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The relationship between thermal spatial variability and mean temperature alters movement and population dynamics

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Abstract

The importance of spatial and temporal environmental variation in shaping ecosystem dynamics is well appreciated, yet the ecological consequences of dynamic spatial variability, that is, the temporal patterning of spatial variation, remain unresolved. Here, we experimentally generate temporally fluctuating thermal environments that have either a negative, positive, or neutral relationship between the mean spatial environmental temperature and the degree of thermal spatial heterogeneity. We test the hypothesis that the timing of spatial variation relative to diel temperature cycles can meaningfully alter movement patterns and population dynamics, using the motile green algae *Chlamydomonas reinhardtii*. Our results indicate that *C. reinhardtii* individuals growing in environments with positive relationships between spatial variability and mean temperature show reduced population growth rates, more directed movement as indicated by a reduced turning angle, and decreased negative thermotaxis over time, relative to those growing in environments with a negative relationship between spatial variability and mean temperature. We additionally document substantial regional variation in the dynamics of natural spatial variability by collecting summer water temperature measurements from five ponds in the Mount Saint Helens watershed, WA, USA. Our results collectively suggest that the dynamics of spatial variation are an underappreciated but salient feature within the broader interwoven fabric of spatiotemporal variation.

KEYWORDS

climate warming, movement behavior, space-time, spatial heterogeneity, thermal variability, thermotaxis

INTRODUCTION

Ecological processes are shaped by variation in environmental conditions through both time and space. An environment's degree of spatial variation has well-appreciated impacts on population (Hanski, 1998; Sears et al., 2016), predator–prey (Hastings, 1977), and community dynamics (Brown, 2003), as well as evolutionary processes (Muñoz & Bodensteiner, 2019; Wellnitz & Poff, 2001). Likewise, temporal variation in environmental conditions has multiscale ecological consequences (Gonzalez & Holt, 2002; Ruel & Ayres, 1999; Vasseur et al., 2014), including those that emerge from overlapping timescales of physiological (Fey et al., 2021) and evolutionary dynamics (Padfield et al., 2016). Research conducted in natural environments unavoidably encompasses consequences of both spatial and temporal variation (Bierman et al., 2006; Smith, 1983; Sweeny et al., 2021), yet the interactions between these forms of variation are rarely explicitly considered (Wolkovich et al., 2014). Here, we address this gap by experimentally isolating and manipulating the relationship between spatial and temporal variation in environmental temperature, one powerful driver of ecological dynamics.

While all environments exhibit some temperature changes across space at a given moment (i.e., thermal spatial heterogeneity), various possibilities exist for how this spatial variation unfolds across time. Theory and empirical research suggest that positive relationships between thermal mean and spatial heterogeneity can be conducive to effective behavioral thermoregulation (Fey et al., 2019; Kearney et al., 2009). Such environments include those with thermal refugia that remain relatively cool regardless of ambient temperatures, such that they become more spatially variable during hotter mean conditions (Scheffers et al., 2014). Environments can also exhibit negative relationships, as when apple leaf surfaces were observed to become more thermally homogenous with warmer air temperatures (Caillon et al., 2014; Jones, 1999). Spatial variation during warmer, thermally stressful periods (i.e., periods over which temperatures approach or exceed critical thermal maxima or CTmax) can yield benefits disproportionate to the associated costs of reduced thermal spatial heterogeneity at low temperatures (Fey et al., 2019; Fey & Vasseur, 2016; Ruel & Ayres, 1999; Sears et al., 2016). As such, the fitness or performance of organisms in these environments may be increased when compared with environments with negative or neutral (i.e., nonexistent) relationships. During instances of high mean temperature, effective thermotaxis coupled with adequate spatial heterogeneity can prevent local extinctions by providing nonlethal microclimates (Sunday et al., 2014). Yet despite these possibilities, explicit tests of the ecological consequences of the timing of thermal spatial heterogeneity remain largely absent from the literature and are thus unresolved.

