack before and after the experiment, corrected for expected microbial decomposition using a microbial degradation factor calculated as the proportion of dry mass lost in each microbial leaf bag (Benfield, 2007).

On Day 50, we destructively sampled all mesocosms to quantify the density (total abundance m^{-3}) and taxon richness of macroinvertebrates. Macroinvertebrates collected from the mesocosms were sorted from the mesocosm substrate, preserved in 90% ethanol and identified subsequently to the highest taxonomic resolution practicable.

2.6 | Data analyses

We calculated the temporal and spatial variability of both total biomass (functional variability) and the composition (compositional variability) of algal communities over two time periods, one encompassing the heatwave peak (5 days) and the other the post-heatwave recovery period (20 days). Functional stability represents the stability of ecosystem processes, such as biomass production or decomposition, performed by particular organism groups (Hillebrand et al., 2018). We calculated functional temporal variability as the coefficient of variation (i.e. the standard deviation divided by the mean) of total chlorophyll *a* concentrations in each mesocosm (from daily mean values on algal colonisation tiles) across each time period, where higher temporal variability corresponds to less stable biomass through time (Ives & Carpenter, 2007; Tilman et al., 2006). In dynamic systems such as streams, temporally stable chlorophyll production (i.e. algal productivity) indicates consistency in energy production capacity, a foundational ecosystem function (Steinman et al., 2007). We calculated functional spatial variability as the

coefficient of variation among the three equidistant algal tiles within each mesocosm (Hunter et al., 2019) on Days 27 and 50 to capture treatment effects on spatial variability on, respectively, the final day of peak heating before the start of the receding limb of the heatwave and on the final day of the 20-day post-heatwave recovery period (Figure 1). In contrast to temporal variability, higher functional spatial variability is stabilising, because spatial asynchrony in biomass provides spatial insurance through patch dynamics (Leibold et al., 2004; Loreau et al., 2003).

Compositional variability of algal communities was quantified from Bray–Curtis dissimilarity matrices calculated from algal biomass data (Baert et al., 2016; White et al., 2020). We measured compositional temporal variability for each mesocosm as the mean Euclidean distance from each date to the mesocosm-specific date-averaged centroid (White et al., 2020) for both the 5-day heatwave peak and the 20-day recovery period, with higher temporal variability (i.e. higher mean Euclidean distances) equating to less stable community composition through time (i.e. lower temporal stability; Hillebrand et al., 2018). We measured compositional spatial variability among mesocosms as the mean Euclidean distance between each mesocosm and their treatment-specific centroid (i.e. for all eight replicates under a given treatment) to produce treatment-level estimates for spatial variability (White et al., 2020). As with functional stability, higher compositional spatial variability is associated positively with stability, owing to the stabilising role of asynchrony in ecosystem dynamics (Leibold et al., 2004; Loreau et al., 2003), whereas homogenisation of community biomass or composition in space is destabilising (Donohue et al., 2009; Olden et al., 2004). To explore whether our measurements were confounded by shifts in mean values over time or space, we detrended our measurements of variability following Tilman et al. (2006). Results for detrended data were consistent with those for non-detrended data, so we present here analyses of non-detrended data only.

We tested the effects of predator presence and heatwaves on algal communities over two time periods: during the 5 days of peak heatwave exposure and at the end of the experiment following 20 days of post-heatwave recovery after cessation of the heatwaves. In contrast, analyses of macroinvertebrate communities and leaf litter decomposition were done only at the end of the experiment. We used ANOVA for univariate responses, after ensuring data homoscedasticity (via $\log_{10}$-transformation where needed; Table S2), and permutational multivariate analysis of variance (PERMANOVA) for multivariate responses, based on Bray–Curtis dissimilarity matrices. The contribution of individual macroinvertebrate taxa or algal groups to treatment differences was quantified using similarity percentage (Simper) analysis (Clarke, 1993). Post hoc comparisons among levels of significant terms were done with Tukey HSD tests for univariate analyses, and with pairwise multilevel comparisons with Bonferroni correction in the *pairwiseAdonis R* package (ver 0.4; Martinez Arbizu, 2020) for multivariate analyses. All statistical analyses were conducted in *R* (ver 4.0.2; R Core Team, 2020) using packages *orddom* (ver 3.1; Rogmann, 2013) and *vegan* (ver 2.5-6; Oksanen et al., 2019).

3 | RESULTS

During the heatwave period, we found no effects of heatwave or predator treatments on the biomass (ANOVA, $p > .05$; Figure 2a), functional temporal variability (ANOVA, $p > .05$; Figure 2b) or functional spatial variability (ANOVA, $p > .05$; Figure 2c) of algal communities (Table S3). However, the presence of fish predators modified the structure of algal community composition (PERMANOVA, $F_{1,42} = 9.67$, $p < .001$; Figure 3a; Table S4) and interacted significantly with heatwaves to modify both the temporal (ANOVA, $F_{2,42} = 3.33$, $p = .046$; Figure 3b) and spatial (ANOVA, $F_{2,24} = 6.65$, $p = .005$; Figure 3c) variability of algal community composition during the heatwave period. Though post hoc tests for compositional temporal variability were inconclusive (Tukey HSD, $p_{adj} > .05$), we found that predators stabilised the mesocosms exposed to current, but not future, heatwaves, by increasing the compositional spatial variability of their algal communities relative to ambient conditions (Tukey HSD, $p_{adj} = .05$; Table 1).

We found legacy effects of our experimental heatwaves that persisted after 20 days of post-heatwave recovery on algal biomass and functional variability. At the end of the experiment, total algal biomass was significantly higher in mesocosms under heatwave treatments (ANOVA, $F_{2,42} = 13.2$, $p < .001$; Figure 2d), with projected future heatwaves yielding higher algal biomass than both current heatwaves and ambient temperatures (Tukey HSD, $p_{adj} < .001$ in both cases; Table 1). Heatwaves also reduced the functional temporal variability of algal communities during the post-heatwave recovery period (ANOVA, $F_{2,42} = 9.46$, $p < .001$; Figure 2e), which was lowest under projected future heatwaves (Tukey HSD, $p_{adj} < .001$ and =.008 for ambient conditions and current heatwaves; Table 1). The presence of predators caused a trophic cascade by the end of the experiment, increasing the total biomass of algal communities (ANOVA, $F_{1,42} = 22.1$, $p < .001$; Figure 2d). Predators also stabilised the mesocosm communities by decreasing their functional temporal variability (ANOVA, $F_{1,42} = 6.06$, $p = .018$; Figure 2e). Though both predator presence and heatwaves affected algal biomass and temporal variability, their interaction was not significant in either case (ANOVA, $p > .05$; Table 1). We found no main or interactive treatment effects on functional spatial variability 20 days after the heatwave (ANOVA, $p > .05$; Figure 2f).

