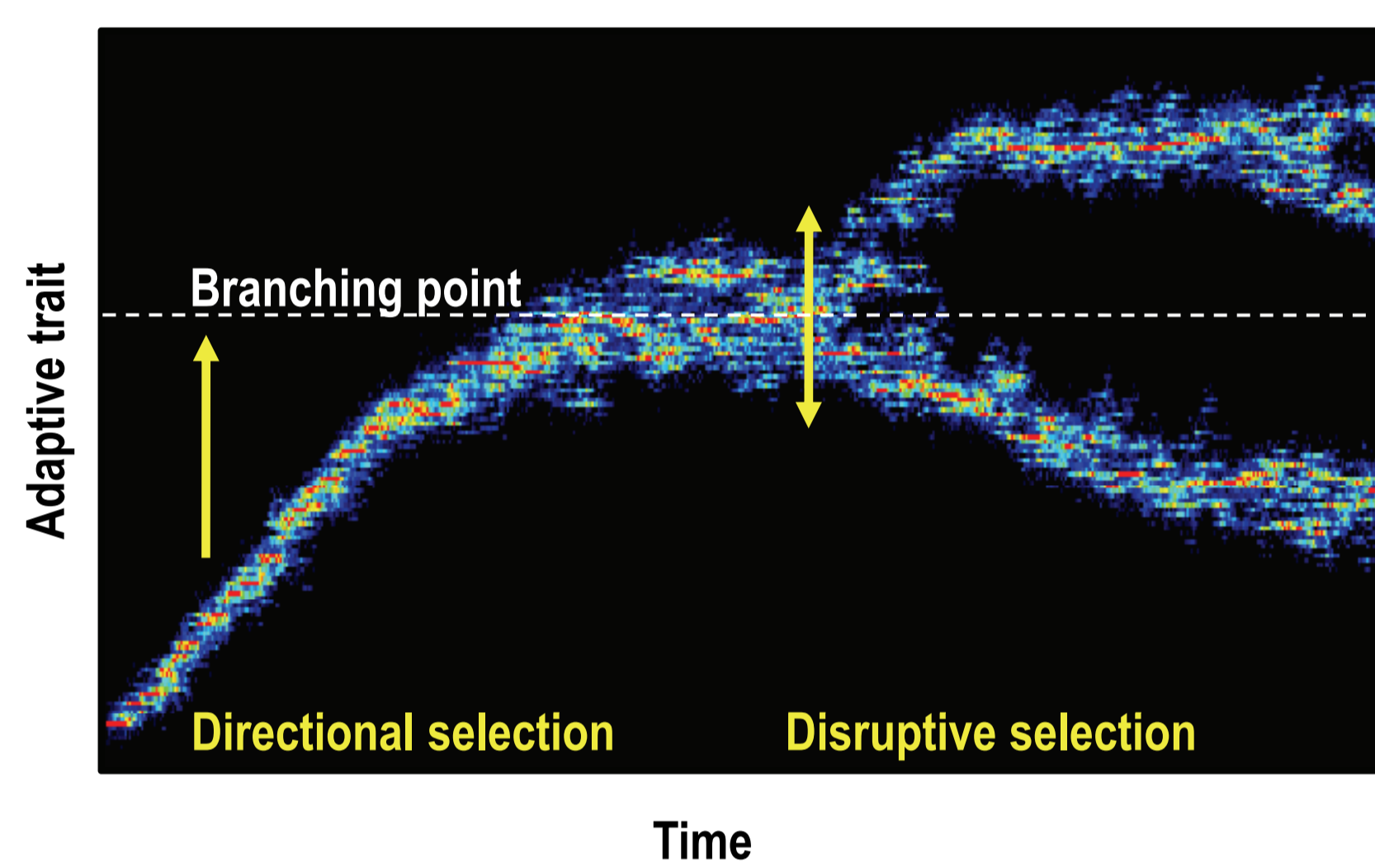


## Introduction

The principle of fitness maximization is widely employed in contemporary studies of adaptation to predict how empirically observed adaptive traits vary with empirically observed environmental conditions.

