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## RESEARCH ARTICLE

# Legacy effects of fish but not elevation influence lake ecosystem response to environmental change

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**Abstract**

1. How communities reorganize during climate change depends on the distribution of diversity within ecosystems and across landscapes. Understanding how environmental and evolutionary history constrain community resilience is critical to predicting shifts in future ecosystem function.
2. The goal of our study was to understand how communities with different histories respond to environmental change with regard to shifts in elevation (temperature, nutrients) and introduced predators. We hypothesized that community responses to the environment would differ in ways consistent with local adaptation and initial trait structure.
3. We transplanted plankton communities from lakes at different elevations with and without fish in the Sierra Nevada Mountains in California to mesocosms at different elevations with and without fish. We examined the relative importance of the historical and experimental environment on functional (size structure, effects on lower trophic levels), community (zooplankton composition, abundance and biomass) and population (individual species abundance and biomass) responses.
4. Communities originating from different elevations produced similar biomass at each elevation despite differences in species composition; that is, the experimental elevation, but not the elevation of origin, had a strong effect on biomass. Conversely, we detected a legacy effect of predators on plankton in the fishless environment. *Daphnia pulex* that historically coexisted with fish reached greater biomass under fishless conditions than those from fishless lakes, resulting in greater zooplankton community biomass and larger average size.
5. Therefore, trait variation among lake populations determined the top-down effects of fish predators. In contrast, phenotypic plasticity and local diversity were sufficient to maintain food web structure in response to changing environmental conditions associated with elevation.

**KEYWORDS**

climate change, *Daphnia pulex*, historical contingency, local adaptation, resilience, temperature

## 1 | INTRODUCTION

The maintenance of critical ecosystem functions during climate change depends on how ecological communities respond to changing selective forces. Ecosystem models typically assume that community functional responses are resilient, and contemporary environmental conditions can predict function (Thuiller et al., 2005; Yates et al., 2018). However, historical contingencies at the population, community or ecosystem level may modulate responses to environmental change. The occurrence of legacy effects is attributable to differences in heritable trait variation (Willi et al., 2006), biodiversity (Isbell et al., 2011) and historical effects on abiotic conditions (Filbee-Dexter et al., 2018).

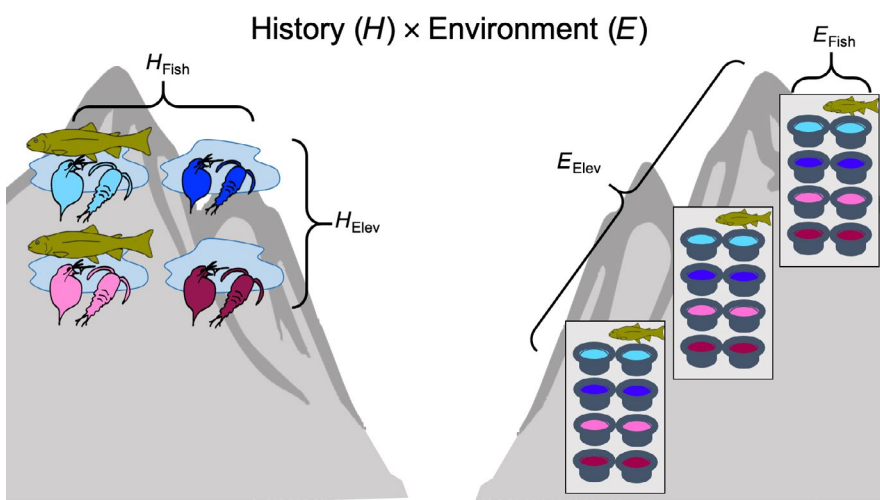
Within populations, responses to new environmental conditions are contingent on heritable trait variation, levels of plasticity and whether current genotypes are 'pre-adapted' to the new conditions due to co-tolerances (Christmas et al., 2016; Vinebrooke et al., 2004). Standing genetic variation determines the potential for adaptation to maintain population fitness in the face of environmental change (Barrett & Schluter, 2008; Bell & Gonzalez, 2009; Carlson et al., 2014). Past selection can constrain the response of organisms to novel conditions by limiting the range of phenotypic variation on which new selective forces can act (Cuddington, 2011). Within communities, changes in the relative abundance of species can stabilize ecosystem functioning during environmental change if species or genotypes that possess traits that match the new conditions are already present in the community (Derry & Arnott, 2007; Walker et al., 1999; Yachi & Loreau, 1999) or arrive via dispersal (Bell & Gonzalez, 2011; Symons & Arnott, 2013; Thompson & Shurin, 2012).

Communities arrayed along broad environmental gradients driven by latitude or elevation are ideal systems in which to test the roles of ecological and evolutionary history in influencing resilience to environmental change. Species composition and traits turnover along elevational gradients (e.g. Swenson et al., 2011; Symons & Shurin, 2016) and populations are often locally adapted to environmental conditions (e.g. Gonzalo-Turpin & Hazard, 2009). Natural gradients therefore contain the range of trait variability that underlies

community resilience to environmental change. Additionally, the steep abiotic gradients mean these communities are relatively close together, making experiments, such as whole-community transplantation, easier (Alexander et al., 2016).

In this study, we used plankton communities found in lakes with contrasting ecological and evolutionary histories due to differences in elevation and the presence of introduced fish predators. The introduction of fish has led to a large turnover in zooplankton species composition (Knapp et al., 2001), especially in high elevation lakes (Symons & Shurin, 2016). However, some zooplankton species are cosmopolitan and locally adapted to different lake environments (Miner et al., 2012). For example, introduced fish drove fixed genetic differences among populations of *Daphnia melanica* such that populations coexisting with fish show smaller body sizes and earlier reproduction (Fisk et al., 2007). Additionally, plastic responses to predator cues amplify the fixed genetic patterns (Latta et al., 2007). Furthermore, the level of plasticity in life-history traits is influenced interactively by elevation and fish presence (Cavalheri et al., 2019). The documented species turnover and local adaptation in zooplankton communities and populations of Sierra Nevada lakes allow us to test the role of environmental history in the resilience of communities to environmental change.

