**Temperature and predation alter metabolic scaling without changing size-based structure community in freshwater macroinvertebrates**

Vojsava Gjoni1,2, Douglas S. Glazier3, Justin Pomeranz4, James Junker5, Jacob Woelber1, Aria Smith1, Staci Reynolds1, Trevor Welch1, Jeff S. Wesner1

*1Department of Biology, University of South Dakota, Vermillion, SD, USA*

*2Institute forMarine Biological Resources and Biotechnology of the National Research Council, Mazzara del Valo, Italy*

*3Department of Biology, Juniata College, Huntingdon, PA 16652, USA*

*4Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, Colorado, USA*

*5Department of Biological Sciences, University of North Texas, Denton, Texas, USA*

**Abstract**

Body size plays a fundamental role in structuring ecological communities, shaping processes such as metabolism, abundance, and species interactions. Metabolic theory predicts a universal scaling of metabolic rate with body mass, yet growing evidence suggests that the scaling exponent is environmentally sensitive. In particular, both temperature and predation can drive deviations from canonical expectations, with potential shift in size–abundance relationships. However, most existing studies focus on individual species or populations, leaving a gap in understanding how these dynamics unfold at the community level. We conducted a mesocosm experiment manipulating temperature and predator presence in freshwater macroinvertebrate communities. Our results show that metabolic scaling is highly responsive to environmental context: heating increased the metabolic scaling exponent in predator-free communities but decreased it in the presence of fish predators. These opposing responses suggest that large individuals reduce activity under predation risk, particularly at higher temperatures, leading to shallower scaling. Despite these changes, the slope of the size–abundance relationship remained stable across treatments, indicating that shifts in individual metabolic scaling did not translate into altered community size structure. These findings highlight the flexibility of metabolic scaling under realistic ecological conditions, while suggesting that links between metabolism and size-abundance relatinoship may be weaker or more complex than previously assumed**.**

**Introduction**

Body size plays a pivotal role in shaping ecological dynamics, influencing key processes such as metabolism, reproduction, and species interactions across biological scales (Peters 1983; Brown et al. 2004; Savage et al. 2004). A central framework explaining these patterns is the metabolic theory of ecology (MTE), which posits that an organism’s metabolic rate (R) scales with body mass (M) following a power-law relationship: R = aMb. The exponent b is generally expected to approximate ¾, a value theoretically derived from models describing internal resource transport networks (West et al. 1997; Banavar et al. 2010). This scaling rule has been widely used to predict how energy flows from individuals to populations and entire ecosystems (Brown et al. 2004; Allen et al. 2005; Ernest et al. 2003).

Nonetheless, empirical work has increasingly shown that the exponent b is far from universal. It often varies across taxa, environments, and life stages (Glazier 2005; White et al. 2007; Killen et al. 2010; Gjoni et al. 2020; Glazier et al. 2020). In aquatic macroinvertebrates, for instance, metabolic scaling can shift in response to both temperature and predation pressure, often becoming shallower than the canonical ¾ expectation (Glazier et al. 2011; Gjoni et al. 2020). These observations suggest that ecological conditions can significantly influence metabolic allometry, revealing flexibility in a trait once considered physiologically constrained.

These variations in metabolic scaling have important implications for the size–abundance relationship—the well-established pattern where smaller organisms tend to occur at higher densities than larger ones (Damuth 1981; Marquet et al. 1990). Assuming energy use is equal across size classes, shifts in b should map directly onto changes in size-abundance relatinoship under equilibrium conditions (Enquist et al. 1998; White et al. 2007; Malerba & Marshall 2019). Yet, the link among matebolic scaling and size-abundance relationship themselve is not fixed empirically. Recent work by Malerba and Marshall (2019) demonstrated that even within a single species, evolutionary changes in body size can decouple metabolic scaling from abundance patterns, underscoring how energetics and demography interact in more nuanced ways than previously assumed.

Environmental temperature adds further complexity to this picture. Rising temperatures elevate metabolic demand through basic biochemical processes (Gillooly et al. 2001), but they can also shift the scaling relationship itself via size-specific physiological and behavioral responses (Killen et al. 2010; Gjoni et al. 2020). Moreover, temperature influences body size more directly through well-documented plastic responses, such as the temperature–size rule (Atkinson 1994; Forster et al. 2012; Saito et al. 2021; Perkins 2021). Warmer environments tend to produce smaller-bodied individuals, especially among ectotherms, and this shift can alter community-level body size distributions. Consequently, these size reductions may influence \lambda, linking thermal conditions to both metabolic scaling and SARs (Malerba & Marshall 2019).

