Cooperation in yeast sucrose metabolism

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Understanding the conditions required for the initiation and maintenance of cooperation is a classic problem in evolutionary biology. Yeast digest sucrose using the enzyme invertase in such a way that a majority of the useable product is lost to the environment and consumed by other cells. We have demonstrated experimentally that this results in cooperative growth in sucrose cultures. We have developed a simple model that explains the cooperative interaction and that accurately predicts the outcome of competition experiments in a variety of conditions between the wildtype cooperator strain and a cheater strain that does not produce invertase.

***Keywords* — cooperation, evolution, yeast, game dynamics.**

I. Introduction

THE evolution of cooperation presents a significant challenge to our understanding of evolution [1,2]. If evolution favors survival of the fittest, then how can costly behaviors that benefit others arise?

The simple monosaccharides glucose and fructose are the preferred carbon sources of the budding yeast *S. cerevisiae*, although when these sugars are not available yeast can utilize alternative carbon sources such as sucrose [3], a disaccharide composed of glucose and fructose. Digesting sucrose requires that the disaccharide be broken down into its constituent sugars, a reaction catalyzed by the enzyme invertase which is secreted into the periplasmic space between the plasma membrane and the cell wall [4]. However, it may be possible for some of the resulting glucose and fructose to diffuse away before the cell is able to import them. Supporting the idea that monosaccharide loss to the environment may be important, it has been shown that at high density on a sucrose plate a "cheater" strain with the invertase gene knocked out is able to outcompete the wildtype strain [5].

II. Results

We have found that the growth rate of yeast in sucrose culture increases with cell density, suggesting that sucrose metabolism is indeed cooperative. After invertase hydrolyzes sucrose at the cell surface there is a competition between monosaccharide import and diffusion away from the cell. Analytical calculations predict that only ~1% of the monosaccharides are captured; the vast majority of the glucose and fructose therefore diffuse away and are eventually consumed by other cells. Experimental measurements of the rate of sucrose hydrolysis and monosaccharide import quantitatively validate these theoretical predictions and provide a framework through which to understand the nature of cooperation in this system. The production and secretion of invertase is a cooperative behavior with a leaky capture of benefits (in this case monosaccharide import).

We have developed a simple game theory model that yields a phase diagram predicting the outcome of competition between wildtype cooperator cells and mutant cheater cells lacking the invertase gene. We are able to probe this phase diagram experimentally by controlling both the sugar concentrations and the cost of cooperation (using a histidine auxotroph cooperator together with limiting histidine concentrations). As the parameters governing the interaction are varied we are able to transform the nature of the "game" and observe qualitatively different experimental outcomes—either coexistence of the two strains or extinction of the cooperating strain. However, over a wide range of parameters we observe coexistence between the cooperator and cheater strains, suggesting that the interaction is a snowdrift game in which the optimal strategy is the opposite of one's opponents [2]. Finally, we have experimentally characterized the wildtype invertase production strategy and find that the response is appropriate for the snowdrift game—wildtype cells cooperate when competing against cheater cells but cheat when competing against cells that always cooperate.

III. Conclusion

This study demonstrates how a given cooperative interaction—in this case a leaky capture of benefits—can lead to qualitatively different outcomes depending upon the conditions of the competition. In the future we plan to extend these experiments to consider competition in spatially structured environments.

References

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