Defect or Die: How Does Low Resource Availability Impact the Preservation of Cooperation in a Quorum-Sensing Regulated Public Good Economy?

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Abstract

Quorum sensing is a mechanism by which bacteria regulate and coordinate group behavior. In quorum sensing regulated cooperation, each bacterium will excrete an auto-inducer, and when the concentration of the auto inducer is sufficient, the colony will act. It is an innate quality of cooperative strategies that they are evolutionarily stable only if there is a net benefit to cooperating organisms. Using Empirical, we attempted to determine if historical quorum sensing-behavior in a colony could be destabilized by low resource availability. We found that low resource availability, under a certain threshold, does select for reduction in cooperation over time. In worlds with randomized offspring spawn location, defecting from cooperation is even more favorable.

Introduction

Quorum sensing is a method of bacterial communication used by bacteria to detect *quorum*, the minimum number of bacteria needed to carry-out colony-wide behaviors. Quorum is detected by individual bacterium producing and secreting auto-inducers (Holm and Vikström, 2014). When the concentration of the auto-inducer is high enough, the population of bacteria will complete some action. The action can be one of a wide array of behaviors, including bioluminescence, biofilm formation, virulence, and antibiotic resistance (Diggle et al., 2007).

Another example of quorum sensing is quorum sensing regulated protease secretion. Proteases are enzymes that cleave peptide bonds and break proteins down into consumable nutrients. The benefit of using quorum sensing to regulate protease secretion is that it allows for individuals in a cooperating population to consume larger resources than each individual would be able to consume by itself.

One such bacteria that use quorum sensing to regulate protease secretion is *Vibrio harveyi* (Bruger and Waters, 2015). *V. harveyi* are a pathogenic marine bacteria found in the gut microflora of a variety of invertebrates and fish including oysters, prawns, lobsters, barramundi, turbot, milkfish, and seahorses ((Austin and Zhang, 2006); (Lee et al., 2002)). They can also be found free floating in tropical waters (Montánchez et al., 2019). Quorum sensing regulated
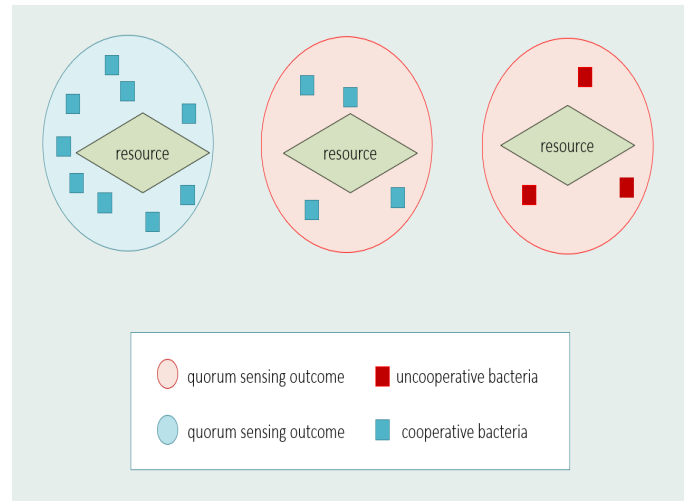

Figure 1: A representation of some of the outcomes of quorum sensing behavior

resource collection is fascinating because it only increases an individual's fitness if they reap a net benefit from the co-operation. Therefore, the question that this investigation is concerned with is this: will a population of organisms using quorum sensing to regulate resource collection cease to do so when resource availability is extremely diminished?

We hypothesized that decreasing the resource levels would lead to decreasing the population cooperation level. We tested this by giving populations differing levels of resources. For each resource level, we ran simulations representing a gut environment and a totally aquatic environment. We found that there exists a threshold of around 8k resources that will cause the population's overall cooperation to decrease over time. We also found that simulations replicating an aquatic environment are less supportive of cooperation.

