## Theory on thermodynamic constraints to biogeochemical and metabolic diversity

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A shared goal of astrobiology, biogeochemistry, ecology, and evolutionary biology is understanding the general principles governing spatiotemporal patterns in the activity and diversity of metabolic reactions. Exergonic richness is the diversity of energy-yielding metabolic reactions harnessed by a living system from geochemical resources. Thermodynamics imposes fundamental constraints on exergonic richness by affecting the energy-yield (Gibbs free energy change) of geochemical reactions. We thus develop a general quantitative theoretical framework integrating thermodynamics, theoretical geochemistry, statistical physics, and ecological theory to predict how temperature, the concentration of geochemical resources, and other physicochemical parameters influence ecosystem exergonic richness for different classes of metabolic reactions, as well as the rate of turnover (beta diversity) in the composition of exergonic reactions along geochemical reactions, to provide and test mathematical predictions of how potential exergonic richness is a function of temperature, pH, and the minimum biological energy quantum. We find that the theoretical predictions matched empirical richness patterns of hot springs at Yellowstone National Park. The developed theory can elucidate the degree to which various physicochemical variables shape exergonic richness, with implications for astrobiology, ecosystem resilience, and patterns of functional, taxonomic and phylogenetic diversity in microbes.