

Mean temperature, fluctuation magnitude, and level of biological organization affect
biological responses amidst thermal variability: a meta-analysis

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Acknowledgements

The future is bright, the future is dark
Time stands still, yet flies like a lark
Memories endure and memories fade
People are rough, yet smooth like suede
The days seem long, the days seem short
It rains all year, until the sunshine retorts
Reed is an experience, Reed is a place
Reed is a journey of learning how to keep pace
Reed is a individual, Reed is a kollektive
Reed is space for being reflective
Reed is the present, Reed is the past
Reed is the net for our future that we cast
To those from Reed
To those from before
To those from the outside
To those at the core
To those I still talk to
To those I talk to no more
To those still here today
To those who now soar
A few words of dear thanks. . . .
Thank you for the laughs, the tears, the screams
Gratitude for the late nights, the dancing, the dreams
Thank you for the walks, the talks, and meals together
Many thanks for the shenanigans I'll cherish forever
Thank you for the compassion, for the coffee and tea
Appreciation for the love, the hate, and learning to be
Thank you for the support, and most ardently, for embracing me

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Abstract

Ecosystems and organisms have experienced variation on many temporal scales, including diurnal changes in light availability, seasonal changes in temperature, and decadal changes in weather patterns. Though scientific literature has continued to highlight the importance of ecologically relevant studies for understanding the persistence and dynamics of ecosystems, there has yet to be a quantitative review of how variability impacts biological responses across taxa and scales of biological organization. Here, we present a quantitative meta-analysis of how thermal variability impacts biological responses across multiple taxa, organism sizes, and levels of biological organization. Our results suggest that the range of temperatures an organism experiences is the most important driver of response magnitude, with the interaction of mean temperature and fluctuation range emerging equally as significant predictors in our model of biological responsiveness to temperature variability. Further, our results also suggest that level of biological organization is a less important, though statistically significant, predictor of organismal responses.

Introduction

Placeholder

- 0.1 The historical significance of variability**
- 0.2 Relevant significance of variability today**
- 0.3 Why this study on variability matters**

