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Trophic cascades and predator-prey dynamics in freshwater ecosystems subjected to thermal fluctuations

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Abstract

This study examines how thermal fluctuations influence predator–prey dynamics and trophic cascades in freshwater ecosystems, with a focus on ecosystem stability under climate variability. A six-week mesocosm experiment was conducted using four thermal treatments: control (19°C), constant warming (23°C), fluctuating (17–27°C), and extreme pulse (30°C peaks). A three-level trophic web (phytoplankton, *Daphnia magna,* and *Notonecta glauca*) was set up. Measured key variables were phytoplankton biomass (chlorophyll a), zooplankton density, predator survival, strength of interaction (OI), trophic transfer efficiency (TTE), and ecosystem stability (σ^2). Statistical tests were repeated-measures ANOVA and Gaussian process regression. These conditions of constant warming (~22.8 µg L^{-1}) created a larger phytoplankton biomass than the control (~15.0 µg L^{-1}) and more variability with extreme pulse conditions (~11.4 µg L^{-1}). Zooplankton density declined from 28.5 ± 3.1 to 12.5 ± 3.0 individuals L^{-1} under combined thermal stress and predation. Predator–prey interaction strength was highest under constant warming (0.035 ± 0.006) and lowest under extreme pulse conditions (0.024 ± 0.008). Under constant warming, the trophic transfer efficiency was maximum at 22.7% and 15.6% but low at limiting conditions. There was a significant decrease in ecosystem stability and the variance, which rose to 6.38 (extreme pulse) compared to a

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control of 1.85, showing non-linear threshold responses. One important cause of trophic dynamics and ecosystem stability is not mean warming, but thermal variability. Middle levels of warming are beneficial in terms of productivity and energy flow, but severe thermal events interfere with the ecological interactions and make the system less resilient.

Keywords: Thermal variability, Trophic cascades, Predator–prey dynamics, Freshwater ecosystems, Ecosystem stability, Climate change, Mesocosm experiment

Introduction

Freshwater ecosystems are dynamic and complex networks with biological interactions determining the structure and functioning of ecosystems. Trophic cascades and predator-prey are among these interactions and are important contributors to ecological stability. Trophic cascades are defined by the indirect impact that alterations at upper trophic levels, especially the presence of predators, have on lower trophic levels, especially the primary producers and detritivores (Duchet *et al.,* 2026). Instead, population stability, the transfer of energy, and community structure are dictated by predator-prey interactions. Over the last few decades, climate change has become a leading cause of environmental variability, specifically causing an increase in temperature and amplification of thermal changes (Fabian and Froneman, 2025). Temperature changes in freshwater systems are very reactive because these systems have a low thermal buffering capacity. Temperature changes can cause changes in metabolic rate, behaviour, breeding, and feeding performance of species, and hence can cause changes in predator-prey relationships. These changes caused by temperature have the potential to upset existing trophic interactions, with possible resultant changes in cascade processes, loss of biodiversity, and ecosystem imbalances. The contribution of changes in the strength of thermal variability to trophic cascades is thus important in forecasting ecosystem responses to climatic changes (Johnson *et al.,* 2024). This is, however, a difficult area of ecological research due to the complexity of interaction among species coupled with the variability of the environment.

This research aims first of all to examine the effects of thermal changes on predator-prey relationships in freshwater ecosystems and to learn the cascading impacts of these relationships through various trophic tiers. Specifically, the study will test the hypothesis that variability of temperatures alters the strength and direction of trophic cascades, species interactions, and ecosystem processes such as feeding behavior, growth, and reproduction. It also seeks to quantify species-specific responses to changes in thermal conditions and elucidate the aggregate implications of such changes to the stability, resilience, and functioning of ecosystems in response to environmental variability due to climate change.

Despite the extensive literature on trophic cascades and predator-prey relationships and interactions, there is limited literature on how these ecological processes are affected by temporary changes in freshwater ecosystems in response to temperature variations (Pintanel *et al.,* 2021). The majority of the available literature has concentrated mainly on constant temperature scenarios or warming tendencies in the long term, neglecting the fact that the frequency and intensity of temperature variability are on the rise due to climate change (Staudinger *et al.,* 2021). Moreover, little focus has been on the ability to include the multi-trophic, species-specific thermal sensitivities and nonlinear ecological responses into an individual framework. Such a deficit of comprehensive, integrative studies limits precise projections of ecosystem reactions and underscores the significance of studies that directly regard the dynamic character of thermal variability.

The hypothesis underpinning this experiment is that thermal variations are potentially able to bring about significant changes in predator-prey interactions and the strength of trophic cascades in freshwater lakes. It is hypothesized that temperature changes alter metabolic rates and behavioral patterns of organisms and thus alter the strength of interactions between predators and prey. More thermal variability will also cause temporal asynchrony among trophic levels, resulting in weakened or distorted cascade interactions. The experiment also assumes that species with a smaller thermal tolerance will respond more to a change in temperature, which may cause changes in community structure. Lastly, it is postulated that these are nonlinear responses that increase unpredictability and decrease ecological stability.

The paper contributes to the literature on freshwater ecology by providing an all-inclusive view of the effects of thermal changes on trophic cascades and predator-prey interactions. It builds upon the existing research by showing the importance of short-term changes in temperature, rather than strictly looking at changes in warming over a long period. The study also incorporates multi-trophic views and species-specific reactions, rendering existing known models more ecological. The research contributes to the general understanding of ecological responses during changes in thermal regimes by establishing the relationship between the stability and resilience of ecosystems and the presence of different thermal regimes when the climate varies. In addition, it assists in developing adaptive water management and conservation policies in the protection of biodiversity in freshwater, and in supporting the sustainability of freshwater ecosystems in the context of increasing environmental variability.