Heatwaves left legacy effects on algal community structure (PERMANOVA, $F_{2,42} = 5.74$, $p = .001$; Figure 3d), which, at the end of the experiment, differed in ambient temperature treatments relative to that following both current (Bonferroni, $p_{adj} = .003$) and future ($p_{adj} = .006$) heatwaves. In both cases, treatment differences were driven primarily by reductions in cyanobacteria biomass after heatwaves (Table S5). While the effect of heatwaves on compositional temporal variability during the post-heatwave recovery period was not statistically significant at the $p < .05$ level (ANOVA, $F_{2,42} = 2.73$, $p = .077$; Figure 3e), for compositional spatial variability, we detected a significant interaction between predator and heatwave treatments (ANOVA, $F_{2,114} = 5.88$, $p = .004$; Figure 3f). Specifically, predators negated the destabilising effect

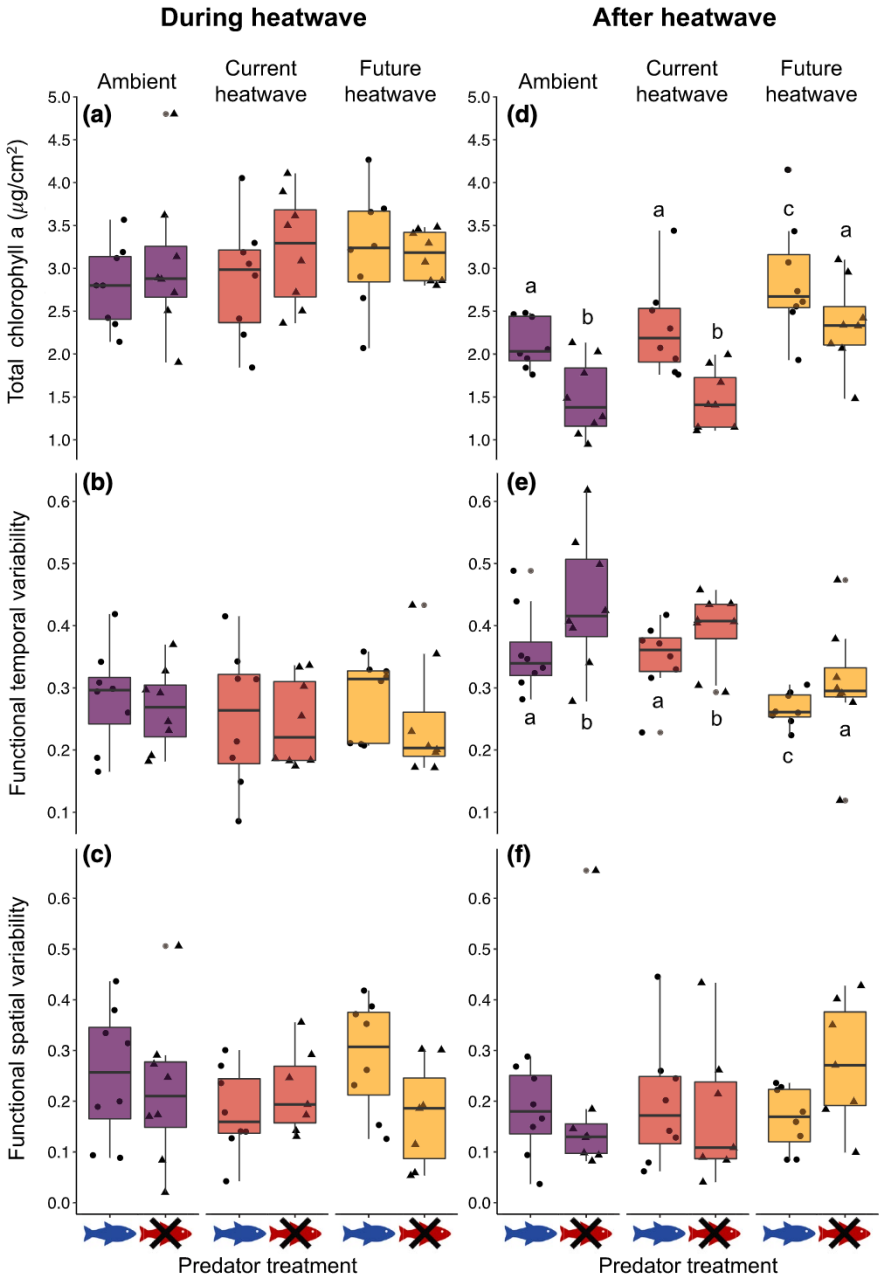

FIGURE 2 Effects of predation and heatwaves on total algal biomass and its temporal and spatial variability during (a–c) and after (d–f) heatwaves. (a, d) Total chlorophyll *a* (μg cm^{-2}) and its corresponding (b, e) temporal and (c, f) spatial variability in our experimental mesocosms (a–c) during the 5-day peak heatwave period (Days 22–27 inclusive) and (d–f) over the 20-day post-heatwave recovery period (Days 30–50 inclusive). Results for total chlorophyll *a* and functional spatial variability were measured at the final day of each period, whereas functional temporal variability was measured throughout the two time periods (over 5 and 20 days respectively). Boxplots represent the range (box = median and interquartile range) of values across the eight mesocosm replicates by treatment in the presence or absence of predatory fish [*X*-axis] under (from left to right) the ambient, current heatwave (+2.76°C) and projected future heatwave (+6.06°C) treatments. Significant ($p < .05$) pairwise contrasts (see Table 1) are denoted with superscript/subscript letters

of heatwaves on spatial variability; in the absence of predators, compositional spatial variability was lower under both current (Tukey HSD, $p_{adj} = .032$) and future ($p_{adj} = .012$) heatwaves, but no difference was detected among heatwave treatments when predators were present ($p_{adj} > .05$; Table 1).

Heatwaves also modified the structure of macroinvertebrate communities (PERMANOVA, $F_{2,46} = 2.19$, $p = .031$; Figure 4a); communities exposed to the higher intensity (i.e. future) heatwaves were significantly different from those under ambient conditions ($p_{adj} = .033$). Differences in community composition were driven mainly by increases in the densities of Chironomidae in mesocosms that experienced heatwaves (Table S6a). The presence of our focal predatory fish also restructured macroinvertebrate communities significantly (PERMANOVA, $F_{1,46} = 7.25$, $p < .001$; Figure 4b), particularly by increasing densities of orthocladiinid chironomids and reducing those of the mayfly *Baetis thermicus* and amphipod *S. yezoensis* (Table S6b). Regardless of heatwave treatment, both the taxon richness (ANOVA, $F_{1,42} = 5.96$, $p = .019$; Figure S2) and the density (ANOVA, $F_{1,42} = 31.4$, $p < .001$; Figure 4c) of benthic macroinvertebrates were significantly higher in the absence of predators. This, in turn, resulted in higher rates of leaf litter processing (ANOVA, $F_{1,42} = 13.5$, $p < .001$; Figure 4d) when predators were absent. Heatwaves or their interactive effects had, however, no effect on macroinvertebrate richness, density or leaf litter decomposition, including microbial degradation (Table 1; Table S3).