Predation, especially when is size-selective, add another layer of ecological influence. In many systems, larger individuals are more susceptible to predation, which can lead to population and community shifts toward smaller body sizes (Brose et al. 2006; Emmerson & Raffaelli 2004). This process not only affects size–abundance patterns directly but can also reshape metabolic scaling by selecting for reduced activity or slower growth among larger individuals. Studies on amphipods show that exposure to fish predators induces size-dependent physiological adjustments: large individuals tend to suppress metabolic activity to avoid detection, while smaller individuals remain more thermally responsive (Glazier et al. 2020; Gjoni et al. 2020).

These behavioral and physiological responses align with a plausible adaptive explanation. In the presence of predation risk, larger individuals maintain lower metabolic rates to reduce exposure, particularly under warmer conditions where predator detection or encounter rates may increase (Dell et al. 2014). Meanwhile, smaller individuals—less likely to be targeted—can afford to increase metabolic output with rising temperatures. This pattern explains why, under predator presence, the scaling exponent b decreases: small individuals ramp up metabolism, while larger ones suppress it. In contrast, when predators are absent, both large and small individuals show similar metabolic increases with temperature, resulting in a more stable exponent.

Taken together, these findings suggest a dynamic and context-dependent link between metabolic scaling and size–abundance structure—one shaped by the interplay of thermal conditions and biotic interactions. However, despite growing evidence, most studies have examined these processes at the level of single species or isolated populations. As a result, we still lack a clear understanding of how these mechanisms play out at the community level, where species with different size profiles and ecological traits interact simultaneously (Glazier 2014; Malerba & Marshall 2019). In particular, empirical studies that explicitly connect temperature- and predation-driven changes in metabolic scaling to shifts in community-wide size–abundance relationships remain scarce.

To address this gap, we conducted a mesocosm experiment manipulating temperature and predator presence in freshwater macroinvertebrate communities. Our aim was to evaluate how these environmental drivers affect metabolic scaling exponents and in turn, community body size distributions. Specifically, we tested: (i) how does ecological context influence *b* at the community scale? and (ii) do changes in *b* predict shifts insize-abundance relationship? By linking individual-level energetics with emergent community structure, our work contributes to a more nuanced and ecologically grounded understanding of metabolic theory under environmental change.

**Materials and methods**

*Study Site*

Data was collected at the University of South Dakota’s Experimental Aquatic Research Site, Vermillion, SD. The site consists of 24 fiberglass tanks (1136 L). The tanks were filled with 714 L of water over a mix of cobble and sand for substrate in May of 2023. Water levels were monitored and maintained over the course of the experiment. Each tank had an overflow spout and a magnetic drive water pump (Danner Supreme Aqua-Mag). Local populations of macroinvertebrates colonized the tanks via oviposition before data collection occurred in late June. AQQA Aquarium 800W Heaters (AQQA Inc.) were placed in half of the tanks and set to ~5 degrees C above ambient nighttime temperatures. Temperature data were taken daily in the middle of the water column using a YSI Pro-Series DSS (YSI Inc., Yellow Springs, OH, USA). Heaters were adjusted to maintain a temperature of ~5 degrees C above ambient. Fish (Lepomis cyanellus) were gathered from a local pond with a seine net and set free in half of the tanks (one fish per tank). The four treatment groups included ambient temperatures with fish, ambient temperatures without fish, heated with fish, and heated without fish.

*Metabolic rate measurments*

Metabolic measurements occurred 30 days after treatments were started. A Hess sampler (0.032 m2, 500 um collection mesh) was used to sample benthic macroinvertebrates following the methods of Henry & Wesner (2018). Macroinvertebrates from the sediment were sorted and placed in containers with filtered water from their corresponding treatment and held without food for 24 hours to empty their guts. After 24 hours, they were separated into individual glass vials with 20 mL of oxygenated, filtered water. Nine vials with a macroinvertebrate and one without (to correct for oxygen changes not due to respiration) were used for each run of measurements. Two O2 readings were taken an hour apart with each vial using a Fibox 4 oxygen sensor (Presens, Regensburg, Germany). The macroinvertebrates were then photographed (lengths measured using ImageJ) before being dried and measured on a microbalance. Oxygen consumption was estimated using the following equation:

*PE* and *PC* represent partial pressures of oxygen in the experimental environment (20 mL vials) and control, respectively, *S* is the solubility coefficient of oxygen in water, *A* is the volume of 1 mol O2 at standard temperature and pressure, *V* is the volume of water in the vials, and t is the time of incubation.

To ensure accurate results, preliminary testing was performed to see how long it would take for a visible drop in dissolved oxygen content to occur. This determined the 60-minute time span between measurements. During the experiment, macroinvertebrates were kept in water that corresponded to their respective treatment.

