Temperature Controls on Soil Microbial Processes:
Including Heat Capacity Explains Temperature Optima and High Q_{10} at Low Temperatures

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Introduction

The response of soil biochemical processes to changing temperature is critical for predicting cycling of nutrients and carbon. Much of our current understanding of the temperature response is based on the Arrhenius equation, which predicts an exponential increase in rate as temperature rises. However, there is a clearly identifiable temperature optimum (T_{opt}) for microbial processes (Fig. 1a). This T_{opt} has previously been explained by enzyme denaturation at higher temperatures. We have recently shown that the decrease in rate above T_{opt} for enzymes *in vitro* is not due to denaturation but the change in heat capacity at constant pressure ($\Delta C^{\ddagger}_p$) associated with enzyme catalysis (ref. 1). Here, we demonstrate the impact of $\Delta C^{\ddagger}_p$ on the response of microbial processes to temperature in soil using a wide range of data from the literature.

Theory

We have recently (ref. 1) expanded the Arrhenius equation to take into account the temperature dependence of the activation energy (Eq. 1, Fig. 1b). From this, it is also possible to derive an equation which describes the temperature sensitivity of biological processes (i.e. Q_{10}; Eq. 2).

$$k = Ae^{\left(\frac{-E_A}{RT}\right)} \quad \text{(Arrhenius equation)}$$

$$E_A = \Delta G^{\ddagger} = \Delta H^{\ddagger} - T\Delta S^{\ddagger} \quad \text{(Gibbs free energy expressed in terms of enthalpy and entropy)}$$

$$k = Ae^{\left(\frac{-(\Delta H^{\ddagger} - T\Delta S^{\ddagger})}{RT}\right)}$$

Temperature dependence of $\Delta H^{\ddagger}$ and $\Delta S^{\ddagger}$ is defined by $\Delta C^{\ddagger}_p$

$$\ln(k) = \ln A - \frac{[\Delta H^{\ddagger}_{T_0} + \Delta C^{\ddagger}_p(T - T_0)]}{RT} + \frac{[\Delta S^{\ddagger}_{T_0} + \Delta C^{\ddagger}_p \ln(T/T_0)]}{R} \quad \textbf{Eq. 1}$$

where k is the rate constant, A is a pre-exponential factor, E_A is the activation energy, R is the universal gas constant, T is the temperature, $\Delta G^{\ddagger}$ is the Gibbs free energy for activation, T_0 is an arbitrary reference temperature, $\Delta C^{\ddagger}_p$ is the change in heat capacity for activation, and $\Delta H^{\ddagger}$ and $\Delta S^{\ddagger}$ are the activation enthalpy and entropy, respectively ($\Delta H^{\ddagger}_{T_0}$ and $\Delta S^{\ddagger}_{T_0}$ are the activation enthalpy and entropy at T_0).