Chapter 1

Background

Placeholder

1.1 Environmental variability

1.1.1 Mean

1.1.2 Amplitude/Range

1.1.3 Duration

1.1.4 Predictability

1.1.5 Link between temporal and spatial variability

1.2 Temperature variability

1.2.1 What is temperature variability?

1.2.2 Why is temperature variability important to ecological processes?

1.2.3 Jensen's Inequality and its impacts on metabolic rate

1.2.4 Relevancy of thermal variability in the modern context

1.3 Objectives, driving questions, hypotheses

Chapter 2

Methods

Placeholder

2.1 Data extraction and analysis

2.2 *Metafor*

Chapter 3

Results

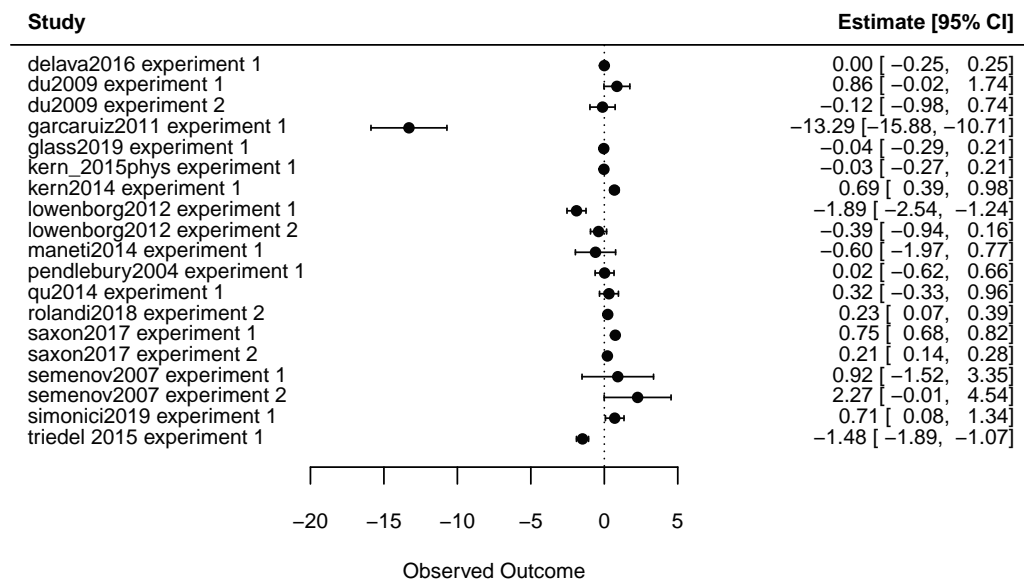


Figure 3.1: Forest plot of effects sizes by study and experiment within a study. Data indicate that both within and across studies, there were a wide range of effect sizes, likely due to experimental design (including fluctuation range, mean temperature, etc.) Each point represents an average of SMD for multiple responses within each experiment in a single study. Accordingly, the error bars represent an average of variance across multiple responses within a single experiment.

Overall, even our simple model demonstrated that the intercept was not significant but there was significant heterogeneity across studies ($n=140$, $z= 0.79$, $p < 0.0001$),

as demonstrated by Figure 3.1. These results allowed us to reject the null hypothesis that there are no significant differences between SMD across the studies included in analysis (see Appendix Figure 1). This then allowed us to proceed in further detail how different covariates were influencing the effect sizes specifically.

Our full model, including 7 covariates (all covariates in Table 2.2, an additional interaction term between fluctuation range and mean temperature, and excluding thermal stress), responses were still significantly different from each other when accounting for the nested structure of responses, experiments, and studies ($QM = 191.3722$, $df = 7$, $p < 0.0001$). Further, fluctuation range and the interaction term between fluctuation range and mean temperature were statistically significant in the model ($n=140$, $df = 7$, $p < 0.00001$). Organization level was also important in the model, as a statistically significant covariate ($n=140$, $df = 7$, $p < 0.05$).

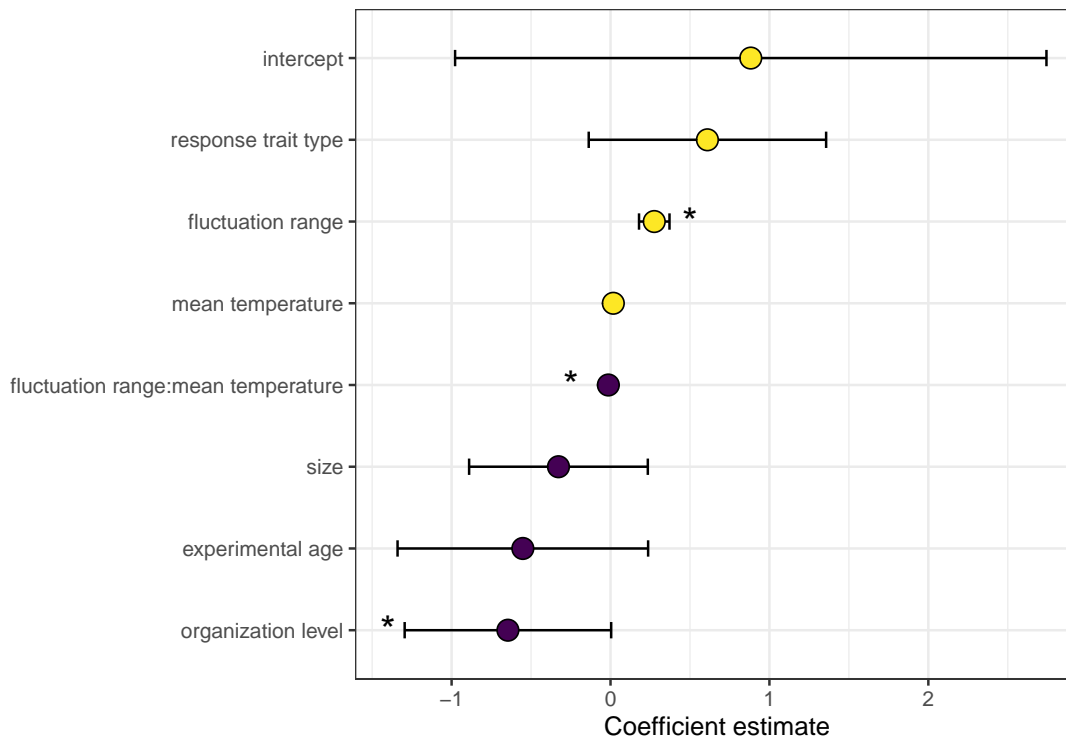


Figure 3.2: Coefficient estimates for each covariate in the full model, where * signify statistically significant model predictors. Error bars represent 95 percent confidence intervals. Yellow indicates a positive coefficient estimate, purple indicates a negative coefficient estimate.