The focus of this article is to explore how thermal variability impacts trophic cascades and predator-prey relations in freshwater ecosystems. It starts with an introduction in section 1 that illustrates the ecological significance of trophic interactions and how temperature changes induced by climate affect these interactions. Section 2 shows the literature review identifies current gaps in the knowledge about short-term thermal variability. In section 3, the methodology refers to a controlled mesocosm experiment of several thermal regimes and trophic levels. Findings include alterations in phytoplankton biomass, zooplankton density, the strength of interaction, and the stability of an ecosystem in section 4. These discoveries are discussed in the context of climate change in section 5, and the conclusion draws on the outlined key findings and future study in section 6.

Literature Review

Predator-prey relationships and trophic cascades are core processes that control freshwater ecosystem structure and dynamics. More recent research is beginning to point to environmental stressors, especially temperature fluctuation, in changing these ecological interactions. Stress may manifest in many different ways, including changes in temperature, which have been documented to remodel tropic cascades and have strong contrasting effects on ecosystem processes, which emphasize the complexity of interacting drivers in freshwater systems (Duchet *et al.,* 2026). On a larger scale, international reviews suggest that the strength of trophic cascades is defined by a set of biotic and abiotic conditions, including productivity, diversity of predators, and environmental factors (Su *et al.,* 2021). These trends of robust top-down control have been seen in aquatic ecosystems as well, further supporting the ecological significance of trophic cascades (Surma *et al.,* 2025).

Temperature is one of the major determinants of predator-prey associations because it affects the rate of metabolism, feeding mechanisms, and performance of species. Experiments have shown that predator-prey interactions can be stabilized when warmed by thermal acclimation (Sohlström *et al.,* 2021). However, the strength of interactions and the stabilization of top-down control could be compromised by non-thermal heterogamy between predators and prey (Meehan and Lindo, 2023). Furthermore, it was also demonstrated that temperature alters the shape of predator-prey cycles, leading to nonlinear and possibly unpredictable interactions between ecology (DeLong and Lyon, 2020).

In addition to temperature, other environmental stress factors that cause complex trophic dynamics are turbidity, eutrophication, and habitat changes. Increased turbidity can hamper predator efficiency and predator-prey interactions (Zanghi and Ioannou, 2025), and eutrophication and warming can potentially partner with each other to trigger significant changes across more than just one trophic level (Marin *et al.,* 2025). Mesocosm experiments also show that freshwater food webs can be restructured as a complex of stressors and can change energy transfer pathways (Xie *et al.,* 2024). These results are consistent with broader ecological studies that predict that climate shifts affect the emergent ecological features of resilience, stability, and ecosystem processes (Staudinger *et al.,* 2021).

Other notable factors that influence trophic interactions include the predator characteristics, including diversity, composition, and functional roles. It has been demonstrated that ratios of predator fauna have an indirect effect on food web processes, expressed in variation in growth rate and prey choice behavior (Laskowski *et al.,* 2022). Predator diversity has been shown to directly benefit prey risk in some studies (Froneman, 2022), whilst others have shown it to be vital to maintain the complexity and stability of microbial and planktonic food webs (Guo *et al.,* 2023). In addition, carnivorous fish that feed on freshwater are also important in controlling the high top-down control trophic structure (Oyeboade and Komolafe, 2025).

The role of eco-evolutionary and trait-mediated elements of trophic cascades has recently been emphasized as well. One possible force of evolution is trophic interaction (including body size changes, Luhring and DeLong, 2020), and local adaptation can also affect cascades of trait strength and direction (Corbett and Trussell, 2024). Also, the intertemporal variability of trophic levels plays a significant role in ecological processes, especially in the changing environment (Siqueira *et al.,* 2024).

On the whole, literature shows that freshwater ecosystem trophic cascades are very sensitive to thermal changes and other interacting environmental stressors. Nevertheless, there has been very limited research on integrative studies between thermal variability and multi-trophic, trait-mediated, and eco-evolutionary processes to date, which can be a valuable line of research going forward.

Methodology

Experimental Design and Mesocosm Setup

A mesocosm experiment was used to test various thermal regimes to investigate the cascades of trophic interactions. The experiment involved the use of twenty-four cylindrical fiberglass mesocosms containing 500 liters of each cylindrical shape and set in an open research facility to expose the mesocosms to natural photoperiod and ambient light conditions. The mesocosms were prepped with 15 kilograms of sterilized silica sand, as a benthic substrate, and were filled with 450 liters of pre-screened freshwater filtered to exclude macro-organisms.

In order to develop a semi-natural aquatic community, 2 liters of concentrated pond water that contained a natural assemblage of microorganisms and phytoplankton were inoculated into each mesocosm. The green alga *Scenedesmus quadricauda* and the diatom *Synedra ulna* dominated the community. A stabilization period of 14 days was allowed to ensure equilibrium in nutrient concentrations and biological interactions. At this stage, the total phosphorus was stabilized to about 20 µg L^{-1}, indicating mesotrophic conditions. Simple physicochemical parameters such as pH, dissolved oxygen, and conductivity were also to be measured on a regular basis to achieve homogeneous baseline parameters in all the units of the experiment.

Trophic Structure and Species Selection

The experimental system was programmed to describe a simplified three-level trophic system comprising primary producers, primary consumers, and secondary consumers. The basal energy source was the phytoplankton community dominated by *Scenedesmus quadricauda*. The major consumer chosen was the cladoceran *Daphnia magna*, which was added at an initial density of 25 individuals per liter, producing about 11, 250 individuals in each mesocosm. This species has been selected because of its documented grazing efficiency as well as sensitivity to the environment.

