

## RESEARCH ARTICLE

# Spatial insurance against a heatwave differs between trophic levels in experimental aquatic communities

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## Abstract

Climate change-related heatwaves are major threats to biodiversity and ecosystem functioning. However, our current understanding of the mechanisms governing community resistance to and recovery from extreme temperature events is still rudimentary. The spatial insurance hypothesis postulates that diverse regional species pools can buffer ecosystem functioning against local disturbances through the immigration of better-adapted taxa. Yet, experimental evidence for such predictions from multi-trophic communities and pulse-type disturbances, like heatwaves, is largely missing. We performed an experimental mesocosm study to test whether species dispersal from natural lakes prior to a simulated heatwave could increase the resistance and recovery of plankton communities. As the buffering effect of dispersal may differ among trophic groups, we independently manipulated the dispersal of organisms from lower (phytoplankton) and higher (zooplankton) trophic levels. The experimental heatwave suppressed total community biomass by having a strong negative effect on zooplankton biomass, probably due to a heat-induced increase in metabolic costs,

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resulting in weaker top-down control on phytoplankton. While zooplankton dispersal did not alleviate the negative heatwave effects on zooplankton biomass, phytoplankton dispersal enhanced biomass recovery at the level of primary producers, providing partial evidence for spatial insurance. The differential responses to dispersal may be linked to the much larger regional species pool of phytoplankton than of zooplankton. Our results suggest high recovery capacity of community biomass independent of dispersal. However, community composition and trophic structure remained altered due to the heatwave, implying longer-lasting changes in ecosystem functioning.

#### KEYWORDS

dispersal, global change, mesocosm experiment, metacommunity, phytoplankton, trophic interactions, warming, zooplankton

## 1 | INTRODUCTION

Global climate change is characterised not only by rising means in annual surface temperatures but also by increasing frequency, magnitude and duration of heatwaves (IPCC, 2021). There is evidence for these increasing trends in heatwaves across the terrestrial (Fischer & Schär, 2010; Perkins-Kirkpatrick & Lewis, 2020), marine (Frölicher et al., 2018; Oliver et al., 2018), and freshwater realms (Woolway et al., 2021). Although the critical role of extreme weather events driving ecosystem changes has long been recognized (Jentsch et al., 2007), much of the previous climate change research has focused on the effects of rising mean temperatures. For example, a large majority of experimental studies aiming to unravel ecosystem responses to temperature increases applied static warming treatments without incorporating extreme events (Thompson et al., 2013; Woodward et al., 2016). Consequently, our understanding of how ecological communities and ecosystems respond to extreme weather events, such as heatwaves, is still limited.

Heatwaves often impose short but intense disturbances. By quickly pushing organisms beyond their thermal tolerance limits, heatwaves may alter community composition and ecosystem functioning more strongly than a gradual rise in mean temperature (Bennett et al., 2021; Gutschick & BassiriRad, 2003; Stillman, 2019; Vasseur et al., 2014). It has been suggested that frequent heatwaves can reshuffle global biodiversity patterns by causing local extinctions coupled with species range shifts (Smale & Wernberg, 2013; Wernberg et al., 2013), modulating population dynamics (Davison et al., 2010; Jiguet et al., 2006) and altering species interactions (Sentis et al., 2013; Zhang et al., 2018). All these changes can in turn impair ecosystem functioning (Eggers et al., 2012; Thompson et al., 2015) and the provisioning of ecosystem services (Smale et al., 2019).

Aquatic ecosystems may be particularly susceptible to heatwaves as aquatic ectotherms tend to exhibit narrower thermal safety margins than terrestrial ones (Pinsky et al., 2019; Sunday et al., 2012). Higher sensitivities to warming imply more frequent extinctions and faster species turnover, with implications for aquatic ecosystem functioning (Comte & Olden, 2017; Pinsky et al., 2019). However, in contrast to a press disturbance of steadily rising mean temperatures,

a short-term pulse disturbance caused by a heatwave is likely to be followed by a certain degree of community and ecosystem recovery (Bender et al., 1984; Harris et al., 2018). Management strategies will therefore critically depend on our understanding of the mechanisms that govern the resilience of ecosystems against heatwaves, in particular of its key components, resistance to and recovery from a disturbance (Hodgson et al., 2015; Ingrisch & Bahn, 2018).

According to the spatial insurance hypothesis, the resilience of local communities to disturbance depends on the connectivity to and diversity of the surrounding regional species pool (Loreau et al., 2003; Thompson et al., 2017). This implies that habitats that are geographically isolated, either naturally or through anthropogenic impacts (e.g., habitat fragmentation), are likely to be more susceptible to environmental change, including more frequent heatwaves. Immigration of species more tolerant to certain disturbances may allow better tracking of the changing environment, allowing for more stable ecosystem functioning if the colonising and resident species are redundant in maintaining specific ecosystem processes (Loreau et al., 2003).

Experimental evidence in support of the spatial insurance hypothesis is however still contradictory and no consensus has been reached. This is partly due to the fact that the insurance effect depends on the type of stressor and the measure of ecosystem functioning (Symons & Arnott, 2013; Thompson & Shurin, 2012). The spatial insurance can also differ among trophic groups due to their different responses to environmental stressors and abilities to disperse (Limberger et al., 2019). Yet, most previous experiments have focused only on simplified ecosystems composed of a single trophic group (de Boer et al., 2014; Eggers et al., 2012; Guelzow et al., 2017), or manipulated dispersal of only a single trophic group (Symons & Arnott, 2013; Thompson & Shurin, 2012). It has also been recently debated whether dispersal can provide spatial insurance against heatwaves. Laboratory experimental manipulations of a single trophic level suggested either positive (de Boer et al., 2014) or neutral effects (Eggers et al., 2012). As dispersal of organisms from different trophic levels can cause different effects on metacommunity structure and ecosystem function (Haegeman & Loreau, 2014), the direct experimental manipulation of multiple trophic levels in a

metacommunity context can provide a more realistic understanding of ecosystem resistance to and recovery from extreme heatwaves on a regional scale.

There has been mounting evidence that the impacts of warming critically depend on the trophic level (and associated traits such as body size) of organisms, driven by their different physiological constraints and changes in the strength of trophic interactions (Kratina et al., 2022; Petchey et al., 1999; Shurin et al., 2012). For instance, increased metabolic demands of ectothermic consumers can result in higher feeding rates, resulting in stronger top-down control (Brown et al., 2004; Romero et al., 2018; Zhang et al., 2020). At the same time, large consumers are more prone to starvation under warmer conditions, which increases the risk of local extinction (Fussmann et al., 2014; Rall et al., 2010). This is further accentuated by their generally smaller population sizes and slower growth rates (Petchey et al., 1999; Purvis et al., 2000). Moreover, the successful establishment of consumer populations in a new habitat strongly depends on the availability of resources (Thompson & Gonzalez, 2017). Therefore, consumers may be more dispersal-limited than their resources, resulting in stronger and longer-lasting responses to and slower recovery from disturbance. Lastly, it is essential to partition dispersal and associated diversity changes at different trophic levels, as responses of ecosystem functioning (e.g., primary production) to diversity changes directly depend on the affected trophic group (Duffy et al., 2007; Thébault & Loreau, 2003).

Here, we tested how multi-trophic plankton communities respond to heatwaves, and whether the spatial insurance provided by dispersal buffers the negative effects. We performed a mesocosm experiment where we first established plankton communities from a geographically isolated mountain lake. We then tested whether an initial dispersal event from a diverse regional species pool contributed to the resistance and recovery of the experimental communities during and after the heatwave manipulation. To be able to partition the effects of dispersal of different trophic levels, dispersal was manipulated separately for phytoplankton and zooplankton. We first predicted that disturbance caused by the experimental heatwave would result in reduced total community biomass. Second, given the different metabolic constraints and sensitivity to resource availability, we predicted that organisms at higher trophic levels (i.e., zooplankton) would be more negatively affected than those at lower levels, resulting in weaker top-down control. Third, we expected that increased connectivity to a regional species pool would enhance community resistance and recovery and this spatial insurance effect would be of higher importance for organisms at higher trophic levels.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental setup

We performed an outdoor mesocosm experiment between June and August 2018 at the Biological Station of WasserCluster Lunz, Austria. We investigated the independent and interactive effects of

heatwave and dispersal on community composition and ecosystem functioning in a full-factorial design. The presence (H+) or absence (H-) of the heatwave was crossed with the manipulation of dispersal, represented by a dispersal event from the regional species pool of natural lakes and applied separately for phytoplankton (P-, P+) and zooplankton (Z-, Z+). The experimental setup thus comprised 8 treatments and 5 replicates per treatment for a total of 40 experimental units.

