

A meta-analysis of temperature sensitivity as a microbial trait

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Abstract

Traits-based approaches in microbial ecology provide a valuable way to abstract organismal interaction with the environment and to generate hypotheses about community function. Using macromolecular rate theory (MMRT), we recently identified that temperature sensitivity can be characterized as a distinct microbial trait. As temperature is fundamental in controlling biological reactions, variation in temperature sensitivity across communities, organisms, and processes has the potential to vastly improve understanding of microbial response to climate change. These microbial temperature sensitivity traits include the heat capacity (ΔC_p^\ddagger), temperature optimum (T_{opt}), and point of maximum temperature sensitivity (TS_{max}), each of which provide unique insights about organismal response to changes in temperature. In this meta-analysis, we analyzed the distribution of these temperature sensitivity traits from bacteria, fungi, and mixed communities across a variety of biological systems (e.g., soils, oceans, foods, wastewater treatment plants) in order to identify commonalities in temperature responses across these diverse organisms and reaction rates. Our analysis of temperature sensitivity traits from over 350 temperature response curves reveals a wide distribution of temperature sensitivity traits, with T_{opt} and TS_{max} well within biological relevant temperatures. We find that traits vary significantly depending on organism type, microbial diversity, source environment, and biological process, with higher temperature sensitivity found in fungi than bacteria and in less diverse systems. Carbon dioxide production was found to be less temperature sensitive than denitrification, suggesting that changes in temperature will have a potentially larger impact on nitrogen-related processes. As climate changes, these results have important implications for basic understanding of the temperature sensitivity of biological reactions and for ecological understanding of species' trait distributions, as well as for improved treatment of temperature sensitivity in models.

KEY WORDS

activation energy, Arrhenius, ecological theory, functional traits, macromolecular rate theory, microbial trait, Q10

1 | INTRODUCTION

Understanding the structure and function of communities is a central theme in ecology. This is particularly difficult to study in microbial communities because the species concept is difficult to apply and

because the communities are highly dynamic (Antwis et al., 2017). Already a common approach in plant and animal ecology, trait-based ecological research is starting to gain traction in microbial ecology as a way to assess the biogeography of microbial communities and

overcome the constraint of species diversity and ambiguity (Crowther et al., 2014; Green, Bohannan, & Whitaker, 2008).

In light of present and future anthropogenic changes in climate, there is rising interest for predicting the response of microbial communities to temperature, and there is theoretical motive to use a traits-based approach in this effort. The response of microbial communities and their metabolism to temperature is of particular interest because (a) virtually all metabolic reactions are highly sensitive to temperature, and (b) with global warming, small changes in temperature have the potential to severely impact organismal performance and consequently ecosystem functioning (Dell, Pawar, & Savage, 2014). Recently, we (Alster, Baas, Wallenstein, Johnson, & Fischer, 2016) introduced a mechanism for characterizing temperature sensitivity as a microbial trait. We found that temperature sensitivity can be characterized as a microbial trait itself with distinct temperature sensitivity trait values, influenced by genetic and environmental variation (Alster, Baas, et al., 2016; Alster, Koyama, Johnson, Wallenstein, & Fischer, 2016). Defining temperature sensitivity as a microbial trait with measurable and intercomparable characteristics adds another technique to predict microbial community assemblage and creates an important tool to evaluate microbial response to climate change and impact on ecosystem function.

We have defined three temperature sensitivity traits (heat capacity, point of maximum temperature sensitivity, and the temperature optimum) derived from Macromolecular Rate Theory (MMRT). This theory, proposed by Hobbs et al. (2013), expands the Arrhenius equation to account for the temperature dependence of activation energy that is a thermodynamic feature of enzyme-catalyzed reactions. The consequence of incorporating these thermodynamic principles is the commonly observed concave response in rate to temperature, instead of the convex, exponential increase in rate that the standard Arrhenius model predicts.

Macromolecular rate theory uses three parameters to characterize temperature sensitivity traits including the change between the ground state and transition state for enthalpy, entropy, and heat capacity ($\Delta H_{T_0}^\ddagger$, $\Delta S_{T_0}^\ddagger$, and ΔC_P^\ddagger), which can be directly estimated from the MMRT equation,

$$\ln(k) = \ln\left(\frac{k_B T}{h}\right) - \frac{\Delta H_{T_0}^\ddagger + \Delta C_P^\ddagger(T - T_0)}{R T} + \frac{\Delta S_{T_0}^\ddagger + \Delta C_P^\ddagger(\ln T - \ln T_0)}{R}, \quad (1)$$

where k is the rate constant, k_B is Boltzmann's constant, h is Planck's constant, R is the universal gas constant, T is temperature, and T_0 is the reference temperature (Hobbs et al., 2013). Enthalpy and entropy are very closely related and reflect the intercept location of the temperature response curve. Heat capacity directly reflects the degree of negative curvature in the temperature response curve where more negative ΔC_P^\ddagger values correspond to a narrower temperature response curve (i.e., more temperature sensitive) and less negative ΔC_P^\ddagger values correspond to a wider temperature response curve (i.e., less temperature sensitive). From these parameters, we derived two temperature sensitivity traits in addition to ΔC_P^\ddagger , the temperature optimum (T_{opt}) and the point of

maximum temperature sensitivity (TS_{max}), which can be estimated by taking the derivative of MMRT (Arcus et al., 2016) and provides perhaps a more practical measure of temperature sensitivity (Figure 1). The temperature optimum denotes the temperature with the greatest rate value, while the point of maximum temperature sensitivity denotes the point where the change in rate is greatest. While T_{opt} and TS_{max} are functions of ΔC_P^\ddagger and $\Delta H_{T_0}^\ddagger$, the relationships between these traits have not yet been reported. Furthermore, although the T_{opt} and TS_{max} do not theoretically need to be correlated, it is possible that higher T_{opt} values correspond to higher TS_{max} values due to biological constraints. Understanding the relationships between these different temperature traits is important for a variety of reasons including generating information about evolutionary trade-offs between traits and developing deeper understanding on how independent these trait distributions are, which has implications for theory development and parameterization of trait-based ecosystem models. From a practical perspective, understanding these relationships would allow us to extrapolate information should a study only provide one trait value, for example T_{opt} .

The concept of temperature sensitivity as a trait could be applied using other concave temperature response models besides MMRT, but commonly used measures of temperature sensitivity, such as Q10 or activation energy, are inadequate for the several reasons. First, our previous work (Alster, Baas, et al., 2016), along with work of others (Pawar et al., 2016; Schulte, 2015), shows that parameters from the commonly used Arrhenius equation can be inappropriate and misleading for traits-based approaches. Unlike most biological processes, the Arrhenius equation predicts monotonically increasing reaction rates with temperature, whereas biological rates are very commonly unimodal functions with distinct rate maxima (DeLong et al., 2017). Second, even if applied within a biologically relevant temperature range, activation energy estimated from the Arrhenius equation is strongly contingent on the experimental temperature range, producing vastly different parameter estimates depending on incubation conditions (Alster, Baas, et al., 2016; Pawar et al., 2016; Schulte, 2015). Besides MMRT, there are several models that modify the Arrhenius equation to better fit unimodal temperature response in biological reactions. These include Johnson-Lewisin (Johnson & Lewin, 1946), Sharpe-DeMichele (Sharpe & DeMichele, 1977), Schoolfield (Schoolfield, Sharpe, & Magnuson, 1981), Ratkowsky (Ratkowsky, Olley, & Ross, 2005), Equilibrium model (Daniel & Danson, 2010), and enzyme-assisted Arrhenius (DeLong et al., 2017), which could also be a basis for the temperature-trait approach. However, except for MMRT and enzyme-assisted Arrhenius, these other models assume an unlimited substrate supply and that reactions would occur in the absence of enzymes, which ignores the purpose of incorporating enzymes in the first place (DeLong et al., 2017).