Here, we experimentally manipulate the relationship between thermal spatial heterogeneity and mean temperature in temporally fluctuating thermal environments, while holding daily mean temperature and mean spatial variation constant. We examine the individual- and population-level consequences of environments with positive, negative, or neutral relationships between spatial variation and mean temperature, using the motile green algae *Chlamydomonas reinhardtii*. We hypothesize that a positive relationship between thermal spatial variation and mean temperature will promote faster growth rates and be associated with a greater amount of movement by individuals, relative to when the two variables are neutrally or negatively related. We additionally demonstrate the diversity of potential timing relationships for spatial variation across freshwater ecosystems, by collecting and analyzing high-resolution water temperature data from a mosaic of small ponds north of Mount Saint Helens, WA, USA. Although we focus on a single species in an idealized thermal environment, our results indicate that the timing of spatial heterogeneity yields ecologically meaningful consequences.

METHODS

We performed all experimental research using the freshwater phytoplankton species, *C. reinhardtii*. This species was selected because it exhibits viable population growth at a wide range of temperatures (Appendix S1: Figure S1) and is a highly motile species, such that individuals can swim at speeds up to 123 μm/s, or 44.28 cm/h (Ojakian & Katz, 1973; Sasso et al., 2018; Sekiguchi et al., 2018).

Establishing thermal environments and initial experimental setup

Thermal environments were established using three independently programmable incubators (I-36, Percival Scientific, Inc., Perry, IA, USA) connected with six horizontal plexiglass tubes (5.08 cm outer diameter × 4.445 cm inner diameter × 182.88 cm length; ePlastics, San Diego, CA, USA) outfitted with holes for access and gas exchange (Appendix S1: Figure S2). Continuous lighting was provided at a photosynthetic photon flux density of ~40 micromoles per square meter per second. Environments were designated as either “positive,” “neutral,” or “negative,” with the name conveying the relationship between mean temperature and spatial standard deviation of temperature (Figure 1). Daily maxima in each environment, while sublethal, exceeded the thermal optimum for *C. reinhardtii* (Appendix S1: Figure S1). The three thermal environment treatments were imposed in random order.

At the start of each assay, five tubes were capped with test plugs and filled with 2 L COMBO media (Kilham et al., 1998); one tube (dedicated to measuring water