Fluctuation range had a positive estimate while the interaction term between range and mean temperature was only slightly negative, both of which were statistically significant ($n=140$, $df=7$, $p < 0.001$ level (Figure 3.2). The most negative estimate, organization level ($n=140$), was also significantly influential in our model ($n=140$, $df=7$, $p < 0.05$). The additional negative estimates of our model coefficients, experimental age and size, were not statistically significant. In our analysis of thermal stress via a separate random effects model, we found thermal stress was not statistically significant ($n=132$, $df=1$, $p = 0.4855$) in explaining the effect size (Table 3.1).

Table 3.1: Model summary statistics for random effects model using thermal stress as sole modifier

Term	estimate	se	zval	pval	ci.lb	ci.ub
intercept	0.2050	0.1846	1.1104	0.2668	-0.1568	0.5669
stressful	-0.0489	0.0702	-0.6975	0.4855	-0.1864	0.0886

The interaction between fluctuation range and mean temperature as well as effect size is best displayed in Figure 3.3. At lower mean temperatures, higher fluctuation ranges generally have a more positive effect on organism responses and performance, though that trend starkly ends at about 24°C. However, at higher mean temperatures, lower fluctuation ranges appear to have an equally positive and negative effect on organism responses and performance (Figure 3.3).

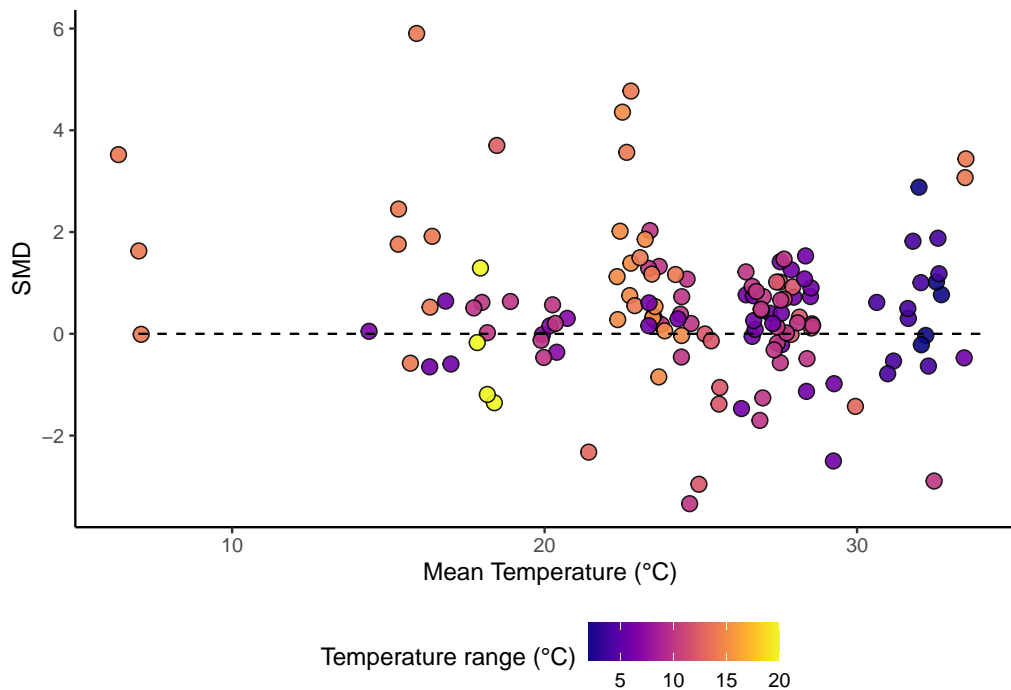


Figure 3.3: Scatterplot describing the relationship between mean temperature, temperature fluctuation range, and SMD. Temperature fluctuation ranged from 0-20°C, mean temperature ranged from 7-33°C. SMD ranged from -4 to 6, restricted based on the distribution of SMD to minimize impact of outliers (see Appendix Figure 2).

The trend between organization level and temperature fluctuation range, suggests that populations perform better at higher fluctuation ranges than organisms (Figure 3.4). Interestingly, there were not any significant differences between thermal stress (Figure 3.5), life history metric (Figure 3.6), body size (Figure 3.7), or age (Figure 3.8).