In the predation treatments together with the introduction of the back swimmer *Notonecta glauca*, the secondary consumer was 10 back swimmers introduced in treatment at a density of 10 individuals per mesocosm. This predator was selected because of its active hunting behavior and strong temperature-dependent metabolic responses. The predator-prey ratio was set to be effective in producing strong top-down control without the extinction of prey, and as such, the ongoing ecological interaction between predators and prey was dynamic.

Thermal Regime Treatments

Four thermal treatments and six replicates of the mesocosms were randomly allocated. The control treatment was kept at a constant temperature of 19°C, which is the ambient temperature. Chronic warming conditions were simulated by keeping the constant warming at 23°C. The changing temperature regimen was based on a diurnal cycle of 17°C to 27°C, with an average temperature of 22°C, which reflects natural thermal variation. The extreme pulse simulation imitated episodic heatwaves, a scenario where the temperature would rise to 30°C over a period of 48 hours, three times in every ten days.

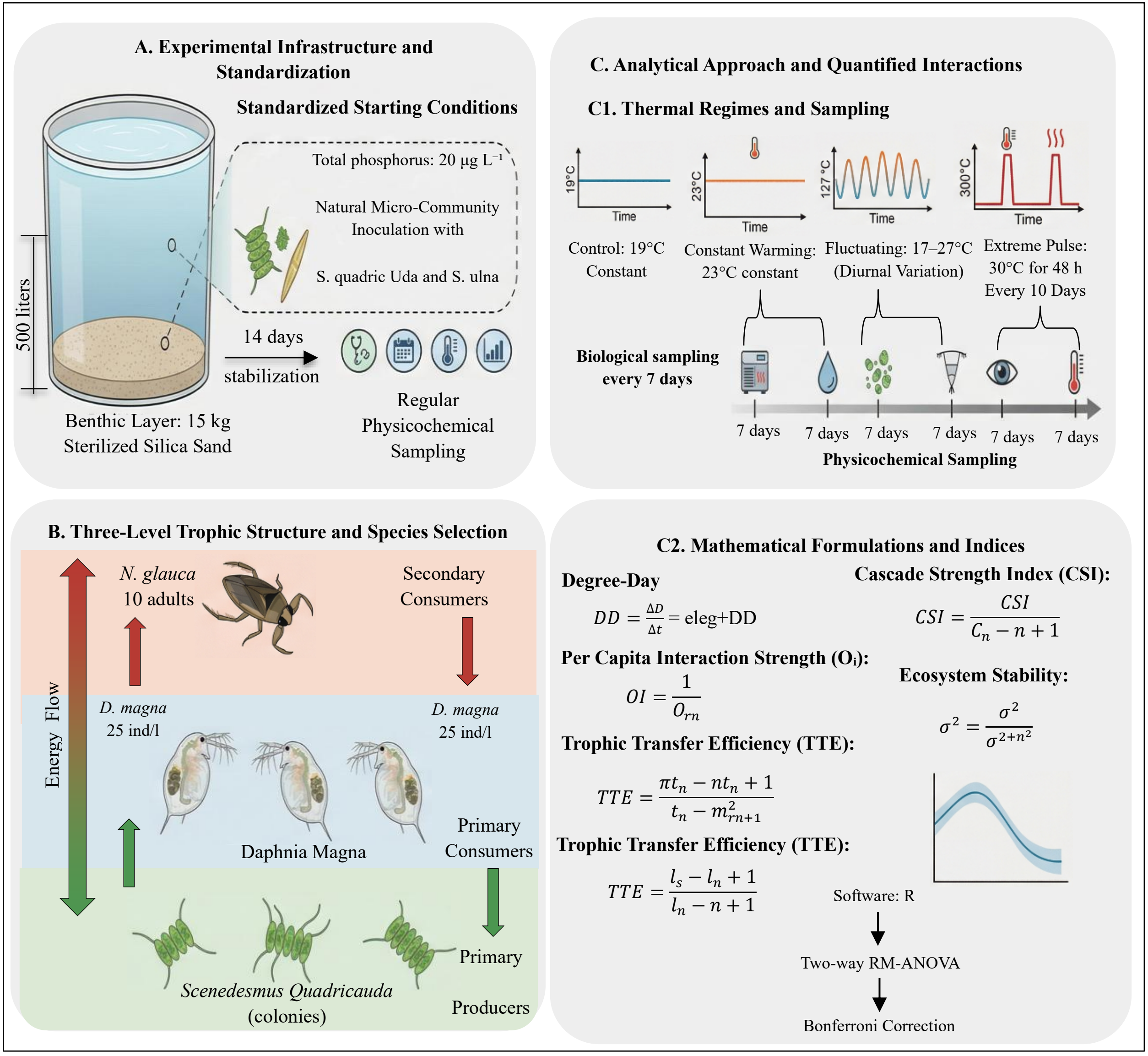

Figure 1: Conceptual framework of experimental design and trophic cascade dynamics under thermal regimes.

Automated heater-chiller systems were used to control temperature, and data were recorded at intervals of five minutes. A degree-day accumulation was used to measure thermal exposure:

$$DD = \sum (T_i - T_{base}) \qquad (1)$$

In equation (1), T_i represents the observed temperature, and T_{base} is the baseline temperature.

The experimental mesocosm system and three-level trophic structure were represented in figure 1 and evaluated to determine the trophic cascade dynamics in different thermal regimes. The diagram illustrates the primary producers (*Scenedesmus quadricauda*), the primary consumers (*Daphnia magna*), and the secondary consumers (*Notonecta glauca*) and directional arrows to show the flow of energy and predator and prey relationships. The four thermal treatments (control, constant warming, fluctuating, and extreme pulse) are depicted as external drivers affecting trophic interactions. And, it also emphasizes the most important response variables to be quantified in the study, such as phytoplankton biomass, zooplankton density, predator survival, interaction strength (OI), trophic transfer efficiency (TTE), and ecosystem stability (variance). This theoretical framework is an overview of the experimental design and analysis of the impact of thermal variability on freshwater trophic dynamics.