Under this innovative approach identifying temperature sensitivity as a biological trait, we are now able to address a new suite of ecological questions and their relevant applications. Because temperature is a foundational property for regulating biological reaction

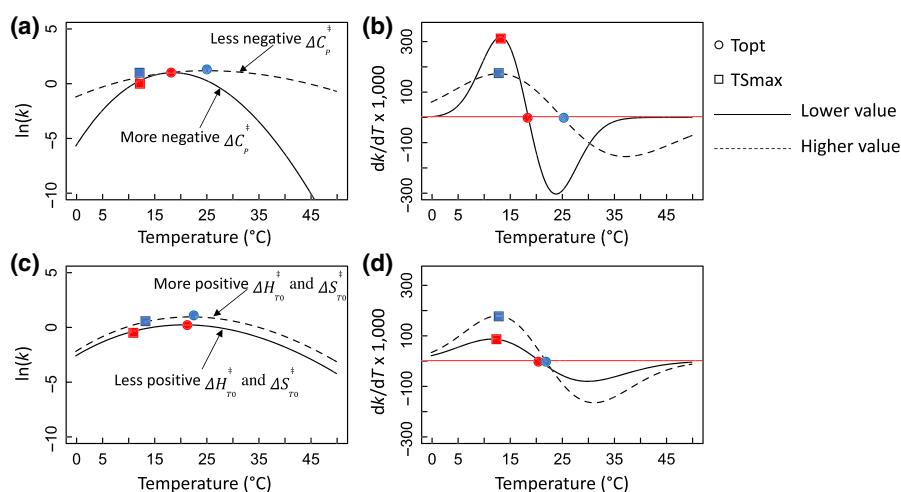


FIGURE 1 Example temperature sensitivity plots fitted with MMRT (a) and (c) and the derivative of MMRT (b) and (d). Plot (b) corresponds to the derivative of plot (a) and plot (d) corresponds to the derivative of plot (c). In plots (b) and (d) T_{opt} can be found where the lines intersect zero (red lines) and TS_{max} can be found at the curve optima. Plots show variable ΔC_p^{\ddagger} (a) and (b) and variable $\Delta H_{T_0}^{\ddagger}$ and $\Delta S_{T_0}^{\ddagger}$ (c) and (d). T_{opt} and TS_{max} for each curve are denoted by circles and squares, respectively. Curves with blue circles and squares have greater T_{opt} and TS_{max} values than curves with red circles and squares. In plots (a) and (b), $\Delta H_{T_0}^{\ddagger}$ and $\Delta S_{T_0}^{\ddagger}$ are the same and ΔC_p^{\ddagger} is more negative (and therefore narrower) in the solid line and less negative (and therefore wider) in the dashed line. T_{opt} and TS_{max} can be the similar or different depending on the specific ΔC_p^{\ddagger} value. In plots (c) and (d), ΔC_p^{\ddagger} is the same and $\Delta H_{T_0}^{\ddagger}$ and $\Delta S_{T_0}^{\ddagger}$ are variable and these parameters control the location of the curve on the plot as well as the curve magnitude

rates (Cossins, 2012), comparing temperature sensitivity traits has the potential to provide nuance into organismal competition, biogeography, and adaptation at various thermal regimes and environmental conditions. Furthermore, assessing temperature sensitivity as a microbial trait is pertinent as it has the potential to improve modeling of organismal and ecosystem response to climate change. For example, differential thermal response of organisms is not currently accounted for in ecosystem climate models (e.g., Wieder, Bonan, & Allison, 2013). Incorporating temperature response as a trait would allow easy incorporation into existing trait-based ecosystems models such as the Decomposition Model of Enzymatic Traits (DEMENT) model or the Microbial-Mineral Carbon Stabilization (MIMICS) model (Allison, 2012; Wieder, Grandy, Kallenbach, Taylor, & Bonan, 2015). Delving into temperature sensitivity traits may also give us a better understanding of functional biodiversity of microbial communities and how we might expect individual taxa and microbial communities to adapt to warming.

In this meta-analysis we explore how temperature sensitivity varies as a biological trait. We identify how broadly temperature sensitivity varies under this new definition of temperature sensitivity traits and assess the relationships between these temperature sensitivity traits. We also begin identifying which characteristics of organismal type and environmental conditions are most important for predicting temperature traits. Our efforts synthesize results from nearly 100 studies by analyzing over 350 different temperature response curves from bacteria, fungi, and communities from a diverse array of systems including natural systems such as soils and oceans, wastewater treatment plants, and a variety of food sources. We hypothesize that organisms from a more variable thermal environment will produce enzymes that are less temperature sensitive

(less negative ΔC_p^{\ddagger}) than organisms from a less variable thermal environment due to thermal adaptation, but there will likely be trade-offs involving resource availability and competition, as well as gene conservation (Alster, Baas, et al., 2016; Wallenstein & Hall, 2012), and that T_{opt} and TS_{max} will reflect the average thermal environment from which the organisms originate. We also hypothesize that measurements of temperature sensitivity of larger groups of organisms or enzymes will result in lower temperature sensitivity, due to those estimates being a summation of a variety of individual temperature responses (Schipper, Hobbs, Rutledge, & Arcus, 2014).

2 | MATERIALS AND METHODS

2.1 | Literature survey

We searched Web of Science and Agricola databases for published papers reporting reaction rate by temperature interactions for bacteria and fungi. Each search contained at least one organismal term: bacteria, bacterium, fungi, microbes, "microbial communities", or microorganism*; at least one rate term: "ammonia oxidation", "carbon use", "denitrification", "microbial growth", "nitrification", or "respiration rate"; and at least one temperature term: "activation energy", Arrhenius, "macromolecular rate theory", MMRT, "rat-kowsky model", or "temperature sensitivity". Other acceptable rates, that were not included as one of our "rate terms", sometimes were identified in the studies that our search yielded and can be found in Table S1. Our search yielded 263 total studies, however, 149 were eliminated after initial review based on preliminary criteria. The majority of exclusions were because the studies measured less than four separate temperatures, and/or the temperature range measured

spanned $<15^{\circ}\text{C}$. We chose these criteria because our preliminary analysis revealed that a narrow temperature range could not statistically resolve the curvature in temperature response rates. Furthermore, we chose four temperature points for statistical purposes because curvature was not well-characterized with fewer than four data points. Several studies were eliminated because they did not measure a rate (e.g., total growth or percent of activity) or did not focus on bacteria and/or fungi (e.g., virus or algae). A few papers were also excluded where data were generated from a model as opposed to experimental data, where English versions of the papers could not be obtained (four studies), or where the paper could not be found by the Colorado State University Library services (four studies). In eight of the papers, the analyzed data were from previous studies, so in those cases we used the data from the original source paper (Table S1).

2.2 | Data acquisition

After initial review, we extracted data from the remaining 113 studies using WebPlotDigitizer, manually entering data from tables, or emailing the authors. After emailing, we were unable to obtain the specific data needed from the authors from six papers that matched the experimental criteria. A total of 661 temperature response curves (rate vs. temperature) were obtained from the 136 papers we extracted data from (note that this number is larger than 113 because some of these papers compiled nonoriginal data from multiple sources, so we extracted the data from the paper with the original data in it, bringing our paper total up to 136). Data from each temperature response was then fitted to the MMRT equation using a numerical Gauss-Newton approach in JMP Pro v.11. MMRT model parameter values ($\Delta H_{T_0}^{\ddagger}$, ΔC_p^{\ddagger} , $\Delta S_{T_0}^{\ddagger}$) and associated standard errors were estimated for each curve. We immediately eliminated temperature response curves that were convex (positive ΔC_p^{\ddagger}) as thermodynamically implausible (Arcus et al., 2016; Alster, Koyama, et al., 2016), leaving a final dataset of MMRT parameter estimates from 549 temperature response curves (Table S2).