When we excluded one highly influential study and included thermal stress in the exclusion model ($n=132$), size became much more important in the exclusion model ($df=8$, $p < 0.001$) as did mean temperature ($df=8$, $p < 0.001$). Organization level, fluctuation range, and the interaction between fluctuation range and mean

temperature became insignificant in the exclusion model ($df=8$, $p < 0.1$).

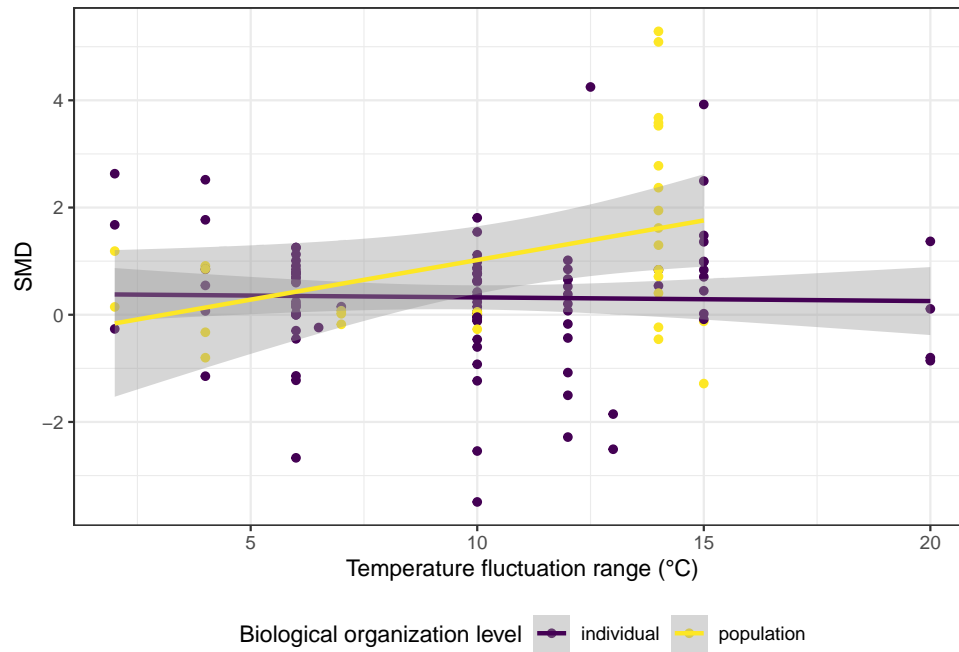


Figure 3.4: Linear regression of SMD across temperature fluctuation ranges from 0 to 20°C, colored by organization level: individual or population level responses reported in studies.