4 | DISCUSSION

Our results demonstrate that predators can help mitigate the destabilising effects of heatwaves on stream ecosystems. In the absence

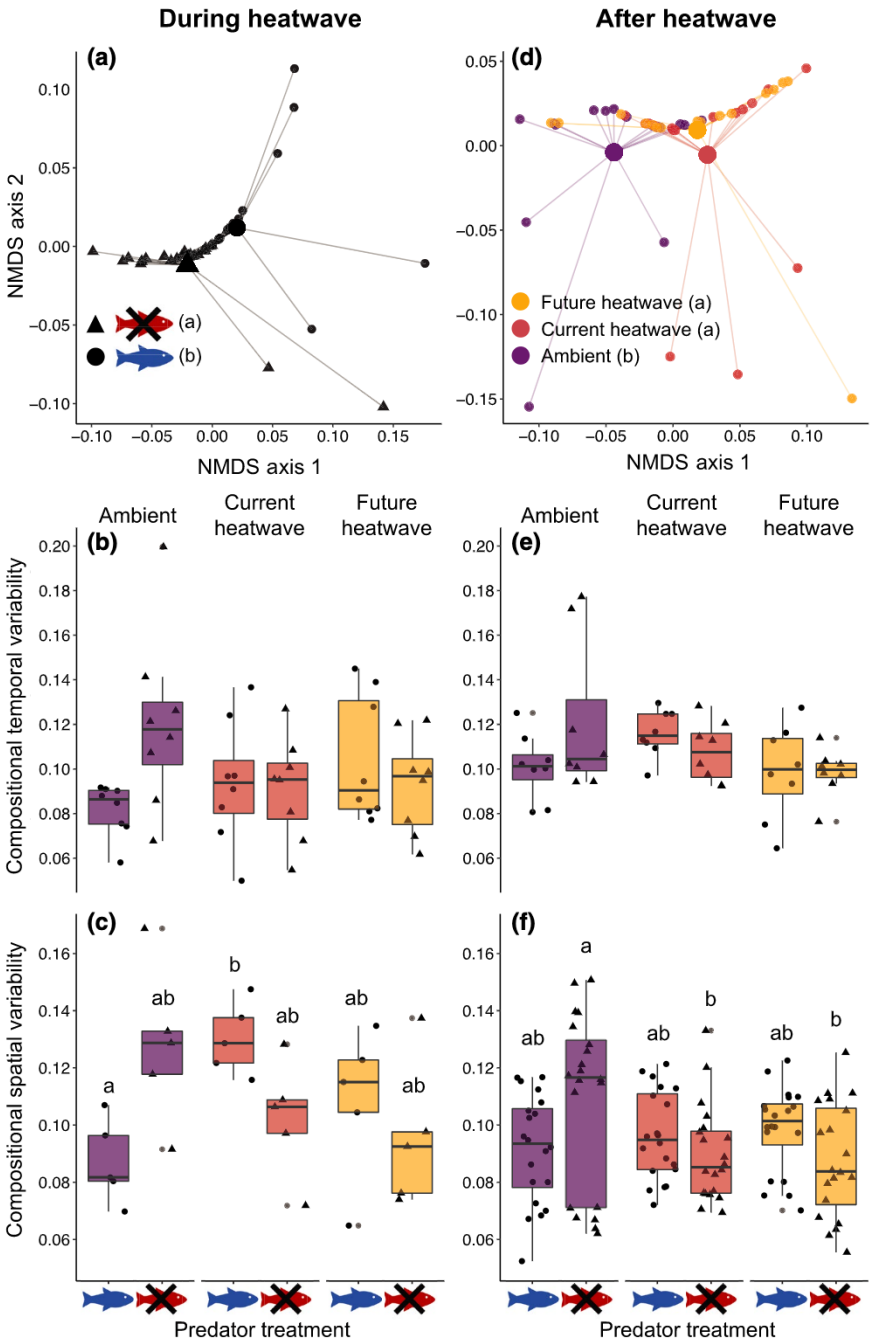

FIGURE 3 Effects of predation and heatwaves on algal structure and compositional variability during (a–c) and after (d–f) heatwaves. (a, d) Nonmetric multidimensional scaling (NMDS) ordinations of algal community composition in mesocosms belonging to the different (a) predator (stress = 0.021) and (d) heatwave (stress = 0.045) treatments. Only significant ($p < .05$) treatment effects are shown in each case (see Table 1). Large points represent treatment-level centroids for significant treatment effects, whereas small points represent algal communities within individual mesocosms. (b, e) Temporal and (c, f) spatial variability in algal composition. Panels (a–c) correspond to the 5-day peak heatwave (Days 22–27 inclusive), while (d–f) are for the 20-day post-heatwave recovery period (Days 30–50 inclusive). Boxplots represent the range (box = median and interquartile range) of values across eight mesocosms (b, e) or across days (c, f) within each treatment in the presence or absence of predatory fish [*X*-axis] under (from left to right) the ambient, current heatwave (+2.76°C) and projected future heatwave (+6.06°C) treatments. Significant ($p < .05$) pairwise contrasts (Table 1) are denoted with superscript/subscript letters

of predatory sculpin, we found that heatwaves homogenised the composition of algal communities in space. However, when present, our focal predator buffered mesocosms against these negative heatwave impacts. The presence of fish predators also reduced macroinvertebrate densities, which, in turn, suppressed leaf litter processing. Taken together, these results suggest that the predator moderated heatwave impacts and modified ecosystem functioning via a classical trophic cascade (Donohue et al., 2017; Kishi et al., 2005; Konishi et al., 2001; Rasher et al., 2020). Though our experimental design does not allow us to explicitly identify the mechanisms underpinning the patterns we observed, our results nonetheless suggest strongly that the stabilising effect of predators on algal communities exposed to heatwaves was an indirect consequence of the effects of the predators on their macroinvertebrate prey. Primary consumers can buffer producer assemblages against the effects of warming in terrestrial and marine systems (Kordas et al., 2017; Post & Pedersen, 2008). For example, Kordas et al. (2017) found that a key mechanism driving this pattern in rocky intertidal communities was the action of herbivores modifying the spatial variability of algal community structure. Our findings suggest predator effects on spatial variability occur indirectly through their effects on macroinvertebrate herbivores, highlighting the importance of both direct and indirect ecological interactions in providing resistance against heatwaves and climate warming more generally (Goldenberg et al., 2018; Kordas et al., 2017; Zarnetske et al., 2012; see also Beauchesne et al., 2021).