We transplanted plankton with different histories to two ecologically relevant stressors: climate change, by using three transplant elevations encompassing an 8°C temperature gradient, and predation by a non-native fish (Figure 1). These environmental treatments are especially relevant because alpine aquatic ecosystems are particularly affected by climate warming and fish introductions (Bradley et al., 2004; Hauer et al., 1997; Sarnelle & Knapp, 2005; Schindler & Parker, 2002). We used this design to ask the following questions: (a) Are communities locally adapted to their environment? We expected that local adaptation should lead communities to produce the greatest biomass in the experimental conditions that match their environment of origin. That is, communities that historically coexisted with fish should maintain a higher abundance in the presence of fish than fish-naïve communities (e.g. Walsh et al., 2016), and high elevation communities should be most productive under high



**FIGURE 1** We conducted a fully factorial experiment crossing community history ( $H$ ) and the contemporary environment ( $E$ ). Plankton communities were collected from lakes at two elevations ( $H_{Elev}$ ), with and without fish ( $H_{Fish}$ ) and exposed to different environments at different elevations ( $E_{Elev}$ ) with and without fish in the mesocosms ( $E_{Fish}$ ). The colours on the Environment side correspond to the community histories. Each factor was fully crossed for a total of 24 treatments each replicated five times for a total of 120 mesocosms, 40 at each site ( $E_{Elev}$ )

elevation conditions (i.e.  $H_{\text{Elev}} \times E_{\text{Elev}}$ ). (b) Does response to one selective agent influence resilience to another? Communities are considered resilient if function is predicted by current environmental conditions alone and not affected by historical conditions (Hawkes & Keitt, 2015). We expected to find interactive effects of past selection by fish and elevation and the experimental conditions. For example, both fish and high temperatures favour smaller-bodied taxa (Brooks & Dodson, 1965; Horne et al., 2015); therefore, we expect plankton from lakes containing fish might respond differently to translocation across elevations than those from fishless lakes (i.e.  $H_{\text{Fish}} \times E_{\text{Elev}}$ ; Loewen et al., 2020; Symons & Shurin, 2016). We examined functional (size structure, effects on lower trophic levels), community (zooplankton composition and abundance) and population (individual species abundance) responses to determine how historical conditions modulate the impact of environmental change on aquatic ecosystems.

## 2 | MATERIALS AND METHODS

### 2.1 | Experiment overview

We collected communities of plankton and micro-organisms from lakes that varied in their environment due to elevation, and history of fish stocking. We transplanted them to different elevations with and without fish (Figure 1). Thus, the treatments were as follows: (a) History of elevation ( $H_{\text{Elev}}$ ): source community elevation [two levels, sub-alpine (average of 2,591 m) and alpine (average of 3,252 m)] (b) History of fish ( $H_{\text{Fish}}$ ): source community fish presence (two levels, +/-) (c) Experimental elevation treatment ( $E_{\text{Elev}}$ ): transplant elevation [three levels, montane (1,200 m), sub-alpine (2,149 m) and alpine (3,093 m)] and (d) Experimental fish treatment ( $E_{\text{Fish}}$ ): fish presence in the transplant environment (two levels, +/-). We used three transplant elevations ( $E_{\text{Elev}}$ ) so that communities from each elevation were exposed to a lower elevation to simulate the directional environmental change these communities are predicted to experience. This results in a total of 24 treatments, each replicated five times for a total of 120 mesocosms, 40 at each experimental elevation (Figure 1).

This experimental design allows us to partition the variance in the response of community and population variables to the present and historical environment and their interaction. We modelled the response of plankton species and aggregate community metrics to the experimental treatments as a function of the current environmental conditions in the experiment ( $E$ ), the ecological and evolutionary history of the community from which they originated ( $H$ ) and the interaction between the two ( $E \times H$ ), where  $E = E_{\text{Fish}} + E_{\text{Elev}} + E_{\text{Fish}} \times E_{\text{Elev}}$  and  $H = H_{\text{Fish}} + H_{\text{Elev}} + H_{\text{Fish}} \times H_{\text{Elev}}$ .  $E_{\text{Fish}}$  is the presence of fish in the mesocosms,  $E_{\text{Elev}}$  is the elevation of the experimental environment and  $E_{\text{Fish}} \times E_{\text{Elev}}$  is the interactive effects of contemporary conditions. History ( $H$ ) represents the conditions in the community of origin, where the presence or absence of fish predators in the source community is  $H_{\text{Fish}}$ , and its elevation is  $H_{\text{Elev}}$ . Each term

represents a treatment or interaction in the mixed-effects model table. The two-way interaction terms  $E \times H = E_{\text{Fish}} \times H_{\text{Fish}} + E_{\text{Fish}} \times H_{\text{Elev}} + E_{\text{Elev}} \times H_{\text{Fish}} + E_{\text{Elev}} \times H_{\text{Elev}}$  describe the eco-evolutionary interactions or the impact of the selection history of the community on the outcome of contemporary ecological interactions. For the rest of this paper, we refer to the current experimental environment as the 'environmental' effects and the ecological/evolutionary history as 'history' effects.

### 2.2 | Experimental set-up

We established mesocosm arrays at three elevations ( $E_{\text{Elev}}$ ,  $n = 40$  for a total of 120 mesocosms), located at three University of California Natural Reserves [White Mountain (WM), 3,093 m, 37.499044, -118.171597; Sierra Nevada Aquatic Research Lab (SNARL), 2,149 m, 37.613240, -118.830226; and the Sierra Nevada Research Institute (SNRI), 1,200 m, 37.540008, -119.657737]. Each site was at least 3 km away from a lake, reducing the chance of overland plankton dispersal into the mesocosms. Using mesocosms at three elevations, we allowed for natural seasonal and daily air thermal variation and other environmental differences associated with elevation, such as vegetation cover. We used three transplant elevations so that communities from each elevation were exposed to higher temperatures than the source lakes to simulate climate change (Figure 1). We filled the mesocosms (1,280 L in volume, 2 m in diameter and 1 m in depth) with well water for the low and high elevation sites and a local stream (filtered through 63- $\mu\text{m}$  mesh) for the sub-alpine site, due to differences in accessibility to water sources at each site. Initial water chemistry data are found in ESM Table S4. We covered the tanks immediately with 60% shade cloth to reduce evaporation and eventually the UV stress on trout. Also, we placed three 15 cm long, 5 cm diameter PVC tubes in each tank as a refuge for fish. We installed temperature loggers on the bottom of three haphazardly chosen tanks at each location to measure the water temperature at 2-hr intervals.