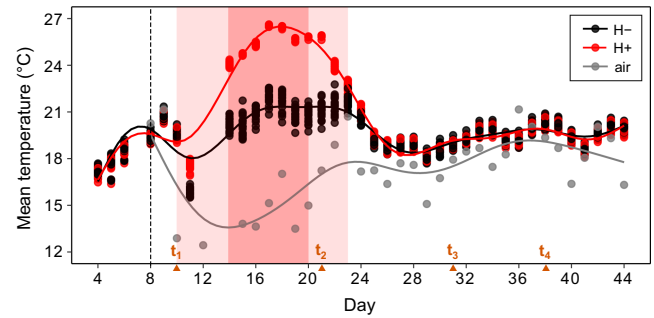
The experimental system consisted of 40 land-based mesocosms (height: 81 cm, inner diameter: 77 cm) made of food-safe PE containers (ARICON Kunststoffwerk GmbH). We placed them on an unshaded meadow approximately 500 m from Lake Lunz, Eastern Alps (N 47°51'15.7", E 15°04'3.8", 608 m a.s.l.). Each mesocosm was insulated with mineral wool and covered by white opaque plastic foil on the outer side to reduce the thermal impact of air temperature and irradiation. As a result, the average diurnal fluctuations in mesocosm water temperatures were in the range commonly seen in the surface water of Lake Lunz. We covered the mesocosms with 250  $\mu\text{m}$ -mesh net lids to minimise the introduction of particles while allowing for air exchange. Each mesocosm was also equipped with a removable, black-coloured plastic inner wall and bottom plates, which we turned every other week of the experiment to minimise the growth of periphyton and its impact on the planktonic system.

At the start of the experiment, we filled the mesocosms with 300 L of water (resulting in a water depth of 66.6 cm) from Lake Lunz. Water was collected from a 2-m depth (i.e., from the lake epilimnion) by a centrifugal pump, transported by a water truck to the experimental site, and randomly pumped into the mesocosms after passing through a coarse sieve (500  $\mu\text{m}$ ) to exclude fish larvae. As mesozooplankton (especially cladocerans) were impaired by pumping, we also introduced natural lake zooplankton from net hauls to set a starting density of approximately three *Daphnia* individuals  $\text{L}^{-1}$  in the mesocosms. This density corresponded to the mean summer density of *Daphnia* in natural lakes in the area (Horváth et al., 2017). In the oligotrophic (5–8  $\mu\text{g}$  total phosphorus  $\text{L}^{-1}$ ) Lake Lunz, phosphorus is the limiting nutrient for primary production. After filling the mesocosms with lake water and organisms, total phosphorus concentrations were raised to 15  $\mu\text{g}$   $\text{L}^{-1}$  by the addition of  $\text{K}_2\text{HPO}_4$  to set slightly mesotrophic conditions, as we expected a reduction of nutrients through sedimentation throughout the experiment. No experimental treatments were applied for 8 days, allowing for local species sorting and community establishment.

To simulate dispersal from the regional species pool, we introduced a pooled inoculum consisting of either phytoplankton (P+ treatment), zooplankton (Z+ treatment) or both (P+Z+ treatment), originating from 15 regional lakes (Table S1). Among these source lakes, we also included peri-alpine lowland habitats that likely harbour more heat-tolerant planktonic taxa than our focal site. To apply the treatments, we first collected samples of phytoplankton and zooplankton from each source lake. For phytoplankton, we collected a 20-L vertically integrated epilimnetic water sample with a Van Dorn bottle. In the next step, samples were pooled and screened

through a plankton net (mesh size: 30  $\mu\text{m}$ ) to remove larger organisms, especially metazoans. Thus, this pooled sample contained all microorganisms  $<30 \mu\text{m}$  (i.e., viruses, bacteria and protists). Still, we label it 'phytoplankton' for simplicity, as phytoplankton comprised an important part of biomass and we have detailed data for all time points only for this group. We collected zooplankton by vertical net hauls (mesh size: 100  $\mu\text{m}$ , opening diameter: 40 cm) from the epilimnion of the 15 source lakes. These samples were first subsampled to the same effective volume per lake (20 L) as in the case of phytoplankton. Next, we performed the dispersal manipulations by introducing an inoculum of standardised volume independently for the phytoplankton (P+) and zooplankton (Z+) dispersal treatments. From the pooled phytoplankton sample, we introduced a 3-L subsample (representing 1% of total mesocosm volume) to inoculate the P+ mesocosms ( $N=20$ ). Before applying the Z+ dispersal treatment, the pooled community was washed gently by retaining zooplankton in a 100- $\mu\text{m}$ -mesh plankton net that was kept submerged in a large bucket just below the rim while gently pouring water in. This way, we ensured the animals did not fall dry while most bacteria and protists were washed out. We then added a zooplankton dispersal inoculum (volume: 0.5 L) corresponding to 3 L of lake water to each Z+ mesocosm. As the volume introduced by the dispersal inocula represented  $\leq 1\%$  of the total volume of water in the mesocosms, we did not immediately compensate for this in the control (P-, Z-) mesocosms. We equalled the water level in the mesocosms after the subsequent sampling. To reliably assess the number of phytoplankton taxa introduced with dispersal (P+), besides microscopic counts of the inoculum sample ( $\sim 33$  new taxa introduced; Table S2), we also performed an estimation based on species accumulation curves using our existing phytoplankton dataset for alpine and peri-alpine lakes. While the microscopic counts likely underestimated the taxonomic richness of the inoculum due to the large fraction of rare taxa, the second approach indicated  $\sim 53$  new taxa for 15 source lakes (Figure S1). With zooplankton dispersal (Z+), we introduced 4 cladoceran and 4 copepod species that were not present in the local community (Table S3), and on average, 160 individuals of cladocerans (corresponding to a density of  $\sim 0.5$  individuals  $\text{L}^{-1}$  in the mesocosms) and 412 individuals of copepods ( $\sim 1.4$  individuals  $\text{L}^{-1}$ ). The dispersal event (P+ and Z+ treatments) was simulated on day 8 of the experiment, prior to the experimental heatwave, which started 48 h later (i.e., on day 10, Figure 1).

The experimental heatwave (H+ treatment) was simulated by gradually increasing temperatures to reach a 5°C offset (required 4 days of initial heating) compared to the control (H-) conditions, which was subsequently maintained for 7 days (heatwave culmination phase). Temperature was regulated by submersible aquarium heaters (200 W, thermocontrol 200, Eheim GmbH) connected to a computer-controlled heating system. To set temperature levels in the H+ treatment, the mean temperature of the control (H-) mesocosms ( $N=20$ ) was used as baseline. While we planned to use the ambient temperatures as baseline, due to unusually cold weather conditions, H- mesocosms were also heated to 21.0°C from the third day of the heatwave until the end of the heating in the H+ mesocosms.



**FIGURE 1** Temporal dynamics of daily mean water temperature and ambient air temperature over the experimental duration. Heatwave treatment (H+) is indicated with red, while control (H-) mesocosms are indicated with black ( $N=20$  per treatment and per day). Red-coloured shading denotes the time interval of the simulated heatwave in H+ treatments (light shading: heating and cooling phases, dark shading: culmination phase with a +5°C offset in H+ vs H-). Triangles show the timing of the four focal sampling campaigns (i.e.,  $t_1$ ,  $t_2$ ,  $t_3$ , and  $t_4$ ). Solid lines represent fitted GAM models illustrating the temperature dynamics. The vertical dashed line indicates the timing of the dispersal manipulations.

After turning off the heating, water temperature in H+ mesocosms cooled to ambient levels within 3 days. The heatwave, including its initial heating, culmination, and cooling phases, thus lasted 14 days (Figure 1) and was followed by a 21-day recovery phase. The entire experiment (including the establishment, heatwave and recovery phases) lasted for 44 days (Figure 1). We applied an airlift system to prevent vertical temperature gradients in the tanks (Striebel et al., 2013). Compressed air released from a tube produced a very gentle upward current in a PVC pipe hanging in the centre of each mesocosm, and this kept the entire water column constantly mixed during the experiment.