We calculated additional temperature trait values (T_{opt} and TS_{max}) for each of the successfully fitted temperature response curves using the first derivative of the MMRT equation and estimated the standard errors for these traits using a parametric Monte Carlo simulation in R version 3.4.1 (R Core Team, 2017). For each study, we simulated new values of the temperature curve parameters by sampling from a normal distribution with the mean given by the parameter estimate and standard deviation given by the standard error. We then calculated the derived temperature curve parameters (i.e., T_{opt} and TS_{max}) and estimated the standard error of the derived parameters by calculating the standard deviation of the derived parameters from the Monte Carlo simulation.

For each temperature response curve, we gathered additional metadata including: average native pH, average experimental pH, organismal type (i.e., bacteria, fungi, or a mix of bacteria and fungi), bacteria type (i.e., gram-positive or gram-negative), assortment of organisms measured (i.e., isolate, group of similar organisms, or

community of organisms), microbial source, average native thermal environment, preincubation temperature, thermally/anthropogenically managed or unmanaged system, aquatic or terrestrial source (if from an unmanaged system), and rate type (Table S1). Unfortunately, we were not able to include several metadata parameters of interest, including substrate availability, due to lack of information from the original papers. We chose the metadata that we did due to a combination of our interest in its relationship with temperature sensitivity and also how likely it was to be included in the diverse assortment of studies used for this analysis. It is important to note that not all of the trait values have all of the metadata, either because the information was not reported in the paper or because the information was not relevant for that particular study (e.g., bacteria type when the paper measured fungal temperature response).

We also gathered some additional metadata concerning the methodology for each of the temperature response curves. These included: number of temperatures measured, range of temperatures measured, highest temperature measured, lowest temperature measured, total sample size (i.e., number of temperatures \times replications), if all of the data points or the average data point from each temperature was used in the MMRT model fit, if the temperature optimum was included in the range of temperature measured, and the mean square error of the MMRT model fit (Table S1).

2.3 | Statistical analysis

We used R (R Core Team, 2017) for the analysis described in this section. We removed temperature response curves that had large standard errors for any of the temperature parameters or trait values ($\Delta H_{T_0}^{\ddagger}$, ΔC_p^{\ddagger} , $\Delta S_{T_0}^{\ddagger}$, T_{opt} , and TS_{max}). We defined a large standard error as one that fell above the upper quartile + 1.5 \times the interquartile range (a total of 133 temperature response curves). We removed these studies because if we were to create a 95% confidence interval for the parameter using these large standard errors, the confidence interval would contain parameter values that are biologically implausible. Additional temperature response curves (63 total) where the standard error was still larger than 200°C for T_{opt} and TS_{max} or larger than $6 \text{ kJ mol}^{-1} \text{ K}^{-1}$ for ΔC_p^{\ddagger} were also removed due to numerical issues in our analysis with the random effects model (REM) (i.e., the ratio of the largest to smallest sampling variance was too large for the model to obtain stable results). These large standard errors caused the studies to be down-weighted in our analysis, rendering them as uninformative. We chose the largest possible cut-off point for standard errors that would allow our model estimation algorithm to converge. Note that small changes in this cut-off point had no effect on our conclusions because our statistical analysis down-weights studies with large standard errors. After removing the uninformative studies, we used 353 temperature response curves for the final analysis from a total of 99 studies. The maximum and minimum number of temperature response curves per paper was 31 and 1, respectively, and the mean number of temperature response curves per paper was 3.6. We calculated the mean, range, standard deviation, and weighted mean (using the standard error) and plotted

histograms for each parameter. We also estimated correlations between each of the temperature traits. We used the R package “metafor” (Viechtbauer, 2010) to fit a random effects model to estimate the means and difference between the means for each of the parameter values as a function of various covariates. By using a REM, we are able to make statistical inferences about the population distribution of temperature trait curves rather than just about the sample distribution of temperature trait curves collected for our meta-analysis. Using this approach, we were able to assess significant differences in means across the different groups and understand how much variability can be explained by covariates. When using categorical covariates, we only reported results when there were at least 10 temperature response curves in the category. We checked the normality of the residuals for every distribution of temperature traits values that we examined and, in all cases, used the natural log of ΔC_p^\ddagger in order to normalize the data. It should be noted that only univariate random effects models were run due to the statistical challenges of combining categorical and numerical covariates and due to the incomplete data available for the covariates for each of the temperature response curves.

3 | RESULTS

3.1 | Summary statistics

One main goal of this meta-analysis was to characterize the frequency distributions of the MMRT parameters and temperature traits ($\Delta H_{T_0}^\ddagger$, ΔC_p^\ddagger , $\Delta S_{T_0}^\ddagger$, T_{opt} , TS_{max}). We found that the shape of the distribution varied among parameters and the ranges of trait values were diverse. The temperature optimum and point of maximum temperature sensitivity had approximately normal distributions, with TS_{max} skewed slightly left with a mean of 18.1°C , a standard deviation of 8.7°C , and range of -15.8 to 45.8°C (Figure 2a). T_{opt} was skewed slightly right with a mean of 29.4°C , a standard deviation of 10.1°C , and a range of 4.6 – 73.9°C (Figure 2b). Heat capacity had a roughly lognormal distribution with a mean of $-8.5 \text{ kJ mol}^{-1} \text{ K}^{-1}$, a standard deviation of $6.4 \text{ kJ mol}^{-1} \text{ K}^{-1}$, and a range from -33.8 to $-0.413 \text{ kJ mol}^{-1} \text{ K}^{-1}$ (Figure 2c). The values closer to zero indicate a more linear temperature response (or the rate is less sensitive to changes in temperature) whereas the more negative ΔC_p^\ddagger values indicate a more curved temperature response, indicating the rate is more sensitive to changes in temperature. Lastly, enthalpy and entropy both had approximately normal distributions with means of 38.2 and $-0.105 \text{ kJ mol}^{-1} \text{ K}^{-1}$, standard deviations of 58.4 and $0.191 \text{ kJ mol}^{-1} \text{ K}^{-1}$, and ranges of -173 to 385 and -0.888 to $0.998 \text{ kJ mol}^{-1} \text{ K}^{-1}$ respectively (Figure 2d,e). Weighted means varied slightly from the reported means with a TS_{max} of 17.5°C , T_{opt} of 26.2°C , ΔC_p^\ddagger of $-4.66 \text{ kJ mol}^{-1} \text{ K}^{-1}$, $\Delta H_{T_0}^\ddagger$ of $36.4 \text{ kJ mol}^{-1} \text{ K}^{-1}$, and $\Delta S_{T_0}^\ddagger$ of $-0.109 \text{ kJ mol}^{-1} \text{ K}^{-1}$.