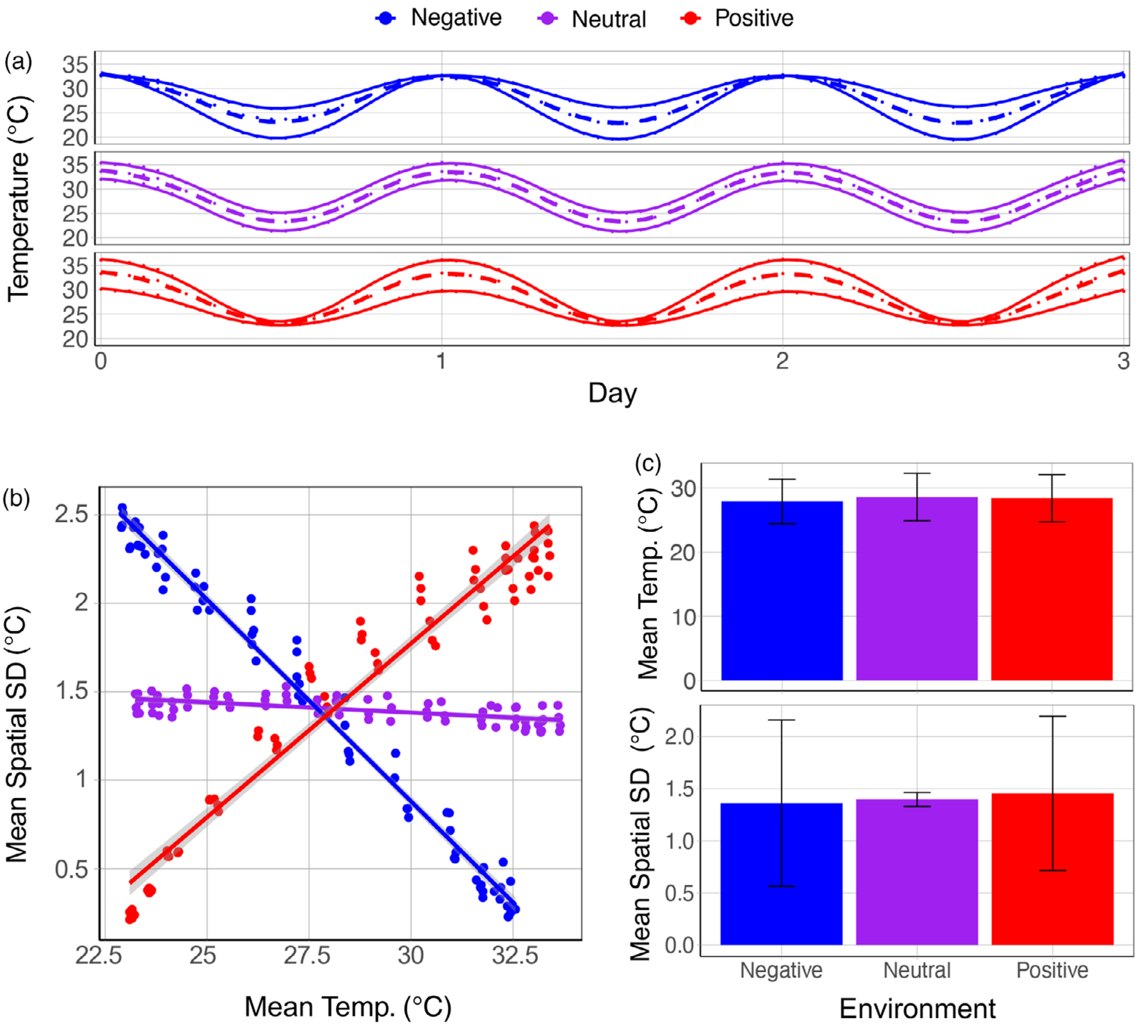

FIGURE 1 Negative (blue), neutral (purple), and positive (red) thermal environments exhibit different patterns of thermal spatial heterogeneity. Solid lines in (a) represent the minimum and maximum temperatures for the first three days of each trial, while dashed lines indicate the spatial mean. (b) The relationships between spatial variability (spatial standard deviation) and mean temperature in each experimental environment, recorded hourly. Lines represent linear estimates of relationships, and environments were referred to by the sign of the slope. (c) The overall means (±1 SD) of the spatial mean temperature (top) and spatial heterogeneity (bottom) for each treatment.

temperature) was filled with deionized water. HOBO pendant temperature loggers (Onset Computer Corp., Pocasset, MA, USA) were placed at five evenly spaced locations along this tube (Appendix S1: Figure S2) for measuring environmental temperature. The media equilibrated to desired temperatures overnight before the assay. *C. reinhardtii* (from E. Litchman, Michigan State University) cultures were acclimated to 25°C in a constant light environment and initially established at a target starting density of 1000 cells/ml (estimated fluorometrically using an empirically derived relationship, $R^2 > 0.99$; Fey et al., 2021). These cultures were maintained in the exponential growth phase and were inoculated evenly across five horizontal locations in each COMBO-filled tube during peak mean temperature, providing an initial thermotaxis index (TI) of 0 (Equations 1 and 2). Additionally, because the thermal environment of the center incubator was similar across assays, we inoculated three 100-ml control beakers containing 50 ml COMBO with 1000 cells/ml of *C. reinhardtii* and placed them in the central incubator during each assay to monitor the consistency of *C. reinhardtii* performance across experimental treatments. A duration of 5 days, approximately eight generations, was chosen for data collection because previous research indicated that this was a sufficient time to estimate growth rates and carrying capacities (Fey et al., 2021), and because this represents a timescale where changes in freshwater phytoplankton community dynamics can be observed (Thomas et al., 2018).

Experimental data acquisition

Density data were collected daily for the 5 days after inoculation, during the hour of peak mean temperature. Each tube was sampled in triplicate at each of the five locations using a micropipette. Control beakers were homogenized and sampled at a single location. The fluorescence of each sample was measured using a fluorometer (Trilogy, Turner Designs, Inc., San Jose, CA, USA, with a chlorophyll *a* in vivo module). On Day 3 (prior to populations reaching carrying capacity), microscope videos were recorded during the hour of peak temperature in the tube by withdrawing 450 μl of culture from Locations 1, 3, and 5 of each replicate onto a slide containing an affixed plastic ring. Samples were filmed at 10× magnification for 1200 frames with a 50-ms exposure per frame (totaling 60 s) using Olympus SZX2 stereomicroscope (Olympus America Inc, Waltham, MA, USA). Videos were processed with TrackMate within FIJI (version 2.1.0) and analyzed using the moveHMM package (Michelot et al., 2019) to determine the average speed and average absolute turning angle (Appendix S1: Figure S3) based on 100 randomly selected particles.