$$Q_{10} \approx e^{\left(\frac{10(\Delta H^{\ddagger} - 5\Delta C^{\ddagger}_p)}{RT^2}\right)} \quad \textbf{Eq. 2}$$
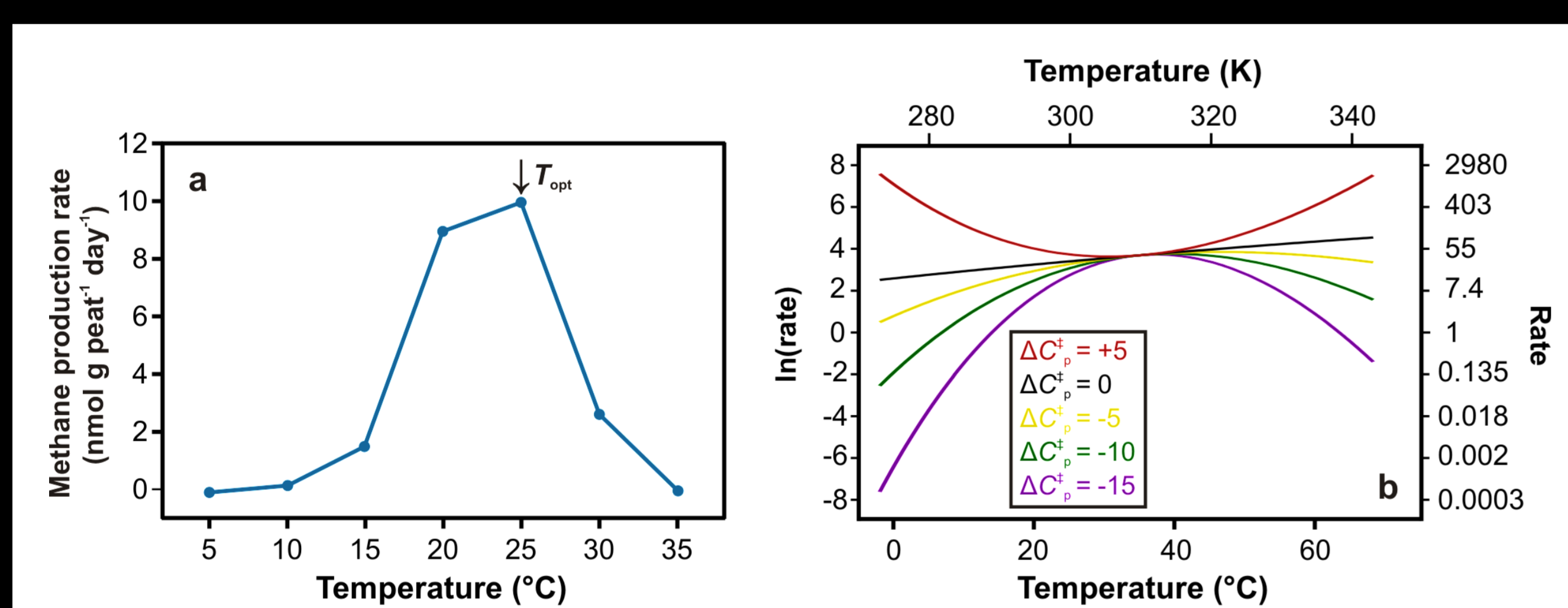

Fig. 1 The relationship between temperature and rate
a) Rate of methane production from KLTS peat with increasing temperature, illustrating a clear T_{opt}. Data retrieved from Fig. 3 of Dunfield et al. (1993) *Soil Biol. Biochem.* 25:321. b) Influence of $\Delta C^{\ddagger}_p$ on the temperature-rate relationship. The black line indicates a standard Arrhenius plot (i.e. $\Delta C^{\ddagger}_p = 0$). $\Delta C^{\ddagger}_p$ values shown are in kJ mol^{-1} K^{-1}.

Applications and Aims

Microbial processes in soil are driven by enzymatic reactions, each with their own $\Delta C^{\ddagger}_p$, therefore we would expect to see a $\Delta C^{\ddagger}_p$ signature in the temperature-rate relationship for these processes. As such, we had two aims in this study:

1. To test the ability of our $\Delta C^{\ddagger}_p$-based theoretical framework to model the temperature response of soil microbial processes using laboratory-derived datasets from the literature
2. To test the predictive power of Eq. 2 in relation to Q_{10} using a dataset of changing respiration rate with increasing temperature summarised in ref. 2
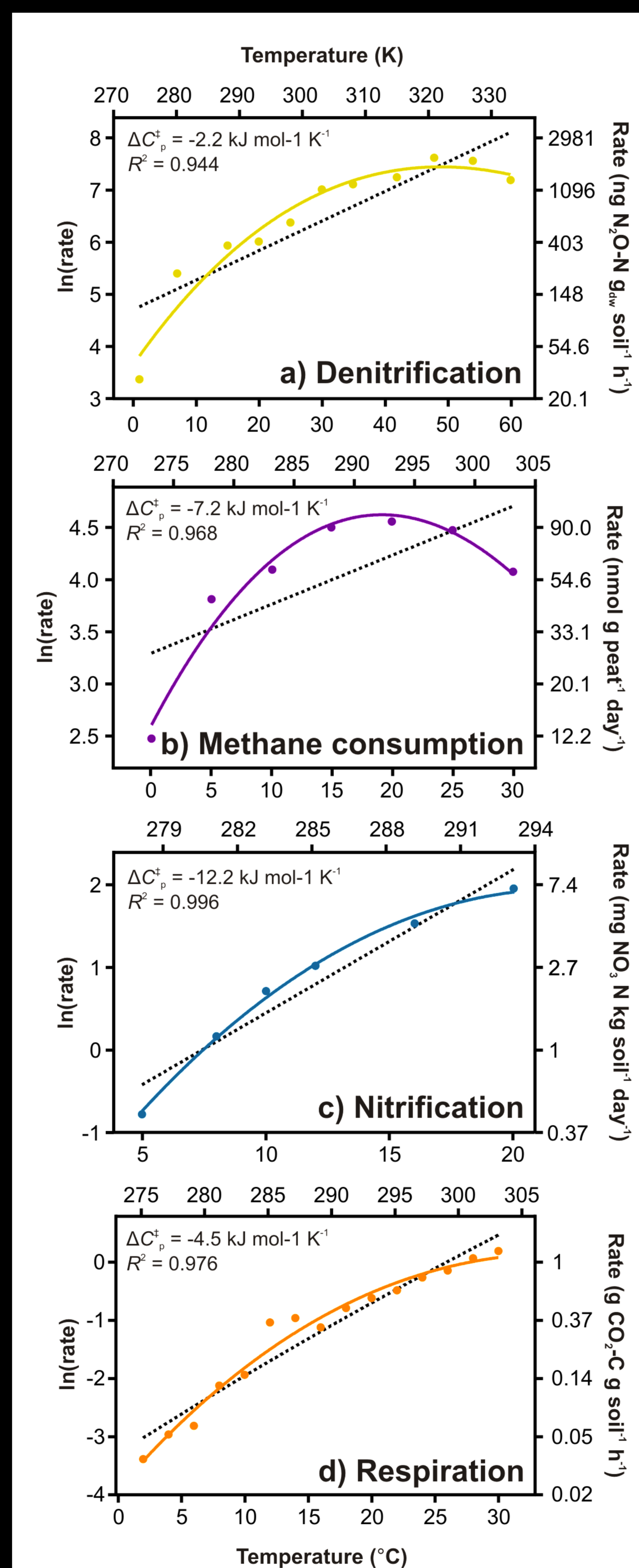

Fig. 2 Fit of Eq. 1 to temperature-rate data for a range of microbial processes in soil
Solid lines represent the fit of Eq. 1 to the data; dashed lines represent a standard Arrhenius plot. a) Fischer & Whalen 2005, *Nutr. Cycl. Agroecosys.* 71:271. b) Dunfield et al. 1993, *Soil Biol. Biochem.* 25:321 (B1 peat). c) Russell et al. 2002, *Commun. Soil Sci. Plan.* 33:1975 (nitrogen source 1). d) Chen et al. 2010, *Soil Biol. Biochem.* 42:2282 (arable soil).