Response	Period	HW	P	HW:P	Contrast
Benthic algae	Heatwave				
Total biomass		N.S.	N.S.	N.S.	
Funct. temporal var.		N.S.	N.S.	N.S.	
Funct. spatial var.		N.S.	N.S.	N.S.	
Composition		N.S.	***	^	P_{Abs} ←
Comp. temporal var.		N.S.	N.S.	*	Inconclusive
Comp. spatial var.		N.S.	N.S.	**	HW_{Cur}:P_{Pres} $\uparrow_{vs}$ HW_{Amb}:P_{Pres}
Benthic algae	Recovery				
Total biomass		***	***	N.S.	HW_{Fut} ↑; P_{Abs} ↓
Funct. temporal var.		***	*	N.S.	HW_{Fut} ↓; P_{Abs} ↑
Funct. spatial var.		N.S.	N.S.	N.S.	
Composition		**	N.S.	N.S.	HW_{Fut} $\rightarrow_{vs}$ HW_{Amb}; HW_{Cur} $\rightarrow_{vs}$ HW_{Amb}
Comp. temporal var.		^	N.S.	N.S.	
Comp. spatial var.		N.S.	N.S.	**	HW_{Cur}:P_{Abs} $\downarrow_{vs}$ HW_{Amb}:P_{Abs}; HW_{Fut}:P_{Abs} $\downarrow_{vs}$ HW_{Amb}:P_{Abs}
Macroinvertebrate	Recovery				
Composition		*	***	N.S.	HW_{Fut} $\leftarrow_{vs}$ HW_{Amb}; P_{Abs} ←
Richness		N.S.	*	N.S.	P_{Abs} ↑
Density		N.S.	***	N.S.	P_{Abs} ↑
Leaf decomposition	Recovery				
Macroinvert. shredding		N.S.	***	N.S.	P_{Abs} ↑
Microbial degradation		N.S.	N.S.	N.S.	

TABLE 1 Summary of heatwave and predator effects on each response variable measured during heatwaves and at the end of the recovery period following the heatwaves. Where a significant ($p < .05$) treatment effect is reported for heatwave (HW_{Amb} = ambient, HW_{Cur} = current, HW_{Fut} = future) or predator (P_{Pres} = present, P_{Abs} = absent) treatment or their interaction (HW:P), significance level is marked (*$p < .05$, **$p < .01$, ***$p < .001$, ^$p < .1$) and corresponding levels for the statistically significant contrasts resulting from post hoc Tukey HSD/Bonferroni tests are shown. Vertical arrows represent an increase (↑) or decrease (↓) in relevant treatment level. Where pairwise comparisons are not explicit ('vs'), contrasts are for all relevant treatment levels. Horizontal arrows represent compositional shifts

Heatwaves left lasting effects on both macroinvertebrate composition and algal biomass in our experimental system, even though many of their impacts were not apparent during or at the end of the heatwaves. However, 20 days after the heatwaves, mesocosms exposed to future heatwaves had higher total biomass and lower temporal variability of algal biomass, and had modified algal and macroinvertebrate communities. If heatwave impacts on algal communities were indeed mediated by macroinvertebrates—as suggested by our finding of predator effects on macroinvertebrate richness, abundance and community structure—the observed lag in heatwave effects on algal biomass and structure is probably a consequence of the time taken for heatwave impacts to propagate through the food web (Donohue et al., 2017; Konishi et al., 2001). Heatwave and predator effects on algal communities were found at the end of the experiment, even though they were less apparent during and immediately following the heatwaves. These effects imply that the consequences of heatwaves for aquatic communities can be considerable even if not immediately detectable, with the potential for legacy effects to compound the impact of prior stressors over longer timescales (Jackson et al., 2021) or insidious effects of press perturbations such as background warming becoming obvious only when interacting with additional stressors (e.g. Rasher et al., 2020). Our results underscore the fundamental role of scale in understanding variability (Clark et al., 2021), including the pitfalls of not considering transience or legacy effects when interpreting the ecological consequences of extreme climatic events (Downing et al., 2008; Miller et al., 2021; Ross, Suzuki, et al., 2021).

Though the predatory sculpin altered both the structure and variability of algal community composition during and after the heatwave, its presence took longer to affect functional variability and algal biomass. This suggests a difference in the time taken for heatwaves to affect functional versus compositional stability, and supports the notion that the drivers of functional and compositional stability are largely independent of one another (Baert et al., 2016; Hillebrand & Kunze, 2020; Jacquet & Altermatt, 2020; White et al., 2020). Our results are thus also consistent with the recent finding that individual species provide complex and frequently contrasting contributions to different dimensions of ecological stability (White et al., 2020). Further work examining the temporal scales of relevance when measuring functional versus compositional stability will help achieve a process-based understanding of disturbance and recovery through a multidimensional lens (Baert et al., 2016; Donohue et al., 2013; Hillebrand & Kunze, 2020; Hillebrand et al., 2018).

As extreme events become more frequent and intense in the future (Easterling et al., 2000; Fischer et al., 2021; Oliver et al., 2018), complex disturbance regimes will likely unfold (Eveleens et al.,

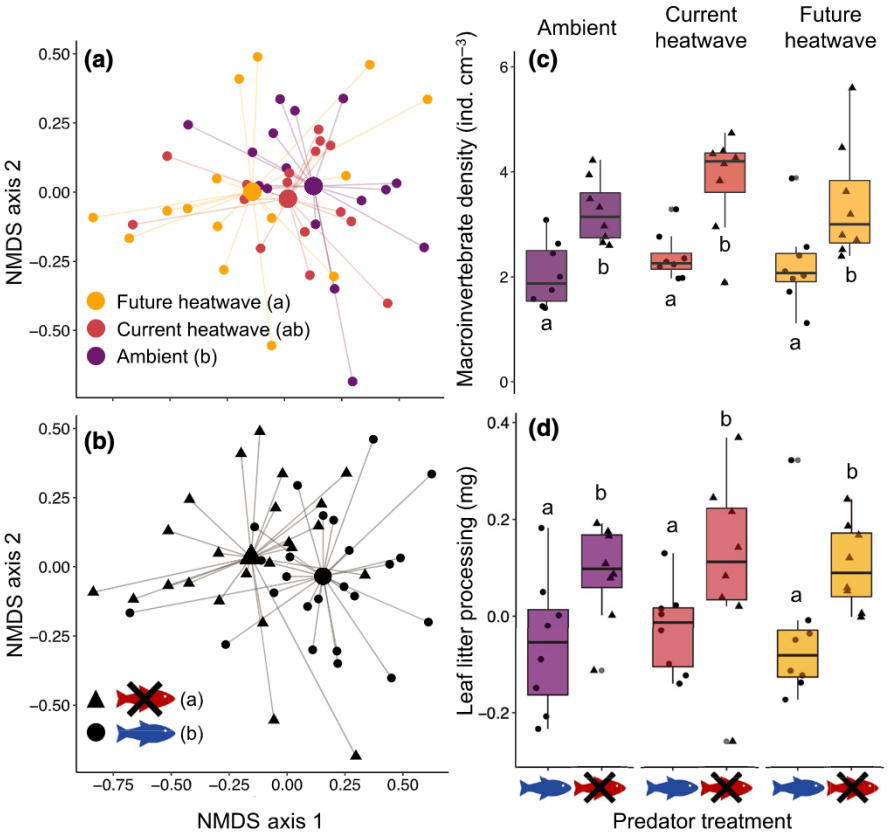

FIGURE 4 Effects of predation and heatwaves on macroinvertebrate community composition, density and leaf litter processing at the end of the experiment. (a, b) Nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition in mesocosms belonging to the different (a) heatwave and (b) predator treatments (stress = 0.166). Large points represent treatment-level centroids and small points, individual mesocosm communities. (c) Macroinvertebrate density (individuals cm^{-3}) and (d) leaf litter processing by macroinvertebrates, the latter calculated as the mesocosm-specific change in leaf mass after correcting for microbial degradation (where negative values represent interactions between macroinvertebrates and microbes; Kominoski et al., 2011, reducing proportional microbial degradation in large vs. small leaf packs). Boxplots represent the range (box = median and interquartile range) of values across mesocosms within treatments in the presence or absence of predatory fish [*X*-axis] under (from left to right) the ambient, current heatwave (+2.76°C) and projected future heatwave (+6.06°C) treatments. Significant ($p < .05$) pairwise contrasts (Table 1) are denoted with superscript/subscript letters