Next, we selected lakes that varied in their history of fish presence and elevation to collect the four different types of source communities (sub-alpine  $\times$  alpine, fish  $\times$  fishless; ESM Table S1). We collected plankton communities from three lakes within each of the four source community types and mixed communities of the same type to create diverse inocula. Nearly all lakes at these elevations are naturally fishless. Stocking of fish started in the early 1900s, and the populations are now self-sustaining (Knapp & Matthews, 2000) resulting in communities that have differed in the presence or absence of fish predators for ~100 years. Lakes at lower elevations have warmer temperatures and higher dissolved organic carbon (DOC) concentrations from more densely vegetated watersheds, whereas higher elevation lakes are colder and nutrient-poor (Piovia-Scott et al., 2016; Sadro et al., 2012; Symons et al., 2019).

We collected plankton at the deepest point in the lake by drawing a 30 cm diameter, 63  $\mu\text{m}$  mesh zooplankton net through the water column, starting 1 m above the lake bottom. We collected the volume

of zooplankton required to inoculate each mesocosm at ambient lake density (ESM Table S2). We placed the zooplankton into surface lake water collected in 2 L Nalgene for transport. We combined the plankton samples from the three lakes in a 20 L bucket and stored them at  $-4^{\circ}\text{C}$  (refrigerator) until mesocosm inoculation. Visual inspection suggested zooplankton survival was high. All zooplankton were added to the mesocosms within 9 days of collection (4–12 July 2014). Also, we collected 6 L of sediment with shovels at  $\sim 0.5$  m water depth at each lake, which we combined, and placed in containers to distribute at each mesocosm array. We chose three lakes in each source community category to ensure that we sampled a diversity of species representative of these conditions and included sediment to ensure that resting stages would be present in the inoculum. We inoculated zooplankton, phytoplankton (*via* the collected lake water) and sediment into the mesocosms at each location over 9 days (4–12 July 2014). We preserved four aliquots of each source community inoculum with 70% ethanol for later enumeration. The plankton communities had nearly 1 year to establish in the mesocosms. The communities remained largely similar to the inocula in the second year when comparing communities that experienced the same environment to which they were historically exposed (e.g. compared  $H_{\text{Elev}} = \text{alpine}$  inocula to  $H_{\text{Elev}} = \text{alpine}$  &  $E_{\text{Elev}} = \text{alpine}$  communities at the beginning of the second year, ESM, Figure S2).

We established the fish presence treatment in the mesocosms ( $E_{\text{Fish}}$ ) by adding five juvenile Rainbow Trout *Oncorhynchus mykiss* between 13 and 16 May 2015 at the montane and sub-alpine elevations. We chose Rainbow Trout because lakes in the Sierra Nevada contain stocked populations of primarily Rainbow Trout and Brook Trout—*O. mykiss* and *Salvelinus fontinalis* (Knapp et al., 2001). Fish were added to the alpine elevation tanks on 4 June 2015, after the mesocosm water melted. We obtained triploid female juvenile Rainbow Trout from the same hatching from Thomas Fish Company. After 24-hr acclimation to ambient temperature at each elevation, we added five juvenile fish (length of  $5.4 \pm 0.13$  cm) to the tanks. Fish were monitored at one location (sub-alpine location, SNARL) every other day for signs of distress. At the other two sites, we monitored fish after stocking and more sporadically throughout the experiment as researchers were not continually present throughout the experiment. Fish survival across the experiment was 88% overall; 67% at low elevation, 100% at mid-elevation and 97% at high elevation. We excluded five tanks in the  $E_{\text{fish}}$  treatment from our analyses as they did not contain any fish at the end of the experiment. Our treatment of fish complied with ethical regulations, approved by IACUC at UC San Diego and UC Santa Barbara. The treatments were replicated 5 $\times$  for a total of 120 units.

### 2.3 | Mesocosm sampling

We sampled the mesocosms monthly for 4 months following the introduction of fish to quantify water chemistry, zooplankton community composition and abundance, and chlorophyll-*a* (a proxy for phytoplankton biomass). We sampled the zooplankton community

using an integrated tube sampler. We collected 20 L from haphazardly chosen locations from each mesocosm, condensed the sample on a 63- $\mu\text{m}$  mesh filter and preserved it with 70% ethanol. We counted zooplankton samples using a protocol designed to estimate the abundance of common species and detect rare species: we identified 200 individuals to the lowest taxonomic resolution possible (generally to species for crustaceans and genus for rotifers) without counting more than 50 individuals of each species towards the total. We scanned the remainder of the sample to detect rare species. While Miner et al. (2013) showed that large-bodied unmelanized *Daphnia* 'pulex-type' species is *D. melanica* using mtDNA sequencing, we classified unmelanized 'pulex-types' as *Daphnia pulicaria* following (Fisk et al., 2007; Knapp & Sarnelle, 2008; Latta et al., 2007).

To calculate zooplankton community biomass, we measured the body length of 15 individuals of the three most common species in each sample. For rare species, we used the average body length of all measured individuals of that species. Body size measurements were done only on the final set of samples (September); for these samples, we used the mesocosm-specific measurements to calculate biomass and mean body length, but for all other sample dates, we used the average length of each species across all treatments. We then used published length–weight regressions to estimate zooplankton biomass (Dumont et al., 1975; McCauley, 1984). To calculate the average body size, we used an abundance-weighted mean length. Community biomass was determined by summing the population biomasses of each species.