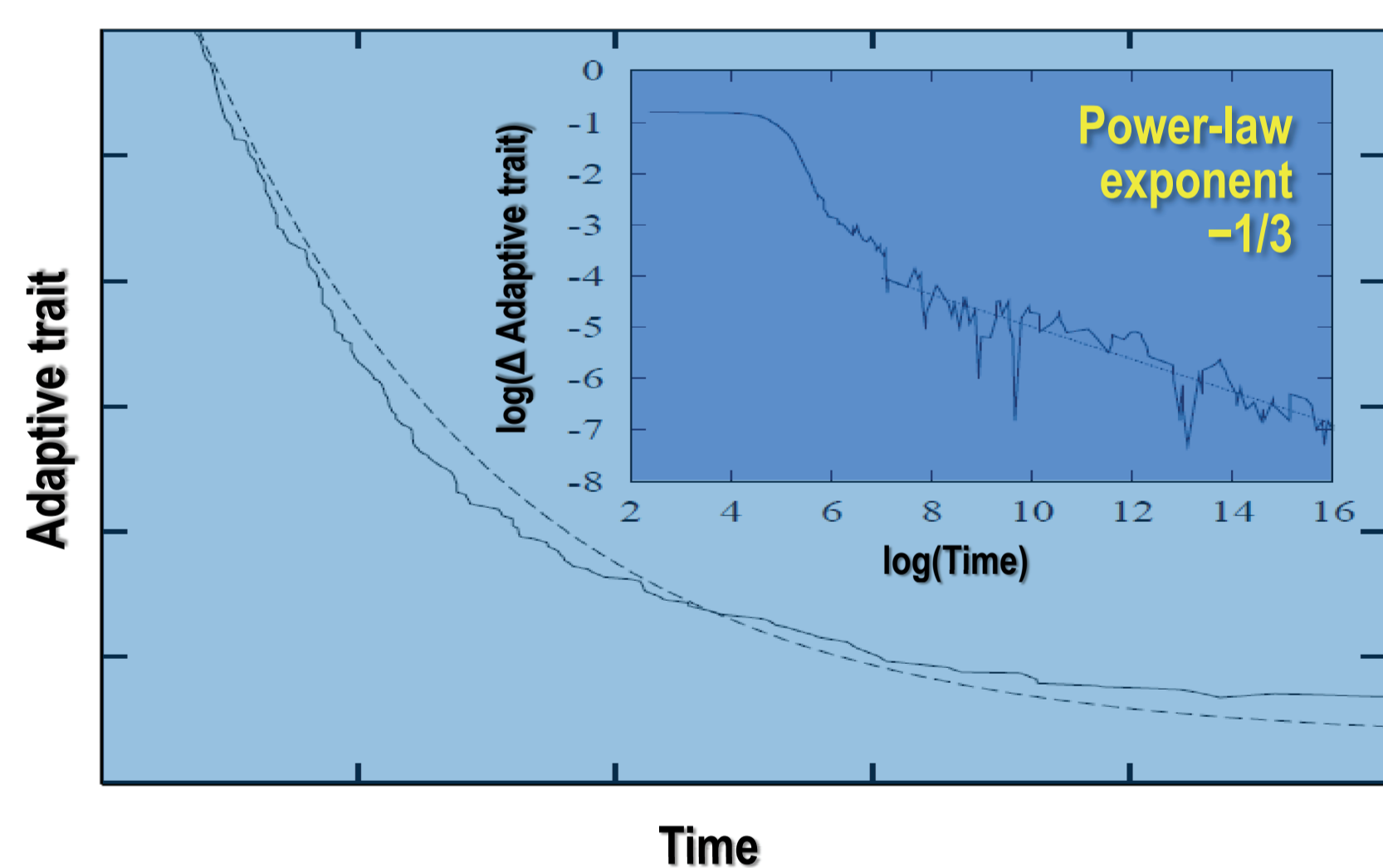
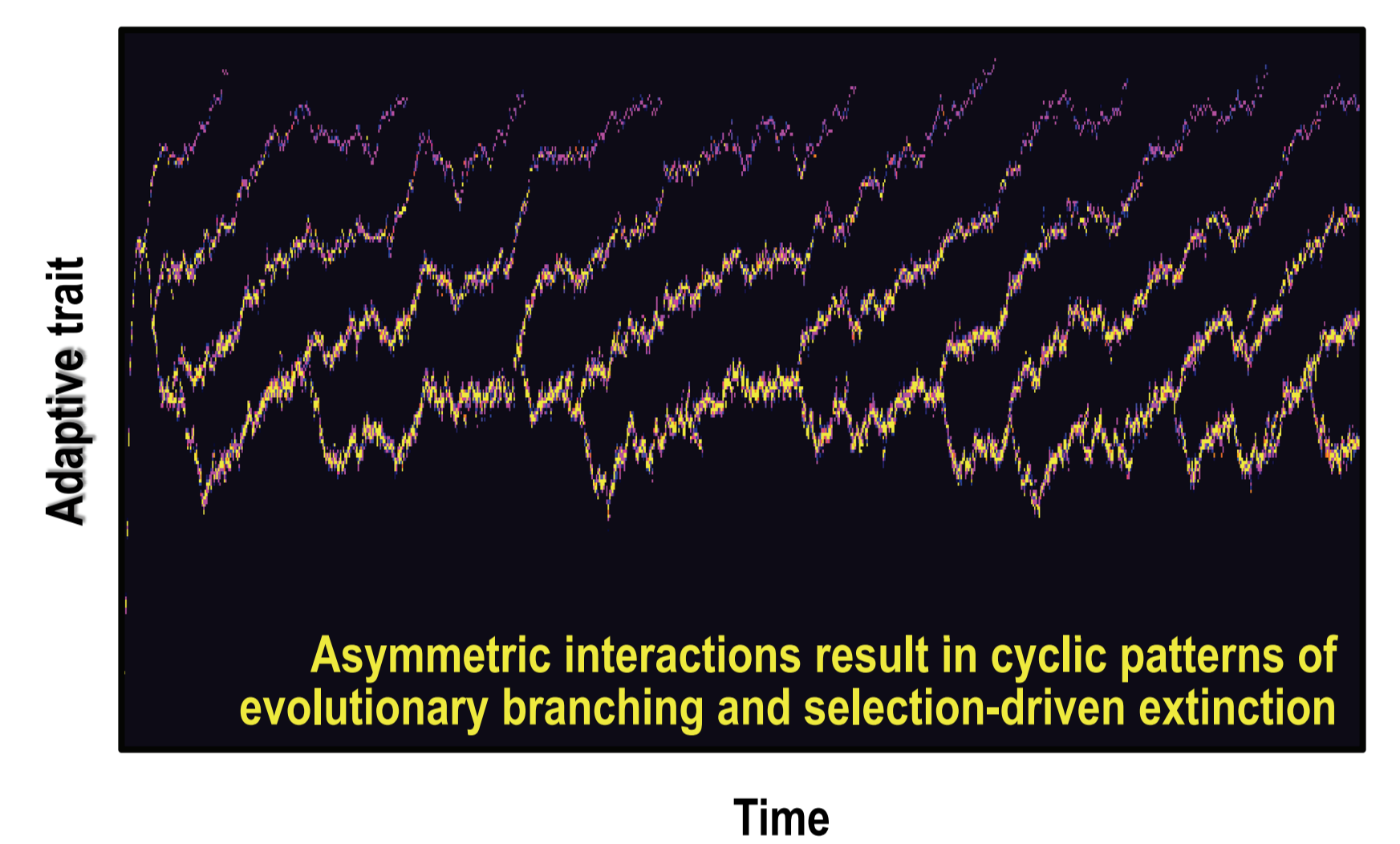
Yet, two fundamental determinants of real social systems and ecosystems have remained unaccounted for in this classical approach: frequency-dependent selection and realistic density regulation. From an evolutionary perspective, these are just flipsides of the same coin: observed adaptations do not usually maximize any absolute measure of fitness, but must instead be understood as outcomes of frequency-dependent evolutionary dynamics determined by the interplay of trait-dependent and density-dependent processes.

Building on these insights, the theory of adaptive dynamics, actively developed at IIASA, is opening up new vistas on studies of adaption, revealing previously unexpected, and often counterintuitive, system behaviors, such as evolutionary branching, evolutionary slowing down, evolutionary self-extinction, and evolutionary cycling.