2019; Jacquet & Altermatt, 2020; Miller et al., 2021). Both disturbance regimes and their legacies can moderate the impact of subsequent disturbance events (Eveleens et al., 2019; Fugère et al., 2020; García Molinos & Donohue, 2011; Miller et al., 2021; Mrowicki et al., 2016). The ecological impacts of heatwaves may, therefore, be compounded if recovery from a previous disturbance is incomplete (e.g. Stockwell et al., 2020). Alternatively, ecological memory may prime ecosystems against repeated disturbances, attenuating their impact or facilitating community rescue (Fugère et al., 2020; Hughes et al., 2019; Jackson et al., 2021; Miller et al., 2021). That said, even communities exposed to frequent climate extremes may exhibit temperature-driven biodiversity change under increasingly severe disturbance regimes (e.g. Harris et al., 2018). A key next step is thus to test experimentally the consequences of increasingly complex disturbance regimes and repeated heatwaves for the functional and compositional stability of multitrophic communities (Eveleens et al., 2019; Jackson et al., 2021; Jacquet & Altermatt, 2020; Kéfi et al., 2019; Miller et al., 2021; Stockwell et al., 2020).

We used predictions from the IPCC RCP8.5 high-emission scenario to inform our future projected heatwaves. RCP8.5 represents a worst-case emission scenario, with previous warming experiments mostly manipulating temperatures less severe than those changes predicted under RCP8.5 (Korell et al., 2020). Our results therefore represent an extreme case, and we are unable to say with certainty whether predators would play similar stabilising roles under future heatwaves constructed based on more moderate emission stabilisation scenarios (RCP6.0-2.6). Nevertheless, CO_2 emissions are currently tracking RCP8.5 projections (Schwalm et al., 2020). Despite RCP8.5 being quite an extreme scenario, projections for the end of the century based on RCP8.5 may yet represent a plausible future (Schwalm et al., 2020). Our finding that several heatwave effects, particularly on algal biomass and macroinvertebrate community structure, were weaker or not detectable under current heatwaves underscores the importance of avoiding extreme warming scenarios by enforcing strict climate change mitigation policies. Locally informed climate change experiments, such as ours, considering a range of future climate scenarios

are essential to provide much more realistic predictions of the likely ecological impacts of climate change (Korell et al., 2020).

As with all field-based ecological experiments, our study is limited in scope by its temporal scale. Longer lasting legacies of heatwaves on community composition, functioning and/or stability that were not detected within the time frame of our measurements may surface at timescales >20 days post heatwave (Clark et al., 2021; Downing et al., 2008; Marcarelli et al., 2020; Ross, Suzuki, et al., 2021). For example, Downing et al. (2008) found that asynchrony among zooplankton taxa occurred only at time periods >80 days in response to recurring nutrient pulses, while synchrony dominated at shorter timescales and in constant environments. Marcarelli et al. (2020) also reported differences in the magnitude and direction of both direct and indirect trophic interactions in the Horonai stream food web through time, revealing scale-dependent top-down control of macroinvertebrates by predatory fish (including *C. nozawae*). Taken together, these results suggest that the role of predators in mitigating heatwave impacts may be more pronounced over longer timescales. Alternatively, heatwave legacies may dissipate over longer timescales (e.g. over months compared to weeks), as transient dynamics converge to long-term system dynamics post-disturbance (Hastings et al., 2018). Nevertheless, the fact that we found interactions between sculpin and heatwaves highlights the importance of top-down control in the Horonai system, even over relatively short timescales, such as in our experiment.

The size of our experimental units also limited the capacity of our experiment to mimic the full complexity of the Horonai stream ecosystem (Goto & Nakano, 1993; Marcarelli et al., 2020; Yagami & Goto, 2000; Yamamoto et al., 1988). Further, the limited availability of microclimatic refugia in our mesocosm systems may have overexposed macroinvertebrates and sculpin to heat stress compared to the natural stream (Isaak et al., 2016). Even so, the natural immigration and dispersal of algae, microorganisms and invertebrates in the experimental system, and continuous exposure to natural environmental fluctuations for the duration of the experiment increased considerably the realism of our experimental communities relative to a closed system. Additionally, immigration to the mesocosms from the stream may have dampened the effects of heating on our multitrophic communities (Fugère et al., 2020; Leibold et al., 2004), because individuals from the regional species pool upstream would not have been exposed to the heatwave until dispersal into our experimental system. Were that the case, the potential for temperature-driven biodiversity change on the stream system could be considerably greater than suggested by our experiment (Fussmann et al., 2014; García Molinos et al., 2016; Inagaki et al., 2020; Konishi et al., 2001; Kishi et al., 2005; Waldock et al., 2018; Wernberg et al., 2013).

By revealing that predators can mitigate the destabilizing effects of heatwaves on multitrophic stream communities, our study adds to a growing body of literature exploring the contribution of individual species to the stability of communities, ecosystem functioning and service supply (Gerhard et al., 2020; Kordas et al., 2017; Oliver et al., 2015; Post & Pedersen, 2008; Ross, Arnoldi, et al., 2021; Smale et al., 2019; White et al., 2018, 2020; Worm et al., 2006). As climate change increases the frequency and intensity of extreme climatic events such as heatwaves (Fischer et al., 2021; Oliver et al., 2018), predators may play a key role in tempering the ecological consequences of such extremes through both their direct and indirect effects on food webs (Kishi et al., 2005; Rasher et al., 2020). Further, our results highlight the potential for human impacts on predators to interact with other elements of global environmental change, worsening the consequences of trophic downgrading on ecosystems (Estes et al., 2011; Rasher et al., 2020). We conclude that much greater focus should be given to biotic multipliers of climate change and the role of community structure and biotic interactions in regulating ecological responses to extreme climatic events (Rasher et al., 2020; Zarnetske et al., 2012).