Statistical analysis of experimental data

We used ANOVA to test for differences between the thermal environments' mean temperature, mean spatial heterogeneity (spatial standard deviation across the five tube locations) and expected growth rate (growth rates predicted in the absence of movement behavior for each environment). The latter was estimated numerically according to previously collected thermal reaction norms for *C. reinhardtii* and the temperature data measured at five locations within tubes (Appendix S1: Figure S2). Whether the relationship between mean spatial heterogeneity and mean temperature differed significantly between environments was tested with analysis of covariance (ANCOVA).

The growth rate of each population was calculated using the growthTools package (Kremer, 2022) as the slope of the relationship between log(density) and time, using density data collected before the effects of density dependence was visible (Appendix S1: Figure S4). Carrying capacities (*K*) were estimated using the R package growthrates (Petzoldt, 2020).

Thermotaxis values were determined similarly to Sekiguchi et al. (2018), where locations along the tube were normalized to values of −2, −1, 0, 1, and 2, with the coldest location as −2 and the warmest at +2. The cell abundance across all positions at each timepoint, D_T, was defined according to Equation (1), where i indicates the horizontal position and D_i indicates the density at position i. The TI for each tube at each timepoint was calculated according to Equation (2), where j indicates the horizontal position of the tube and D_j indicates the density measured at position j:

$$D_T = \sum_{i=-2}^{2} D_i \tag{1}$$

$$\mathrm{TI} = \sum_{j=-2}^{2} j\left[\frac{D_j}{D_T}\right]. \tag{2}$$

A TI value was also calculated for Days 1–3 of each treatment based solely on how the predicted growth rates diverged along the length of the tube's temperature gradient, assuming cells exhibited no thermotactic behavior.

To determine if thermotaxis was influenced by time, treatment, or their interaction, we performed repeated-measures ANOVA (RM-ANOVA), restricting the data to Days 1–3, before all treatments reached carrying capacity, as to focus on the process of behavioral thermoregulation over the thermal dependence of growth rate. We used separate one-way ANOVAs to determine whether mean absolute angle, growth rate, or carrying capacity differed among treatments, and used a Welch's one-way test to determine whether mean speed differed among treatments because these data failed to meet assumptions of homogeneity of variance. All above analyses were conducted in R (version 4.1.2) and significance was determined at $\alpha = 0.05$.

Evaluating variation in the timing of thermal heterogeneity in natural systems

To characterize the diversity in the relationships between spatial variability and mean temperature in pond ecosystems, we collected observational field temperature measurements. HOBO temperature loggers (Onset Computer Corporation; Bourne, MA, USA) equipped with white plastic protective coverings were installed in pairs at five ponds within a 750-m radius in the Mount Saint Helens watershed, WA, USA (Appendix S1: Figure S5). One of each pair floated at the surface and the other rested on the bottom. Temperature loggers were deployed at the location that gave the maximum pond depth. Ponds had a median surface area of 2552 m^2 (interquartile range = 1678 m^2) (Crisafulli et al., 2005). Loggers collected hourly water temperature readings between 1 and 31 July 2020. To examine patterns in the timing of spatial variation, we regressed thermal spatial heterogeneity (intra-pond temperature range) against the mean water temperature at each timepoint.

RESULTS

Quantifying thermal environments

The three thermal environments (negative, neutral, and positive) were indistinguishable by many metrics (Figure 1). The average spatial temperature across the trial did not differ among treatments ($F_{2,363} = 1.40$, $p = 0.25$; Figure 1c), nor did the mean spatial heterogeneity observed across horizontal positions ($F_{2,363} = 0.75$, $p = 0.47$; Figure 1c) or the predicted overall growth rates (Appendix S1: Figure S6). The timing of thermal spatial heterogeneity did differ as intended, such that negative environments had minimal spatial variation during times when the mean temperature was highest, while positive environments had maximal spatial variation during times when the mean temperature was highest (Figure 1a,b). Neutral environments had intermediate, but temporally constant, levels of spatial variation (Figure 1). As such, the relationship between thermal spatial heterogeneity and mean temperature significantly differed among environments (ANCOVA, spatial heterogeneity × environment, $F_{2,360} = 384.77$, $p < 0.001$).

