Cooperation is favored in expanding populations

Manoshi S. Datta[1], Kirill Korolev[2], Carmel Dudley[2], Ivana Cvijovic[3], and Jeff Gore[1,2]

***Short Abstract* — The evolution of cooperation is a major enigma in evolutionary biology, and the forces driving the maintenance of cooperation in nature are still unclear. Theory predicts that, during range expansions, cooperation is favored at the front of the expanding population wave. We use a yeast model system of cooperative dynamics to demonstrate the enrichment of cooperation on the front of an expanding population. This study provides a demonstration of a novel mechanism by which cooperation could evolve in nature.**

***Keywords* — evolution, cooperation, range expansion, metapopulation**

I. Introduction

EXPLAINING the origin and maintenance of cooperation in nature remains a key challenge in evolutionary biology [1]. By definition, a "cooperator" is an individual that provides a benefit to other members of the population at a cost to itself [2]. Although such behaviors are beneficial to the survival of the population as a whole, theory predicts that they are evolutionarily unstable, as they are easily invaded by opportunistic "cheaters" in the population that can take advantage of the benefit without incurring the cost of cooperation [1,2]. Nonetheless, examples of stable cooperative behaviors are ubiquitous in the wild – ranging from siderophore production in bacteria to the formation of communities in human populations [2].

Natural populations throughout the tree of life have been shown to undergo environmentally induced range shifts and range expansions, during which a population wave (consisting of a low-density front and a high-density bulk population) expands into new territory [3,4]. Recent theoretical work suggests that such range expansions can lead to the fixation of rare alleles (typically via genetic drift) at the low-density front of an expanding population wave, even if such alleles are disfavored in the bulk population [4]. Moreover, cooperative behaviors are often favored at low densities, suggesting that cooperation could even be enhanced by selection on the expanding wave front [5]. Thus, range expansions provide an attractive, potentially widespread mechanism through which cooperation could be maintained in nature.

Acknowledgements: The laboratory acknowledges funding from an NIH R00 Pathways to Independence Award, an NSF CAREER Award. In addition, J.G. thanks the Pew Scholars Program and the Sloan Foundation.

[1]Computational and Systems Biology, Massachusetts Institute of Technology, Cambridge, MA, USA.

[2]Department of Physics, Massachusetts Institute of Technology, Cambridge, MA, USA

[3]Department of Physics, Cambridge University, Cambridge, England, UK

II. Objective & Approach

We hypothesize that range expansions provide a mechanism through which cooperation can be maintained in nature. To test this hypothesis, we have studied the effect of range expansions on the evolution of cooperation in the context of a yeast model of cooperative growth in sucrose. Previous work shows that this model exhibits many of the hallmarks of cooperative behaviors, including negative frequency-dependent growth [5].

In our system, we consider a yeast metapopulation consisting of several discrete, well-mixed subpopulations of cooperators and cheaters. Every subpopulation undergoes daily dilution, as well as fixed migration into the neighboring regions to simulate "range expansion" into novel territory. We monitor the cell density and the frequency of cooperators in all subpopulations each day.

III. Results & Conclusions

We have analyzed the spatio-temporal dynamics of microbial populations undergoing range expansions, both with and without the presence of cheaters. Consistent with the theory, when cheaters are present, we observe a dramatic enrichment of cooperators on the front of the expanding population wave. This enrichment significantly increases the frequency of cooperation in the population as a whole compared to any individual subpopulation, providing traction for the idea that range expansions could allow for the maintenance of cooperation in the wild.

More broadly, this study suggests a strong coupling between the ecological dynamics of expanding populations and the evolutionary dynamics of cooperation. These dynamics are typically assumed to occur on vastly different timescales such that there is very little coupling between them. However, our study suggests that the fate of the population is driven by the interplay of the spatio-temporal dynamics of spreading populations and density-dependent cooperative growth.

References

[1] Xavier, JB (2011) Social interaction in synthetic and natural microbial communities. *Mol. Sys. Bio.* 7, 483.

[2] Nowak MA (2006) Five Rules for the Evolution of Cooperation. *Science* 314, 1560-1563.

[3] Moreau, C, Bherer, C, Vezina, H, Jomphe, M, et al (2011). Deep human genealogies reveal a selective advantage to be on an expanding wave front. *Science* 334, 1148-1150.

[4] Hallatschek, O & Nelson, DR (2007). Gene surfing in expanding populations. *Theor. Pop. Bio.* 73, 158-170.

[5] Gore, J & van Oudenaarden, A (2009). Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459, 253-256.