To characterize the environment in our mesocosms, we measured a series of water chemistry variables. First, total nitrogen (TN) and total phosphorus (TP) were measured by filtering water through 63- $\mu\text{m}$  mesh, collecting it in triple-rinsed 20 ml high-density polyethylene (HDPE) bottles, then preserving it with  $\text{H}_2\text{SO}_4$  to a pH < 2 and storing it at  $-4^{\circ}\text{C}$  until later analysis. TN and TP (mg/L) were measured using an auto-analyser (LaChat QuikChem 8500, persulfate digestions, LaChat). We collected DOC samples by filtering water through precombusted glass fibre filters (Whatman GF/F, pore size 0.45  $\mu\text{m}$ , Whatman) into triple-rinsed 20 ml glass vials and preserved with HCl to a pH < 2. DOC (mg/L) was measured using a total organic carbon analyser (TOC-V CSN, Shimadzu Scientific Instruments). Chlorophyll-*a* concentration (chl-*a*,  $\mu\text{g/L}$ ), a proxy for phytoplankton biomass, was measured in a known volume of water filtered through a GF/F that was frozen before processing. Chl-*a* concentration was measured using a Turner Trilogy fluorometer (Turner) following a 24 hr  $-4^{\circ}\text{C}$  methanol extraction. We added water ( $\sim 200$  L) to each mesocosm after sampling to replenish evaporated water. The evaporation rate was similar between the three locations.

### 2.4 | Statistical analyses

We modelled total zooplankton community biomass, chl-*a*, average body size and total abundance of zooplankton using a linear mixed-effects model. The fixed effects included in the model are  $E_{\text{Fish}}$  and  $E_{\text{Elev}}$  (the contemporary impacts of fish and elevation),  $H_{\text{Fish}}$  and  $H_{\text{Elev}}$

(the presence of fish and elevation of the source environment) and the two-way interactions among them. Here we present models with only two-way interactions and main effects to simplify interpretation. We show the results of the analysis with all higher-order interactions in ESM Table S4. Sample date and mesocosm were included as random effects to account for temporal pseudoreplication. Variables were  $\log(x)$ , or  $\log(x + 1)$  transformed to improve normality and homoscedasticity. We ran models using the function `LME` in the `NLME` package, and we assessed the significance of fixed effects terms using the ANOVA function (Pinheiro et al., 2016). All  $p$  values for LMEs were corrected for multiple comparisons using the Benjamini and Hochberg (2000) false discovery rate correction. For individual species abundance responses, data transformations were unable to improve normality as species responses included many zeros. In these cases, we modelled species responses using a permutational LME approach followed by Benjamini–Hochberg false discovery rate correction. We examined the effect of treatments on *D. pulicaria* body size using ANOVA as we only measured individuals on one sample date.

To examine how community structure responded to treatments we used a permutational multivariate analysis of variance (multivariate PERMANOVA) based on a Bray–Curtis distance matrix (pairwise.adonis2 function in the `PAIRWISEADONIS` package) on the species biomasses at the end of the experiment with the four experimental factors and all two-way interactions as the predictors. Pairwise.adonis2 uses the adonis function in the `VEGAN` package (Oksanen et al., 2019) and uses Bonferroni corrections for multiple comparisons. To visualize changes in species composition, we used non-metric multidimensional scaling (nMDS), though this visualization is not mathematically a perfect match to the multivariate PERMANOVA statistical results.

We conducted all analyses in R (R Core Team, 2016).

## 3 | RESULTS

### 3.1 | Initial conditions

Mesocosms filled with water at different elevations varied in water chemistry (see ESM). Nutrients (TN and TP) were uniformly low at all three sites, but DOC was highest at the low elevation montane site, and conductivity was highest at sub-alpine elevation (ESM Table S4). After sediment and plankton were added to the mesocosms and the mesocosms were left to over-winter, the water chemistry changed (ESM Table S5). More detrital inputs to the mesocosms at low elevation resulted in higher nutrient and DOC concentrations over time (ESM Figures S3–S6). These patterns are consistent with observed changes in the water chemistry of natural lakes in the Sierra over natural elevation gradients (Symons & Shurin, 2016), which is why we describe this treatment as an ‘elevation’ treatment instead of a ‘temperature’ treatment. In addition, climate warming will increase lake water temperatures in addition to causing upward elevational expansion of vegetation and greater

DOC loading into aquatic systems (Walther et al., 2005). Our elevation treatment is, therefore, a relatively faithful representation of the effects of climate change at different elevations.

### 3.2 | Treatments

Temperature differed among the three elevations (linear mixed model,  $p < 0.001$ ). The montane, sub-alpine and alpine mesocosms averaged 19.2, 16.7 and 13.4°C, respectively (ESM Figure S7). The community inoculum differed among lake types (ADONIS,  $p < 0.001$ , ESM Figure S1). We found 6 of the 11 inoculum species in all lake types.

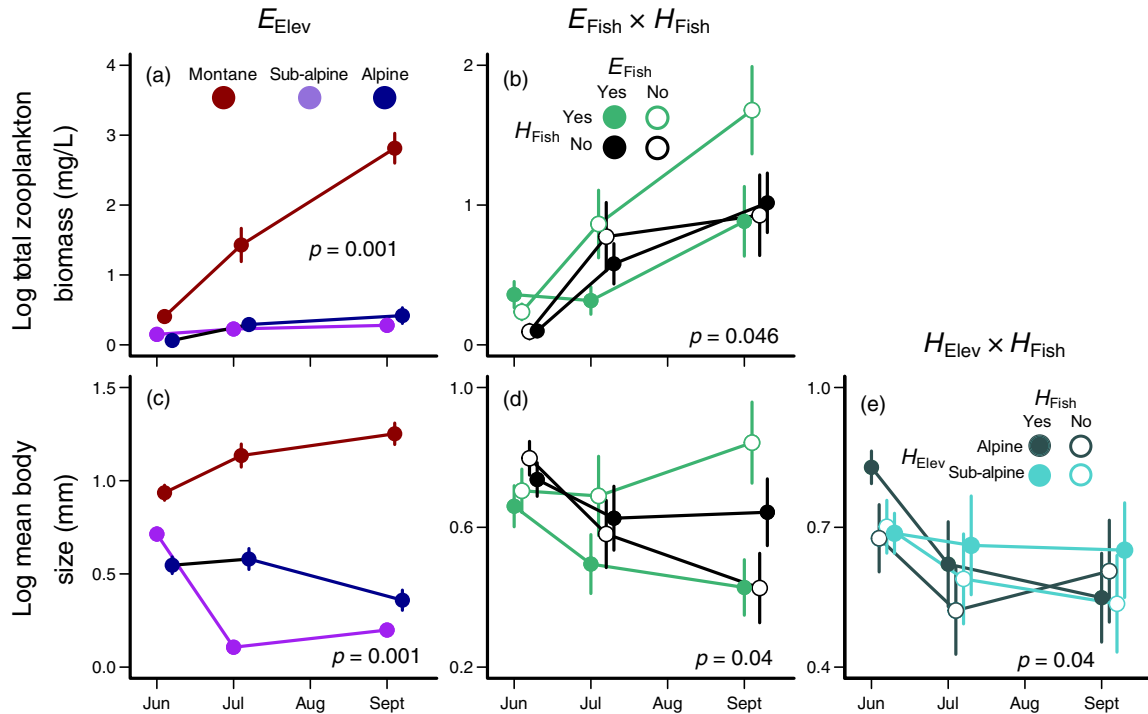
### 3.3 | Zooplankton community structure