3.2 | Temperature trait correlations

Correlations among the MMRT parameters and temperature traits varied considerably. There was a nearly perfect positive correlation

between $\Delta H_{T_0}^\ddagger$ and $\Delta S_{T_0}^\ddagger$ ($R^2 = 0.98$). We also found a strong positive correlation between T_{opt} and TS_{max} ($R^2 = 0.87$, slope = 1.10 , Figure 3a) with an offset of T_{opt} approximately 11.3°C higher than TS_{max} , which has not been reported previously to our knowledge. We observed no correlation with ΔC_p^\ddagger for $\Delta H_{T_0}^\ddagger$ or $\Delta S_{T_0}^\ddagger$ ($R^2 = -0.05$ and -0.03). Correlations between $\Delta H_{T_0}^\ddagger$ and $\Delta S_{T_0}^\ddagger$ with T_{opt} and TS_{max} were positive with correlation coefficients between 0.65 and 0.78 . The relationships between ΔC_p^\ddagger and T_{opt} and TS_{max} (Figure 3b,c) had a T-shaped or right-angled scatter plot where a variety of T_{opt} and TS_{max} values are possible when ΔC_p^\ddagger is smaller than about $-10 \text{ kJ mol}^{-1} \text{ K}^{-1}$, but values for higher negative ΔC_p^\ddagger values T_{opt} and TS_{max} fall within a very narrow temperature range.

3.3 | Variation in temperature sensitivity traits

Using a random effects model, we examined how ΔC_p^\ddagger , T_{opt} , and TS_{max} varied as a function of different organism types and environmental factors. We found that bacteria had a higher T_{opt} and TS_{max} than fungi or than the mix of organisms ($p < 0.01$, Figure 4a), however fungi had a more negative ΔC_p^\ddagger than bacteria or than the mix of organisms ($p < 0.0001$, Figure 5a). We also found considerable variation in temperature sensitivity between gram-positive and gram-negative bacteria. Gram-positive and gram-negative bacteria were found to differ in all of their temperature sensitivity traits, with gram-positive bacteria having a higher TS_{max} , T_{opt} , and more negative ΔC_p^\ddagger ($p < 0.05$, Figures 4b and 5b).

Temperature sensitivity traits also varied with environmental conditions. We found significant positive relationships with average native thermal temperature for T_{opt} and TS_{max} ($p < 0.05$, Figure 6a,b) and lower T_{opt} and TS_{max} values in sources where we might expect lower average temperatures like marine water and ice, and marine sediments (Figure 4d). We found higher T_{opt} and TS_{max} values in sources where we might expect to have high average temperatures, like wastewater and sludge and food animal products (Figure 4d). Heat capacity also varied considerably depending on the source of incubated material (Figure 5d). Terrestrial systems were found to have a higher T_{opt} and TS_{max} values than aquatic systems ($p < 0.01$, Figure 4c), but no difference in ΔC_p^\ddagger ($p = 0.358$, Figure 5c). Similarly, we found that in thermally managed systems (i.e., wastewater and sludge and food animal products) T_{opt} and TS_{max} was higher ($p < 0.0001$, Figure 4e), but there is no difference in ΔC_p^\ddagger ($p = 0.963$, Figure 5e). We found only weak relationships between the temperature sensitivity traits and pH (Figure 6g–l).

Temperature traits also varied with the type of rate measured and the assortment of organisms measured. The different assortments of organisms measured (i.e., isolate, selected group of similar organisms, and community) had significantly different temperature trait values. TS_{max} and T_{opt} were both lowest for the community, followed by the isolate, and then by the group of similar organisms ($p < 0.01$, Figure 4f). Heat capacity was least negative at the community level and for groups of similar organisms and most negative at the isolate level ($p < 0.0001$, Figure 5f).

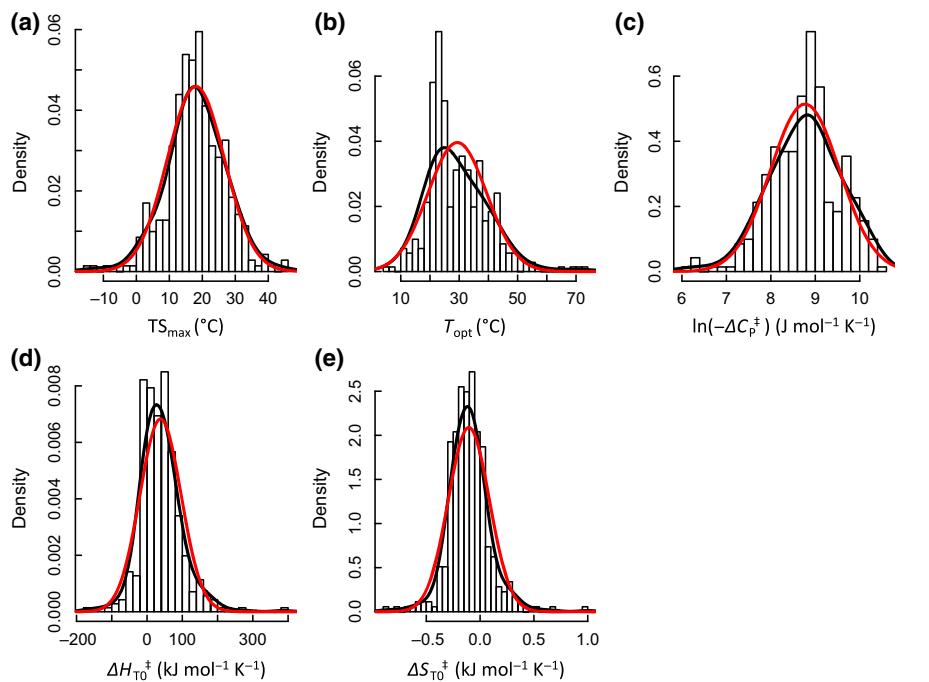


FIGURE 2 Histograms of TS_{\max} (a), T_{opt} (b), $\ln(-\Delta C_p^{\ddagger})$ (c), $\Delta H_{T_0}^{\ddagger}$ (d), and $\Delta S_{T_0}^{\ddagger}$ (e). The black lines are a smoothed version of the empirical distribution, while the red lines are a normal distribution (or lognormal distribution for ΔC_p^{\ddagger}) with the same mean and standard deviation as the data

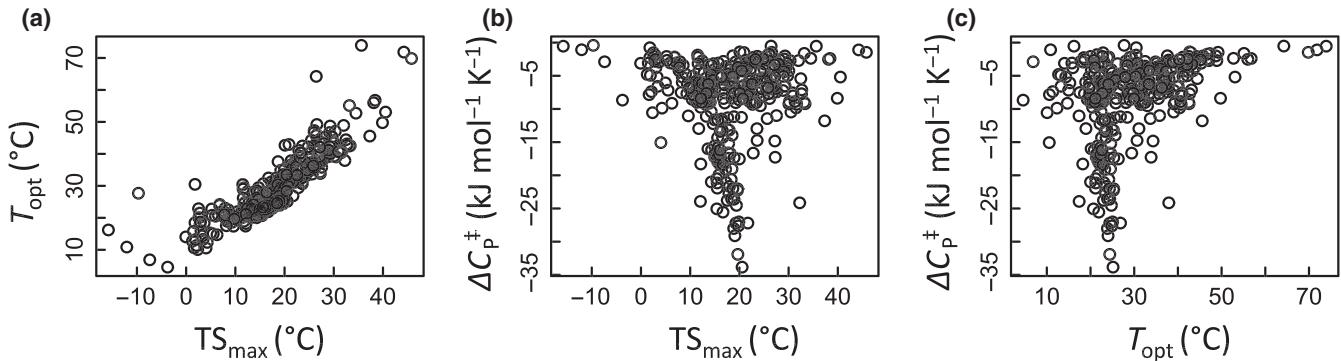


FIGURE 3 Correlations among temperature sensitivity traits

Interestingly, we found that temperature traits varied among types of rates measured in the analysis. Carbon dioxide flux and enzyme activity had the least negative ΔC_p^{\ddagger} values, but carbon dioxide flux had the largest TS_{\max} and T_{opt} values whereas enzyme activity had one of the lowest TS_{\max} and T_{opt} values (Figures 4g and 5g). Growth rate and nitrogen-related rates had more intermediate TS_{\max} and T_{opt} values, but more negative ΔC_p^{\ddagger} values (Figures 4g and 5g).