Thermal environment's influence on movement

C. reinhardtii in the three thermal environments exhibited a tendency for negative thermotaxis during the first three days of data collection (RM-ANOVA intercept, $F_{1,44} = 9.59$, $p = 0.003$; Figure 2a), with disproportionately high population densities in the colder positions along tubes indicated by significantly negative TI values. Additionally, the strength of thermotaxis in each environment differed across days (RM-ANOVA time × environment, $F_{2,44} = 3.53$, $p = 0.0062$), such that populations in the positive environment initially exhibited the strongest negative thermotaxis but by Day 3 exhibited no thermotaxis, while populations in the negative environment initially exhibited the weakest thermotaxis but by Day 3 exhibited the strongest negative thermotaxis of any environment.

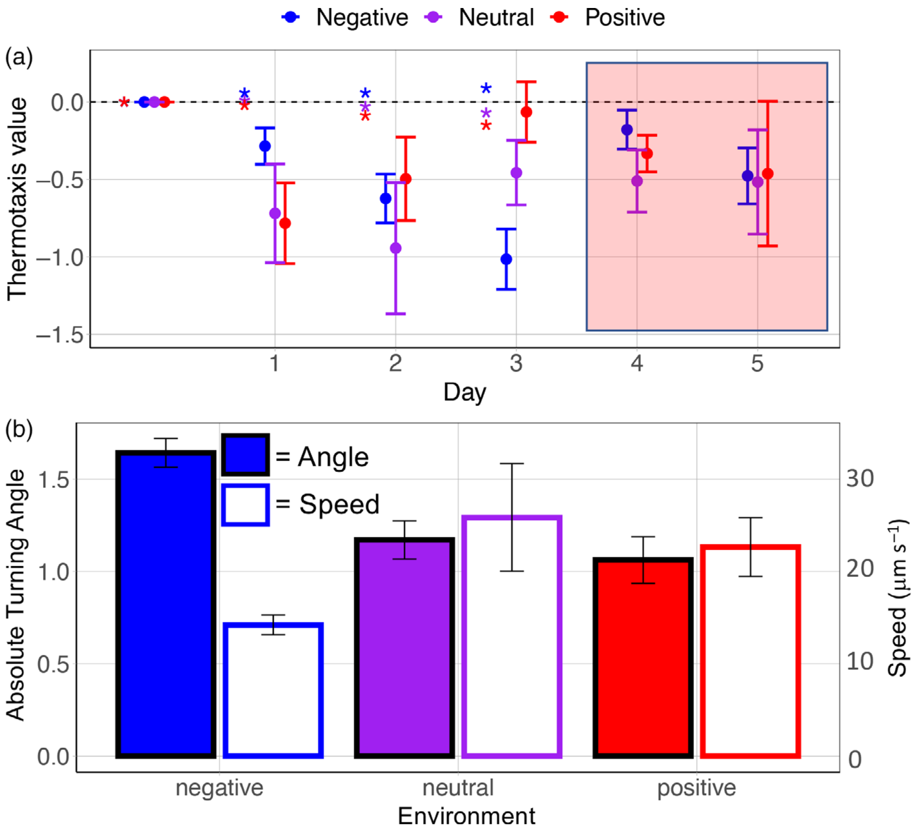

FIGURE 2 *Chlamydomonas reinhardtii* movement differs across the three environments. (a) The predicted thermotaxis index (TI) (asterisk symbols), calculated assuming no motility, remains close to 0, while the observed thermotaxis (filled circles, mean ± 1 SE) varies widely across time and between treatments. TI values are bounded between −2 and 2, with negative values indicating negative thermotaxis. The boxed points indicate days (4 and 5) in which cultures reached carrying capacity. (b) Mean absolute angle (filled bars ±1 SE; left axis, in radians) and mean swimming speed (empty bars ±1 SE; right axis) of *C. reinhardtii* individuals on Day 3.