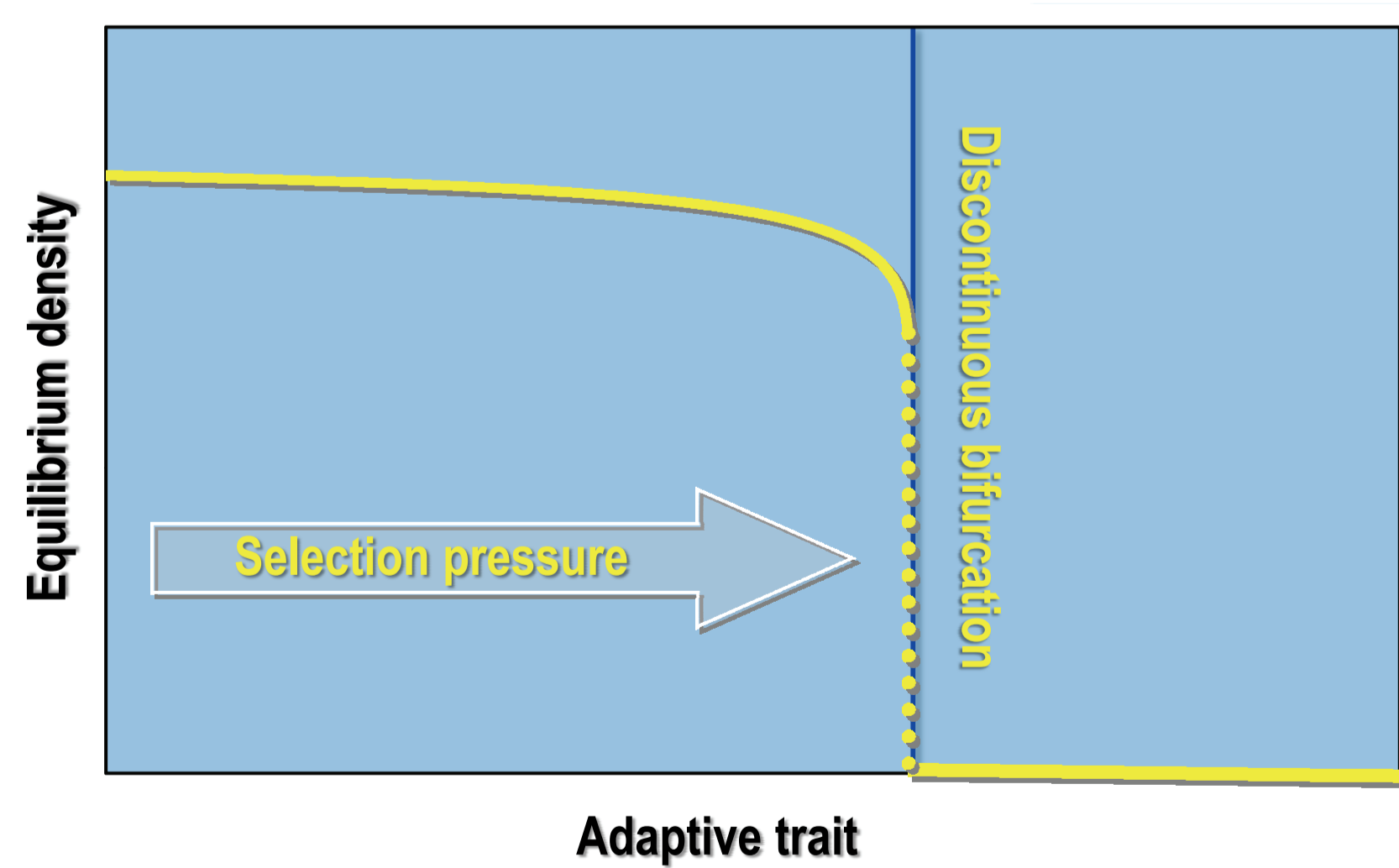
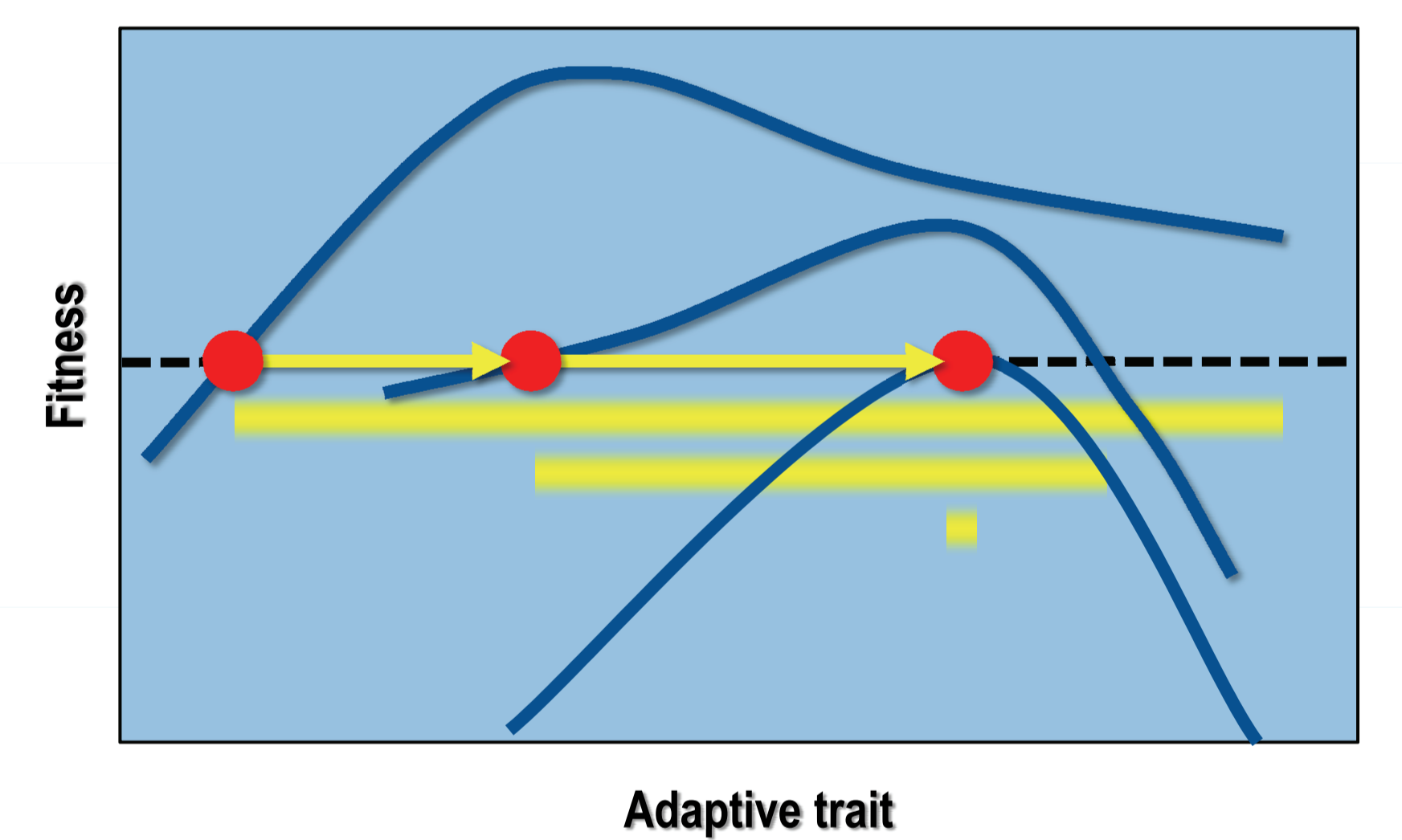
## Evolutionary Branching

Evolutionary branching explains the endogenous creation of diversity. It occurs when evolution counterintuitively converges to a fitness minimum, so that directional selection is followed by disruptive selection. Evolutionary branching can also occur sequentially, resulting in complex evolutionary trees.