3.4 | Methodological considerations

We also considered the possibility that methodological approaches from each of the studies impacted our temperature sensitivity trait results. While we found a number of significant methodological

factors impacting ΔC_p^{\ddagger} , T_{opt} , and TS_{\max} , R^2 values remained relatively low for each of these factors. The number of temperatures measured, the highest temperature measured, the total sample size, and the mean square error of the MMRT model fit either were insignificant in predicting ΔC_p^{\ddagger} , T_{opt} , and TS_{\max} ($p > 0.05$) or had an R^2 value of less than 5% (Table 1). We found that the range of temperatures measured did not impact the T_{opt} or TS_{\max} values, but suggests a potentially less negative ΔC_p^{\ddagger} with larger temperature ranges. Several factors did significantly impact ΔC_p^{\ddagger} , T_{opt} , and TS_{\max} values. These included: the lowest temperature measured, whether all of the data points or the average data point from each temperature was used in the MMRT model fit, and if the temperature optimum was included in the range (Table 1). These factors also seemed to have relatively higher R^2 values compared with the other

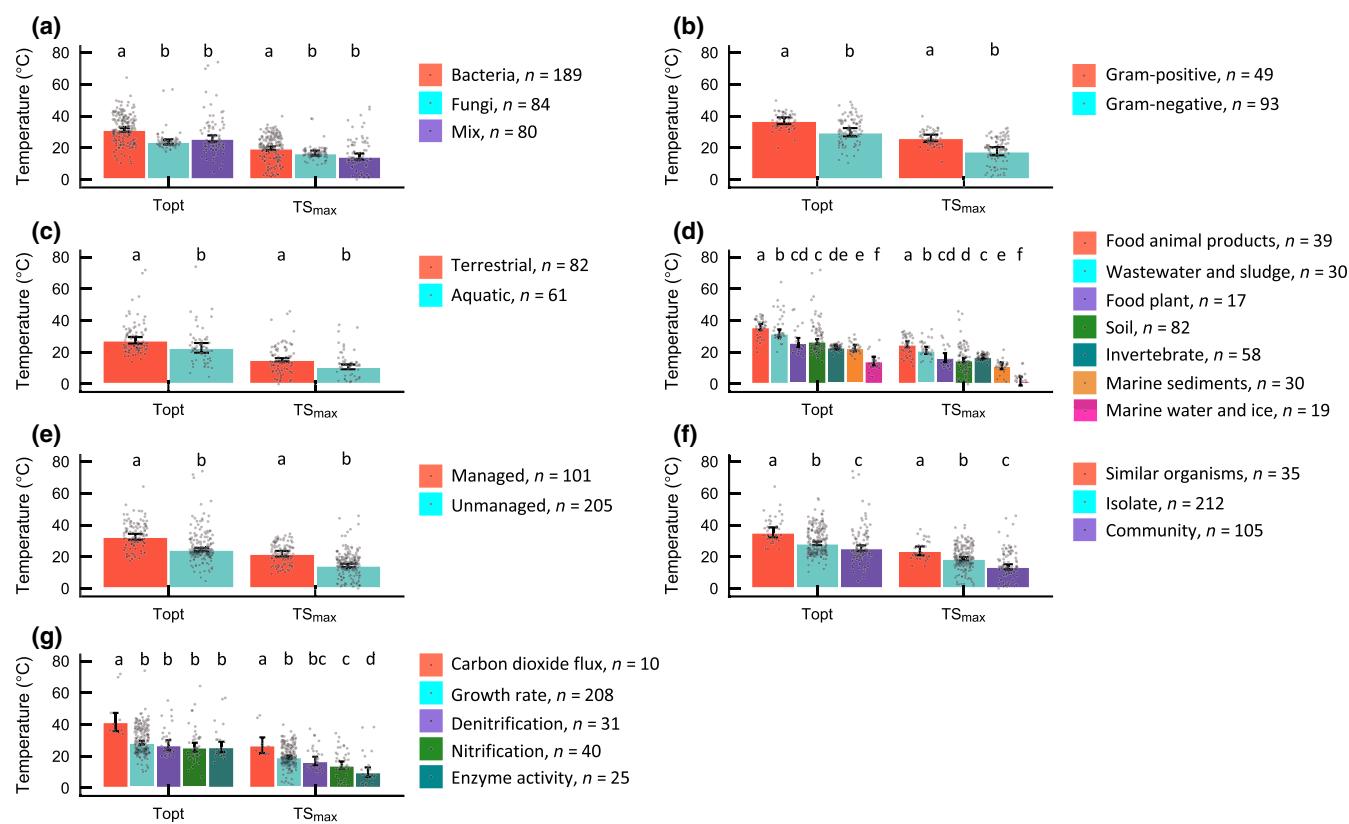


FIGURE 4 Mean $T_{S\text{max}}$ and T_{opt} for organismal type (a), bacterial type (b), aquatic or terrestrial source (c), microbial source (d), thermally/anthropogenically managed or unmanaged system (e), assortment of organisms measured (f), and rate type (g). Data points from each group underlay the bar plots. Error bars represent ± 2 standard errors above and below the mean. Letters group similar means ($p < 0.05$) between groups within $T_{S\text{max}}$ or T_{opt} (but not between the two temperature traits)

methodological factors measured (Table 1) according to the random effects model results.

4 | DISCUSSION

4.1 | Relationships among temperature traits

Our study documents the distribution of temperature sensitivity traits for microorganisms and explores how they diverge for different organisms, environments, and biological processes, and examines the relationships between those traits. Among temperature sensitivity parameters, we find a T-shaped or right-angled type of relationship between ΔC_p^{\ddagger} and T_{opt} , and between ΔC_p^{\ddagger} and $T_{S\text{max}}$. Although the literature is thin in this area, the relationship between ΔC_p^{\ddagger} and T_{opt} has been examined previously for a handful of enzymes (Hobbs et al., 2013) and for ammonia-oxidizing archaea and bacteria (Taylor, Giguere, Zobelein, Myrold, & Bottomley, 2017), and both experiments partially corroborate our results. These studies generally found that larger ΔC_p^{\ddagger} values correspond to lower T_{opt} values, however, Taylor et al. (2017) found this relationship to be linear while Hobbs et al. (2013) found that this relationship saturates at higher temperatures, neither of which match our results completely. This discrepancy is likely due to the many more data points we have in our

study, the broader temperature range, and the diversity of metabolic rates included. Regardless, these relationships suggest a trade-off between ΔC_p^{\ddagger} and T_{opt} making it is rare to have high temperature sensitivity with very high T_{opt} or $T_{S\text{max}}$. Interestingly, we also found a positive, linear relationship between T_{opt} and $T_{S\text{max}}$, with a slope nearly identical to the one found by Liang et al. (2017), which looks at respiration rates from plants across different biomes. This similarity suggests that the relationship between T_{opt} and $T_{S\text{max}}$ is consistent across organisms and perhaps optimized for enzymatic activity.

