Modeling reciprocal altruism and quorum sensing in biofilms

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Bacterial cells in biofilms cooperate through the secretion of public goods, such as digestive enzymes and iron chelators. This cooperative behavior is subject to exploitation by non-producing cells. Quorum sensing (QS) is thought to mitigate exploitation by directing cooperative benefit to other cooperators. However, QS is also vulnerable to exploitation by "mimic" cells that produce QS signals without producing public goods. Here, we consider the special case where the QS signal is also the public good, leading to a novel form of reciprocal altruism among cooperators. We find that this mechanism is sufficient for the evolution of cooperation in a computational biofilm model.

***Keywords* — Quorum sensing, evolution of cooperation, kin selection, reciprocal altruism, biofilms, bacteria, game theory.**

[1] Introduction

BIOFILMS are diverse microbial populations characterized by a high degree of intercellular cooperation. Many biofilm cells export public goods such as chelators, virulence factors and digestive enzymes. In many cases, either the public good or its product can diffuse away from a producing cell [1]. In these cases, producing cells are subject to exploitation unless they can preferentially direct the benefits of shared resources to other public-good producers ("cooperators"). It has been shown that quorum sensing (QS) can facilitate kin selection among cooperators [2]. But QS is itself vulnerable to cheating, in that some cells may produce QS signals without actually cooperating. Here, we look at the special case where the QS signal is also the public good, leading to a form of reciprocal altruism [3]. This behavior has been observed in *Pseudomonas aeruginosa*, where the presence of phenazine triggers additional phenazine production [4]. We consider the difference between this strategy and more general quorum-sensing strategies, and seek to identify the conditions under which each would be favored.

[2] Computational Model

To explore the effect of public good diffusion on the evolution of cooperation in biofilms, we developed a model consisting of a discrete cellular population coupled to the concentrations of three diffusible solutes: a catalyst, its substrate, and its product. All cells grow at a basal rate and divide at some threshold biomass. Cooperators produce catalyst, reducing their growth rate, while non-cooperators do not. The catalyst's product can accelerate growth in any cell. The catalyst is subject to decay, yielding a finite range of catalyst activity around producing cells. "Naïve" cooperators produce catalyst at a constant rate. "Reciprocal" cooperators produce catalyst in proportion to the amount present at their site, with a small baseline production rate.

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[3] Preliminary results & Discussion

We competed "naïve" and "reciprocal" cooperators against non-producing cells. Naïve cooperators are easily exploited by cheaters (Fig. 1, left). However, "reciprocators" tend to dominate over cheaters (Fig. 1, right). Reciprocity is therefore sufficient to direct cooperative benefit to other cooperators. However, typically QS signals are not public goods. Such pure signals are vulnerable to exploitation by individuals that signal but fail to cooperate. Given the sufficiency of a reciprocal strategy for the evolution of cooperation, why is pure QS so prevalent? One possibility is that, in addition to preventing exploitation, QS also facilitates complex social coordination. A pure QS signal may provide additional flexibility and efficiency that outweighs the risk of exploitation. Using our simulation framework, we seek to identify the conditions under which QS is favored over reciprocal public good production, despite its vulnerability to cheating. We hope this work will provide new insights into the evolution and social role of quorum sensing.

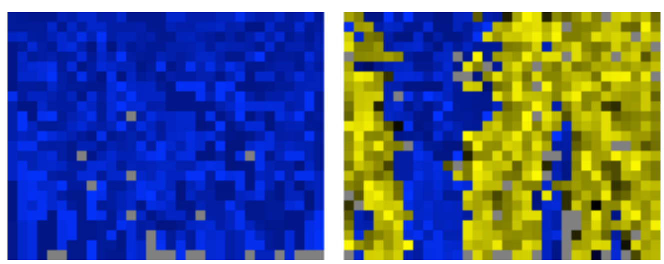

Figure 1. Final population distribution for constitutive (left) and reciprocal (right) public good production. Non-producers in blue; producers in yellow; dead cells in grey. Color intensity shows biomass.

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