Both the current environment ( $E$ ) and the ecological/evolutionary history ( $H$ ) influenced zooplankton community structure. Regardless of the origin, communities in montane mesocosms had higher biomass and larger-bodied zooplankton than alpine and subalpine communities (Environment effect, Figure 2a,c). Communities that originated from lakes containing fish showed different responses to the presence or absence of fish in the experiment in terms of biomass and size structure. Communities previously coexisting with fish increased in biomass compared to other communities when fish were absent from the mesocosms (Environment  $\times$  History interaction, Figure 2b). We examined species responses, and the community biomass change was driven by changes in the biomass of the ecologically dominant species, *D. pulicaria* (Environment  $\times$  History interaction, Figure 3c), whereas other species did not show a significant response to treatments.

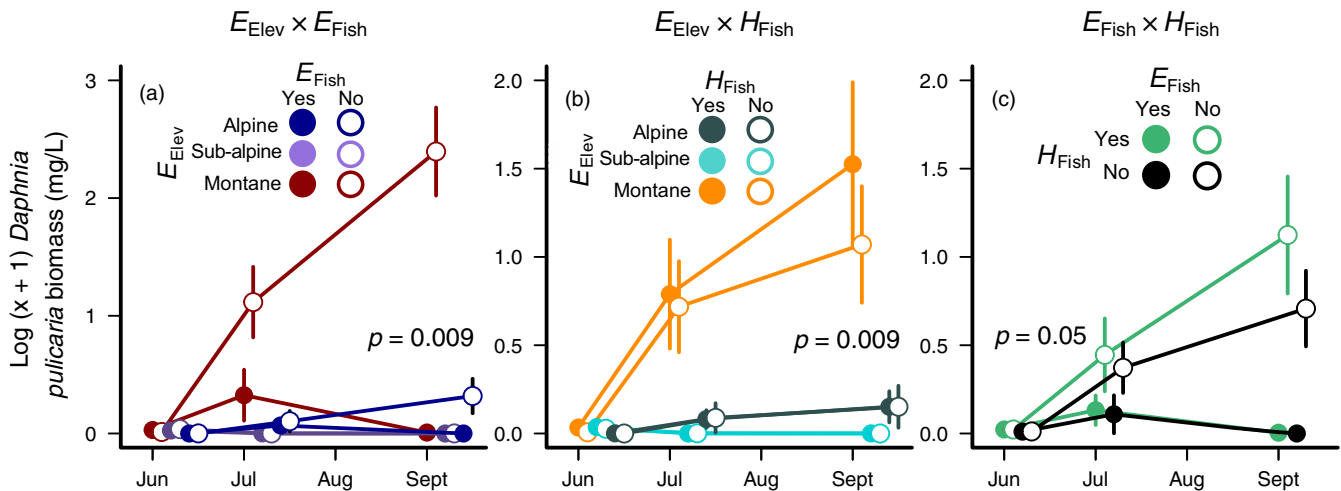
The shift in total community biomass (Figure 2) was not due to a difference in total abundance (Table 1), but instead due to a change in the mean body size of the community (Environment  $\times$  History interaction, Figure 2d; Table 1). Large bodied species, including *D. pulicaria*, were more abundant in communities with a history of fish in the treatments without fish present (Environment  $\times$  History interaction Figure 3c). The biomass, abundance and average body size of zooplankton were greatest at the lowest  $E_{\text{Elev}}$  elevation (Environment effect, Figure 2a,c; Table 1). History also influenced body size, and we found a significant interaction between  $H_{\text{Elev}}$  and  $H_{\text{Fish}}$ , where in June, mean body size was greatest in communities originating from high elevation fishless lakes (History effect, Figure 2e).

The response of *D. pulicaria* explains much of the zooplankton community response to the history and environment treatments. The environment ( $E_{\text{Fish}}$  and  $E_{\text{Elev}}$ ) had the greatest impact on *D. pulicaria*, which was excluded from tanks with fish at the end of the experiment and was most abundant at low elevations (Environment effect, Figure 3a; Table S3). The weaker  $E_{\text{Fish}}$  effect at the alpine site may be due to the shorter period of time fish were present in the  $E_{\text{Fish}}$  + treatment because their addition was delayed by a snowstorm (ESM, Table S3).  $H_{\text{Fish}}$  had the largest





**FIGURE 2** The response of (a, b) total zooplankton biomass and (c–e) mean community body size to experimental treatments in 2015. Biomass and mean community body size were calculated with species mean size in June and July, and mesocosm-specific sizes in September. Error bars represent standard error. Points are offset along the x-axis for clarity. Only significant results are presented; therefore, data are averaged across all other effects for each panel



**FIGURE 3** The response of *Daphnia pulicaria* biomass to experimental treatments in 2015. Biomass and mean community body size were calculated with species mean size in June and July, and mesocosm-specific sizes in September. Error bars represent standard error. Points are offset along the x-axis for clarity. Only significant results are presented; therefore, data are averaged across all other effects for each panel

impact on *D. pulicaria* biomass at the montane site, where populations originating from lakes containing fish populations obtained higher biomass (History  $\times$  Environment interaction, Figure 3b; Table S3), though their individual body size was not affected by  $H_{Fish}$  (ANOVA,  $p = 0.78$ ). Finally, *D. pulicaria* biomass was highest in populations with a history of fish exposure in the tanks when fish were absent (History  $\times$  Environment interaction, Figure 3c; Table S3).