Methods

To conduct our investigation into the effect of low resource availability on the preservation of quorum sensing, we utilized Empirical, an open source artificial life platform, to
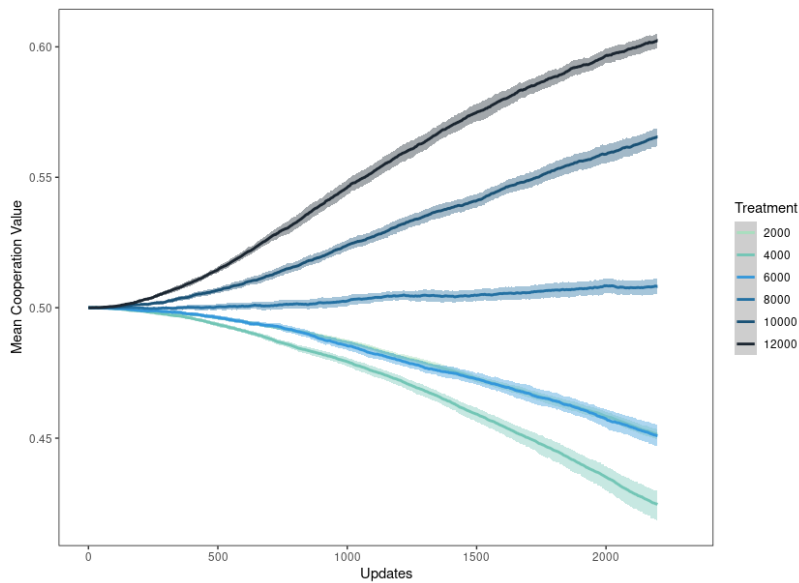
Figure 2: Cooperation evolving across different resource levels with population mixing.

replicate the environment of *V. harveyi*. In the environment we created, we coded in the following axioms: 1) the pre-existence of quorum sensing behavior, 2) the necessary features for evolution via natural selection (horizontal transmission, mutation and competition), 3) the ability of individual bacterium to identify the presence of their neighbors, and sense quorum, 4) the existence of a quorum threshold, or minimum number of necessary cooperators for quorum sensing to take place, and 5) the ability of bacterium to reproduce when they have collected a certain value of resource points.

In our world, we began with a population of 1,000 bacteria, and had a population max of 10,000. Each bacterium has a genome representing their likelihood of attempting to participate in quorum sensing, represented by a single float on a scale of 0.0 to 1.0. To represent the preexistence of quorum sensing in the population, we set the beginning genome of all organisms to 0.5. We set the threshold of cooperating neighbors necessary for quorum sensing to 60% (Vostinar et al., 2018). On each grid space in the world, there exists a resource with a value ranging from 0 to the user selected maximum resource value.

During each update, each organism is given the opportunity to individually collect resources, and to participate in cooperation. If an organism attempts to individually acquire resources, it must have a genome value below some randomly generated float. If an individual has the appropriate genome, there is a baseline successful acquisition rate of 30%, which represents the increased difficulty of producing the protease necessary to consume a resource individually. Organisms who attempt to collect resources individually will receive the full value of the resource added to their

resource points. On the other hand, if an organism attempts to cooperate, it must have a genome value higher than some randomly generated float. All of its neighbors within a 8x8 grid centered on the organism will be checked for a genome appropriate for cooperation. If there is a cooperator concentration of at least 60%, the bacterium will receive the value of the resource they are on divided by the number of cooperators.

After bacteria are given the chance to collect resources, they will be checked if they are eligible to reproduce. If an individual has 1000 resource points, they will reproduce and pass down their genome with a mutation value chosen from a normal distribution centered at 0.0 with a standard deviation of 0.002.

To replicate both the aquatic and gut environments of *V. harveyi* we added or removed a structured population grid. When a population grid is absent, offspring have randomized spawn location, and when it is present offspring spawn next to their parents. Randomized offspring spawn locations represent free floating bacteria, and offspring spawning next to their parents represents a structured environment.

The focus of this experiment is on the effect of low resources on the bacterial population's aggregate cooperation level. To investigate this, we ran experiments with maximum resources values of 2k, 4k, 6k, 8k, 10k, and 12k. We ran each resource value for 20 random seeds, and ran experiments with an environmental structural grid turned on and off.

Results and Discussion

The key question addressed in this investigation is as follows: does lowering the resources available to a population
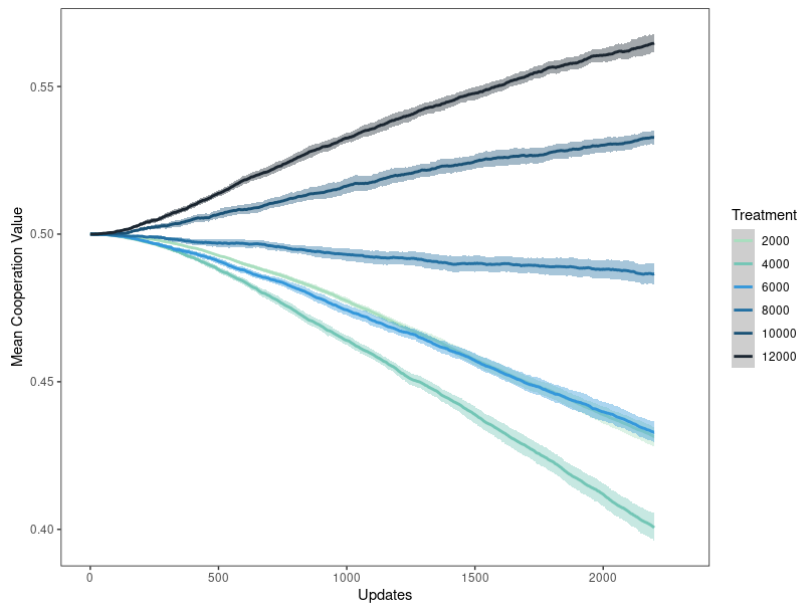
Figure 3: Cooperation evolving across different resource levels with population mixing.

