Physiological and ecological constraints on TEX_{86} and GDGT provenance revealed by pure culture experiments and quinone biomarkers

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Archaeal glycerol dibiphytanyl glycerol tetraether (GDGT) membrane lipids are ubiquitous in the environment. They are used both as biomarkers for the abundance of living archaea and in the reconstruction of past sea surface temperatures using the TEX_{86} proxy. However, widely observed discrepancies between *in situ* and TEX_{86} temperatures in the marine water column indicate that the physiological and ecological controls on lipid composition in planktonic archaea are still poorly understood. Moreover, the relative contributions of *Eury-* and *Thaumarchaeota* to the total GDGT signal remain controversial.

Here, we demonstrate that the responses of membrane lipid compositions, and resulting TEX_{86} values, to growth temperature strongly diverge in three closely related thaumarchaeal pure cultures, including *Nitrosopumilus maritimus* and two novel isolates from South Atlantic surface water. Moreover we show that GDGT composition in *N. maritimus* depends on growth stage, growth rate, and pH, but not on salinity. This indicates that the TEX_{86} paleotemperature proxy is not solely dependent on temperature, but amalgamates several physiological and environmental factors such as phylogenetic composition and metabolic state of marine archaeal communities.

In order to identify diagnostic lipid biomarkers for the activity and abundance of specific archaeal clades, we studied the lipidomes of >30 cultivated representatives of the three major archaeal phyla *Eury-*, *Cren-*, and *Thaumarchaeota* using novel, comprehensive analytical protocols. We identified respiratory quinones that are involved in cellular energy transfer in *Thaumarchaeota*, as well as the unique membrane lipid methoxy archaeol. We demonstrate that these novel biomarkers are well suited for tracing the presence and activity of planktonic *Thaumarchaeota* independently from GDGTs, thus offering high potential for distinguishing thaumarchaeal and euryarchaeal sources of GDGTs.