## 2.2 | Sampling and sample processing

In vivo chlorophyll *a* (Chl-*a*) autofluorescence (hereinafter referred as Chl-*a* fluorescence) was measured daily by a handheld fluorometer (AquaPen-C AP-C 100, PSI) after a 30-min dark-adaptation period and served as a proxy for phytoplankton biomass. Samples were taken from the central surface water of the mesocosms. Over the experimental duration, samples were collected twice per week for total phosphorus, Chl-*a* (based on pigment extraction), particulate organic carbon (POC) as well as phyto- and zooplankton. Microscopic analysis of plankton community samples was carried out on four focal sampling dates: (i) 2 days after the introduction of the regional inoculum but before starting the heatwave manipulation (day 10,  $t_1$ ), (ii) at the end of the culmination phase of the experimental heatwave when the heaters were turned off (day 21,  $t_2$ ), as well as (iii) 10 days (day 31,  $t_3$ ) and (iv) 17 days (day 38,  $t_4$ ) later, in the recovery phase (Figure 1). Samples were collected through a tap at the side of each mesocosm (inner diameter: 10 cm, height from the ground: 50 cm) to reduce the risk of unintentional dispersal (e.g., by a sampling device)

among the experimental units. Prior to the sampling, we increased airflow and gently mixed the water column of each mesocosm with a clean plastic tube, ensuring a homogenous distribution of plankton. We then collected zooplankton samples by releasing 20L from the tap into a clean container, thereby ensuring fast flow that prevents the zooplankton from escaping the suction. Subsequently, we filtered the volume through a 30- $\mu\text{m}$  mesh plankton net and preserved the retained organisms in absolute ethanol. To obtain samples of phytoplankton, Chl-*a*, POC and water for nutrient analysis, another 3-L water sample was collected and filtered through a 100- $\mu\text{m}$  mesh to remove large zooplankton. For phytoplankton samples, 200mL of water was preserved with Lugol's iodine solution. 500mL of water were filtered through glass microfiber filters (Whatman GF/F, pore size: 0.7  $\mu\text{m}$ ) for analyses of Chl-*a* and POC, and filters were kept frozen ( $-20^{\circ}\text{C}$ ) until analysis. We then replaced the sampled water volume in each mesocosm with sterile-filtered (polyethersulfone membrane, pore size: 0.2  $\mu\text{m}$ , MTS & APIC Filter), chlorine-free tap water, and added  $15\mu\text{gL}^{-1}\text{K}_2\text{HPO}_4$  corresponding to the exchanged volume of water. As a result, total phosphorus concentrations generally varied between 10 and  $15\mu\text{gL}^{-1}$  over the experimental period, and we did not find any systematic deviations across treatments (Figure S2).

Chl-*a* concentration in water samples was determined by fluorometry after acetone extraction (Arar & Collins, 1997), without correcting for pheophytin. POC content was measured by an elemental analyser (vario MICRO cube™, Elementar Analysensysteme GmbH). The concentration of total phosphorus was measured by the ascorbic acid colorimetric method (Hansen & Koroleff, 1999) after persulfate digestion (Clesceri et al., 1999).

## 2.3 | Microscopic analyses

We estimated phytoplankton densities according to Utermöhl (1958) method with an inverted microscope (DMI3000 B, Leica Microsystems). We counted and identified (to species level when possible) at least 400 sedimentation units (filaments, colonies, or single cells) in each sample (Lund et al., 1958). To obtain taxon-specific biovolume and wet weight, we applied conversion factors for corresponding geometrical shapes (Hillebrand et al., 1999), based on measurements of axial dimensions of at least 30 individuals for dominant taxa. We then converted wet weight to carbon mass by a conversion factor of 14% (Vadstein et al., 1988).

To obtain zooplankton density data, we counted all crustacean individuals in the 20-L samples. For rotifers, we counted all individuals in subsamples representing 10% of the sampled volume. Individuals were identified to species level when possible. Specimens belonging to the *Daphnia longispina* species complex were pooled due to the difficulty of reliable phenotypic differentiation between parental taxa and interspecific hybrids during routine identification (Dlouhá et al., 2010). We determined crustacean zooplankton body size by measuring the length of the first 20 individuals of each dominant species using a stereo microscope (Stemi 2000-C, Carl

Zeiss AG), while we used published average length data for rotifers (Koste, 1978). Body length of cladocerans was measured from the top of the head to the base of the caudal spine, while length of copepods was measured from the tip of the cephalothorax to the base of the furca (Bottrell et al., 1976). For rare crustacean species, we used mean body size measurements obtained from replicates of the same treatment combination with higher densities. When a species occurred at low densities in all replicates of a treatment combination, mean body size was obtained from all the individuals available. For copepod nauplii, we used the published mean body length of *Cyclops abyssorum* nauplii, the dominant species in our experiment (Ludovisi et al., 2008). We subsequently converted body length to dry mass following the length-weight relationships (McCauley, 1984), and applied a factor of 0.4 to convert dry mass to carbon mass (Reiss & Schmid-Araya, 2008).

Due to the high time demand for taxonomic identification, counting and size measurements, three randomly selected replicates per all treatment combinations were processed. These data (i.e.,  $N=3$  per treatment) were then used to analyse species richness and community composition. For zooplankton, the dominant taxa (i.e., cladoceran genera, Cyclopoida, and Calanoida) were identified in all five replicates per treatments, which we used to calculate taxon-specific biomass and to analyse resistance and recovery of zooplankton. As rotifers occurred in very low abundances from  $t_2$  till the end of the experiment (contributing on average <1% to total zooplankton biomass at  $t_2$  and  $t_4$ ), we considered the biomass of crustaceans as a representative proxy for total zooplankton biomass.

## 2.4 | Data analysis

### 2.4.1 | Temperature dynamics and the effect of dispersal on species diversity

Temporal dynamics of daily mean temperatures were visualised by smoothed conditional mean curves based on generalised additive models (GAM) with the *stat\_smooth* function (using *mgcv* gam fitting and formula:  $y \sim s(x, k=12)$ ) of the 'ggplot2' R package (Wickham et al., 2021).

To visualise the effect of the dispersal treatments at  $t_1$  (before the heatwave manipulation) on phytoplankton and zooplankton alpha diversity, we compared rarefied (i.e., testing for density-independent differences in taxon richness) mean taxon richness between the treatments with and without dispersal manipulations by the 'mobr' R package (McGlinn et al., 2021). Effect sizes were calculated as the mean absolute differences between treatments ( $\bar{D}$ ), and *p*-values were determined by a Monte Carlo permutation procedure ( $n=1000$  permutations) following the framework described in McGlinn et al. (2019). To visualise the effect of dispersal on gamma diversity, we constructed sample-based rarefaction curves for both phyto- and zooplankton based on 1000 random permutations using the *specaccum* function of the 'vegan' R package (Oksanen et al., 2020).

## 2.4.2 | Community composition

To test how taxa responded to treatments, we analysed the changes in community composition based on taxon-specific biomass and tested for significant associations between specific taxa and treatments. We tested for significant treatment effects using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) based on Bray-Curtis distances and 1000 random permutations. Taxa with less than three occurrences were excluded from the analysis given their minor contribution to similarities between samples. We then visualised phytoplankton and zooplankton composition across all treatment combinations with non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices. To identify taxa with the strongest contribution to compositional changes among significantly different treatments, we performed a similarity percentages (SIMPER) analysis. Significant associations between taxa and treatments were tested by 1000 random permutations. The analyses were performed with the functions *metaMDS* (NMDS), *adonis2* (PERMANOVA), and *simper* in the 'vegan' R package.

## 2.4.3 | Biomass resistance and recovery of different trophic levels

To assess the effect of the experimental treatment on the resistance and recovery of community biomass, which is a widely used measure of ecosystem functioning (Cardinale et al., 2012), we fitted linear models (LMs) on multiple measures characterising the biomass of different trophic levels. We quantified resistance based on the biomass change from the pre-disturbance state ( $t_1$ ) to the end of the heatwave ( $t_2$ ) and recovery on the change in biomass between  $t_1$  and the final sampling date  $t_4$  (Figure 1 and Figure S3). With biomass change used as dependent variable, we accounted for potential temporal asynchrony and differences among mesocosms developed during the establishment phase. By calculating biomass change from the pre-disturbance state (i.e.,  $t_1$ ), we were able to test temporal patterns of biomass over the experiment in each treatment combination, as well as the individual effects of the dispersal treatments.

For both resistance and recovery, we created separate LMs with the following dependent variables: (1) change of total plankton biomass, that is, the sum of zooplankton carbon mass and POC, (2) change of zooplankton biomass (expressed as carbon mass), (3) change of Chl-*a* and (4) change of POC. POC was used as a proxy for phytoplankton biomass (even though it included all microorganisms <100  $\mu\text{m}$ ) as it generally corresponded well to phytoplankton carbon mass estimated from biovolumes (Text S1 and Figure S4). To test potentially different responses of the major zooplankton groups, we also created separate LMs with the biomass change of Cladocera and Copepoda as dependent variables.

All models included heatwave with two levels (H+, H-) and dispersal with four levels (P-Z-, P+Z-, P-Z+, and P+Z+), together with their interaction as fixed factors. In this model structure, heatwave

and dispersal parameters show whether changes in average biomass were different in mesocosms as a response to a single treatment (heat or dispersal) compared to the control mesocosms, while the interaction terms indicate the potential insurance effect of dispersal against the heatwave. To account for any potential differences in initial (i.e.,  $t_1$ ) biomass values, mean-centred initial biomass was also included in all models as a predictor. Assumptions of normality and homoscedasticity of residuals were assessed by diagnostic plots. In case assumptions were violated, data were log-transformed, except for Cladocera and Copepoda biomass, where square-transformation was applied.