ACKNOWLEDGEMENTS

We thank Susumu Igarashi and Tomoaki Sato for help in constructing our experimental system and for help with sample processing; Hinako Katsushima, Gen Kusakabe, Hiroyuki 'Dani' Matsuyama, Azusa Sekishita, Ryohei Sugime, Muku Tsujino and Saori Yoshida for help with sample processing and data collection; Junjiro Negishi, Daisetsu Ito and Janine Tolod for help during macroinvertebrate identification; Emi Yoshida and all staff members of Tomakomai Experimental Forest for additional support; and Jay Piggott and Hannah White for helpful discussion. We also thank Jason Stockwell and one anonymous reviewer for their helpful comments on our manuscript. Authorship order of authors YM through HS was determined through a maggot eating race by Japanese grass lizards. This work was supported by a National Geographic Early Career Grant [EC-51224R-18] to S.R.P.-J.R., J.G.M. and I.D., a Japan Society for the Promotion of Science (JSPS) KAKENHI [17H03725] to O.K. and a JSPS KAKENHI Grant-in-Aid for Scientific Research (B) [19H04314] to J.G.M. S.R.P.-J.R. was supported by an Irish Research Council Postgraduate Scholarship [GOIPG/2018/3023]. J.J. was supported by a JSPS Summer Research Fellowship Grant (Summer 2019) [SP19005/Y]. K.A. was supported by a Grant-in-Aid for JSPS Research Fellows [18J10096].

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study and all R code are available in the Zenodo digital repository http://doi.org/10.5281/zenodo.5018448 (Ross, García Molinos, et al., 2021).

ORCID

Samuel R. P.-J. Ross https://orcid.org/0000-0001-9402-9119
Jorge García Molinos https://orcid.org/0000-0001-7516-1835
Keisuke Atsumi https://orcid.org/0000-0002-8206-4977
Ryo Futamura https://orcid.org/0000-0001-8128-3476
Maureen A. Williams https://orcid.org/0000-0001-7886-9353
Osamu Kishida https://orcid.org/0000-0002-2663-8155
Ian Donohue https://orcid.org/0000-0002-4698-6448

REFERENCES

Baert, J. M., De Laender, F., Sabbe, K., & Janssen, C. R. (2016). Biodiversity increases functional and compositional resistance, but decreases resilience in phytoplankton communities. *Ecology*, *97*, 3433–3440. https://doi.org/10.1002/ecy.1601

Beauchesne, D., Cazelles, K., Archambault, P., Dee, L. E., & Gravel, D. (2021). On the sensitivity of food webs to multiple stressors. *Ecology Letters*, *24*(10), 2219–2237. https://doi.org/10.1111/ele.13841

Benfield, E. F. (2007). Decomposition of leaf material. In R. F. Hauer & G. A. Lamberti (Eds.), *Methods in stream ecology* (pp. 711–720). Academic Press.

Bernhardt, J. R., & O'Connor, M. I. (2021). Aquatic biodiversity enhances multiple nutritional benefits to humans. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e1917487118. https://doi.org/10.1073/pnas.1917487118

Birk, S., Chapman, D., Carvalho, L., Spears, B. M., Andersen, H. E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A. D., Cardoso, A. C., Couture, R.-M., Cremona, F., de Zwart, D., … Hering, D. (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*, *4*, 1060–1068. https://doi.org/10.1038/s41559-020-1216-4

Cardinale, B. J. (2011). Biodiversity improves water quality through niche partitioning. *Nature*, *472*, 86–91. https://doi.org/10.1038/nature09904

Chen, Y., Huang, Y., Niklaus, P. A., Castro-Izaguirre, N., Clark, A. T., Bruelheide, H., Ma, K., & Schmid, B. (2020). Directed species loss reduces community productivity in a subtropical forest biodiversity experiment. *Nature Ecology & Evolution*, *4*, 550–559. https://doi.org/10.1038/s41559-020-1127-4

Clark, A. T., Arnoldi, J.-F., Zelnik, Y. R., Barabas, G., Hodapp, D., Karakoç, C., König, S., Radchuk, V., Donohue, I., Huth, A., Jacquet, C., Mazancourt, C., Mentges, A., Nothaaß, D., Shoemaker, L. G., Taubert, F., Wiegand, T., Wang, S., Chase, J. M., … Harpole, S. (2021). General statistical scaling laws for stability in ecological systems. *Ecology Letters*, *24*, 1474–1486. https://doi.org/10.1111/ele.13760

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Comte, L., & Olden, J. D. (2017). Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change*, *7*, 718–722. https://doi.org/10.1038/nclimate3382

Donohue, I., Jackson, A. L., Pusch, M. T., & Irvine, K. (2009). Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology*, *90*, 3470–3477. https://doi.org/10.1890/09-0415.1

Donohue, I., Petchey, O. L., Kéfi, S., Génin, A., Jackson, A. L., Yang, Q., & O'Connor, N. E. (2017). Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. *Global Change Biology*, *23*, 2962–2972. https://doi.org/10.1111/gcb.13703

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, *16*, 421–429. https://doi.org/10.1111/ele.12086

Downing, A. L., Brown, B. L., Perrin, E. M., Keitt, T. H., & Leibold, M. A. (2008). Environmental fluctuations induce scale-dependent compensation and increase stability in plankton ecosystems. *Ecology*, *89*, 3204–3214. https://doi.org/10.1890/07-1652.1

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, *289*, 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333*, 301–306. https://doi.org/10.1126/science.1205106

Eveleens, R. A., McIntosh, A. R., & Warburton, H. J. (2019). Interactive community responses to disturbance in streams: Disturbance history moderates the influence of disturbance types. *Oikos*, *128*, 1170–1181. https://doi.org/10.1111/oik.05868

Fausch, K. D., Power, M. E., & Murakami, M. (2002). Linkages between stream and forest food webs: Shigeru Nakano's legacy for ecology in Japan. *Trends in Ecology & Evolution*, *17*, 429–434. https://doi.org/10.1016/S0169-5347(02)02572-7

Fischer, E. M., Sippel, S., & Knutti, R. (2021). Increasing probability of record-shattering climate extremes. *Nature Climate Change*, *11*, 689–695. https://doi.org/10.1038/s41558-021-01092-9

Fugère, V., Hébert, M.-P., da Costa, N. B., Xu, C. C. Y., Barrett, R. D. H., Beisner, B. E., Bell, G., Fussmann, G. F., Shapiro, B. J., Yargeau, V., & Gonzalez, A. (2020). Community rescue in experimental phytoplankton communities facing severe herbicide pollution. *Nature Ecology & Evolution*, *4*, 578–588. https://doi.org/10.1038/s41559-020-1134-5

Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A., & Rall, B. C. (2014). Ecological stability in response to warming. *Nature Climate Change*, *4*, 206–210. https://doi.org/10.1038/nclimate2134

García Molinos, J., & Donohue, I. (2011). Temporal variability within disturbance events regulates their effects on natural communities. *Oecologia*, *166*, 795–806. https://doi.org/10.1007/s00442-011-1923-2

García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., Poloczanska, E. S., Richardson, A. J., & Burrows, M. T. (2016). Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, *6*, 83–88. https://doi.org/10.1038/nclimate2769

Gerhard, M., Mori, C., & Striebel, M. (2020). Nonrandom species loss in phytoplankton communities and its effect on ecosystem functioning. *Limnology and Oceanography*, *66*, 779–792. https://doi.org/10.1002/lno.11642

Goldenberg, S. U., Nagelkerken, I., Marangon, E., Bonnet, A., Ferreira, C. M., & Connell, S. D. (2018). Ecological complexity buffers the impacts of future climate on marine consumers. *Nature Climate Change*, *8*, 229–233. https://doi.org/10.1038/s41558-018-0086-0

Goto, A., & Nakano, S. (1993). Distribution and ecology of freshwater fishes in Hokkaido. In S. Higashi, A. Osawa, & K. Kanagawa (Eds.), *Biodiversity and ecology in the Northernmost Japan* (pp. 114–126). Hokkaido University Press.