The timing of thermal heterogeneity additionally altered microscale movement behaviors of individuals. The mean absolute turning angle differed across the three thermal environments (ANOVA $F_{2,12} = 8.75$, $p = 0.005$; Figure 2b, filled bars) such that *C. reinhardtii* exhibited significantly less linear movement in the negative environment relative to the neutral and positive environments (Tukey honestly significant difference, neutral–negative $p = 0.019$; positive–negative $p = 0.005$). On average, the absolute turning angle was 40% and 55% greater than the angle in neutral and positive environments, respectively. The average *C. reinhardtii* speed tended to be lowest in negative environments (Welch test, $F_{2,6.02} = 4.31$, $p = 0.069$; Figure 2b, open bars), showing 46% and 38% reductions from the neutral and positive environments, respectively. Treatments exhibited similar ratios of moving to nonmoving particles such that a mean of 24%, 22%, and 30% of *C. reinhardtii* individuals were moving in negative, neutral, and positive environments, respectively.

Thermal environment's influence on population-level processes

Exponential growth rates differed across the three environments ($F_{2,12} = 24.07$, $p < 0.001$; Figure 3a), with the mean neutral environment (1.441 day^{-1}) and negative environment (1.293 day^{-1}) outperforming the mean positive environment (1.022 day^{-1}). Unlike growth rates, the mean carrying capacity did not significantly differ among thermal environments ($F_{2,12} = 0.0789$, $p = 0.92$; Figure 3b), nor did the population growth rate of control *C. reinhardtii* populations ($F_{2,6} = 3.741$, $p = 0.09$).

The timing of variability in natural ecosystems

Ponds in the Hummocks complex exhibited marked differences in their relationship between mean spatial temperature and spatial heterogeneity, with observed slopes ranging from nearly neutral (slope = 0.24) to strongly positive (slope = 1.76; Figure 4). During the warmest periods observed in ponds, Pond H55 exhibited the greatest spatial variation, diverging by up to 15°C between the pond surface and bottom. Other ponds exhibited an average range of less than 5°C during the warmest overall periods. No example of a negative relationship between spatial variability and mean pond temperature was observed. Within the sampling period, ponds also exhibited substantial diversity in the R^2 values, ranging from 0.17 to 0.96. For all ponds besides H55, various spatial temperature ranges were observed for a given mean temperature, likely indicating the effects of seasonal dynamics on pond thermal stratification.

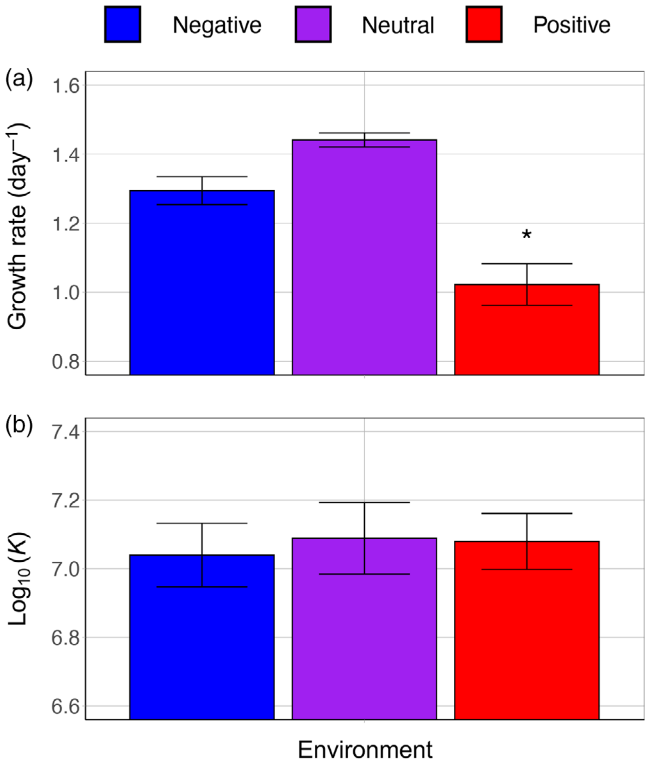

FIGURE 3 The timing of spatial heterogeneity influenced mean population growth rate (a) but did not have a significant impact on *K*, carrying capacity (b). Error bars show ±1 SE and an asterisk indicates significant post hoc differences.

DISCUSSION

Differentiating between the three environments in this study would be impossible using common summary statistics such as mean temperature or mean spatial variability, yet our results indicate that changing the relationship between thermal spatial variability and mean temperature had meaningful consequences for the movement and dynamics of *C. reinhardtii* populations. These data indicate that emergent, population-level processes may complicate expectations of how individual-level responses can scale to population dynamics in spatiotemporally variable environments. Additionally, the freshwater pond thermal data indicate that the key feature we experimentally manipulated (the relationship between spatial variability and mean temperature) differs between pond ecosystems during the summer months.