4.2 | Temperature sensitivity traits vary among organisms

In this meta-analysis we primarily explore how temperature sensitivity varies as a microbial trait. Although the differences in temperature sensitivity traits among the different measured categories could be a function of variation in organismal physiology and adaptation, competition between organisms, thermal regime and other environmental trade-offs, and/or measurement approaches, our results reveal that temperature sensitivity varies with organism type. We found that fungi had a more negative ΔC_p^{\ddagger} than bacteria, but a lower T_{opt} and $T_{S\text{max}}$ (Figure 4a and 5a). A more negative ΔC_p^{\ddagger} implies that fungi are

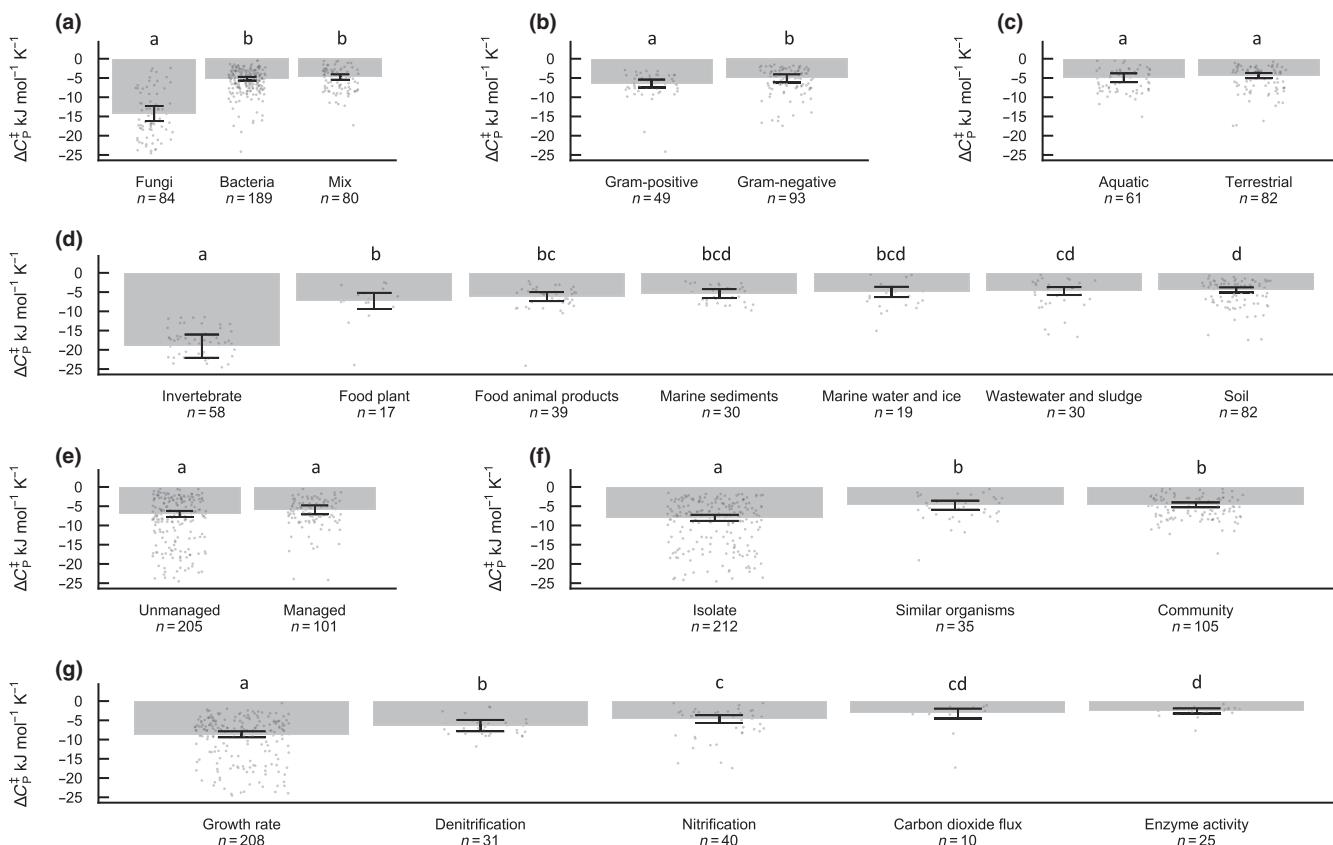


FIGURE 5 Mean ΔC_p^{\ddagger} for organismal type (a), bacterial type (b), aquatic or terrestrial source (c), microbial source (d), thermally/anthropogenically managed or unmanaged system (e), assortment of organisms measured (f), and rate type (g). Data points from each group underlay the bar plots. Error bars represent ± 2 standard errors above and below the mean. Letters indicate significant differences ($p < 0.05$) between groups

more sensitive to changes in temperature than bacteria. This could be due to either adaptation strategies or fundamental differences in physiology. Although we were unable to find studies directly comparing heat capacities between fungal and bacterial enzymes, several studies report no change in the bacterial-fungal ratios with temperature in soils (Allison & Treseder, 2008; Strickland & Rousk, 2010), suggesting similarities in temperature sensitivity between bacteria and fungi, which contrasts our results. This difference in findings could emerge because the studies have a narrower scope (i.e., they study within-site and not between-site differences) and do not measure and define temperature sensitivity in the same manner as our meta-analysis. There are more examples comparing T_{opt} between bacteria and fungi, but results are overall inconsistent; the T_{opt} of bacteria have been observed as higher, lower, or the same as fungi (Bárcenas-Moreno, Gómez-Brandón, Rousk, & Bååth, 2009; Immanuel, Dhanusha, Prema, & Palavesam, 2006; Pietikäinen, Pettersson, & Bååth, 2005). Although not fully comprehensive, our study perhaps comprises a broader comparison of bacterial vs. fungal temperature response than previous studies, which typically compare T_{opt} within a single system.

We also found differences in temperature sensitivity between gram-positive and gram-negative bacteria. Although both types of bacteria are ubiquitous, with exceptionally high and low temperature

optima found for each (Huston, Krieger-Brockett, & Deming, 2000; Pask-Hughes & Williams, 1975), the gram-negative bacteria are thought to better tolerate extreme temperatures due to their strong but elastic outer membranes (Beveridge, 1999). Interestingly, this notion contrasts with our results. It is possible that thicker cell walls in gram-positive bacteria or other features of their cell wall allow them to have the higher TS_{max} and T_{opt} values observed in our study. The result of gram-negative bacteria having a less negative ΔC_p^{\ddagger} is also surprising. Both Schwab, Gastmeier, and Meyer (2014) and Eber, Shardell, Schweizer, Laxminarayan, and Perencevich (2011) report higher densities of gram-negative bacterial pathogens in warmer months as opposed to cooler months, but little change in densities of gram-positive bacteria throughout the year. Thus, gram-negative bacteria were more temperature sensitive in these studies, while our meta-analysis reveals that gram-negative bacteria are less temperature sensitive. It is possible that the results from Schwab et al. (2014) and Eber et al. (2011) are specific to those pathogenic bacteria or due to other environmental conditions unrelated to temperature. However, it is also plausible that the differences in the temperature traits observed between gram-positive and gram-negative bacteria in our study are an artifact of the meta-analysis itself. All gram-positive bacteria in our study were derived from