Gross, K., & Cardinale, B. J. (2005). The functional consequences of random vs. ordered species extinctions. *Ecology Letters*, *8*, 409–418. https://doi.org/10.1111/j.1461-0248.2005.00733.x

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., … Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, *8*, 579–587. https://doi.org/10.1038/s41558-018-0187-9

Hastings, A., Abbott, K. C., Cuddington, K., Francis, T., Gellner, G., Lai, Y.-C., Morozov, A., Petrovskii, S., Scranton, K., & Zeeman, M. L. (2018). Transient phenomena in ecology. *Science*, *361*, eaat6412. https://doi.org/10.1126/science.aat6412

Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, *23*, 575–585. https://doi.org/10.1111/ele.13457

Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., & Striebel, M. (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters*, *21*, 21–30. https://doi.org/10.1111/ele.12867

Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuysen, J. A., Burrows, M. T., Donat, M. G., Feng, M., Holbrook, N. J., Moore, P. J., Scannell, H. A., Sen Gupta, A., & Wernberg, T. (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, *141*, 227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Hughes, T. P., Kerry, J. T., Connolly, S. R., Baird, A. H., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Jacobson, M., Liu, G., Pratchett, M. S., Skirving, W., & Torda, G. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change*, *9*, 40–43. https://doi.org/10.1038/s41558-018-0351-2

Hunter, W. R., Ogle, N., & O'Connor, N. (2019). Warming affects predatory faunal impacts upon microbial carbon cycling. *Functional Ecology*, *33*, 924–935. https://doi.org/10.1111/1365-2435.13304

Inagaki, K. Y., Pennino, M. G., Floeter, S. R., Hay, M. E., & Longo, G. O. (2020). Trophic interactions will expand geographically but be less intense as oceans warm. *Global Change Biology*, *26*, 6805–6812. https://doi.org/10.1111/gcb.15346

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of United States of America*, *113*, 4374–4379. https://doi.org/10.1073/pnas.1522429113

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, *317*, 58–62. https://doi.org/10.1126/science.1133258

Jackson, M. C., Pawar, S., & Woodward, G. (2021). The temporal dynamics of multiple stressor effects: From individuals to ecosystems. *Trends in Ecology & Evolution*, *36*(5), 402–410. https://doi.org/10.1016/j.tree.2021.01.005

Jacquet, C., & Altermatt, F. (2020). The ghost of disturbance past: Long-term effects of pulse disturbances on community biomass and composition. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20200678. https://doi.org/10.1098/rspb.2020.0678

Kahlert, M., & McKie, B. G. (2014). Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environmental Science: Processes & Impacts*, *16*, 2627–2634. https://doi.org/10.1039/C4EM00326H

Kärcher, O., Hering, D., Frank, K., & Markovic, D. (2019). Freshwater species distributions along thermal gradients. *Ecology and Evolution*, *9*, 111–124. https://doi.org/10.1002/ece3.4659

Kéfi, S., Dominguez-Garcia, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*, *22*, 1349–1356. https://doi.org/10.1111/ele.13340

Kishi, D., Murakami, M., Nakano, S., & Maekawa, K. (2005). Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*, *50*, 1315–1322. https://doi.org/10.1111/j.1365-2427.2005.01404.x

Kominoski, J. S., Marczak, L. B., & Richardson, J. S. (2011). Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology*, *92*, 151–159. https://doi.org/10.1890/10-0028.1

Konishi, M., Nakano, S., & Iwata, T. (2001). Trophic cascading effects of predatory fish on leaf litter. *Ecological Research*, *16*, 415–422. https://doi.org/10.1046/j.1440-1703.2001.00406.x

Kordas, R. L., Donohue, I., & Harley, C. D. G. (2017). Herbivory enables marine communities to resist warming. *Science Advances*, *3*, e1701349. https://doi.org/10.1126/sciadv.1701349

Korell, L., Auge, H., Chase, J. M., Harpole, W. S., & Knight, T. M. (2020). We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology*, *26*, 325–327. https://doi.org/10.1111/gcb.14797

Kreyling, J., Jentsch, A., & Beierkuhnlein, C. (2011). Stochastic trajectories of succession initiated by extreme climatic events. *Ecology Letters*, *14*, 758–764. https://doi.org/10.1111/j.1461-0248.2011.01637.x

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280. https://doi.org/10.1007/s004420100716

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Loreau, M., Mouquet, N., & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 12765–12770. https://doi.org/10.1073/pnas.2235465100

Marcarelli, A. M., Baxter, C. V., Benjamin, J. R., Miyake, Y. O., Murakami, M., Fausch, K. D., & Nakano, S. (2020). Magnitude and direction of stream–forest community interactions change with timescale. *Ecology*, *101*, e03064. https://doi.org/10.1002/ecy.3064

Martinez Arbizu, P. (2020). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis

Miller, A. D., Inamine, H., Buckling, A., Roxburgh, S. H., & Shea, K. (2021). How disturbance history alters invasion success: Biotic legacies and regime change. *Ecology Letters*, *24*, 687–697. https://doi.org/10.1111/ele.13685

Miyasaka, H., Genkai-Kato, M., Kuhara, N., & Nakano, S. (2003). Predatory fish impact on competition between stream insect grazers: A consideration of behaviorally- and density-mediated effects on an apparent coexistence pattern. *Oikos*, *101*, 511–520. https://doi.org/10.1034/j.1600-0706.2003.12001.x

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., Carter, T. R., Emori, S., Kainuma, M., Kram, T., Meehl, G. A., Mitchell, J. F. B., Nakicenovic, N., Riahi, K., Smith, S. J., Stouffer, R. J., Thomson, A. M., Weyant, J. P., & Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, *463*, 747–756. https://doi.org/10.1038/nature08823

Mrowicki, R. J., O'Connor, N. E., & Donohue, I. (2016). Temporal variability of a single population can determine the vulnerability of communities to perturbations. *Journal of Ecology*, *104*, 887–897. https://doi.org/10.1111/1365-2745.12533

Nagelkerken, I., Goldenberg, S. U., Ferreira, C. M., Ullah, H., & Connell, S. D. (2020). Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science*, *369*, 829–832. https://doi.org/10.1126/science.aax0621

Nakano, S., Miyasaka, H., & Kuhara, N. (1999). Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, *80*, 2435–2441. https://doi.org/10.2307/176923

O'Connor, N. E., Bracken, M. E. S., Crowe, T. P., & Donohue, I. (2015). Nutrient enrichment alters the consequences of species loss. *Journal of Ecology*, *103*, 862–870. https://doi.org/10.1111/1365-2745.12415