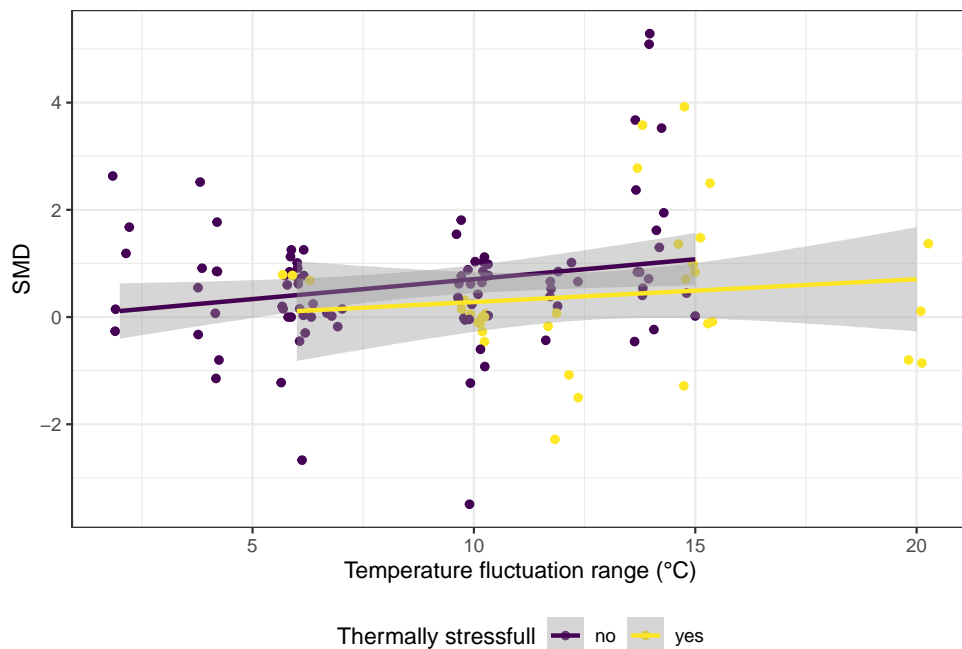


Figure 3.5: Linear regression of SMD across temperature fluctuation ranges from 0 to 20°C, colored by thermal stress.

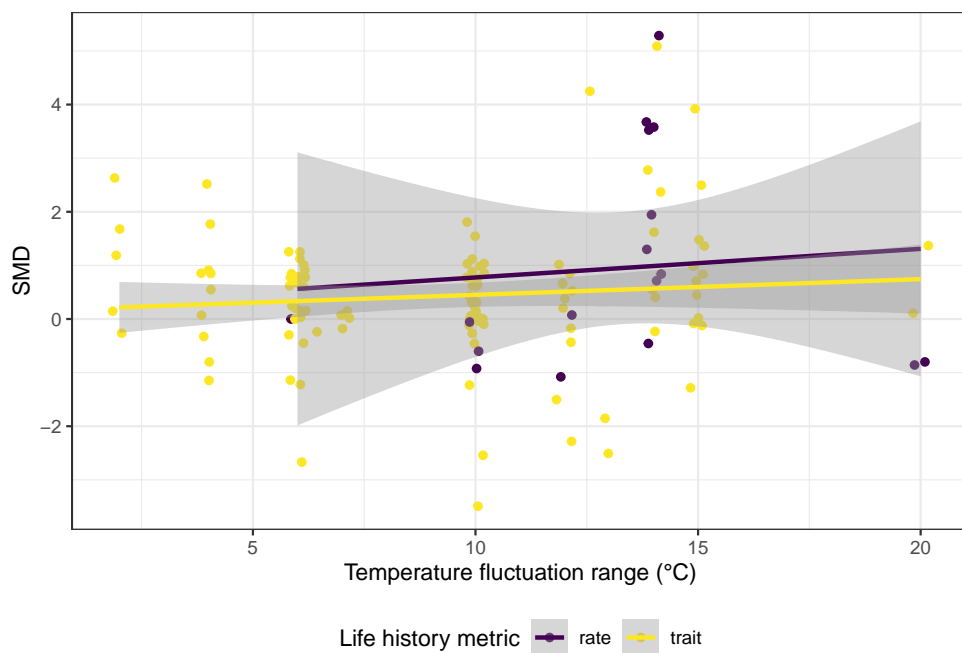


Figure 3.6: Linear regression of SMD across temperature fluctuation ranges from 0 to 20°C, colored by life history metric: responses categorized as rate or trait.