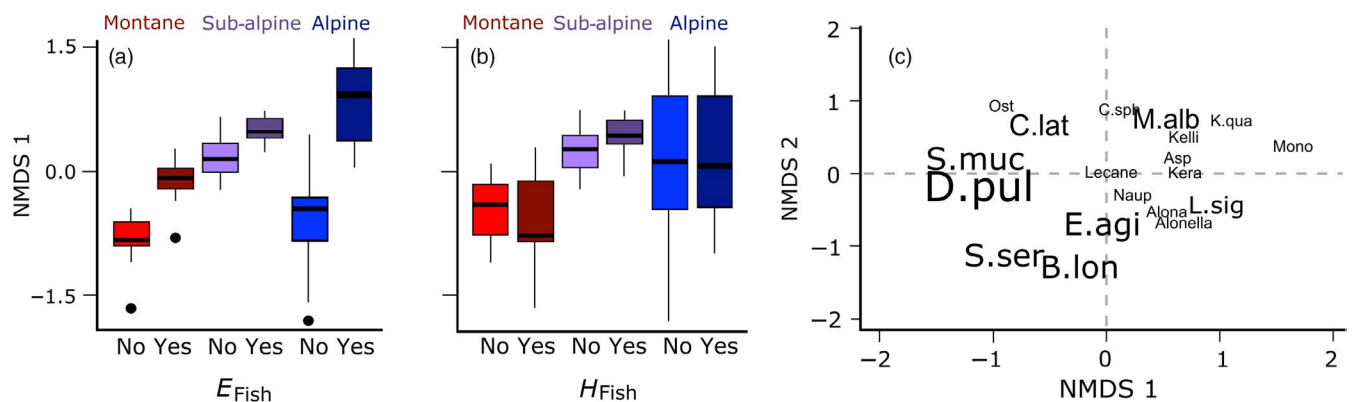
### 3.4 | Zooplankton species composition

Regardless of their origin, communities diverged between the six mesocosm environments ( $E_{Fish} \times E_{Elev}$ , Environment effect, Figure 4a). However, we found evidence that ecological/evolutionary history determined the response of zooplankton communities to contemporary environmental conditions (ADONIS, Table 1; Figure 4). The effect of  $H_{Fish}$  interacted with  $E_{Elev}$ , although the shift

**TABLE 1**  $F$  statistics and  $p$  values for mixed-effects models and  $r^2$  and  $p$  values for ADONIS permutational analysis of community composition at the end of the experiment.  $p$  values for were corrected for multiple comparisons using the Benjamini and Hochberg (2000) false discovery rate correction

Test:	Community biomass		Abundance		Average body size		Chlorophyll- <i>a</i>		<i>Daphnia pulicaria</i> biomass		Community composition	
	LME		LME		LME		LME		Randomization		Permutation	
	$F$	$p$	$F$	$p$	$F$	$p$	$F$	$p$	$F$	$p$	$r^2$	$p$
$E_{\text{Fish}}$	3.59	0.20	<0.01	0.99	16.70	<b>0.007*</b>	5.97	0.067	12.82	<b>0.009*</b>	0.06	<b>0.001*</b>
$E_{\text{Elev}}$	74.5	<b>0.001*</b>	36.84	<b>0.007*</b>	170.65	<b>0.001*</b>	16.16	<b>0.001*</b>	13.43	<b>0.009*</b>	0.14	<b>0.001*</b>
$H_{\text{Fish}}$	1.87	0.44	0.65	0.91	0.02	0.97	0.18	0.967	3.62	0.09	0.01	0.17
$H_{\text{Elev}}$	0.01	0.97	0.04	0.97	0.01	0.97	1.92	0.436	0.91	0.40	0.01	0.10
$E_{\text{Fish}} \times E_{\text{Elev}}$	0.01	0.99	0.18	0.97	1.16	0.73	2.02	0.436	10.16	<b>0.009*</b>	0.07	<b>0.001*</b>
$E_{\text{Fish}} \times H_{\text{Fish}}$	6.35	<b>0.046*</b>	0.09	0.97	7.24	<b>0.04*</b>	0.29	0.967	4.85	<b>0.05*</b>	0.01	0.05
$E_{\text{Fish}} \times H_{\text{Elev}}$	1.43	0.58	2.01	0.44	0.35	0.97	0.08	0.967	0.70	0.42	0.01	0.05
$H_{\text{Fish}} \times E_{\text{Elev}}$	0.13	0.97	0.34	0.97	0.79	0.92	0.39	0.967	5.08	<b>0.009*</b>	0.02	<b>0.01*</b>
$H_{\text{Fish}} \times H_{\text{Elev}}$	0.03	0.97	0.29	0.97	7.54	<b>0.04*</b>	4.4	0.141	1.25	0.35	0.01	0.07
$H_{\text{Elev}} \times E_{\text{Elev}}$	1.43	0.97	0.45	0.97	0.12	0.97	0.49	0.967	1.40	0.35	0.02	0.09

\*Bold values denote significance at  $p < 0.05$ .