O'Connor, N. E., & Donohue, I. (2013). Environmental context determines multi-trophic effects of consumer species loss. *Global Change Biology*, *19*, 431–440. https://doi.org/10.1111/gcb.12061

Oksanen, J. F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Peter Solymos, M., Stevens, H. H., Szoecs, E., & Wagner, H. (2019). vegan: Community ecology package. R package version 2.5-6. https://github.com/vegandevs/vegan

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic

homogenization. *Trends in Ecology & Evolution*, *19*, 18–24. https://doi.org/10.1016/j.tree.2003.09.010

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*, 1324. https://doi.org/10.1038/s41467-018-03732-9

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, *30*, 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, *81*, 443–450. https://doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214. https://doi.org/10.1126/science.aai9214

Piggott, J. J., Townsend, C. R., & Matthaei, C. D. (2015). Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology*, *21*, 1887–1906. https://doi.org/10.1111/gcb.12861

Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L., & Sunday, J. M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, *569*, 108–111. https://doi.org/10.1038/s41586-019-1132-4

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 12353–12358. https://doi.org/10.1073/pnas.0802421105

Purvis, A., Agapow, P.-M., Gittleman, J. L., & Mace, G. M. (2000). Nonrandom extinction and the loss of evolutionary history. *Science*, *288*, 328–330. https://doi.org/10.1126/science.288.5464.328

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rasher, D. B., Steneck, R. S., Halfar, J., Kroeker, K. J., Ries, J. B., Tinker, M. T., Chan, P. T. W., Fietzke, J., Kamenos, N. A., Konar, B. H., Lefcheck, J. S., Norley, C. J. D., Weitzman, B. P., Westfield, I. T., & Estes, J. A. (2020). Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem. *Science*, *369*, 1351–1354. https://doi.org/10.1126/science.aav7515

Rogmann, J. J. (2013). orddom: Ordinal dominance statistics. R package version 3.1. https://www.rdocumentation.org/packages/orddom/versions/3.1/topics/orddom

Ross, S. R. P.-J., Arnoldi, J.-F., Loreau, M., White, C. D., Stout, J. C., Jackson, A. L., & Donohue, I. (2021). Universal scaling of robustness of ecosystem services to species loss. *Nature Communications*, *12*, 5167. https://doi.org/10.1038/s41467-021-25507-5

Ross, S. R. P.-J., García Molinos, J., Okuda, A., Johnstone, J., Atsumi, K., Futamura, R., Williams, M. A., Matsuoka, Y., Uchida, J., Kumikawa, S., Sugiyama, H., Kishida, O., & Donohue, I. (2021). *Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities (version v1.0)*. Zenodo. https://doi.org/10.5281/zenodo.5018448

Ross, S. R. P.-J., Suzuki, Y., Kondoh, M., Suzuki, K., Villa, M. P., & Dornelas, M. (2021). Illuminating the intrinsic and extrinsic drivers of ecological stability across scales. *Ecological Research*, *36*, 364–378. https://doi.org/10.1111/1440-1703.12214

Sasaki, H., Murata, A., Hanafusa, M., Oh'izumi, M., & Kurihara, K. (2011). Reproducibility of present climate in a non-hydrostatic regional climate model nested within an atmosphere general circulation model. *Scientific Online Letters on the Atmosphere*, *7*, 173–176. https://doi.org/10.2151/sola.2011-044

Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020). RCP8. 5 tracks cumulative CO_2 emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 19656–19657. https://doi.org/10.1073/pnas.2007117117

Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, *9*, 306–312. https://doi.org/10.1038/s41558-019-0412-1

Smit, A. J., Oliver, E. C. J., & Schlegel, R. W. (2018). *RmarineHeatWaves: Package for the calculation of marine heat waves [version 0.16.1]*. University of the Western Cape. https://github.com/ajsmit/RmarineHeatWaves

Steinman, A. D., Lamberti, G. A., & Leavitt, P. R. (2007). Biomass and pigments of benthic algae. In R. F. Hauer & G. A. Lamberti (Eds.), *Methods in stream ecology* (pp. 357–380). Academic Press.

Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., De Senerpont Domis, L. N., Dur, G., Frassl, M. A., Grossart, H.-P., Ibelings, B. W., Lajeunesse, M. J., Lewandowska, A. M., Llames, M. E., Matsuzaki, S.-I., Nodine, E. R., Nõges, P., Patil, V. P., Pomati, F., … Wilson, H. L. (2020). Storm impacts on phytoplankton community dynamics in lakes. *Global Change Biology*, *26*, 2756–2784. https://doi.org/10.1111/gcb.15033

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, *2*, 686–690. https://doi.org/10.1038/nclimate1539

Tanentzap, A. J., Morabito, G., Volta, P., Rogora, M., Yan, N. D., & Manca, M. (2020). Climate warming restructures an aquatic food web over 28 years. *Global Change Biology*, *26*, 6852–6866. https://doi.org/10.1111/gcb.15347

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*, 629–632. https://doi.org/10.1038/nature04742

Waldock, C., Dornelas, M., & Bates, A. E. (2018). Temperature-driven biodiversity change: Disentangling space and time. *BioScience*, *68*, 873–884. https://doi.org/10.1093/biosci/biy096

Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., De Bettignies, T., Bennett, S., & Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*, 78–82. https://doi.org/10.1038/nclimate1627

White, L., Donohue, I., Emmerson, M. C., & O'Connor, N. E. (2018). Combined effects of warming and nutrients on marine communities are moderated by predators and vary across functional groups. *Global Change Biology*, *24*, 5853–5866. https://doi.org/10.1111/gcb.14456

White, L., O'Connor, N. E., Yang, Q., Emmerson, M. C., & Donohue, I. (2020). Individual species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology & Evolution*, *4*, 1594–1601. https://doi.org/10.1038/s41559-020-01315-w

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., & Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*, 787–790. https://doi.org/10.1126/science.1132294

Yagami, T., & Goto, A. (2000). Patchy distribution of a fluval sculpin, *Cottus nozawae*, in the Gakko River system at the southern margin of its native range. *Ichthyological Research*, *47*, 277–286. https://doi.org/10.1007/BF02674251

Yamamoto, E., Goto, A., Nakaya, K., & Amaoka, K. (1988). Aquatic insect fauna and feeding habits of two *Cottus* species in the Daitobetsu

River of southern Hokkaido. *Bulletin of the Faculty of Fisheries Hokkaido University*, *39*, 237–256 (in Japanese with English summary). https://hdl.handle.net/2115/24007

Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change. *Science*, *336*, 1516–1518. https://doi.org/10.1126/science.1222732

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Ross, S. R. P.-J., García Molinos, J., Okuda, A., Johnstone, J., Atsumi, K., Futamura, R., Williams, M. A., Matsuoka, Y., Uchida, J., Kumikawa, S., Sugiyama, H., Kishida, O., & Donohue, I. (2022). Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities. *Global Change Biology*, 28, 403–416. https://doi.org/10.1111/gcb.15956