## 2.4.4 | Resistance and recovery of phytoplankton based on daily Chl-*a* fluorescence

The temporal dynamics of daily Chl-*a* fluorescence over the experimental duration was visualised by fitting GAMs using the same method as in the case of daily mean temperature (see above). To account for the high temporal variability of phytoplankton biomass, we also tested the responses of the daily Chl-*a* fluorescence (dependent variable) to the experimental treatments to analyse resistance and recovery. To this end, three separate linear mixed-effect models (LMEMs) were constructed, covering the experimental period from the start of the experimental heatwave until the end of the experiment. To determine resistance, the first model was fitted to the data of the heatwave period (from days 10 to 21,  $n = 12$  days). As microorganisms such as phytoplankton can rapidly respond to disturbances due to high population growth rates, we decided to analyse short-term and delayed effects of the experimental treatments by building separate models for the first and second part of the recovery phase. We tested short-term recovery immediately after the culmination phase of the heatwave (from days 22 to 33,  $n = 12$  days). We chose this period as Chl-*a* fluorescence values were lowest at the end of the experimental heatwave in all treatment groups and started to increase from day 22 (Figure S5). In the third model, we analysed the temporal pattern of Chl-*a* in the second part of the recovery phase (from days 34 to 44,  $n = 11$  days) to test for any lagged effects of the experimental treatments. In all LMEMs, we included the experimental treatments, time (with starting day set to 1 in each model), as well as their two- and three-way interactions as fixed factors. Here, a significant interaction with time can be interpreted as a temporal trend within the experimental treatments, and the three-way interactions show the potential insurance effect of dispersal against the heatwave. We also included initial zooplankton biomass observed at the beginning of the three analysed periods as an explanatory variable to account for the effect of top-down control. We set individual mesocosm as a random intercept and included the AR(1) error structure to account for temporal autocorrelation (Pinheiro & Bates, 2000). Model comparison by the Akaike information criterion indicated that accounting for temporal autocorrelation improved the model fit in all models. Chl-*a* fluorescence data were

log-transformed in all models to normalise residuals and improve the homoscedasticity of variances. Linear mixed-effects models were constructed with the *lme* function of the 'nlme' R package (Pinheiro et al., 2022). Marginal and conditional  $R^2$  of the models were calculated by the *r.squaredGLMM* function of the 'MuMIn' R package (Bartoń, 2022).

#### 2.4.5 | Relative strength of top-down versus bottom-up control

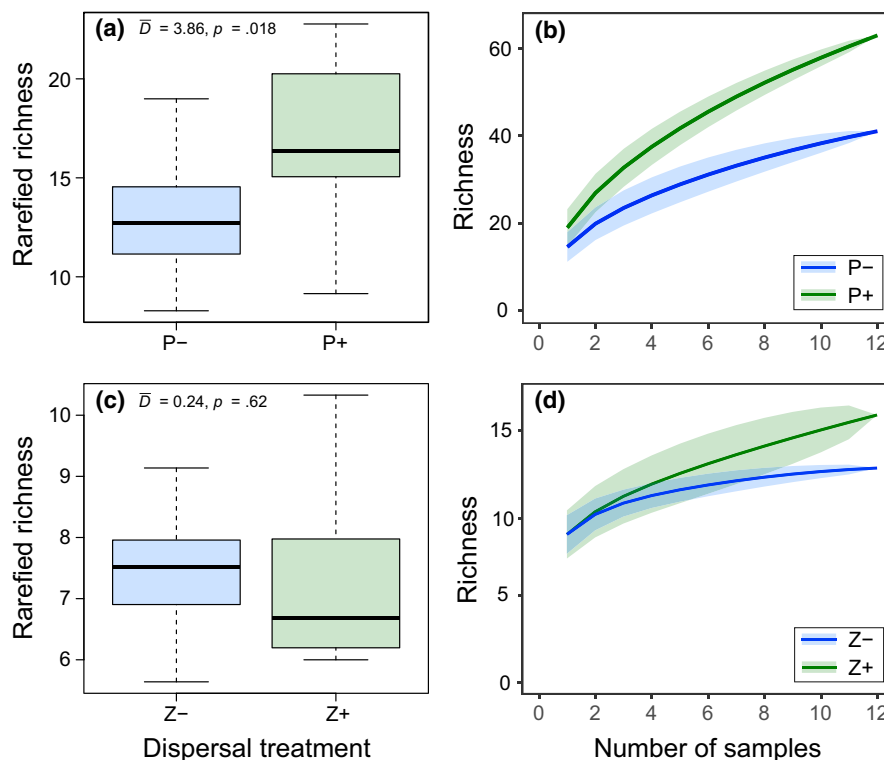
To reveal how trophic structure and trophic transfer efficiency changed in response to the experimental manipulation, we tested treatment-specific differences in the ratio of zooplankton carbon mass to POC. This biomass ratio between organisms with higher and lower trophic positions is a proxy for the strength of top-down control (Shurin et al., 2012). We constructed separate LMs for all four time points with heatwave and dispersal as fixed factors, treated the same way as in the models for resistance and recovery. We assured that normality and homoscedasticity of residuals were met by using diagnostic plots.

All data analyses and visualisations were performed in R version 4.0.2 (R Core Team, 2020).

### 3 | RESULTS

In total, 147 phytoplankton taxa were identified (Table S2). Based on their mean biomass at each focal sampling date, the communities were dominated by the chrysophyte *Chromulina* sp. ( $t_1$ ), the diatom *Nitzschia* sp. and the green alga *Ankyra judayi* ( $t_2$ ), and *Nitzschia* sp. and the green algae *Scenedesmus* group *Acutodesmus* ( $t_4$ ). We found 21 zooplankton taxa (Table S3), of which four were dominant (based on the frequency of occurrence and contribution to total biomass) during the experiment. These were the cladocerans *Daphnia* cf. *longispina* and *Bosmina longispina*, and the copepods *Eudiaptomus gracilis* and *Cyclops abyssorum*. The most dominant taxon was *D.* cf. *longispina*, which accounted for  $47.5 \pm 18.9$  (at  $t_2$ ) to  $61.5 \pm 15.1\%$  (at  $t_3$ ) of total zooplankton biomass during the experiment (mean  $\pm$  SD,  $N=24$ ).

During the 7-day-long culmination of the heatwave period, we maintained an approximately  $5^\circ\text{C}$  offset between the H+ and H- treatments (Figure 1), which resulted in mean water temperatures of  $25.5 \pm 1.3^\circ\text{C}$  (mean  $\pm$  SD,  $N=20$ ) in the H+ treatment and  $20.9 \pm 1.2^\circ\text{C}$  (mean  $\pm$  SD,  $N=20$ ) in the H- treatment. Experimental phytoplankton dispersal (P+) had an immediate positive effect on phytoplankton taxonomic richness expressed as both alpha and gamma diversity (Figure 2a,b). Rarefied richness at the local scale



**FIGURE 2** Richness of (a, b) phytoplankton and (c, d) zooplankton at time point  $t_1$ , i.e., after applying the dispersal treatments (P+ and Z+), but prior to the experimental heatwave. (a) Boxplots illustrate that rarefied richness of phytoplankton at the local scale (i.e., alpha-diversity) increased significantly in the presence of dispersal (P+).  $\bar{D}$  stands for mean absolute differences between treatments, the  $p$ -values are obtained from a Monte Carlo permutation procedure with 1000 permutations. (b) Species accumulation curves (mean  $\pm$  2SD based on 1000 random permutations) show that P+ also increased gamma-diversity. (c) Boxplots illustrate that rarefied richness of zooplankton at the local scale (i.e., alpha-diversity) was not significantly different among the dispersal treatments. (d) Species accumulation curves (mean  $\pm$  2SD based on 1000 random permutations), however, show a higher zooplankton gamma-diversity with Z+.

(i.e., alpha-diversity) was significantly higher compared to the control ( $\bar{D}=3.86$ ,  $p < .05$ , Figure 2a). Zooplankton dispersal (Z+) did not result in increased zooplankton alpha-diversity relative to the control ( $\bar{D}=0.24$ ,  $p = .62$ , Figure 2c), even though there were overall more zooplankton species (i.e., greater gamma-diversity) in the Z+ treatments (Figure 2d).