Biological Sampling and Measurements

Sampling was done on a 7-day interval for a six-week period of the total experiment. The phytoplankton was estimated using one liter of water collected as an integrated sample in each mesocosm. The samples were filtered, and the concentration of chlorophyll a was determined by the use of standard spectrophotometric methods, and the result was expressed in micrograms per liter.

A Schindler-Patalas trap was used to sample the zooplankton, which filtered five liters of water through a 64 µm mesh. Direct counting with a dissecting microscope was used to determine the abundance of *Daphnia magna*. Also, a subsample of thirty individuals in each mesocosm was measured to determine body length in order to determine the effects of size-structured predation.

Daily, the survival and activity of predators were tracked visually. The rates of survival were documented, and the activity was qualitatively measured to estimate the effect of temperature on predator performance.

Quantification of Trophic Interactions

Per capita interaction strength and trophic transfer efficiency were used to quantify the strength of trophic interactions. Per capita interaction strength was determined by the log ratio of prey densities with and without predators, divided by predator density and time.

$$OI = \frac{\ln (N/N_p)}{P \times t} \qquad (2)$$

In equation (2), OI is the per capita interaction strength, N is the prey density in the absence of predators, N_p is the prey density in the presence of predators, P is the number of predators, and t is the duration of the experiment in days. This is a measure of how well predators can depress prey populations across varying temperatures.

The proportion of energy transfer between trophic levels was calculated as the trophic transfer efficiency:

$$TTE = \left(\frac{Biomass_{n+1}}{Biomass_n}\right) \times 100 \qquad (3)$$

In equation (3), TTE is the trophic transfer efficiency in percent, $Biomass_n$ is the biomass in the trophic level n (e.g., primary producer), and $Biomass_{n+1}$ is the biomass in the next higher trophic level (e.g., primary consumer or predator). This index measures the efficiency of energy flow amongst trophic levels in different temperature regimes.

Moreover, a cascade strength index was estimated to measure the indirect response of the predators to the primary producer biomass:

$$CSI = \frac{B_{producer}^{+predator} - B_{producer}^{-predator}}{B_{producer}^{-predator}} \qquad (4)$$

In equation (4), CSI is the cascade strength, $B_{producer}^{+predator}$ is the biomass of the primary producers when predators are present, and $B_{producer}^{-predator}$ is the biomass when predators are absent. This index gives an idea of the size of the trophic cascade effects in the system.

Statistical Analysis

R software was used to perform statistical analyses. A repeated-measures two-way analysis of variance (ANOVA) was used to evaluate the changes in biological response variables, such as phytoplankton biomass and zooplankton density, and predator survival rates based on temperature regime and the presence of predators. The general model of the analysis can be described as:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k + \epsilon_{ijk} \quad (5)$$

In equation (5), Y_{ijk} is the measured response variable, μ is the overall mean, αi is the effect of the temperature treatment, β_j is the effect of predator presence, $(\alpha\beta)_{ij}$ is the interaction effect, γ_k is the time effect, and ϵ_{ijk} is the difference.

The statistical significance of treatment effects was evaluated using the F-statistic shown in equation (6):

$$F = \frac{MS_{treatment}}{MS_{error}} \qquad (6)$$

Model assumptions of normality and homogeneity of variance were tested using the Shapiro–Wilk test and Levene's test, respectively. Where it was required, data transformations have been performed to meet these assumptions. The Bonferroni correction was used to commit post-hoc comparisons to determine the significance of differences between treatments.

Gaussian process regression was used to estimate the association between the amplitude of temperature variability and ecosystem stability to capture non-linear responses to thermal variability. The measure of ecosystem stability was the change in biomass over time; this measure was achieved by calculating:

$$\sigma^2 = \frac{1}{n-1}\sum_{i=1}^{n} (x_i - \grave{x})^2 \qquad (7)$$

In equation (7), x_i denotes biomass at time i and $\grave{x}$ the average biomass during the study period. The smaller the value of variance, the more stable the trophic system. This compound analytical system allowed detecting both linear effects of treatment and non-linear ecological responsiveness in changing thermal conditions.

Experimental Controls and Reproducibility

Treatment was assigned randomly to all mesocosms in order to reduce bias. All units had similar conditions, such as exposure to light and nutrient availability. In each treatment, replication provided adequate statistical power to detect important effects. No random sampling, measurement, and data analysis procedures were used to guarantee reproducibility and comparability with other ecological studies.

Results

Effects of Thermal Regimes on Phytoplankton Biomass

The phytoplankton biomass was also greatly affected by thermal regimes in the six-week experimental course. Constant warming mesocosms were characterized by a gradual rise in chlorophyll a concentration relative to their control, whereas fluctuating and extreme pulse mesocosms were characterized by a greater variability. This radical pulse treatment had the effect of causing periodic reductions in biomass after heatwave events, which showed thermal stress on primary producers.

Repeated-measures ANOVA showed that the temperature treatment had a significant effect on phytoplankton biomass ($F_{3,20} = 12.84$, $p < 0.001$), and a significant interaction between temperature and time ($F_{15,100} = 3.72$, $p < 0.01$). A trophic cascade also indirectly influenced phytoplankton biomass by the presence of predators ($F_{1,20} = 9.16$, $p < 0.01$).

Table 1: Mean chlorophyll-a concentration (μg L⁻¹) across treatments.

