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## Pattern formation in filaments of nitrogen-fixing cyanobacteria: evolvability through criticality

Cyanobacteria produce a significant fraction of the oxygen on the environment and, together with archaea, they fix atmospheric nitrogen used by all other organisms. One of the first forms of multicellular organisms on Earth are filamentous cyanobacteria, which constitute a paradigmatic model organism of the transition between unicellular and multicellular living forms. The genus *Anabaena* forms colonies with cells arranged in one-dimensional filaments; under nitrogen-limiting conditions some cells can differentiate into nitrogen-fixing heterocysts, forming regular patterns to effectively provide nitrogen for the colony. We present a mathematical model to understand the regulation of heterocyst differentiation in *Anabaena* PCC 7120. The model quantitatively reproduces the appearance and dynamics of this pattern, allowing to explore the impact of different factors like fixed-nitrogen diffusion, cell division, or stochasticity on pattern formation. From this model we develop a minimal theoretical framework studying a system of two cells, and find that this analysis faithfully recapitulates the pattern forming properties of a whole filament. The use of such a model lets us identify that the system is poised in the vicinity of a critical point of the dynamics, allowing for robust development while making possible evolutionary flexibility. Our results, together with recent findings in other systems, indicate that criticality in the dynamics is a generic characteristic of developmental evolvability.

**Date:** May 16, 2019

**Place:** Room C1/028

**Time:** 14:30