*Individual Size Distribution*

On the last day of the experiment, we collected benthic macroinvertebrates with a 0.09 m2 Hess sampler. The sampler was forced through the sediment and rock substrate so it was flush with the bottom of the mesocosm. Then we disturbed the substrate by hand for 10 seconds and flushed the substrate through a 250 𝜇m mesh net (Wesner 2010, Henry andWesner 2018). The sample was then placed on a 250 𝜇m sieve, large debris (e.g., rocks) was scrubbed and removed, and the remaining sample was preserved in 95% EtOH. To measure body sizes of benthic macroinvertebrates, we sorted a subsample and retained the first 200-500 individuals. This approximates the number of individuals in simulation studies for which estimates of individual size distributions stabilize (Wesner et al. 2024). These individuals were placed on a gridded watch glass, photographed, and measured for length to the nearest pixel using ImageJ. The pixels were converted to mm using the grid as a reference and adjusting for changes in magnification. Then the dry mass (mg) of each individual was determined using family-specific length-mass equations (Benke et al. 1999).

**Results**

Metabolic scaling exponents were more responsive to both heating and predation treatments (Figure 1b; Table 1). In the presence of fish predators, heating caused a clear reduction in the metabolic scaling exponent, from 0.46 under ambient conditions to 0.35 under heated conditions. This pattern is consistent with a suppression of metabolic rate in larger individuals, as previously hypothesized in predator-sensitive taxa. In contrast, when fish were absent, heating increased the metabolic scaling exponent substantially, from 0.31 at ambient temperature to 0.45 under heated conditions. These opposing trends demonstrate a strong interactive effect of temperature and predation on the metabolic scaling relationship.

The slope of the size–abundance relationship (𝜆) remained largely consistent across both temperature and predation treatments (Figure 1; Table 1). Across all experimental conditions, 𝜆 values ranged narrowly between –1.63 and –1.56, with overlapping credible intervals indicating no meaningful differences. Specifically, neither warming nor the presence of fish predators significantly altered the value of 𝜆. This suggests that, despite changes in community temperature and predator cues, the overall structure of abundance relative to body size remained stable. Thus, while temperature and predation clearly influenced individual metabolic scaling (see below), these effects did not directly translate into detectable shifts in community-level size–abundance patterns.

Together, these results support the hypothesis that warming increases metabolic rate scaling in the absence of predator risk, but that this effect is reversed when predators are present. This context dependence highlights the plasticity of metabolic scaling and its potential to influence community structure. Moreover, the parallel shifts in 𝜆 and metabolic scaling slopes across treatments suggest a mechanistic link between individual-level energetics and emergent size–abundance patterns at the community level.

A graph showing different types of scales

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**Figure 1** – *Effects of temperature and predation on size–abundance scaling (λ) and metabolic scaling slopes in freshwater macroinvertebrate communities.* Violin plots show the posterior distributions (mean ± 95% credible intervals) of (a) the size–abundance relationship slope (λ) and (b) the metabolic scaling slope across four treatments in a factorial experiment: Ambient vs. Heated temperature, crossed with presence vs. absence of fish predators. Color indicates treatment group: light and dark gray for fish-present treatments under ambient and heated conditions, and light and dark orange for no-fish treatments. While heating did not alter λ (panel a), it significantly influenced metabolic scaling (panel b), with contrasting effects depending on predation regime. Specifically, heating reduced the metabolic scaling slope in the presence of fish but increased it in their absence, indicating interactive effects of temperature and predation on metabolic allometry, independent of changes in community size structure.

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**Main Discussion Points**

1. The study shows that metabolic rate scaling with body mass is not fixed, as predicted by the Metabolic Theory of Ecology (MTE), but is highly responsive to environmental conditions. Both temperature and predation had significant, yet opposing, effects on metabolic scaling.

2. In predator-free environments, warming increased the metabolic scaling exponent — suggesting that larger individuals increased their metabolism in response to heat. In the presence of fish predators, warming decreased the scaling exponent — indicating that larger individuals suppressed their metabolism, likely to reduce detection risk under high temperatures.

3. Despite significant changes in metabolic scaling, the size–abundance slopes (λ) remained consistent across all treatments. This suggests that individual-level metabolic shifts did not translate into community-level structural change, decoupling metabolism from abundance patterns — a challenge to the classical MTE framework.

4. The opposing patterns of metabolic scaling are interpreted as adaptive behavioral responses: Large individuals reduce activity in high-risk, heated conditions. Small individuals, facing less predation risk, are free to increase metabolic activity in warmth. This aligns with previous findings on amphipod responses to predation and temperature (e.g., Glazier et al. 2011, 2020; Gjoni et al. 2020).

5. A critical insight from this study is that macroinvertebrates colonized the mesocosms naturally, creating a realistic, self-assembling community. Because of this continuous recruitment and natural community cycling, community structure remained robust against both heating and predation treatments. This natural dynamic likely buffered the system from structural shifts — even though metabolic processes at the individual level changed.

6. These findings reinforce the idea that metabolic scaling is flexible, influenced by thermal conditions, species interactions, and behavioral strategies. They question the universality of MTE’s assumptions and emphasize that predicting ecological responses to warming requires integrating biotic context and community dynamics — not just temperature effects in isolation.