Week	Control (19°C)	Constant (23°C)	Fluctuating (17–27°C)	Extreme Pulse (30°C peaks)
1	12.5 ± 1.2	14.3 ± 1.5	13.8 ± 2.0	13.1 ± 1.8
2	13.2 ± 1.4	16.5 ± 1.7	15.2 ± 2.5	12.6 ± 2.3
3	14.1 ± 1.6	18.7 ± 2.1	16.8 ± 2.8	11.9 ± 2.7
4	13.8 ± 1.5	20.2 ± 2.3	17.1 ± 3.0	10.7 ± 3.2
5	14.5 ± 1.7	21.5 ± 2.5	16.5 ± 3.4	12.2 ± 3.6
6	15.0 ± 1.8	22.8 ± 2.7	17.3 ± 3.6	11.4 ± 3.8

The table 1 shows the changes in phytoplankton biomass in terms of chlorophyll a concentration (μg L⁻¹) within the four thermal treatments and a six-week time span. The uninterrupted warming regime reflects a steady growth in biomass, which implies improved growth of the phytoplankton at stable high temperatures. The control treatment has fairly constant values with slight variation. In contrast, the fluctuating treatment shows moderate variability, reflecting the influence of diurnal temperature changes. The extreme pulse treatment demonstrates a general decline with higher variability, suggesting that episodic heat stress negatively affects phytoplankton stability and growth. Values are reported as mean ± standard deviation, stating variability of replicates.

The figure 2 shows how phytoplankton biomass (chlorophyll a) varies during a six-week period with varying thermal regimes. Biomass increases steadily under constant warming, while the control shows relatively stable trends. The moderate variability is seen in the fluctuating treatment, and the declines and more severe fluctuations are seen in the extreme pulse treatment. Dark areas

(± SD) reveal greater variability when there is a thermal stress effect.

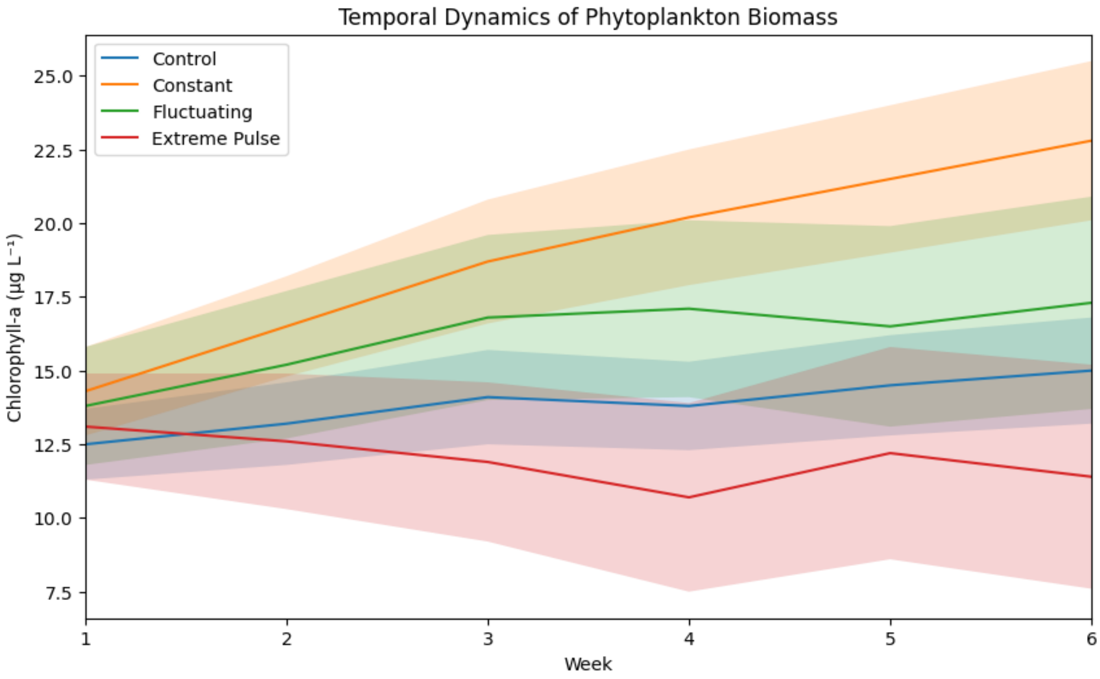

Figure 2: Temporal dynamics of phytoplankton biomass under thermal regimes.

Zooplankton Dynamics and Predator Effects

The abundance of *Daphnia magna* did differ significantly among treatments, and there was strong suppression in the presence of predators. Zooplankton densities were greatest in predator-free control mesocosms, and less so in predator treatments, especially at high temperatures.

The main effects of temperature and predator presence on zooplankton density ($F_{3,20} = 15.67$, $p < 0.001$; $F_{1,20} = 28.45$, $p < 0.001$, respectively) and a significant interaction effect ($F_{3,20} = 4.92$, $p < 0.01$) were observed. Higher temperatures caused predators to feed faster, resulting in stronger top-down control.

Table 2: Mean daphnia magna density (individuals L^{-1}).

Treatment	Without Predator	With Predator
Control	28.5 ± 3.1	18.2 ± 2.4
Constant Warming	26.7 ± 3.5	14.6 ± 2.1
Fluctuating	24.9 ± 4.2	13.8 ± 2.6
Extreme Pulse	22.3 ± 4.8	12.5 ± 3.0

The table 2 presents the average density of *Daphnia magna* (individuals L^{-1}) during the presence and absence of predators subjected to various thermal regimes. However, in all the treatments, zooplankton density is always greater when predators are absent, which confirms a high level of top-down control by *Notonecta glauca*. The density of *Daphnia* is gradually reduced with control compared to extreme pulse treatments, suggesting that increasing thermal stress has a negative effect on population abundance. The overall impact of high temperature and predation is the lowest densities occurring at the extreme pulse condition, indicating that extreme temperature enhances the predator effect. Values are given in the form of standard deviation, which represents variation between replicates.