of bacteria who utilize quorum sensing select for drift from quorum sensing behavior? To test this, we gave a maximum resource value of 2k, 4k, 6k, 8k, 10k, and 12k and ran each resource value in a world representing an aquatic environment and a gut environment.

Low resource availability and structured population grid

We hypothesized that there would exist a particular threshold value for level of resources where any value below it would cause cooperation to decrease over time. It does not increase individual fitness to collaborate in situations where there is no net resource benefit to the individual. Therefore, cooperation is not an evolutionarily advantageous method of resource collection in extremely low resource situations.

We found that the set of resource values below 8k do select for lower cooperation over time. Figure 2 shows the evolution of cooperation across the six treatment resource levels. When a simulation is treated with a maximum resource value lower than 8k, the population will decrease in cooperation. The highest rate of decrease in cooperation occurs when there is a maximum resource level of 4k. When treated with a maximum resource level of 2k, the cooperation decrease is most similar to 6k. While this result may seem peculiar, it becomes intuitive when one considers that 2k is likely too low of a resource value for the bacteria to reproduce and evolve during the same time frame as the higher maximum resource treatments.

When a simulation is treated with a maximum resource value of 8k - 12k, the overall population cooperation increases. The increase in cooperation is highest at a maxi-

mum resource treatment of 12k resources. There seems to be no upper bound on the resources to cause an increase in cooperation.

These results indicate that populations that have a structured population grid will experience an overall decrease in the cooperation value if you starve them of resources. This means that it is more evolutionarily viable to defect from cooperation when there is extreme decrease in resource availability. Additionally, this suggests that short term resource acquisition is more important than the long term benefits of cooperation (i.e kin selection).

Low resource availability and unstructured population grid

The results from our trials with an unstructured population grid are very similar to those produced with a structured population grid. The main differences are: 1) the reaction to the 8k resource treatment, 2) the magnitude of cooperation change and 3) the variation from the median. Figure 3 shows the results from each resource value over time.

In the structured population grid, there was a slight increase in community cooperation in response to the 8k resource treatment. However, in an unstructured population grid the same treatment causes a decrease in community cooperation. This result suggests that cooperation in worlds with unstructured population grid is more vulnerable to destabilization.

The fact that unstructured population grids are less tolerant to low resource availability is further supported by the magnitudes of change in cooperation across grid treatments. When we treated the worlds with a 12k max resource, the

treatment that causes the highest increase in cooperation, the unstructured world evolved to a significantly lower cooperation value than the structured world evolved to at the final time step (Wilcoxon rank sum pairwise $p < 0.00005$). Additionally, the 4k treatment, the treatment that causes the highest decrease in cooperation, caused a significantly lower final cooperation in the unstructured grid than the structured grid (Wilcoxon rank sum pairwise $p < 0.00005$).

There is lower tolerance toward cooperation present in worlds with no population grid because sub-populations of cooperators cannot isolate themselves from the larger general population. When offspring are randomly placed on the board, significant regional genomic differences are not permitted to form.

As aforementioned, the variance within the two treatments are also unique from each other. As seen in Figure 4 and Figure 5, there are several lower bound outliers found in trials with population grid turned on. These outliers would be typical data points for trials with unstructured populations. These outliers likely occurred in simulations where there happened to be no smaller sub-populations of cooperators forming in the world.

Taken together, these results show that cooperation in grid-less worlds is less resilient to low resources. Additionally, grid-less worlds are less supportive to cooperative systems overall. In the real-world system of *V. harveyi*, this means that gut microflora environments are more supportive of cooperation than open world environments. This is corroborated by studies of real bacterial behavior in laboratory settings ((Lion and van Baalen, 2008); (Bruger and Waters, 2015))

Conclusion

We have shown that when choosing between defecting from cooperation or cooperating with a non-certain net benefit, there is indeed a point where it increases fitness to defect. Furthermore, we have shown that worlds with structured grids are more tolerant towards low resources; the resource level that is required to destabilize cooperation in a population with a unstructured population grid is less than that required to destabilize a population with a structured grid.