Results

We fitted Eq. 1 to 40+ datasets for different soil processes and in all cases obtained a better fit than an Arrhenius function (e.g. Fig. 2). Furthermore, the derived $\Delta C^{\ddagger}_p$ values for these processes are similar to those reported for individual enzymes and microbial growth rates (ref. 1).
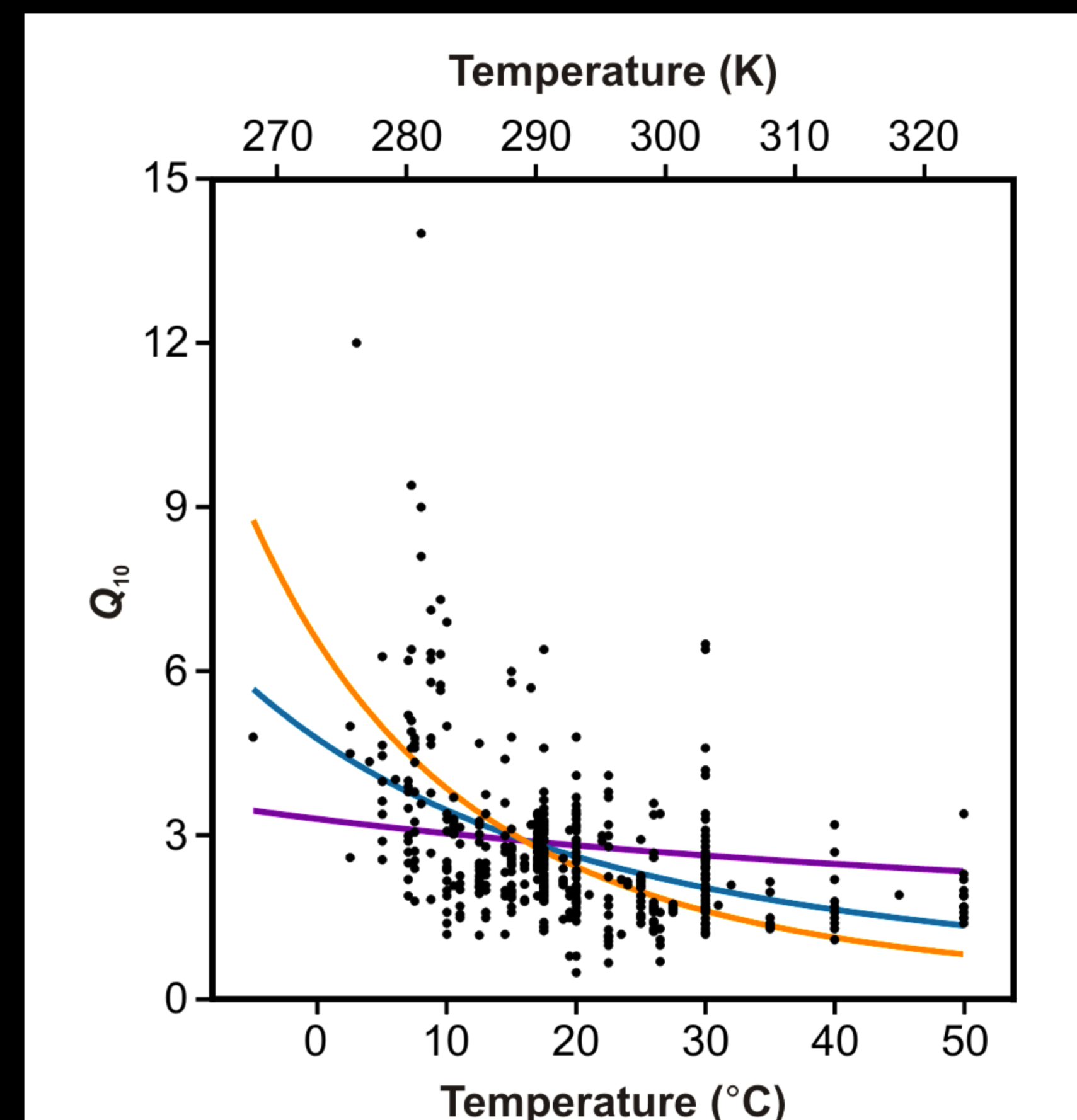
Fig. 3 shows that Q_{10} decreases with increasing temperature. This phenomenon is predicted by Eq. 2, and $\Delta C^{\ddagger}_p$ governs the curvature of the fit. For example, the fitted orange line shows greater curvature than the blue line ($\Delta C^{\ddagger}_p$ of -2.7 vs. -1.4 kJ mol^{-1} K^{-1}). A $\Delta C^{\ddagger}_p$ value of zero gives an Arrhenius function (purple line). We expect $\Delta C^{\ddagger}_p$ to increase from -2.7 kJ mol^{-1} K^{-1} to zero as temperature increases.

Fig. 3 The relationship between Q_{10} and temperature for soil respiration
Two fits of Eq. 2 are shown with different $\Delta C^{\ddagger}_p$ values: $\Delta C^{\ddagger}_p \sim$2.7 kJ mol^{-1} K^{-1} (orange) and $\Delta C^{\ddagger}_p \sim$1.4 kJ mol^{-1} K^{-1} (blue). The fit of a standard Arrhenius function is shown for comparison (purple). Data were taken from ref. 2.

Discussion

Our theoretical framework provides an evidence-based explanation for the frequently observed disparity between low soil process T_{opt} values and high enzyme denaturation temperatures. Furthermore, the temperature sensitivity of a process declines as the temperature approaches T_{opt}, which is relevant even if T_{opt} is rarely reached in the ecosystem.

This framework also predicts high Q_{10} values at low temperatures and that, as frequently observed in soils, Q_{10} decreases with increasing temperature. There are a number of other empirical equations developed to model this decrease in Q_{10} (ref. 3 and 4), however our equation provides a theoretical explanation for this phenomenon and a workable alternative.

References

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