That *C. reinhardtii* initially exhibited negative thermotaxis across treatments is consistent with the

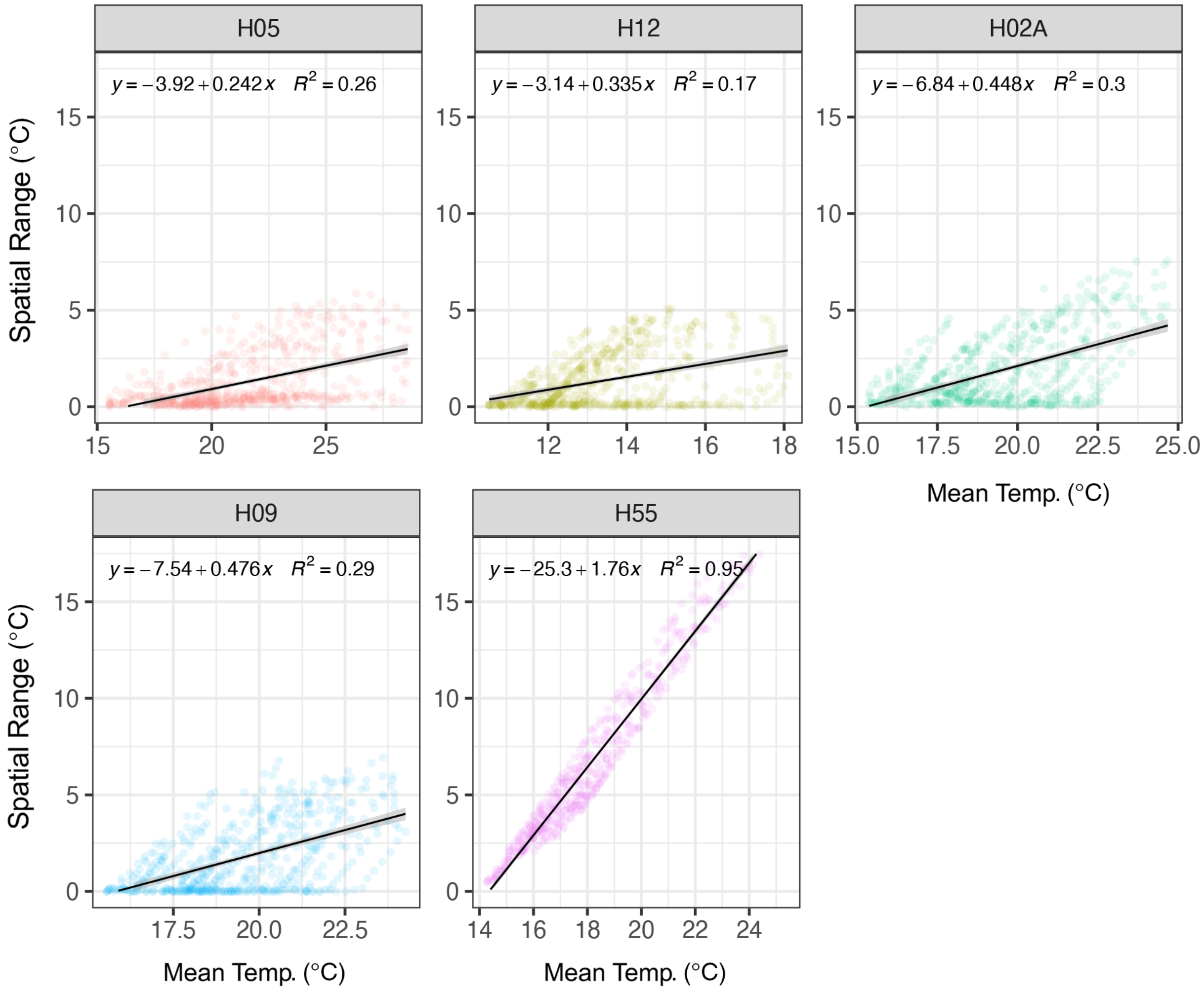

FIGURE 4 The timing of spatial heterogeneity varies significantly in nature. Spatial thermal heterogeneity (difference between surface and bottom temperature) and mean pond temperature were recorded hourly between 1 and 31 July for five ponds. Points indicate raw hourly data and trend lines represent linear fits for each pond.