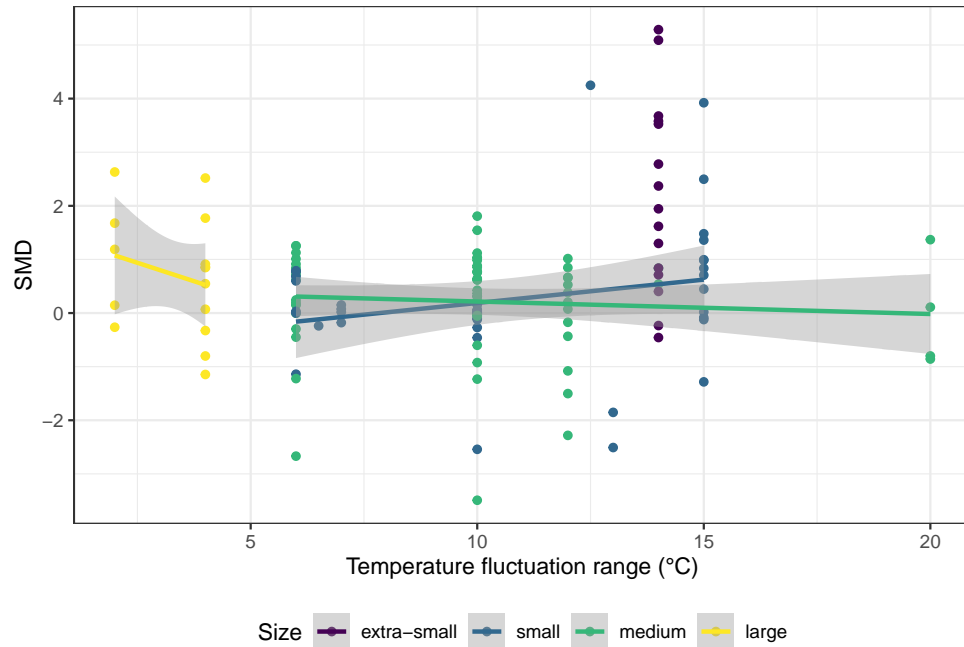


Figure 3.7: Linear regression of SMD across temperature fluctuation ranges from 0 to 20°C, colored by body size: extra-small, small, medium, or large.

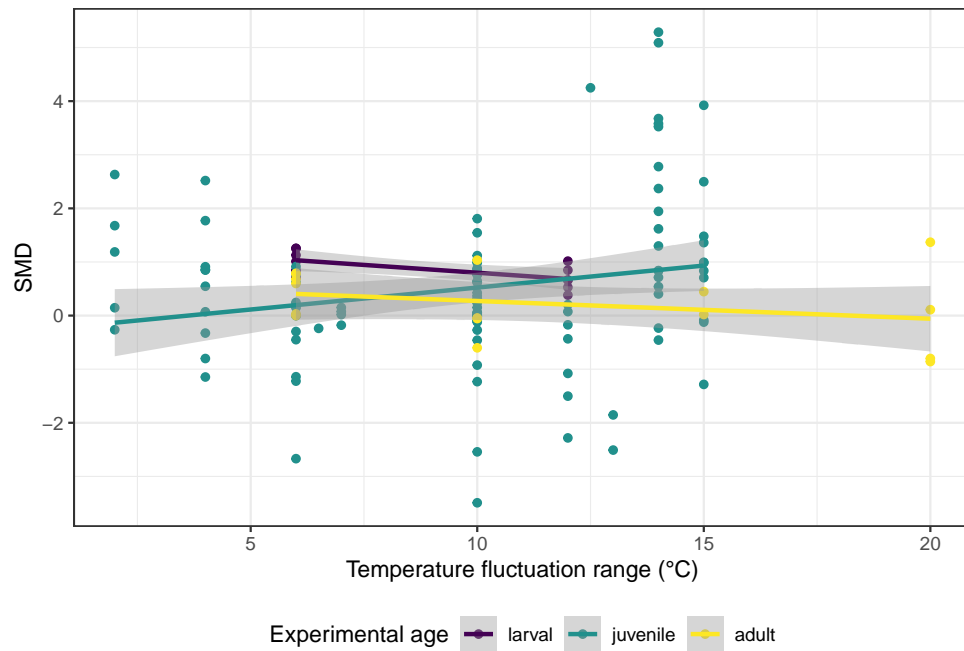


Figure 3.8: Linear regression of SMD across temperature fluctuation ranges from 0 to 20°C, colored by experimental age: larval, juvenile, or adult.

Chapter 4

Discussion

The results of this meta-analysis suggest that fluctuation range is of significant importance to performance, both at the individual and population level. There were not overall differences in the direction of thermally variable environments positively or negatively impacting performance relative to constant environments. However, a considerable amount of variation exists in whether thermally variable environments positively, negatively, or minimally impact performance across studies. Our model results highlight the importance of fluctuation range, mean temperature, and organization level to better understand the variety of effects thermal variation has on organismal responses. These results suggest that mean temperature and fluctuation range must be considered together when understanding the impacts of environmental variability, i.e. higher fluctuation ranges at lower mean temperatures generally have higher effect sizes compared to higher and lower effects sizes of lower fluctuation ranges at higher mean temperatures. The ways in which organisms, populations, and communities have dealt with natural disturbances has become even more significant in the face of climate change (Sunday, Bates, & Dulvy, 2012; Vasseur et al., 2014). With global mean temperatures expected to exceed the crucial 2 degree centigrade threshold scientists have deemed “the point of no return” (Russill & Nyssa, 2009), understanding how organisms will cope is key for understanding how ecosystem composition will change at all scales in the next several decades (Cheung, Close, Lam, Watson, & Pauly, 2008; West, Woodruff, & Brown, 2002). In this context, perhaps the range of temperatures experienced is of greater importance to predictions of performance under future conditions than simply mean temperature (Vasseur et al., 2014).

