

EVOLUTIONARY INNOVATION AND CONSTRAINT IN THERMAL TRAITS FROM PSYCHROPHILIC TO HYPERTHERMOPHILIC MICROBES.

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Introduction: Owing to vast physiological diversity, microbes inhabit practically every habitat capable of supporting life as we know it. An understanding of microbial traits and their evolution has the potential to expand our search for extraterrestrial life to environments previously assumed inhospitable to life, and may inform our understanding of how life may arise and evolve in such environments. Among their greatest evolutionary achievements are those allowing microbes to exist, even thrive, at temperatures ranging from well below 0 to over 100 °C. However, cellular biochemistry fundamentally constrains a given physiological trait (e.g. maximum population growth rate) to a common temperature-dependent functional form across taxa, regardless of absolute trait values. For example, the average fitness of a microbial population (its maximum growth rate, μ_{\max}) increases with temperature up to some optimum, and then decreases precipitously, producing a unimodal curve (Figure 1); this curve is usually, though not always, left-skewed.

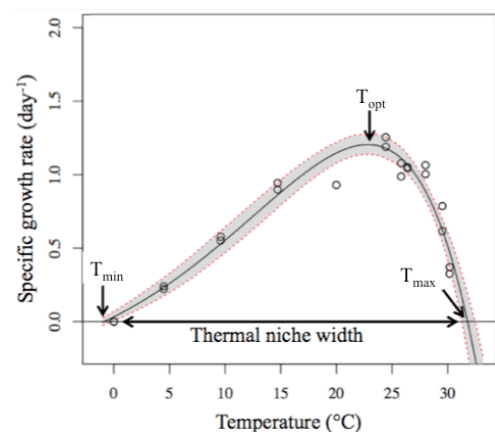


Figure 1: Example thermal performance curve (marine diatom *Thalassiosira pseudonana*, D. O'Donnell, unpublished data).

While its parameters vary tremendously among taxa, the general form of this thermal performance curve (TPC) is universal across microbes, and it can be modeled using any of a number of theoretical functions, (see, e.g., [1] or [2]). Several quantifiable and informative traits emerge from the TPC, such as thermal optimum (T_{opt}), lower and upper critical temperatures (T_{min} , T_{max}), thermal niche width (TNW), and skew (Figure 1). Understanding patterns in variance and covariance of these traits across the range of temperatures at which life is known to exist (and especially of devia-

tions from the patterns) can tell us a great deal about the evolutionary innovations and obstacles that may allow or constrain the origin and subsequent diversification of life in extreme environments on extraterrestrial bodies. Furthermore, using phylogenies to infer the frequency of evolutionary innovation allowing for extremophilia may inform us as to the likelihood that such innovations might arise by random mutation and subsequently lead to the persistence and diversification of extremophilic clades.

We conducted a meta-analysis of over 300 bacterial and archaeal thermal performance curves, characterizing the variance and covariance of thermal traits across a temperature range from < 0 to >100 °C to elucidate evolutionary innovation events, physiological trade-offs, and fundamental constraints to thermal adaptation in a broad range of microbial taxa. We mapped thermal traits onto a phylogeny of all taxa included in the study to determine how often traits allowing extremophilia have arisen, and to infer rates of diversification of microbes in extreme versus moderate environments.

Preliminary results indicate that TNW is narrowest in taxa with very low T_{opt} , and in thermophiles with T_{opt} of 60-70 °C. Mesophiles (T_{opt} of 20-40 °C) possess the broadest TNW. Some hyperthermophiles (strains with T_{opt} >70 °C) seem to have much broader TNW than would be extrapolated from a statistical model including only strains with T_{opt} <70 °C. Intriguingly, strains with T_{opt} >70 °C represent several distantly related clades, indicating the possibility of multiple adaptive events giving rise to hyperthermophilic strategies. Photoautotrophs have narrower TNW, on average, than other microbes with comparable T_{opt} . Exploration of trends in other traits, e.g. T_{min} , T_{max} , and skew of the TPC is ongoing, as is that of broad evolutionary trends inferable from phylogenies.

The data presented here will elucidate broad trends in microbial thermal trait variance and covariance across the range of habitable thermal environments on Earth, as well as patterns in trait evolution. This study may help narrow (or broaden) the parameter space of the search for extraterrestrial life.

References: [1] Norberg, J. (2004) *Limnol. Oceanogr.*, 49, 1269–1277. [2] Corkrey, R.; McMeekin, T. A.; Bowman, J. P.; Ratkowsky, D. A.; Olley, J. and T. Ross (2014) *PLoS One*, 9, e96100.