The heatwave (H+) and phytoplankton dispersal (P+) treatments both had a significant effect on community composition of phytoplankton, which became evident towards the end ( $t_4$ ) of the experiment (PERMANOVA,  $p < .05$ , Table 1, Figure 3a). Among the most influential taxa in terms of total explained variation across treatments, the green algae *Scenedesmus* group *Acutodesmus*, *Ulotrichales* sp. 1, *Monoraphidium minutum* and *Ankyra* sp. were positively associated with H+ (Figure 3a, SIMPER,  $p < .05$ , Table S4). Another green alga, *Mougeotia* sp., exhibited significantly lower biomass values in the P- vs P+ treatments (SIMPER:  $p < .05$ , Table S4). Zooplankton community composition was only affected by H+, which was evident already from  $t_2$  (PERMANOVA:  $p < .01$ , Table 1, Figure S6) and lasted until the end of the experiment (PERMANOVA,  $p < .01$ , Table 1, Figure 3b). At both  $t_2$  and  $t_4$ , *D. cf. longispina* had the largest contribution to the overall dissimilarity across treatments, and it had significantly lower biomasses in the H+ treatments (SIMPER,  $p < .01$ , Table S4). Another cladoceran,

*B. longispina*, was negatively associated with H+ at  $t_2$  (SIMPER,  $p < .01$ , Table S4).

The H+ treatment suppressed total plankton biomass (LM,  $p < .001$ , Table 2, Figure 4a, Figure S3). This significant decrease in biomass was primarily driven by zooplankton (LM,  $p < .001$ , Table 2). The biomass of cladocerans declined significantly in response to H+ (LM,  $p < .001$ ), while the negative effect on copepods was only marginally significant (LM,  $p = .07$ , Table S5, Figure S7). Besides the biomass decline, the proportion of egg-carrying females in the populations of the dominant cladoceran, *D. cf. longispina*, also dropped from  $35.1 \pm 9.4\%$  ( $t_2$ ) to  $0.0 \pm 0.0\%$  ( $t_5$ ) in the H+ treatments (mean  $\pm$  SD,  $N=20$ ), but this decrease was similar in the control treatments (mean  $\pm$  SD at  $t_2$ :  $31.6 \pm 8.0\%$ ,  $t_5$ :  $0.3 \pm 0.6\%$ ,  $N=20$ ). In contrast to the negative effects of H+ on total plankton and zooplankton biomasses, we did not find any significant effect of the heatwave on Chl-*a* concentration and POC (LM,  $p > .1$ , Table 2), nor on the pattern of daily Chl-*a* fluorescence (LMEM,  $p > .1$ , Table 3). Our results did not provide evidence for enhanced resistance to H+ following dispersal from the regional species pool. None of the experimental dispersal treatments mitigated the heatwave-driven decline observed in total plankton biomass and zooplankton (LM,  $p > .1$ , Table 2, Figure 4a). Zooplankton dispersal (P-Z+ and P+Z+) had a negative effect on zooplankton

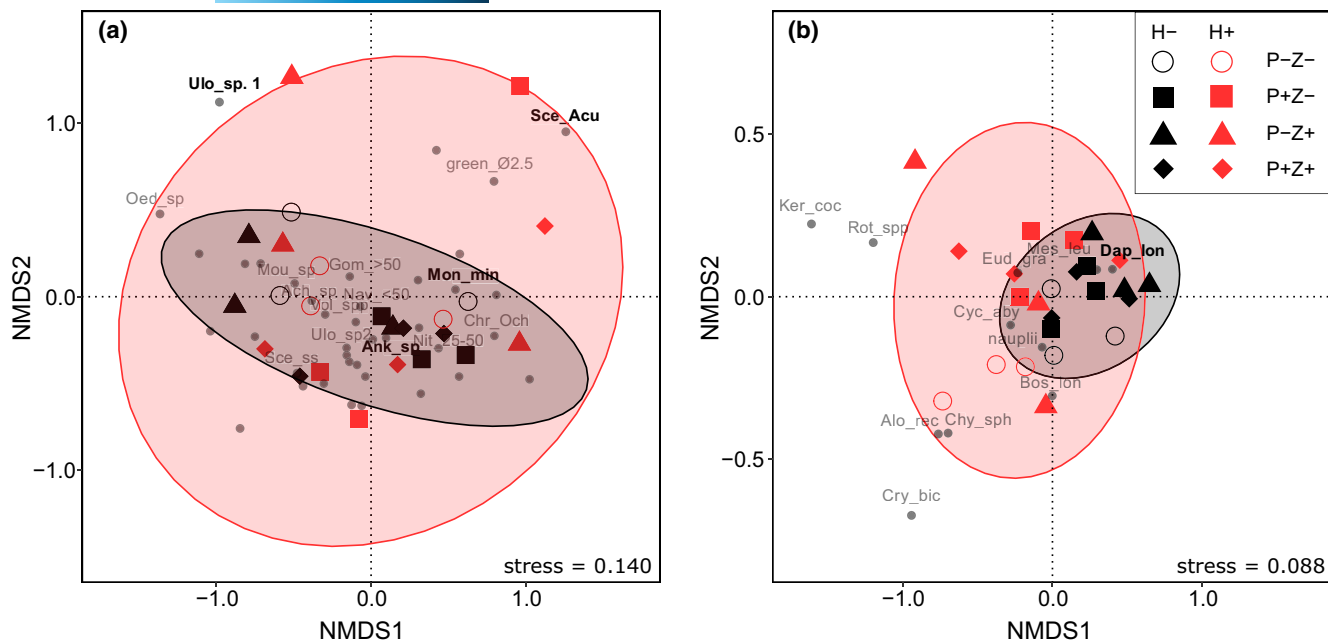
TABLE 1 Summary statistics of PERMANOVA testing for treatment-specific differences in community composition (based on biomass) of phytoplankton and zooplankton at the end of the heatwave ( $t_2$ ) and at end of the experiment ( $t_4$ ).

	Phytoplankton					Zooplankton				
	df.	Sum of sqs	F	R <sup>2</sup>	p	df.	Sum of sqs	F	R <sup>2</sup>	p
Sampling $t_2$										
H+	1	0.059	0.790	.034	.525	1	<b>0.414</b>	<b>16.636</b>	<b>.423</b>	<b>&lt;.001</b>
P+	1	0.018	0.238	.010	.959	1	0.030	1.191	.030	.268
Z+	1	0.185	2.475	.107	.069	1	0.070	2.815	.072	.074
H+ × P+	1	0.070	0.938	.040	.412	1	0.006	0.260	.007	.835
H+ × Z+	1	0.068	0.910	.039	.429	1	0.027	1.100	.028	.328
P+ × Z+	1	0.109	1.454	.063	.206	1	0.025	1.003	.026	.335
H+ × P+ × Z+	1	0.027	0.363	.016	.882	1	0.007	0.281	.007	.815
Residuals	16	1.196		.691		16	0.398		.407	
Total	23	1.732		1.000		23	0.977		1.000	
Sampling $t_4$										
H+	1	<b>0.458</b>	<b>2.189</b>	<b>.092</b>	<b>.029</b>	1	<b>0.379</b>	<b>6.497</b>	<b>.232</b>	<b>&lt;.001</b>
P+	1	<b>0.434</b>	<b>2.074</b>	<b>.087</b>	<b>.044</b>	1	0.084	1.432	.051	.220
Z+	1	0.085	0.406	.017	.943	1	0.045	0.778	.028	.512
H+ × P+	1	0.249	1.188	.050	.285	1	0.060	1.026	.037	.387
H+ × Z+	1	0.164	0.784	.033	.619	1	0.026	0.438	.016	.793
P+ × Z+	1	0.097	0.461	.019	.915	1	0.041	0.698	.025	.576
H+ × P+ × Z+	1	0.136	0.647	.027	.769	1	0.069	1.180	.042	.321
Residuals	16	3.350		.674		16	0.939		.570	
Total	23	4.972		1.000		23	1.637		1.000	

Note: Significant ( $p < .05$ ) results are highlighted in bold.

Abbreviations of treatments: H+: heatwave, P+: phytoplankton dispersal, Z+: zooplankton dispersal.





**FIGURE 3** NMDS plots illustrating (a) phytoplankton and (b) zooplankton community composition (based on biomass) as a function of the heatwave (H-, H+) and dispersal treatments (phytoplankton: P-, P+, zooplankton: Z-, Z+) at the end of the experiment ( $t_4$ ).  $N=3$  for each treatment combination. Ellipses indicate 95% confidence intervals for samples of the H+ and H- treatments, as H+ had a significant influence on the composition of both communities (PERMANOVA,  $p < .05$ , Table 1). Taxa are indicated with points and labels (for full names see Tables S2 and S3), where font type indicates the results of a SIMPER analysis, with taxa significantly related to the H+ treatment ( $p < .05$ ) presented by bold black letters. For phytoplankton, labels are only presented for the 15 taxa with the highest contribution to overall variability (based on SIMPER analysis).

resistance, i.e., suppressed biomass during the heatwave manipulation (LM,  $p < .05$ , Table 2).

