

# Non-equilibrium dynamics in evolutionary game theory and population genetics

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Complex life would be impossible without cooperation at all levels of biological organization: genes cooperate to create regulatory networks and signaling pathways, cells become parts of multicellular organisms, animals participate in intricate cooperative arrangements both within and between species. Cooperation is ubiquitous in human societies and is credited with the rise and development of modern civilization. However, Darwinian evolution is believed to promote selfish behavior - societies of cooperators are vulnerable to free-riders or cheaters that ultimately take over, destroying cooperation and leading to societal collapse. This apparent paradox has puzzled evolutionary biologists for over half a century. A quintessential model of the paradox is provided by the celebrated Prisoner's Dilemma, a mathematical framework which favors cheaters, even though participating in a cooperative society comes with greater rewards. Here we use tools from non-equilibrium statistical mechanics to study Darwinian evolution in finite and infinite populations. We demonstrate that it is possible to achieve high levels of cooperativity in the game of Prisoner's Dilemma if the probability of cooperation varies depending on the physical appearance and behavior of the opponent. We discuss the role of deception and manipulation in evolutionary games. Finally, we show that fluctuation theorems can be used to re-derive and extend well-known results in population genetics. Taken together, our findings enable deeper understanding of the fundamental evolutionary processes that underpin emergence and development of life on Earth.