These findings underscore the significance of better understanding why differences across studies and experimental designs occurred. Jensen’s inequality is one way to

conceptualize why responses differ, as averaging nonlinear responses linearly will not accurately predict anticipated performance, in fact, it will underestimate performance (Bernhardt, Sunday, Thompson, & O'Connor, 2018; Ruel & Ayres, 1999). The ramifications of underestimating performance and not accounting for environmental variability are innumerable, the biggest of which may be our inability to gauge the critical tipping point for many species' ability to survive. Acclimation may also explain differences in response across studies as the scale on which variation occurs influences how organisms may respond. If organisms' non-genetic phenotypic changes lag behind environmental changes but outpace changes in the constant environment (e.g. inducing gradual plasticity), acclimation duration may explain mismatches in responses across studies (Kremer, Fey, Arellano, & Vasseur, 2018). In terms of variability pattern, if an organism experiences environmental variability in uneven intervals, acclimation to previous conditions could explain increases or decreases in performance. Rapid evolution could further explain differences in responses across studies. If organisms are able to keep evolutionary pace with environmental changes via genetic phenotypic changes, responses could be positively affected, as demonstrated in predator-prey system dynamics (Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003). It is important to note that rapid evolution will only be relevant to population levels responses and not individual level responses.

Equally as interesting as the significant model coefficients were the insignificant model coefficients: body size, thermal stress, life history traits, and experimental age. Body size has been identified as important in the allometric scaling of MTE and it is interesting that in these subsets of studies, body size did not explain the differences in responses across studies. This could simply be because we had a small sample size of studies ($n=15$). Though multiple responses within each study contributed to a large sample of effect sizes ($n=140$), there were only a subset of relative body sizes included. It could also provide support for the argument against allometric scaling in MTE, such that there only individualized trends amongst taxonomic groups as opposed to general trends across individuals, populations, and communities of organisms (Clarke, 2006; Clarke & Johnston, 1999). This theory may also explain why thermal stress was not a significant predictor in our model, if MTE does not aptly describe the patterns that variability in temperature drives.

An important side note is that our full model and thermal stress model differed in the number of studies, as one study, García-Ruiz, Marco, & Pérez-Moreno (2011), did not have any supplemental information on thermal performance curve points for the taxa used in that study (*Xylotrechus arvicola*). Further, this study happened

to contribute highly influential points to our model and subsequent analysis, as our model results change drastically when excluding García-Ruiz et al. (2011) from our full model. We decided to include this study in our analysis because data were extracted from a table, therefore there were no inaccuracies in obtaining the data. It provides an important counter and discussion for how and why responses from different studies may be so different from others.

While body size and thermal stress emerging as not statistically significant coefficients in our model may contradict MTE and its allometric scaling component, an additional analysis, with explicit masses for each of these organisms, would better explore the relationship between thermal variability and MTE. If we were able to obtain additional information about the CTmax, CTmin, thermal breadth, and tolerance range for each of the species included in the analysis, we may also be able to better understand the trends and the significance of variability patterns in dictating responses.

Both the type of response (i.e. whether it was a rate or trait) and experimental age were also not important predictors in our full model. We expected rates and traits to have different effects, as traits may be more heavily affected by variability because they are not as temporally dynamic as rates. The lack of difference between rates and traits may be because variability is not differentially acting on rate or trait based responses, simply dampening their overall effects. Again, this may be an artifact of having a small sample size, with mainly trait based responses as opposed to rate based responses.

We also expected for experimental age to be an important predictor, as the time period in which an organism experiences thermal variability has been demonstrated to be important for organisms like turtles, relying on TSD for development (Bowden and Paitz 2018). This may again be the result of studies not focused on the larval stage of development, but instead on the juvenile stage. However, there have been meta-analyses, both qualitative (Massey, Holt, Brooks, & Rollinson, 2019), and quantitative (Noble, Stenhouse, & Schwanz, 2018), that explicitly looked at the effects of incubation temperature on reptile development, concluding that there is a moderate to large effect of incubation temperature on the magnitude of response (Noble et al., 2018). These results align with patterns of juvenile organisms (e.g. fish) routinely having higher CTmax values than adults, such that life stage during experimental duration is of importance to thermal tolerance and performance (Moyano et al., 2017; Portner & Farrell, 2008).