prediction that our highest imposed environmental temperatures were approaching the limits of thermal tolerance (Appendix S1: Figure S1). In our experimental positive environment, despite having access to high spatial variability during thermal maxima, *C. reinhardtii* population grew at a significantly slower rate. *C. reinhardtii* individuals evidently were able to use this variation to behaviorally thermoregulate, as the TI was comparable to that of the other two environments during exponential growth and diverged from the values we estimated would exist in the absence of movement. Our results showed that *C. reinhardtii* can swim at 25.8 μm/s, or 9.29 cm/h. Thus, an individual *C. reinhardtii* at the center of the tube could reach either end of the gradient in approximately 5 h, which is less than half of the 12-h warming or cooling period. Microscope video analysis also indicates effective motility, showing that individuals from the positive environment had fast and linear movement compared with the other treatments during thermally stressful periods. Finally, *C. reinhardtii* are of sufficient body size to take advantage of environmental variation at ecologically relevant scales in freshwater settings, even if steep energetic costs are incurred (Dusenbery, 1997). The observed slower growth in the positive environments thus suggests that thermotaxis occurred but did not compensate for reductions in population growth during higher daily maxima.

Additionally, temperature itself can be considered a limiting resource (Magnuson et al., 1979), and populations can reach higher densities in more optimal thermal environments (Calsbeek & Sinervo, 2002). Continually increasing densities in these spatially limited but thermally optimal regions may have precluded individuals from realizing maximal reproductive rates, particularly if resource use efficiency is modified at higher environmental temperatures (Toseland et al., 2013).

Strong density-dependent effects during the final experimental days may have also accounted for the convergence of thermotaxis indices among treatments, suggesting that population density may interact with the timing of spatial variability.

Our initial hypotheses focused on the potential benefits of a hot, variable environment, as previous theory predicts that organisms should benefit from a positive relationship between mean spatial heterogeneity and mean temperature by access to nonlethal conditions during periods of heat stress (Fey et al., 2019). Conversely, such predictions could be approached by considering the downsides of an invariably cold environment during daily thermal minima. The benefit of refugia during thermal stress may not offset the costs incurred while cool refugia are unnecessary, when heterogenous cold temperatures decrease growth relative to the neutral and negative environments (Ruel & Ayres, 1999). The maximum possible growth rate we calculated for *C. reinhardtii* in the positive environment was lower than the other environments, in part due to reduced access to warm temperatures during cold periods of time (Appendix S1: Figure S7). This suggests that pronounced refuges from thermal stress in the positive environment (e.g., Scheffers et al., 2014) may trade off and reduce performance during non-thermally stressful times. The extent to which climate warming may reframe the value of refugia remains an open question.

While these experimental environments are deliberately simplified relative to natural ecosystems, we observed both strongly positive and neutral relationships within pond environments in the Hummocks complex that qualitatively resemble our experimental conditions. Importantly, these thermal data represent two depths from a single location within a pond, and thus likely underrepresent the entirety of thermal spatial variation that exists for motile organisms in these ecosystems. Yet, these data indicate that natural pond ecosystems include habitats where overall warmer conditions are accompanied by increased thermal spatial heterogeneity, as well as ponds where overall warmer temperatures remain spatially homogenous. In contrast to our experimental environments that held average spatial variability constant across environments, the average spatial variation varied among natural ponds. While our experimental results indicate that positive environments resulted in decreased growth rates, it is possible that motile species with greater heat sensitivity than *C. reinhardtii* may indeed benefit from the existence of spatial variation during high temperature events, especially under climate warming. Further research should thus seek to determine whether such trade-offs in performance between periods of low or high temperature regimes exist within natural environments.

In conclusion, our results indicate that the timing, in addition to the magnitude or configuration of spatial heterogeneity, can have movement- and population-level consequences for *C. reinhardtii*. To what extent these results, collected in idealized thermal environments over a few generations, can provide an understanding of current or future ecological process remains to be investigated. Despite not detecting the existence of negative aquatic environments, we did observe significant differences in the timing of spatial variability in natural environments within a small geographic area. Incorporating such nuance in describing thermal environments may be necessary for the desired improvements in thermal vulnerability indices (Clusella-Trullas et al., 2021) and ecological forecasts in a warming world.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Schuman et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.6898200.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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