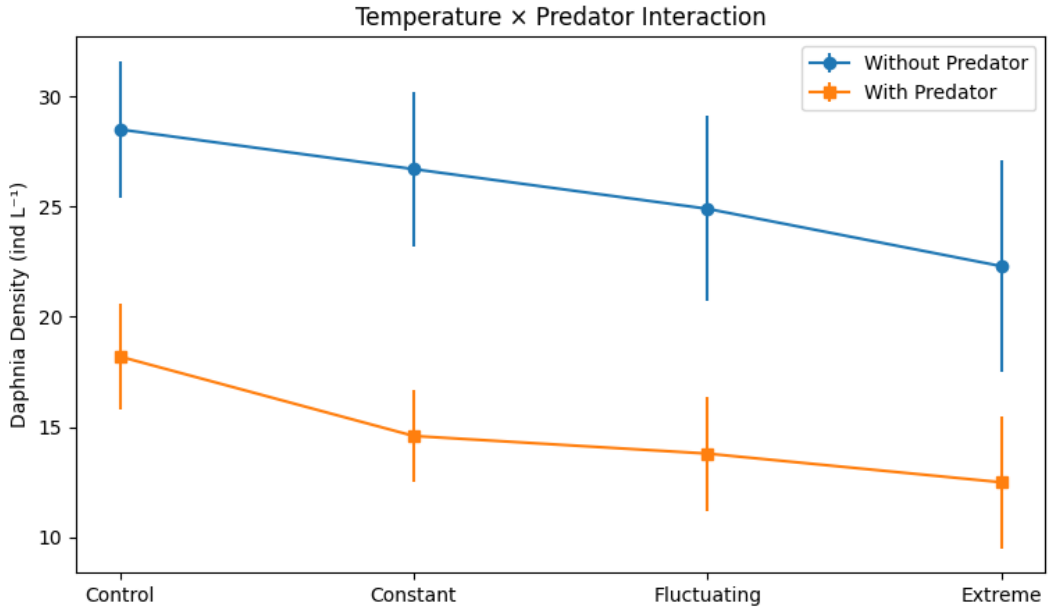

Figure 3: Interactive effects of temperature and predation on *daphnia magna* density.

In figure 3, the interaction between temperature and predator presence is plotted in relation to *Daphnia magna* density. In all thermal treatments, the density of zooplankton is always greater without predators, which supports the high level of top-down control. An increase in temperature results in a slight decrease in density of the predator and the non-predator conditions, and the most intense decrease in density occurs under extreme pulse conditions. This is because the error bars increase as temperature increases, meaning that thermal stress enhances the variability, implying that thermal stress increases the variability in zooplankton populations.

Predator Survival and Activity

In control and constant warming treatments, predator survival was high, and survival rates were greater than 85% over the course of the experiment. Conversely, unstable and extreme pulse treatment caused a decrease in survival, especially after thermal peaks.

The glauca temperature was associated with high activity of *Notonecta glauca*, which showed strong metabolic rates. Nevertheless, there were also times of low activity, indicating thermal stress due to extreme temperatures.

Table 3: Predator survival rate (%) of *notonecta glauca* across thermal treatments.

Treatment	Week 3	Week 6
Control	92%	88%
Constant Warming	90%	85%
Fluctuating	85%	78%
Extreme Pulse	80%	70%

The table 3 provides the survival rate (%) of *Notonecta glauca* at Week 3 and Week 6 at different thermal regimes. Constant temperature conditions prefer predator survival because the highest predator survivors are the control and constant warming treatments. Instead, survival is lowest under extreme and fluctuating pulse conditions and extreme temperature conditions. The gradual reduction between Weeks 3 and 6 in all treatments indicates an increase in thermal stress with time. These findings suggest that thermal variability and extreme temperature events have an adverse effect on the survival of predators, which might undermine top-down control of the trophic system.

Trophic Interaction Strength

Thermal treatments were found to differ greatly in per capita interaction strength. Greater interaction strengths also occurred when keeping the warming constant, suggesting increased predator efficiency. On the contrary, fluctuating and extreme pulse treatments decreased the strength of interaction, probably because of physiological stress and behavioral changes.

The table 4 shows the per capita strength of interaction (OI) of predators at various thermal regimes. Optimal interaction strength is realized at constant warming, with higher predator effectiveness in reducing prey populations at relatively high temperatures. The level of interaction is less in the control treatment, representing the predation level at the baseline in a stable environment.

Table 4: Per capita interaction strength (OI) across thermal treatments.

Treatment	OI Value
Control	0.021 ± 0.004
Constant Warming	0.035 ± 0.006
Fluctuating	0.028 ± 0.007
Extreme Pulse	0.024 ± 0.008

The interaction strength between the fluctuating treatment fluctuates, indicating that the effectiveness of predators is disrupted partially by temperature changes. The weakest interaction strength in the extreme pulse treatment means that thermal stress alters predator performance and decreases top-down control. Represented values are expressed as mean standard deviation, indicating variability between replicates.