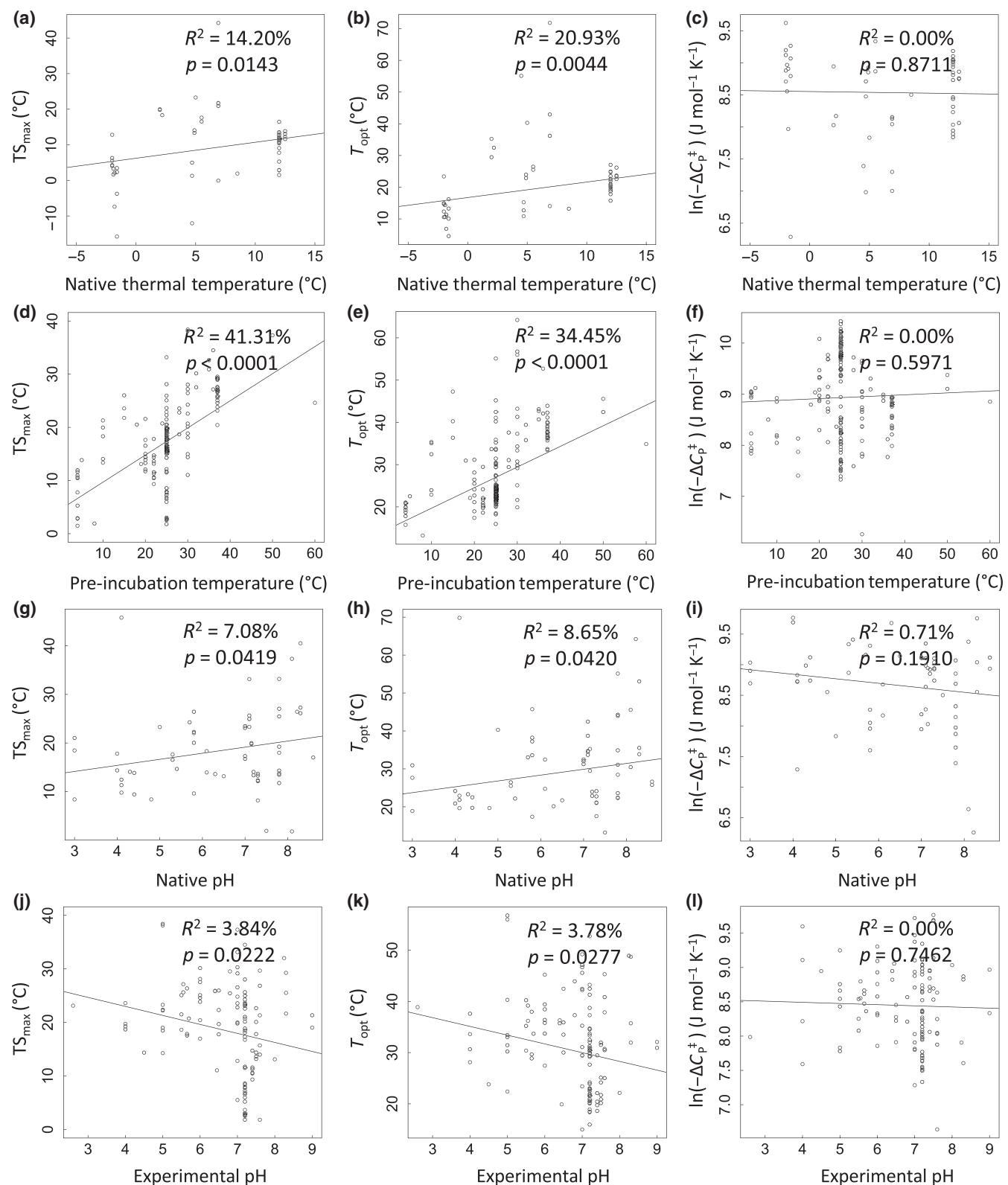


FIGURE 6 Regressions for temperature traits (TS_{max} , T_{opt} , and $\ln(-\Delta C_p^{\dagger})$) and native thermal temperature, preincubation temperature, native pH, and experimental pH

thermally managed (mostly food systems), where the temperature was likely higher and more constant and were also found to have high TS_{max} and T_{opt} values and more negative ΔC_p^{\dagger} values. The

environmental source for gram-negative bacteria was much more varied, but included sources where the native thermal temperature was likely lower and more variable (e.g., soil).

TABLE 1 R^2 and p values from the random effects models for TS_{max} , T_{opt} , and ΔC_p^\ddagger associated with each of the factors collected for methodological purposes. Significance of $p < 0.05$ is bolded

	TS_{max}		T_{opt}		ΔC_p^\ddagger	
	R^2	p	R^2	p	R^2	p
Number of temperatures	0.00%	0.69	0.38%	0.24	0.76%	0.057
Range of temperatures	3.75%	0.0012	0.00%	0.66	14.3%	<0.0001
Mean square error	1.89%	0.0097	3.98%	0.0006	0.84%	0.059
Lowest temp	36.6%	<0.0001	12.9%	<0.0001	17.4%	<0.0001
Highest temp	0.18%	0.1420	3.14%	0.0013	2.98%	0.0011
Total sample size	2.53%	0.0021	1.67%	0.0064	0.00%	0.94
Average or all data	3.31%	0.0008	12.2%	<0.0001	7.65%	<0.0001
T_{opt} in temperature range	10.3%	<0.0001	19.4%	<0.0001	15.3%	<0.0001

4.3 | Temperature sensitivity traits vary among environments

The source environment was a surprisingly poor predictor of variation in temperature sensitivity traits. At the outset of this study, we expected temperature sensitivity to be highly dependent on the source environment—a function of the thermal regime (average temperature and stability of temperature), substrate quality and quantity, and pH. Specifically, we predicted that T_{opt} and TS_{max} would follow average temperature from the source environment, while ΔC_p^\ddagger would more strongly reflect the temperature variation. Unfortunately, the studies in our dataset did not typically quantify variation in temperature and so we were unable to directly test the effect of temperature variance on temperature traits. However, as expected, T_{opt} and TS_{max} were positively correlated with environmental temperature (Figure 6a,b,d,e) and sources with lower average temperatures (e.g., marine water and ice and marine sediments) had lower T_{opt} and TS_{max} values than sources where average temperatures would be expected to be higher (e.g., food animal products, and wastewater and sludge; Figure 4d).

We found that ΔC_p^\ddagger did not vary with differences in environment. Based on our hypothesis, ΔC_p^\ddagger should be most negative (greatest temperature sensitivity) for environments that experience large changes in temperature (Wallenstein & Hall, 2012), have more recalcitrant substrate (Conant et al., 2008; Craine, Fierer, & McLauchlan, 2010; Davidson & Janssens, 2006; Fierer, Craine, McLauchlan, & Schimel, 2005), or that have low substrate availability (Nedwell, 1999; Pomeroy & Wiebe, 2001). We did find some variation in ΔC_p^\ddagger based on the source environment, however, no differences in ΔC_p^\ddagger between aquatic and terrestrial systems and between managed and unmanaged systems were detected despite anticipated differences in thermal stability, substrate availability, and substrate recalcitrance. When looking deeper into the source environment characteristics, we found some support for our hypotheses (Figure 5d). Microbes found in invertebrates had the most negative heat capacity, while microbes found in soils were the least negative, which potentially reflects the greater temporal stability found within invertebrates as compared to soils. Lower substrate availability and/

or more recalcitrant substrates in soils may also contribute to the lower temperature sensitivity. A trade-off between substrate type and temperature sensitivity has been widely documented in the literature where increasing temperature sensitivity corresponds to increasing substrate complexity or recalcitrance (Conant et al., 2008; Craine et al., 2010; Fierer et al., 2005). Furthermore, in resource poor environments, a tradeoff may also exist between temperature response and nutrient acquisition, where temperature sensitivity must be lower to compete for resources (Hall, Neuhauser, & Cotner, 2008; Manzoni, Taylor, Richter, Porporato, & Ågren, 2012). However, it is beyond the scope of this study to disentangle the constraints on temperature sensitivity due to substrate complexity and total substrate availability beyond speculation. Greater detail on substrate availability and recalcitrance may provide further insight into predicted temperature response of organisms from different environments.