While we found no indication for enhanced resistance to heatwave, our results showed that phytoplankton dispersal contributed to faster growth of phytoplankton biomass (measured as Chl-*a* fluorescence) in the presence of heatwave. This was visible in the first part of the post-heatwave recovery phase, indicated by the significant interaction between day  $\times$  H+  $\times$  P+Z- (LMEM,  $p < .05$ , Table 3, Figure 5), but not when combined with Z+ (LMEM,  $p > .1$ , Table 3, Figure 5). The insurance effect of P+ was no longer detectable in the second part of the recovery phase. We also found that H+ enhanced phytoplankton biomass, but only towards the end of the experiment (i.e., significant day  $\times$  H+ interaction, LMEM,  $p < .05$ , Table 3, Figure S8). At the same time, zooplankton biomass had a significant negative effect on Chl-*a* fluorescence (i.e., negative effect on the intercept, LMEM,  $p < .05$ , Table 3), indicating that top-down control was a major driver of phytoplankton dynamics in the recovery phase. Dispersal had no significant effect either on the recovery of total plankton biomass (LM,  $p > .1$ , Table 2, Figure 4b), zooplankton biomass, or the phytoplankton biomass proxies (Chl-*a*, POC) when analysed between  $t_1$  and  $t_4$  (LM,  $p > .1$ , Table 2, Figure 4b). Relative strength of top-down control decreased as a response to H+, indicated by the significant negative effect on zooplankton carbon mass to POC ratios (LM,  $p = .007$ , Figure 4c,d, Table S6). This effect became evident after the heat wave and lasted until the end of the experiment (Table S6).

## 4 | DISCUSSION

The experimental heatwave had a strong negative effect on total community biomass, supporting our first prediction. This negative effect was driven by the decline in zooplankton biomass. The heatwave-driven disruption of the trophic structure resulted in weakened top-down control in agreement with our second prediction. Weakened top-down control contributed to elevated phytoplankton biomass, however, this effect became visible only about 2 weeks following the heatwave. These results illustrate that some consequences of heatwaves may only manifest with a time lag after disturbance as a result of cascading interactions (Ross et al., 2022).

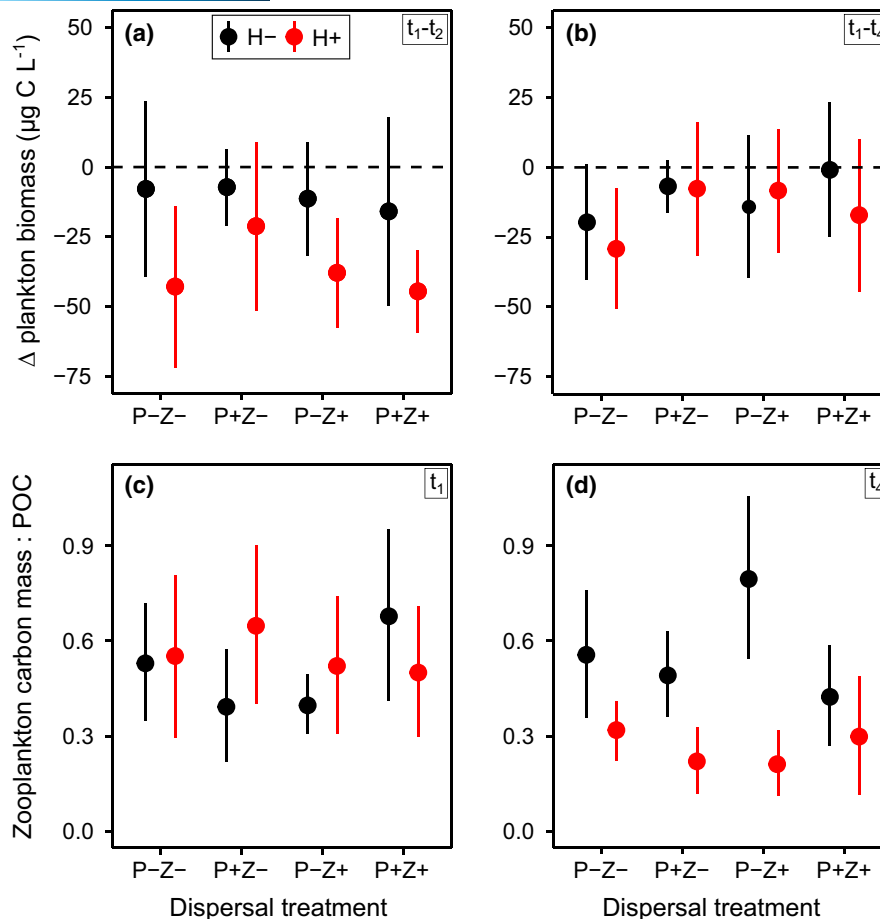
Experimental dispersal did not increase total plankton and zooplankton biomass resistance to the heatwave. In contrast to our third expectation, our results provided no evidence for the buffering effect of dispersal on zooplankton recovery either. Regardless of the dispersal treatments, the negative heatwave effect on total plankton and zooplankton biomass diminished by the end of the experimental period, indicating a high capacity for community recovery. In contrast to no effect of dispersal on zooplankton, the analysis of daily Chl-*a* fluorescence data provided some evidence for a positive dispersal effect on phytoplankton biomass recovery. Specifically, we found faster phytoplankton growth following the heatwave with phytoplankton dispersal, which can be interpreted as spatial insurance, as higher biomass of primary producers may provide a basis for faster recovery of secondary producers and

TABLE 2 Summary statistics (estimated parameters, standard error and *p*-values) of multiple linear regression models testing the effect of the experimental treatments (H+: heatwave, P+: dispersal of phytoplankton, Z+: dispersal of zooplankton) on resistance and recovery of plankton community biomass.

	Total plankton biomass			Zooplankton biomass			log Chl- <i>a</i>			POC		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
<b>Resistance</b>												
Intercept	-7.92	7.48	.298	15.40	3.45	<.001	-0.38	0.27	.168	-23.05	5.94	<.001
Initial	-1.03	0.15	<.001	-1.27	0.13	<.001	-0.45	0.06	<.001	-0.86	0.14	<.001
H+	-26.23	10.67	.020	-24.88	4.89	<.001	-0.33	0.35	.357	-1.91	1.07	.822
P+Z-	-3.54	10.60	.741	-7.84	4.97	.125	-0.40	0.35	.272	2.55	1.08	.767
P-Z+	-6.35	10.59	.553	-11.06	4.96	.033	-0.26	0.35	.465	2.96	1.07	.727
P+Z+	-10.30	10.58	.338	-13.01	4.91	.013	-0.19	0.36	.585	4.34	1.18	.611
H+ × P+Z-	15.71	14.99	.303	6.36	7.00	.370	0.78	0.50	.132	13.11	1.56	.284
H+ × P-Z+	-0.88	15.03	.954	6.33	6.91	.367	0.46	0.50	.361	-4.91	1.52	.685
H+ × P+Z+	5.25	14.96	.728	9.41	6.97	.187	0.67	0.50	.189	-6.40	1.63	.595
<i>R</i> <sup>2</sup>	.62			.83			.57			.53		
<b>Recovery</b>												
Intercept	-19.71	8.94	.035	-0.14	0.17	.408	1.39	0.28	<.001	-0.24	0.11	.036
Initial	-0.58	0.19	.005	-0.00	0.20	<.001	-0.60	0.06	<.001	-0.90	0.18	<.001
H+	-4.59	12.75	.722	-0.38	0.24	.128	0.15	0.36	.676	0.14	0.16	.367
P+Z-	3.88	12.66	.762	0.25	0.24	.319	-0.51	0.36	.164	-0.11	0.16	.468
P-Z+	10.54	12.67	.412	0.05	0.25	.839	-0.04	0.36	.908	0.15	0.16	.338
P+Z+	17.51	12.66	.177	0.00	0.24	.989	-0.03	0.36	.930	0.29	0.16	.074
H+ × P+Z-	10.14	17.97	.577	-0.51	0.34	.143	0.66	0.51	.207	0.31	0.22	.178
H+ × P-Z+	5.70	17.92	.752	-0.26	0.35	.465	0.51	0.51	.324	0.06	0.22	.799
H+ × P+Z+	-7.29	17.89	.687	-0.05	0.34	.885	0.47	0.51	.370	-0.20	0.22	.366
<i>R</i> <sup>2</sup>	.17			.60			.73			.50		

Note: Resistance is defined as the biomass change between the time points before ( $t_1$ ) and at the end ( $t_2$ ) of the heatwave, while recovery is the biomass change between  $t_1$  and the final sampling date ( $t_4$ ). The models for Chl-*a* and the models testing recovery of zooplankton biomass and POC are based on log-transformed data. Significant results ( $p < .05$ ) are highlighted in bold, while marginally significant ones ( $p < .1$ ) with italics.