The ultimate phase of evolution is stable preservation of the evolved trait. Therefore, we are interested in conducting further research investigating the plateau of cooperation levels caused by different resource treatments. Additionally, we are interested in examining if the trajectory of cooperation change can be altered by changing the resource treatment.

Further investigation into the roles of cheaters in public good cooperation is also of interest. In human public good economies, the ability to punish cheaters is essential to the maintenance of reciprocal altruism, and general high-levels of cooperation (Melis and Semmann, 2010). Some bacteria who use quorum sensing to regulate public goods, such as *P. aeruginosa* and *B. thailandensis*, have systems of punishing cheaters (Abisado et al., 2018), while *V. harveyi* does not. Therefore an investigation into the conditions for the *de novo* evolution of a punishment system *V. harveyi* could contribute evidence to the existence of reciprocal investment in non-human public good economies.

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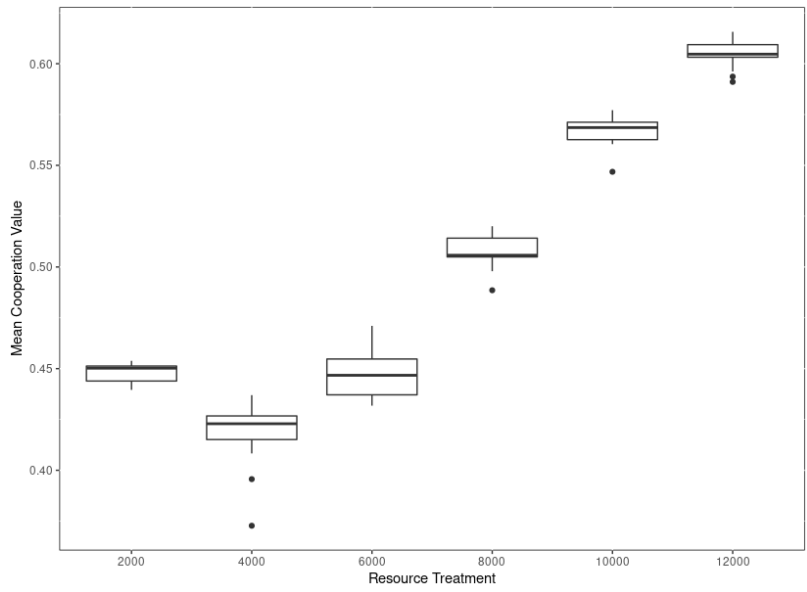
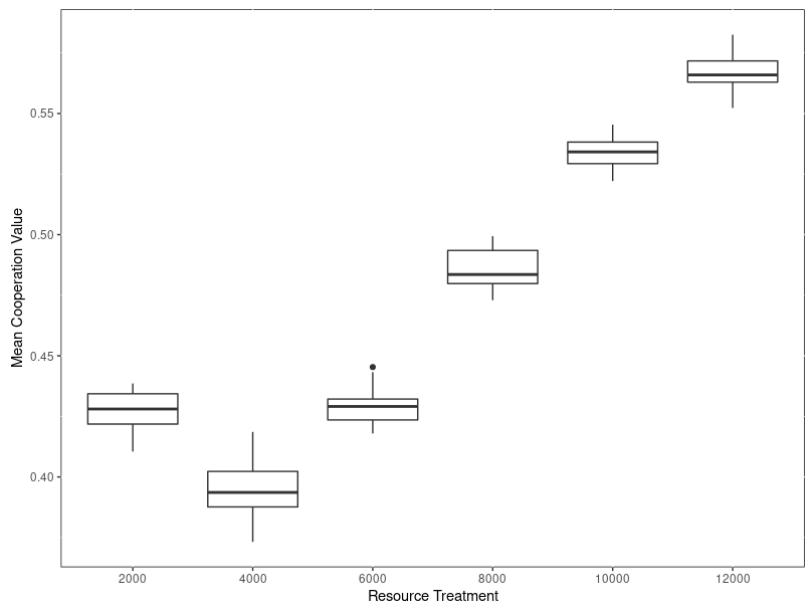Figure 4: Cooperation at the last time step across different resource levels without population mixing

Figure 5: Cooperation at the last time step across different resource levels with population mixing.