Finally, we predicted that pH would be a critical driver of microbial temperature sensitivity. Although pH is a major driver of microbial diversity patterns (Fierer, Strickland, Liptzin, Bradford, & Cleveland, 2009) and its intrinsic relationship with temperature suggests a potential relationship with temperature sensitivity (increase in temperature corresponds to a decrease in pH), we did not find strong support for this in our analysis. Similar to our observation, Craine et al. (2010) found no relationship between pH and activation energy. It is possible the interactive effect of pH and environmental temperature would have a stronger impact on temperature sensitivity. However, this is beyond the scope of this analysis. All together, these results suggest that the source environment is less important in predicting temperature sensitivity than the organism itself or type of enzymatic activity.

4.4 | Temperature sensitivity traits vary based on measurement types

We found some interesting relationships between temperature sensitivity trait values, the type of rate measured and the assortment of organisms measured. The results supported our hypothesis that ΔC_p^\ddagger would be less negative in communities than in isolates (Figure 5f),

suggesting that temperature responses of a community are the summation of individual temperature response curves. This effect lowers the ΔC_p^\ddagger and effectively flattens the temperature response curve (see Schipper et al., 2014, Figure 2). Heat capacity may also be less negative in communities vs. individual isolates because increasing biodiversity can increase ecosystem functioning (Paul, 2014; Wagg, Bender, Widmer, & Heijden, 2014), potentially allowing microbes to be active at a larger range of temperatures. Persisting in a community vs. individually could lessen the apparent temperature sensitivity due to reducing other environmental constraints (i.e., increasing resource acquisition).

The type of rate measured also explains variation in the observed temperature traits. Interestingly, the heat capacity results did not match our hypotheses, which predicted that rates involving a broader range of activities (i.e., carbon dioxide flux) would be less temperature sensitive than rates involving single enzymes (i.e., enzyme activity rates). Consistent with our hypothesis, we found carbon dioxide flux to be among the least temperature sensitive (Figure 5g) as it involves many different enzymes, which might combine to produce an overall less temperature sensitive response. Also, among the least temperature sensitive, we found enzyme activity to have the smallest ΔC_p^\ddagger (Figure 5g). Since enzyme activity is a measurement of a single enzyme, we expected this rate type to be most temperature sensitive. This discrepancy might arise because individual enzymes have different temperature sensitivities (Alster, Baas, et al., 2016; Koch, Tscherko, & Kandeler, 2007; Steinweg, Jagadamma, Frerichs, & Mayes, 2013; Trasar-Cepeda, Gil-Sotres, & Leirós, 2007), and so grouping them into one large group in the meta-analysis may have misconstrued the results. Alternatively, the pure enzymes activities measured in this analysis may just have had lower temperature sensitivity compared with enzymes from the other types of rates measured. Growth rate and nitrogen-related functions had the highest temperature sensitivities (most negative ΔC_p^\ddagger). Despite involving many enzymes, growth rate has been found to exhibit a high degree of temperature sensitivity and often does not adapt to environmental conditions (Clarke, 2003). Denitrification also involves several different enzymes yet was also found to exhibit higher levels of temperature sensitivity. Denitrification takes place under very specialized conditions (i.e., high nitrate availability, low oxygen concentrations, and electron donor availability) compared with the other metabolic functions (Seitzinger et al., 2006), so it is possible that a trade-off exists between substrate acquisition and temperature response that is apparent in denitrification. The relationship between temperature sensitivity and resource acquisition rate requires further investigation within the MMRT framework.

It is widely assumed in microbial systems that reaction rates of all kinds will increase exponentially with temperature (Davidson & Janssens, 2006), unless limited by other factors such as water or other nutrients (Bouletreau et al., 2014) until reaching a very high temperature. The results found in this study indicate that the temperature at which reaction rates might be expected to decline is lower than previously assumed, or at least the temperature where there is exponential growth in the rate term is lower than expected

(Figure 4g). Although a plethora of studies exist on the covariation of metabolic rates and temperature, variation in temperature sensitivity among different rates for the same microbe or same environment is not as commonly compared. In agreement with our results, Pietikäinen et al. (2005) (included in this meta-analysis) found that the T_{opt} for respiration rate in soils was higher than the T_{opt} for growth rate. Furthermore, many respiration studies do not capture the T_{opt} , which implies that the T_{opt} might be quite high (e.g., Lloyd & Taylor, 1994), which is consistent with our data.

A key result of our analysis is identification of which types of microbial functions might be most impacted by global warming and impact ecosystem models the greatest. Microbial transformations involving nitrogen appear to have large temperature sensitivity, defined by a highly negative ΔC_p^\ddagger , as well as moderate TS_{max} and T_{opt} values. Thus, modest increases in temperature could strongly affect how much nitrous oxide could be released from our soils and water, and modeling of those changes could be largely inaccurate (Butterbach-Bahl, Baggs, Dannenmann, Kiese, & Zechmeister-Boltenstern, 2013).

4.5 | Methodological suggestions for future temperature sensitivity studies

Several studies (e.g., Alster, Baas, et al., 2016; Arcus et al., 2016; Schipper et al., 2014) have clearly demonstrated that MMRT is a superior model to use when measuring temperature sensitivity of microorganisms. However, just as activation energy values can change based on the temperatures measured (Alster, Baas, et al., 2016; Pawar et al., 2016), MMRT estimated values can also change based on several methodological factors. Here, we consider some of the methodology-associated metadata collected which allows us to make several recommendations when planning new experiments measuring temperature response and avoid future biases. First, it is important to capture the T_{opt} within the range of temperatures that you are measuring in order to accurately assess temperature sensitivity. Studies not capturing the T_{opt} resulted in a high average T_{opt} and TS_{max} , and less negative ΔC_p^\ddagger . Failure to capture this peak could lead to highly inflated temperature sensitivity values. Second, the highest temperature measured appears to be less critical than the lowest temperature measured for determining TS_{max} , T_{opt} , and ΔC_p^\ddagger (Table 1). Although it is difficult to disentangle the mechanism underlying this pattern, it may arise as an artifact of the design of studies that we analyzed. A priori knowledge likely drives the choice of relevant experimental temperatures, rather than it actually being a critical factor in estimating the temperature traits. Finally, it is less important to include a large number of temperatures and replications than it is to be thoughtful about the range of temperatures chosen to measure for predicting MMRT parameters.

4.6 | Future directions

In this meta-analysis we established the relative distributions for five different temperature sensitivity traits and began exploring how

these traits might vary for different groups of organisms, functions, and environments. This work is groundbreaking in that it is the first synthesis of traits-based temperature sensitivity and provides a starting point for incorporating temperature sensitivity traits into models. There are several open questions that arose from our work that provide avenues of further exploration and research. First, due to deficiencies in the data set we were unable to examine several factors that are hypothesized to strongly impact temperature sensitivity, including substrate quality and quantity. Conducting future experiments using the MMRT traits-based framework that specifically target this question would be beneficial. Second, it would be useful to evaluate the relative importance of the different factors that we tested (e.g., pH, source environment, organism type) on temperature sensitivity as well as assess the interactive effects of these different drivers. This was beyond the scope of this experiment but warrants further investigation as we attempt to understand what forces are shaping temperature sensitivity traits. Lastly, it should be noted that the MMRT traits-based framework is modeled via enzyme-kinetics and thus assumes a physiological time-scale. When looking at larger time-scales it is worth considering other factors, such as changes to other cellular structures and compounds, impacting temperature response.

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SUPPORTING INFORMATION

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

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