Beyond the data included in our meta-analysis, it is also important to note that

there was little variety in the pattern of variation (diurnal, colored noise, etc.) as was initially a question of interest for this project. Diurnal cycles are more correlated than reddened cycles, like seasonal temperatures (Figure 1.3). It is surprising that so many thermal variability studies are focused on diurnal cycles, when in fact, longer-term temperature patterns are more stable than diurnal cycles, and less autocorrelated. Are these diurnal temperature fluctuations accurate for what is expected under natural conditions? This lack of variety in pattern may be due to a lack of consensus on the language used to classify and discuss thermal variability. Though there is a large body of literature that investigates temperature variation, there appears to be dissonance in the scientific literature about the language used to discuss such variation. Many of the background papers pulled from the systematic literature search used temperature variation to mean just different temperatures (Amarasekare & Savage, 2012) as well as different ranges of temperature, both of which are different concepts. For instance, Amarasekare & Savage (2012) addressed the need for more complexity when we think about the processes underlying temperature dependent fitness, as fitness is an amalgamation of interactions between different life-history traits. Though temperature variation appeared in the keywords of the article, there was little to no mention of actual thermal variation or variation pattern. Additionally, a subsection of the papers included in our search specifically defined thermal variability as short term changes in temperature, though these studies were mainly focused on explicitly ecologically irrelevant thermal regimes (Colinet, Rinehart, Yocum, & Greenlee, 2018; Colinet, Sinclair, Vernon, & Renault, 2015). Using standardized language to describe specific patterns or durations of variability may be helpful in better summarizing the results and conclusions from previous studies.

Many of these studies failed to justify why certain temperatures were chosen as mean temperatures as well as the range of temperatures studied. In order to compile information on the thermal stress of each of the organisms included in the studies of this meta-analysis, additional resources were needed (see Appendix Table 1). Understanding where these organisms' performance falls in relation to temperature on its TPC is crucial for drawing reliable conclusions of how thermal variability affects performance. Without it, only broad conclusions can be drawn, as have been drawn here, that variability and range affects thermal performance.

Several studies made little to no mention of generation time with respect to duration of their experiments or study organisms used. How organisms' life cycles and life spans interact with and are impacted by fluctuation patterns is important for understanding the layers variation permeates and how organisms respond (Bernhardt,

O'Connor, Sunday, & Gonzalez, 2020). This is also pertinent to the scale at which we study variability, given the overrepresentation of diurnal fluctuation patterns featured in our meta-analysis. Diurnal thermal fluctuations may affect organisms with shorter generation times differentially compared to organisms with longer generation times. The converse is true for seasonal or decadal thermal fluctuations.

The results of this analysis differ from previous attempts to understand variability as they quantitatively address how variability affects organisms across taxa, not simply one group. Understanding how allometric scaling and thermal variability patterns interact is important for predicting realistic organismal responses in the face of variable conditions in the environment.

Conclusions and Future Directions

While there are limitations to the reach of this meta-analysis and its results, it is the first cross-taxa quantitative summary of how environmental variability has been studied in the literature. Our results suggest that thermal variability influences responses across several studies, positively as lower mean temperatures with higher fluctuation ranges, and less so at high mean temperatures with lower fluctuation ranges.

However, most importantly, our results highlight the importance of learning from previous research to push how environmental variability is studied further. It has been noted for years the importance of including thermal variability in ecological research, yet there are still an overwhelming number of studies that employ the same patterns of variability with the same lack of reference to thermal performance. Going forward, experiments that explicitly account for and justify variation patterns with respect to generation time, organization level, duration, and relevance to natural conditions are needed. In order to draw conclusions that are relevant to natural conditions, patterns of variability across colors of noise (red, white, etc.) and across lengths of time must be investigated. A larger sample size of studies to draw more robust conclusions with respect to support for or against allometric scaling and MTE with respect to thermal variability would be useful. There is more to be studied on how additional experimental designs, e.g. acclimation or heat-wave simulations, as well as how biological performance responds to environmental variability. However, this is an important first step in quantitatively summarizing progress so far.

Appendix

Placeholder

References

Placeholder

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