**FIGURE 4** NMDS results highlighting significant predictors of community composition. (a)  $E_{\text{Fish}} \times E_{\text{Elev}}$  mesocosm elevation is denoted by colour, red, purple and blue representing montane, sub-alpine and alpine sites, respectively. Lighter colours denote mesocosms with fish. (b)  $H_{\text{Fish}} \times E_{\text{Elev}}$  treatments are indicated as in panel (a) but represent source habitat conditions instead of environmental conditions. (c) Species loadings are shown, with the size of the text scaled to the average body size of each taxon. Species depicted are *Alona* spp., *Alonella* spp., *Asplanchna* spp. (*Asp*), *Bosmina longirostris* (*B.lon*), *Ceriodaphnia laticaudata* (*C.lat*), *Chydorus sphaericus* (*C.sph*), *Daphnia pulicaria* (*D.pul*), *Eucyclops agilis* (*E.agi*), *Kellicottia* spp. (*Kelli*), *Keratella* spp. (*Kera*), *Keratella quadrata* (*K.qua*), *Lecane* spp., *Leptodiptomus signicauda* (*L.sig*), *Macrocyclus albidus* (*M.alb*), *Monostyla* spp. (*Mono*), nauplii (*Naup*), Ostracoda (*Ost*), *Scapholeberis mucronata* (*S.muc*) and *Simocephalus serrulatus* (*S.ser*). See ESM Figure S9 for results in ordination space

in multivariate space is low (History  $\times$  Environment interaction, Figure 4b). The presence of fish in the mesocosms ( $E_{\text{Fish}}$ ) caused a more substantial directional change in zooplankton composition than the presence of fish in the lakes of origin ( $H_{\text{Fish}}$ ), where  $E_{\text{Fish}}$ (+) caused a large shift towards smaller-bodied species (Figure 4a,c).

### 3.5 | Phytoplankton biomass

Chlorophyll-*a* throughout the experiment was highest at low elevation ( $E_{\text{Elev}}$  = montane) and was unaffected by other treatments

or interactions, though tended to be higher in the presence of fish (NLME,  $E_{\text{Fish}}$   $p = 0.06$ ,  $E_{\text{Elev}}$   $p = 0.001$ ; Table 1).

## 4 | DISCUSSION

We found that the impact of contemporary perturbations on lake plankton communities was dependent on the history of long-term selection on species and populations. Communities transplanted to different elevations and predation regimes were resilient to changes in elevation but retained a legacy effect of predation. Zooplankton originating from lakes with fish reached higher total community biomass in



the absence of fish than communities originating from fishless lakes. This pattern was primarily driven by changes in *D. pulicaria* biomass, suggesting fish select for a faster intrinsic growth rate in *Daphnia* populations, resulting in larger population sizes. The history of fish predation played a more significant role in contemporary community structure and response to environmental change than the history of elevation despite the considerable variation in temperature and other conditions among lakes at different elevations. Our experiment indicates that different selective environments impose changes in populations and communities that determine their resilience to changing conditions. Long-term evolutionary and ecological changes therefore shape the response of ecosystems to contemporary environmental perturbations (Bell & Gonzalez, 2009; Derry & Arnott, 2007; Lajoie & Vellend, 2018).

We hypothesized that communities originating from different elevations would be locally adapted and therefore exhibit lower fitness when transplanted to different climate zones. However,  $H_{\text{Elev}}$  showed no significant independent effect on our response variables or interactions with any of the  $E$  treatments (Table 1). This result was surprising given the substantial differences in elevation (and therefore temperature and nutrients) among the lakes from which our plankton communities originated (ESM Table S1). Though we cannot exclude the possibility that elevation effects take more than two growing seasons to manifest or that the novel constraints of the mesocosms environment masked  $H_{\text{Elev}}$ , the communities responded similarly to treatments regardless of their elevational history (Table 1). One possible explanation may be that zooplankton show high phenotypic plasticity in responses to temperature variation (Cavalheri et al., 2019; Mitchell et al., 2000). Populations experience broad interannual, seasonal and vertical within-lake variation in temperature, and therefore may have evolved broad thermal niches (Miner et al., 2005). Therefore, our results indicate that zooplankton populations in the Sierra are resilient in the face of environmental change associated with elevation but more constrained in their response to fish predation. Another possibility is that zooplankton show large genetic diversity in thermal tolerances within a lake so that transplanting communities to different elevations resulted in dominance by either warm- or cold-adapted genotypes. Turnover in genetic composition within a season can maintain population fitness as temperatures rise and fall (e.g. Bergland et al., 2014); therefore, local genetic diversity may have resulted in the similar response to temperature change by communities originating from lakes in different climates. Similarly, turnover in species composition and increases in formerly rare species may have allowed the communities to maintain biomass and trait structure. In this region, many taxa occur along the entire elevational gradient (e.g. *Keratella* sp., *Leptodiptomus signicauda*, *Bosmina longirostris*), allowing communities that begin with different compositions to converge during the experiment in the absence of immigration. High local diversity in thermal responses among species may therefore confer community resilience to warming.

Our results indicate that past selection by predators leaves a stronger imprint on contemporary response to predation than a history of different climate conditions. We found that past coexistence with fish increased the biomass of *D. pulicaria* above naturally fishless populations when growing in fishless conditions. This result is particularly important

because *Daphnia* spp. play an ecologically dominant role in lake food webs as preferred prey of fish and strong grazers of algae (Carpenter et al., 1987), though we found no differences in chl-*a* (Table 1). We expected weaker top-down control in communities with a history of fish exposure due to local adaptation and the evolution of prey defence traits (Ingram et al., 2012). However, fish and fishless lake plankton communities were equivalent in terms of zooplankton size, and biomass in the presence of experimental fish exposure, indicating that past coexistence with fish did not increase abundance when predators were present. Instead, the strongest effect of coexisting with fish was on the growth rate of *Daphnia* populations in environments when fish were absent. Fish can select for changes in *Daphnia* life-history parameters that result in increased population growth rates (earlier reproduction and smaller body size; Riessen, 1999), as is documented in *D. melanica* in response to fish in Sierra Nevada lakes (Fisk et al., 2007). This selection is driven by a fish-induced reduction in survival to maturity, causing *Daphnia* to reproduce earlier and increase clutch size, in an example of counter gradient variation where phenotypic variation counteracts the environmental (predation) effects. Indeed, another *Daphnia* species (*Daphnia ambigua*) from lakes with higher planktivory show a greater  $r$  than those from low planktivory lakes in controlled laboratory experiments (M. R. Walsh & Post, 2011). Similarly, we would expect that *Daphnia* with historic exposure to fish should have higher population growth rates in the presence of fish than naive *Daphnia*. However, *Daphnia* did not coexist with the fish at the end of the experiment regardless of their history (Figure 3c). It is likely that the mesocosm environment does not provide enough refuge for *Daphnia* to survive regardless of their population growth rate. Our finding shows that this type of legacy effect (sensu Cuddington, 2011) can persist over many generations (the 2 years of our experiment), and is sufficiently strong to alter zooplankton biomass and size structure within a community context.

