



The homeostatic ensemble for living cells

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Cells are quintessential examples of out of equilibrium systems but they maintain a homeostatic state over a timescale of hours to days. As a consequence, the statistics of all observables is remarkably consistent. Here we develop a statistical mechanics framework for living cells, on par with conventional statistical thermodynamics, by including the homeostatic constraint over the interphase period of the cell cycle. As a first application, the framework is shown to accurately predict the observed effect of the mechanical environment on the in-vitro response of smooth muscle cells. This includes predictions that both the mean values as well as diversity/variability in the measured values of observables such as cell area, shape and tractions decrease with decreasing stiffness of the environment. Thus, we argue that the observed variabilities are inherent to the homeostatic equilibrium of cells and not a result of in-vitro experimental errors.

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