Abbreviations: Chl-*a*, chlorophyll *a* concentration; initial, mean-centred initial ( $t_1$ ) biomass; POC, particulate organic carbon.



**FIGURE 4** (a) Resistance and (b) recovery of the plankton community measured as the change of total plankton biomass (carbon mass; mean  $\pm$  SD) between the pre-disturbance state and (a) the end of the heatwave (difference between  $t_1$  and  $t_2$ ) and (b) the final sampling date in the recovery period (difference between  $t_1$  and  $t_4$ ).  $N=5$  for each treatment combination. (a) The experimental heatwave (H+) had a significant negative effect on plankton biomass ( $p < .05$ , Table 2), with no significant effects of the dispersal treatments (phytoplankton: P- and P+; zooplankton: Z- and Z+). (b) None of the experimental treatments had a significant influence on the recovery of total plankton biomass. Summary statistics are presented in Table 2. The ratio of carbon mass (mean  $\pm$  SD) between zooplankton and POC as a proxy for the strength of top-down control shown at (c) the beginning (sampling point  $t_1$ ) and (d) the end ( $t_4$ ) of the experiment.  $N=5$  for each treatment combination. The ratio decreased as a response to the heatwave (H+) treatment at  $t_4$  (LM with log-transformed data,  $p < .05$ , see Table S6 for the statistical summary).

hence total community biomass over time. Even though the overall dispersal effects were relatively weak, our finding corroborates earlier observations from laboratory microcosm experiments that dispersal can potentially buffer the negative effect of heatwaves (de Boer et al., 2014). Also, dispersal effects may be more evident in unicellular organisms than in larger organisms at upper trophic levels (Limberger et al., 2019).

The decline of total plankton biomass during the heatwave is consistent with the prediction that increasing temperatures reduce total community biomass (O'Connor et al., 2009). This prediction is based on the differential temperature scaling of respiration- and photosynthesis-limited metabolism, which implies a greater sensitivity and, therefore, stronger responses of heterotrophic organisms to temperature changes compared to autotrophs (López-Urrutia et al., 2006; O'Connor et al., 2011). Increased grazing pressure in aquatic ecosystems with moderate warming, driven by increased metabolic demands, generally results in a shift towards

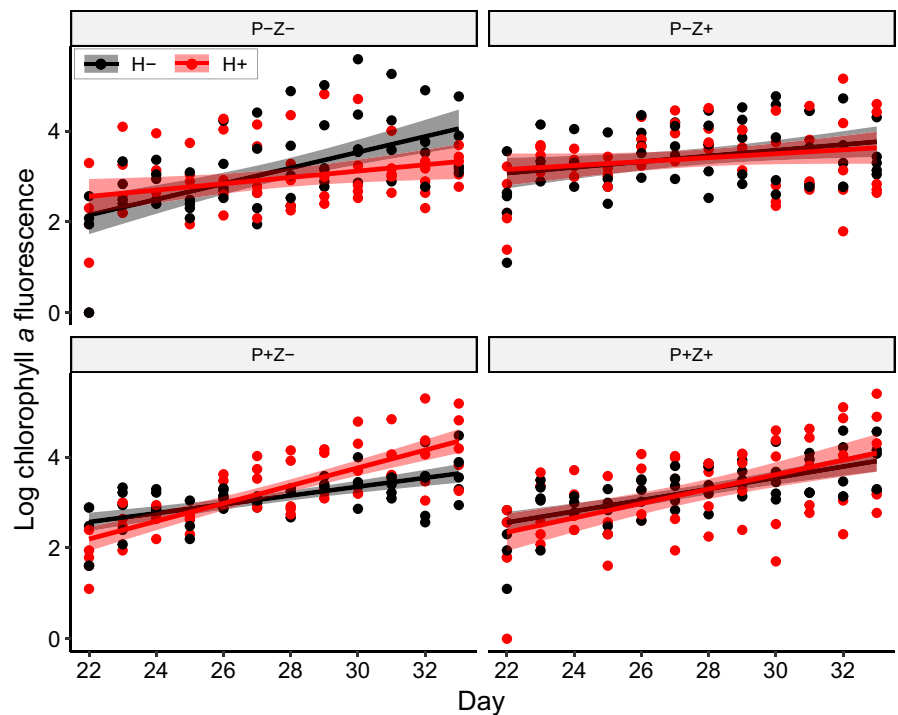
stronger top-down control and decreasing autotroph relative to heterotroph biomass (Kratina et al., 2012; O'Connor et al., 2009; Shurin et al., 2012; Velthuis et al., 2017). However, a greater proportion of consumers is expected to result in a decline in total biomass given the inefficient conversion of phytoplankton to consumer biomass (Persson et al., 2007; Slobodkin, 1959). In contrast, we observed weakened top-down control following the experimental heatwave resulting from the negative (direct or indirect) temperature effects on zooplankton biomass.

The biomass of cladocerans (dominated by *Daphnia cf. longispina*) declined strongly as a result of the heatwave, which was the major driver of the observed decline in total plankton biomass. While cladocerans can rapidly respond to temperature stress by adjusting their physiology (e.g., Yampolsky et al., 2014), the abrupt decline in biomass may indicate a failed acclimation. Besides direct temperature effects, the timing and magnitude of temperature fluctuations, and their interactions with food-limited periods, are also crucial for

**TABLE 3** Summary statistics (estimated parameters, standard error and *p*-values) of linear mixed-effects models testing the effects of the experimental treatments (H+: heatwave, P+: dispersal of phytoplankton, Z+: dispersal of zooplankton) on resistance and recovery of phytoplankton biomass (estimated by log-transformed chlorophyll *a* in vivo fluorescence).

	Resistance			Recovery 1			Recovery 2		
	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>	Estimate	SE	<i>p</i>
Intercept	<b>4.07</b>	<b>0.24</b>	<b>&lt;.001</b>	<b>2.73</b>	<b>0.64</b>	<b>&lt;.001</b>	<b>4.68</b>	<b>0.49</b>	<b>&lt;.001</b>
H+	0.22	0.27	.431	-0.16	0.54	.766	-0.79	0.52	.143
P+Z-	0.23	0.27	.410	0.53	0.46	.259	0.30	0.50	.556
P-Z+	0.10	0.27	.724	0.80	0.46	.097	-0.48	0.49	.341
P+Z+	-0.13	0.27	.629	0.31	0.48	.532	0.40	0.49	.810
Day	<b>-0.19</b>	<b>0.03</b>	<b>&lt;.001</b>	<b>0.20</b>	<b>0.04</b>	<b>&lt;.001</b>	<b>-0.09</b>	<b>0.04</b>	<b>.022</b>
Zooplankton biomass	<b>-0.01</b>	<b>0.01</b>	<b>&lt;.01</b>	-0.01	0.00	.087	<b>-0.02</b>	<b>0.01</b>	<b>.027</b>
H+ × P+Z-	-0.28	0.38	.474	-0.70	0.65	.290	0.44	0.71	.543
H+ × P-Z+	-0.26	0.38	.504	-0.26	0.65	.696	0.48	0.70	.494
H+ × P+Z+	-0.15	0.38	.699	-0.44	0.66	.512	0.59	0.70	.401
Day × H+	0.01	0.04	.822	-0.08	0.06	.181	<b>0.13</b>	<b>0.06</b>	<b>.024</b>
Day × P+Z-	-0.01	0.04	.837	-0.09	0.06	.151	-0.03	0.06	.546
Day × P-Z+	0.02	0.04	.663	-0.12	0.06	.054	0.03	0.06	.658
Day × P+Z+	0.06	0.04	.120	-0.05	0.06	.375	-0.03	0.06	.649
Day × H+ × P+Z-	0.00	0.06	.936	<b>0.18</b>	<b>0.08</b>	<b>.030</b>	-0.01	0.08	.917
Day × H+ × P-Z+	0.02	0.06	.759	0.08	0.08	.347	-0.04	0.08	.583
Day × H+ × P+Z+	-0.01	0.06	.806	0.13	0.08	.126	-0.11	0.08	0.179
Marginal $R^2$	.57			.36			.33		
Conditional $R^2$	.57			.36			.33		

Note: Models were built for the period of the experimental heatwave (12 days between days 10 and 21 and  $t_2$ , 'Resistance'), and for the first (12 days between days 22 and 33, 'Recovery 1') and second part (11 days between days 34 and 44, 'Recovery 2') of the recovery phase. Significant results ( $p < .05$ ) are highlighted in bold, while marginally significant ones ( $p < .1$ ) with italics.