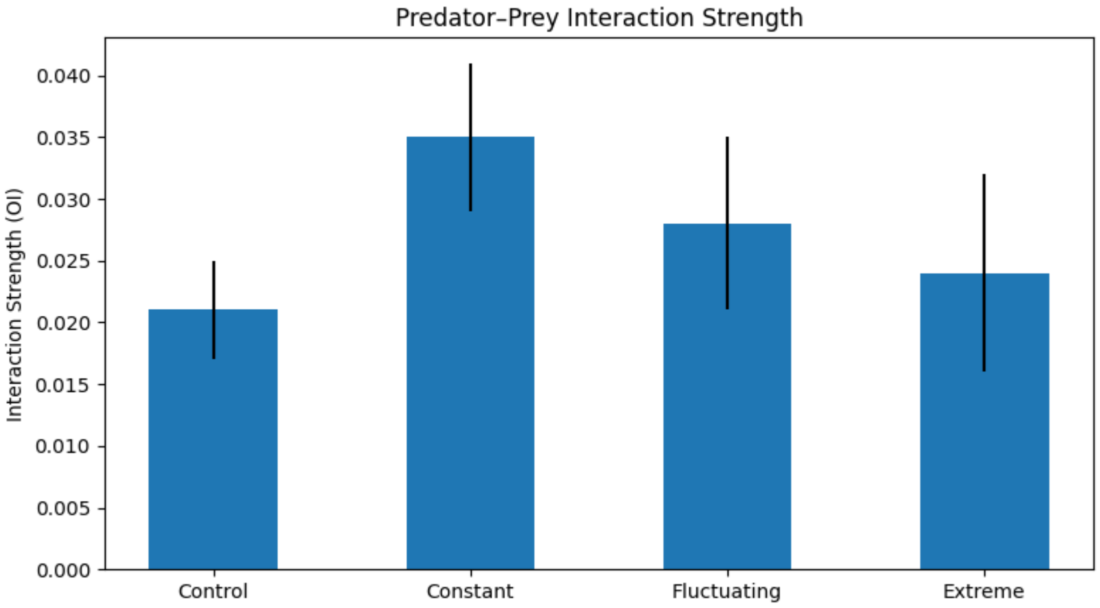

Figure 4: Variation in predator–prey interaction strength across thermal regimes.

The figure 4 shows an example of a change in predator-prey interaction strength (OI) between thermal regimes. The strongest interaction occurs at a constant warming, which means higher predator efficiency at relatively high temperatures. Contrastingly, lower control and extreme pulse treatment values imply decreased predation competence in both stable ambient and thermally stressful environments. The larger dispersion in fluctuating and extreme treatments is evidence of instability in predator performance through a shift in temperature.

Trophic Transfer Efficiency

Trophic Transfer Efficiency was greater with moderate warming than with extreme thermal variability. This implies that stable warming improves the energy transfer efficiency, whereas the thermal extremes interfere with energy transfer across trophic levels.

Table 5: Trophic transfer efficiency (%) across thermal treatments.

Transfer Level	Control	Constant	Fluctuating	Extreme Pulse
Producer → Consumer	18.5	22.7	20.3	17.8
Consumer → Predator	12.2	15.6	13.4	11.9

The table 5 shows the efficiency of trophic transfer (%) between consecutive trophic levels in varied thermal regimes. Producers transfer energy best to consumers through sustained warming, implying a greater grazing performance and use of resources at mid-level warming temperatures. The fluctuating treatment has intermediate values, and the control and extreme pulse treatments have lower values. The same trend can be seen in energy transfer between consumers and predators; whereby maximum efficiency is achieved in warm conditions of constant warming and at the extreme pulse conditions. These findings indicate that, in contrast to thermal variability and extreme temperature events, stable warming boosts energy transfer within the food web, and so does trophic efficiency.

Ecosystem Stability and Non-linear Responses

Ecosystem stability, as a measure of temporal variance of phytoplankton biomass, was significantly different between treatments. The control treatment had the least variance and, thus, was highly stable, whereas the extreme pulse treatment had the largest variability.

The regression of temperature fluctuation amplitude versus ecosystem stability using Gaussian process regression showed a non-linear correlation, with an apparent cut-off at which an ecosystem becomes more than stable.

Table 6: Temporal variance in phytoplankton biomass (σ^2) across thermal treatments.

Treatment	Variance (σ^2)
Control	1.85
Constant Warming	2.74
Fluctuating	4.12
Extreme Pulse	6.38

The table 6 shows the temporal variance (σ^2) of phytoplankton biomass under varying thermal regimes that can provide a measure of ecosystem stability. Control treatment has the least variance, which implies that the biomass of the control treatment has remained relatively constant over time, at constant ambient conditions. The increase in variability with constant warming, and even more with changing temperature, is a measure of increasing instability to thermal variability. The greatest variance is found in the extreme pulse treatment, implying that the episodic heat stress is causing significant variation in the biomass. Generally, there is a decrease in ecosystem stability with increased variability in temperature.