Interestingly, our results are consistent with a pattern found in a previous survey of Sierra Nevada lakes. Knapp et al. (2001) surveyed the biota of lakes in three categories: (a) naturally fishless lakes, (b) lakes stocked with fish and (c) formerly stocked lakes restored to a fishless condition (formerly stocked fishless). They found similar invertebrate communities in the formerly stocked fishless lakes and the always-fishless lakes except that the abundance of *Daphnia rosea* was nearly twice as great in the formerly stocked fishless community (result marginally significant, figure 7a in Knapp et al., 2001). Our results suggest that this pattern may be due to the past selection by fish on *Daphnia* traits. The survey of Knapp et al. (2001) suggests that these effects may persist for at least 10 years post-fish-removal. The increase in *Daphnia* biomass following the removal of fish could affect trophic dynamics and lake water clarity (Carpenter et al., 1987). Our results indicate that coexisting with fish results in faster population growth rates for *Daphnia* that increase biomass in fishless environments. Still, it remains unclear if this is a transient phenomenon or long-term change.

Though some of the zooplankton patterns are consistent with patterns found in nature, other results are less intuitive. The dominance of *Daphnia* at the low elevation site ( $E_{\text{Elev}}$  = montane) is responsible for driving some of the unexpected patterns. For example, we expect to see smaller body sizes at warmer elevations

(Loewen et al., 2020; Symons & Shurin, 2016), whereas our montane site had the largest average body size (Figure 2c). The dominance of large-bodied *Daphnia* at the montane site may be related to the higher concentration of nutrients at the low elevation site (ESM Table S4; Figures S4 and S5) which can increase *Daphnia* abundance through shifts in competitive hierarchies (Vanni, 1986). Additionally, we would expect communities below tree-line in the montane and sub-alpine sites to be more similar to each other than the alpine site (Schulhof et al., 2020; Symons & Shurin, 2016); however, we found that  $E_{\text{Elev}} = \text{alpine}$  and  $E_{\text{Fish}} = \text{fishless}$  communities were more similar to the montane site. Typically, fishless alpine lakes contain *D. melanica* (Knapp & Sarnelle, 2008). Although *D. melanica* was present at the high elevation site for 13 months, it was not present by the end of the experiment (ESM Figures S1 and S9). A replacement by *D. pulicaria* caused these communities to become more similar to the montane site over time, which could be related to lower UV stress caused by shade cloth, as melanization is a costly trait (Hessen, 1996).

Though zooplankton biomass depended on the interactive effect of  $E_{\text{Fish}} \times H_{\text{Fish}}$ , we found no cascading impacts of community history on chl-*a* (Figure 5). Instead, we found that mesocosms with fish had marginally higher chl-*a* in a classic tri-trophic cascade where fish reduced zooplankton biomass, releasing phytoplankton from grazing pressure, though this effect was not significant ( $p = 0.06$ ; Carpenter et al., 1985). We expected chl-*a* to be impacted by  $E_{\text{Fish}} \times H_{\text{Fish}}$  because important determinants of zooplankton grazing rates, namely biomass and body size, were related to the interaction of environment and history (Table 1). However, we did not directly measure community grazing rates or primary productivity, which may not be related to zooplankton biomass, body size or chlorophyll-*a*. Our result contrasts with Ingram et al. (2012) who found that adaptation of sticklebacks to sculpin predators dampened the cascading trophic effects of sculpins on invertebrates and Walsh et al. (2012) who found that adaptation of zooplankton to alewife *Alosa pseudoharengus* had a cascading effect on chlorophyll concentrations. The imprint of past selection by fish was apparent in the biomass and size structure of

the zooplankton community, but not the density of algae as indicated by chlorophyll-*a*.

Our results show that contemporary conditions and past selection interact to determine community response to changes in climate and predation regimes. We found legacy effects from non-native fish predators where zooplankton communities showed strong effects of fish removal possibly due to past selection on prey life-history traits, particularly *Daphnia*. Zooplankton communities coexisting with fish were therefore more abundant and contained larger individuals than allopatric communities under fishless conditions in mesocosms. Therefore, changes that persist after predation extirpation may shape top-down trophic interactions. By contrast, variable past selection in different climate zones had no impact on the effect of contemporary climate change on plankton biomass or size structure. Loss of top-predators is one of several global changes affecting aquatic and terrestrial ecosystems. Studies of predator loss often use experimental exclusion or removal of predators (Shurin et al., 2002); however, our results suggest that community response over experimental time-scales may differ substantially from longer-term effects as evolutionary change and compositional turnover unfold. Legacies of past environments can influence community composition and biomass, leading to asymmetrical responses to the addition or removal of stressors.

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#### AUTHORS' CONTRIBUTIONS

C.C.S. and J.B.S. developed the research questions and designed the experiment; C.C.S. completed the analyses and wrote the first draft of the manuscript; C.C.S., J.B.S., M.A.S. and H.B.C. aided in data collection and edited the manuscript.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4b8gthtd> (Symons et al., 2020).

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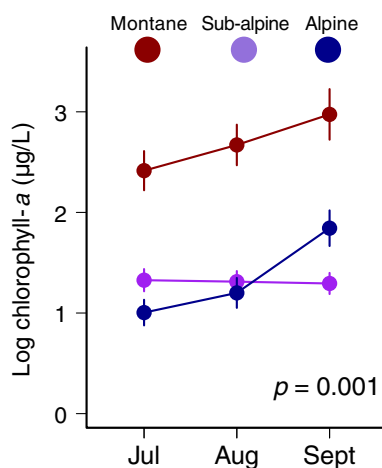
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**FIGURE 5** The response of chlorophyll-*a* to experimental treatments in 2015. Error bars represent standard error. Only significant results are presented; therefore, data are averaged across all other treatment

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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