**FIGURE 5** Increases in daily in vivo fluorescence of chlorophyll *a* following the experimental heatwave, grouped according to the dispersal treatments (phytoplankton: P- and P+; zooplankton: Z- and Z+) and coloured according to the heatwave treatment (H- and H+).  $N=5$  for each treatment combination per day. Solid lines represent fitted linear models (error bands: 95% confidence intervals) to visualise temporal trends. Based on linear mixed-effects models, recovery in the H+ treatments after the heatwave was enhanced by P+ (LMEM: significant day × H+ × P+Z-,  $p < .05$ , Table 3).

zooplankton phenology (Huber et al., 2010). In our study, the period of experimental heatwave coincided with a 'clear-water phase' in all treatments, that is, a trophic cascade where zooplankton increase leads to phytoplankton decrease to the point zooplankton likely becomes food-limited (Lampert et al., 1986). This clear-water phase was indicated by the general decrease in POC and Chl *a* fluorescence during the period of the experimental heatwave. Average POC concentration reached minimum values ( $0.046 \pm 0.012$  and  $0.045 \pm 0.014$  mg C L<sup>-1</sup> in H- and H+) by the end of the heatwave period, representing values below the threshold ( $0.05$  mg C L<sup>-1</sup>) where food limitation is likely to occur in *Daphnia* (Gliwicz, 1990). Furthermore, zooplankton biomass also decreased in the first part of the recovery period even in the H- treatments (Figure S7). Altogether, these lines of evidence suggest that the negative effect of elevated temperature was amplified by starvation of key consumers. The lack of egg-carrying females even in the control (i.e., H-) mesocosms further indicated that *Daphnia* did not have sufficient food supply to invest into reproduction. While the experimental heatwave clearly affected population dynamics of cladocerans, it had a weaker impact on copepod biomass (marginally significant negative effect), possibly because copepods have a broader diet which includes rotifers and ciliates (Adrian & Schneider-Olt, 1999; Brandl, 2005). Copepods are also more buffered against starvation due to their greater ability to accumulate storage lipids (Brett et al., 2009; Lampert & Muck, 1985). Taken together, these findings also indicate that copepods may be generally more robust to temperature fluctuations than cladocerans.

The decrease of crustacean zooplankton in the H+ treatments resulted in elevated phytoplankton biomasses due to weakened top-down control, which occurred with a time lag at the end of the experiment. H+ was associated with the dominance of green algae, which are superior competitors under warm, nutrient-rich conditions. Small-sized green algae (*Scenedesmus* gr. *Acutodesmus*, *Monoraphidium minutum*, *Ankyra* sp.) likely benefited from nutrient-rich conditions once released from grazing pressure. We cannot exclude that the cladoceran decline released herbivorous protists from competition, compensating for reduced crustacean zooplankton grazing on phytoplankton. However, the heatwave had only a marginally significant negative effect on copepods, the main predators of ciliates and large phytoplankton (Sommer & Sommer, 2006). Therefore, it is likely that predation pressure on microzooplankton did not change substantially. Moreover, the biomass of algalivorous ciliates collapsed during the heatwave in all treatments, and the ciliate community shifted towards the dominance of benthic and primarily bacterivorous taxa with low abundances (E. Mironova, personal observation). Therefore, it is unlikely that microzooplankton could significantly compensate for the reduced grazing pressure on phytoplankton.

Phytoplankton taxon richness responded much stronger to dispersal than of zooplankton, which reflected the richness differences in the regional dispersal inocula. The richness and abundance of introduced zooplankton cannot be considered low, as it fell in the ranges observed in studies of natural dispersal and colonisation rates

(Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel et al., 2008). Still, a single dispersal event did not provide a buffering effect on zooplankton biomass. In contrast, phytoplankton dispersal enhanced the growth of phytoplankton biomass (as estimated by Chl-*a* fluorescence) following the heatwave. However, this was only observed for a limited period (ca. 2 weeks) and only in the phytoplankton dispersal treatment without zooplankton dispersal (H+ × P+Z-). Besides, by the end of the experiment, species originally initially present in the local (i.e., Lake Lunz) community dominated even in the phytoplankton dispersal treatments.

A possible explanation for the limited effect of dispersal on biomass resistance and recovery may be related to the timing of the experimental dispersal manipulations. Colonisation success depends on arriving at a window of opportunity, that is, empty niche space in the resident community (Clark & Johnston, 2011; Symons & Arnott, 2014; Thompson & Gonzalez, 2017). Generally, high levels of available resources in a local community increase the opportunity for successful invasion (Davis et al., 2000). By the time of the dispersal manipulation, experimental plankton communities were strongly consumer-controlled, and high zooplankton grazing depleted phytoplankton during the period of the heatwave (i.e., even in the H- treatments). Therefore, zooplankters introduced from the regional pool faced intense competition for limited food resources, which may have reduced their establishment success in the mesocosms. Their chances would likely have been higher following the heatwave, after the decline in zooplankton and increase of phytoplankton biomass in the recipient communities. In contrast, phytoplankton dispersal took place when phytoplankton biomass in the recipient community was steadily declining. The heatwave may have also contributed to a successful establishment by suppressing their grazers (zooplankton) and thereby releasing available nutrients. While this might have contributed to the positive dispersal effect on phytoplankton biomass, our overall results suggest a high recovery capacity of local communities from the effects of a single heatwave independent of dispersal.

It is important to highlight to what extent our conclusions apply to natural ecosystems. Mesocosm experiments are powerful tools for studying the impacts of climate change by balancing experimental power with ecological realism (Kratina et al., 2012; Spivak et al., 2011; Stewart et al., 2013). Like other mesocosm studies, our experiment was limited in the number of replicates, with relatively low habitat complexity (e.g., no vertical gradients), and contained simplified pelagic communities (e.g., top predators such as fish were missing). However, plankton taxonomic diversity and composition were very similar to natural lakes in the region (Horváth et al., 2017), providing sufficient trophic complexity to investigate the effects of heatwaves on pelagic multi-trophic ecosystems. Our results also imply that the consequences of the relative timing of heatwaves and dispersal are likely to be substantial. The experimental setup consisted of a single dispersal event preceding the heatwave, thereby testing the effects of initial differences in species pools for spatial insurance. In natural ecosystems, dispersal events occur repeatedly over time, creating more opportunities for successful

colonisation (Havel & Shurin, 2004). Besides, we applied one heatwave in our experiment. However, disturbance frequency and intensity jointly affect the community and ecosystem recovery (Jacquet & Altermatt, 2020), and the effect of repeated pulse disturbances may accumulate over time (Villnäs et al., 2013). Consequently, recurring heatwaves may have more lasting effects on natural communities, whereas more frequent dispersal from the regional pool could provide stronger spatial insurance than we found in our study. These considerations warrant promising venues for future research.

Global climate warming is accelerating with more frequent and severe heatwaves in the aquatic (Woolway et al., 2021) and terrestrial realms (Perkins-Kirkpatrick & Lewis, 2020), with negative consequences for biodiversity, ecosystem functioning, and services. Our results illustrate that a relatively short heatwave can alter the main pathways of energy flow in pelagic ecosystems through differential responses across trophic groups. While total plankton biomass appeared to recover from the experimental heatwave in approximately 20 days, phytoplankton and zooplankton community compositions remained altered. This supports the observation that compositional recovery from pulse disturbances occurs less frequently than functional recovery (Hillebrand & Kunze, 2020). The altered trophic structure (i.e., top-down control) at the end of the experiment also suggests potentially long-lasting consequences for ecosystem functioning that our experiment could not reveal. We did not find strong evidence for spatial insurance. However, our results indicate that dispersal from the regional species pool can enhance biomass recovery at the level of primary producers, which may contribute to more stable levels of total community biomass over time. As a consequence of accelerating habitat loss and fragmentation, aquatic habitats become spatially more isolated (Davidson & Davidson, 2014; Hassall, 2014), which results in biodiversity loss (Horváth et al., 2019) and consequently lower buffering capacity against ongoing and future climate change. We therefore call for future studies in ecologically realistic settings and longer time scales to better understand the vulnerability of aquatic ecosystems to heatwaves.

#### AUTHOR CONTRIBUTIONS

C.F.V. and R.P. conceived the main study idea and coordinated the experiment. All authors contributed to practical works, including sampling, sample processing and laboratory works. Specifically, C.F.V., A.H.-E., A.A., E.M., D.S.M., L.S., I.T., C.P., M.M.B. and R.P. set up the experiment, C.P., E.M., D.S.M., E.S. and S.S. performed the chemical and nutrient analyses, and I.T. performed the daily fluorescence measurements. A.A. performed taxonomic identification and abundance estimation of phytoplankton, while L.S. performed the analysis of zooplankton with the input of C.F.V. and A.P. A.H.-E. and C.F.V. performed the data analyses with suggestions by P.K., H.T., E.S., S.S. and R.P. All authors contributed substantially to scientific discussions during the Transnational Access. C.F.V. wrote the first draft of the manuscript after which all authors provided feedback and edited subsequent versions.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.02v6wwq75>.

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