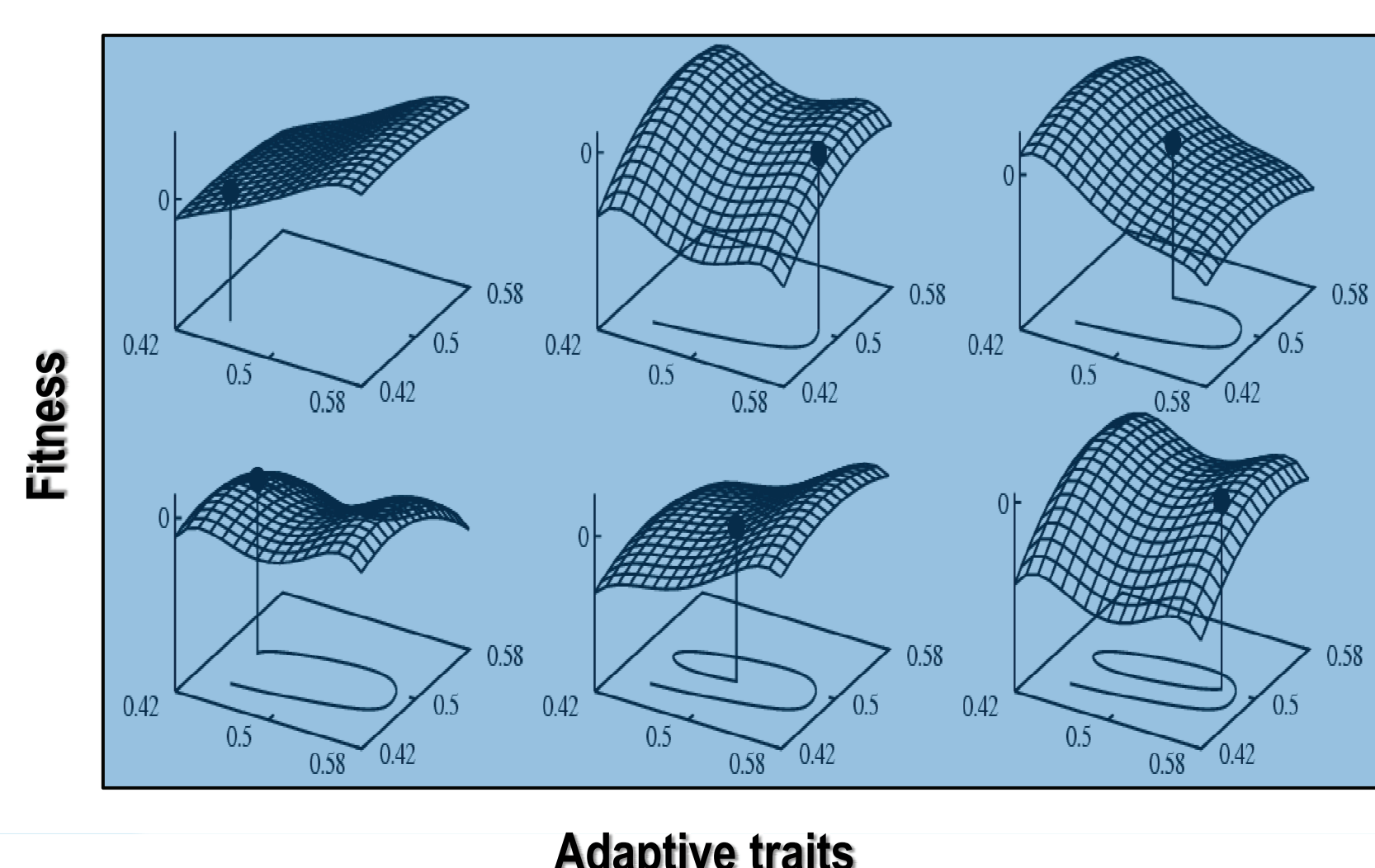
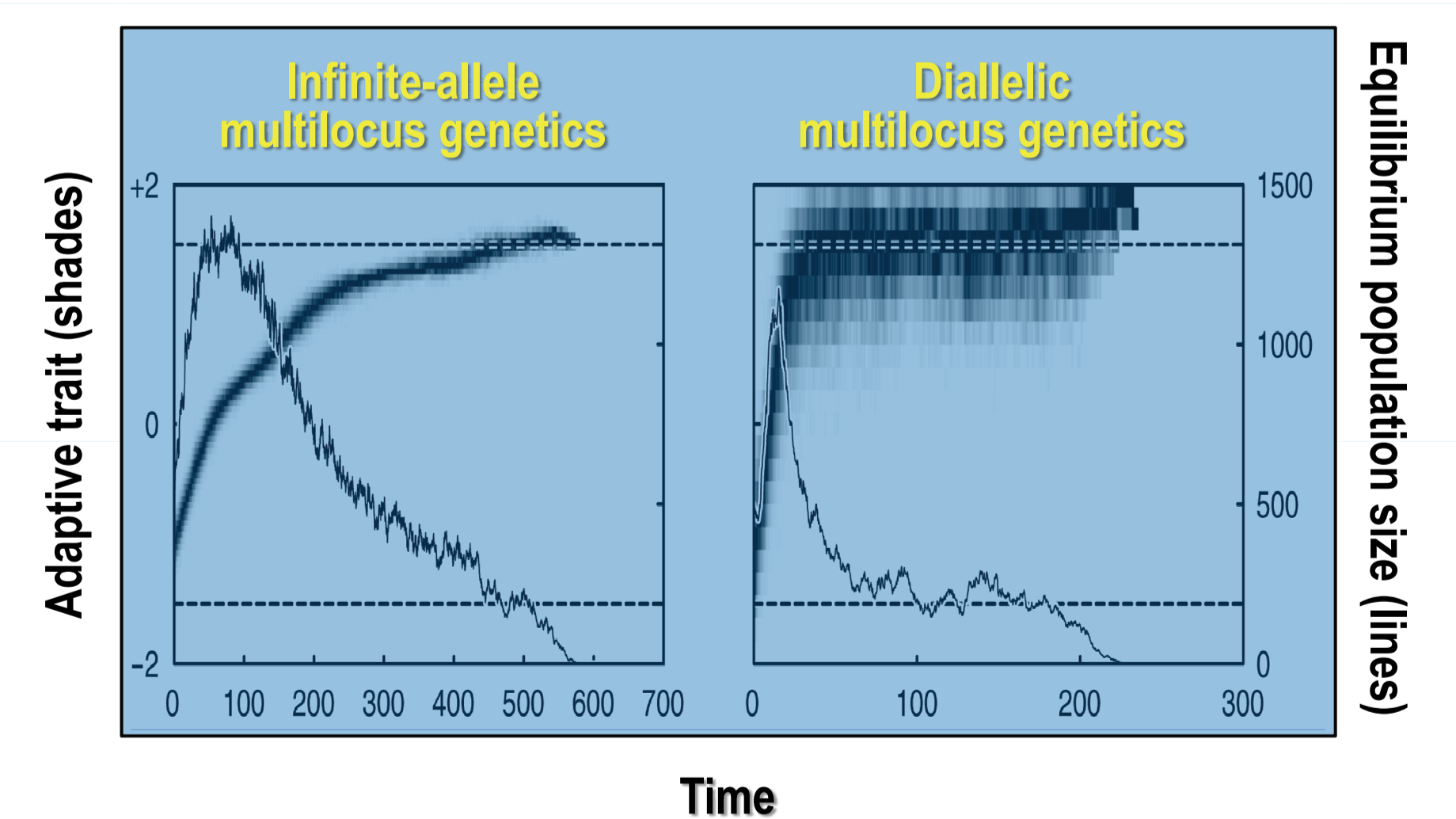
## Evolutionary Slowing Down

Owing to evolutionary slowing down, adaptive outcomes are not approached exponentially fast but algebraically slow. The resultant power law reflects the closing "window of opportunity" for advantageous adaptations, and the power-law exponent  $-(2n+1)^{-1}$  reveals the dimensionality  $n$  of the underlying trait space.



## Evolutionary Self-Extinction

Evolutionary self-extinction occurs when the evolution of an adaptive trait induces a bifurcation in the underlying population dynamics that involves a discontinuous transition to extinction. In this way, a system's gradual adaptation can cause its own demise.



## Evolutionary Cycling

Evolutionary cycling results from an adaptive arms race between traits or populations. As evolution climbs the underlying fitness landscape, this landscape keeps reshaping underfoot, showing how endogenous dynamics can result in incessant adaptations that never settle on any one stationary outcome.