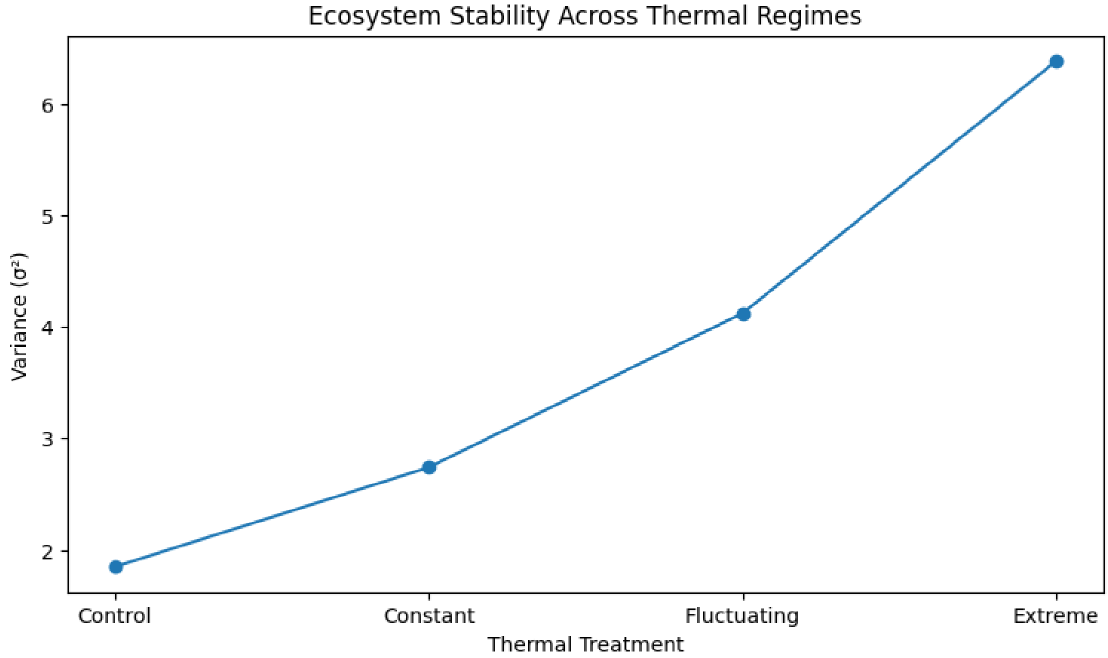

Figure 5: Thermal effects on ecosystem stability.

The figure 5 indicates the change in stability of the ecosystem (σ^2) among the thermal treatments. The variance (between control and extreme pulse) increases gradually as the condition undergoes changes in temperature, implying a decrease in the stability of the ecosystem as the variability of temperatures increases. The extreme pulse treatment indicates an extreme rise, which implicates a threshold response, where episodic heat stress can result in significant instability of phytoplankton biomass.

Discussion

Thermal regimes significantly altered trophic dynamics and ecosystem stability over the six-week experiment. The biomass of phytoplankton grew steadily with constant warming, reaching a value of ~22.8 μg L^{-1} by Week 6, in comparison to comparatively steady values in the control (around ~15.0 μg L^{-1}). In contrast, extreme pulse treatments caused declines (~11.4 μg L^{-1}) and higher variability. Zooplankton (*Daphnia magna*) density decreased with increasing temperature and predator presence, dropping from 28.5 ± 3.1 to 12.5 ± 3.0 individuals L^{-1} under extreme pulse conditions. Predator–prey interaction strength peaked under constant warming (0.035 ± 0.006) but declined under thermal extremes (0.024 ± 0.008). The efficiency of trophic transfer was greatest at the conditions of constant warming (22.7% and 15.6%) and least at the conditions of extreme pulse (17.8% and 11.9%). Stability in ecosystems declined as the variance rose to 1.85 (control) and 6.38 (extreme pulse).

These results suggest that moderate, consistent warming increases the primary productivity, predator efficiency, and transfers of energy among trophic levels.

However, such processes are disrupted by extreme pulse events and especially thermal variability. A reduced stability of phytoplankton under conditions of high and low temperatures reflects the physiological stress of primary producers, and a declining density of the zooplankton reflects both direct thermal stress and the intensity of predation. Although predator function increases with temperature, high temperatures reduce survival capacity, and predictability impairs trophic regulation, even though predator activity increases. The non-linear upward trend in variance has indicated a possible existence of ecological thresholds above which ecosystem stability quickly suffers.

This paper points out that mean warming is not a key and critical driver of ecosystem responses, but instead, temperature variability is a key driver. Limited-time warming of the ecosystem can lead to improvements in ecosystem operations, but intensifying climate extremes could cause food web destabilization, ineffective trophic relationships, and energy imbalances. The findings are especially pertinent to the contemporary climate change conditions, when heatwaves occur more often and more intensely, and may result in less predictable and less resilient aquatic ecosystems.

The experiment was carried out in controlled mesocosm settings, which are not necessarily representative of natural ecosystems, in terms of the diversity of species as well as their migration and adaptation over time. The experimental time scale was quite low, which restricted the information on the ecological responses in the long term. Also, the variability of such environmental factors as nutrient availability was not explicitly considered.

Longer-term experiments and multi-species communities should be included in future work to more closely represent natural systems. The ecological realism would be enhanced by investigating combined stressors (e.g., temperature, nutrients, and oxygen). Mechanistic or predictive model analysis might be useful to determine tipping points and predict ecosystem responses to future climate conditions.

Conclusion

This paper discussed the response of various thermal regimes, including stable warming and extreme temperature pulses, on the trophic interactions, energy flow, and stability of the ecosystem in freshwater systems. To persist in the face of climate change, which is on the rise, it is essential to understand these dynamics as the average temperature and the frequency of extreme events are rising. The overall finding of the results is that the moderate, constant warming improves ecosystem functioning, whereas thermal variability and extreme events disrupt trophic dynamics. Primary productivity was improved as phytoplankton biomass steadily rose under constant warming to an average of ~22.8 µg L^{-1} versus ~15.0 µg L^{-1} in the control. Extreme pulse conditions, by contrast, decreased biomass to ~11.4 µg L^{-1} and produced increased variability. Combined thermal stress and predation resulted in a significant decrease in zooplankton density, reducing it by a factor of 28.5 ± 3.1 to 12.5 ± 3.0 individuals L^{-1}. The strength of predator-prey interaction was greater when the warming was constant

(0.035 ± 0.006) than when the warming was extreme (0.024 ± 0.008). On the same note, the efficiency of trophic transfer was higher in conditions of constant warming (22.7% and 15.6%) and reduced in extreme pulse conditions. There was a significant decrease in ecosystem stability, as the variance was 1.85 in the control and 6.38 in the extreme. The primary lesson is that warming driven by variability in temperatures but not by a mean temperature increase alone is the major cause of ecosystem responses. Although moderate warming can temporarily improve productivity and trophic efficiency, escalating thermal extremes can disrupt interactions between species, decrease ecosystem stability, and destabilize ecosystems. The next research in this field should be on long-term experiments and multi-stressor experiments, which should include other variables in the environment, like the dynamics of nutrients and oxygen. It will be imperative to develop predictive models to detect ecological thresholds in order to forecast ecological responses and guide adaptation to climate change.

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