Spatial reciprocity limits public good diffusion in bacterial colonies growing on a surface

Thomas Julou[1], Thierry Mora[1], Isabelle J. Schalk[2], David Bensimon[1], Nicolas Desprat[1*]

***Short Abstract* — Siderophores shuttle between cells and the environment to deliver iron to bacteria. To study the spatial management of this public good, we measured the single-cell dynamics of an endogenously fluorescent siderophore in micro-colonies growing on a solid surface. We showed that the dynamics was heterogeneous and correlated over very short distances. A microscopic model of exchange between adjacent cells was able to capture the spatio-temporal dynamics of the whole colony. We further showed that individual growth rates were correlated with the siderophore concentration in neighboring cells. These results emphasize the stabilizing role of spatial reciprocity on the maintenance of cooperation.**

***Keywords* — cooperation, bacteria, single-cell, pyoverdine, spatial interactions, image analysis, tit-for-tat, ecology, evolution**

I. Context

Iron is an essential cofactor of many enzymes. To overcome the low solubility of iron, bacteria produce and release in their environment iron-chelating molecules called siderophores [1]. After iron chelation, the ferric form of the siderophore is transported back into the bacteria by specific membrane transporters. Since siderophores may benefit other cells than those that produced by them, they are a prototypical example of a public good [2]. In stirred liquid cultures, the secreted siderophores are shared uniformly: every individual enjoys the same benefit, in proportion to the average concentration of public goods. However siderophore production and secretion have a metabolic cost. Consequently, in stirred cultures production mutants out-compete wild type cells [3][4], eventually leading to population collapse. In fact, since production (cooperation) can easily be defected by mutants, it may seem surprising that production mutants did not displace the producers on evolutionary timescales [5].

II. Data and Modeling

To investigate the spatial effects of siderophore usage [6][7], we measured the fluorescence of siderophore in individual bacteria of micro-colonies of *P. aeruginosa* growing on solid agar surface under a microscope. We followed individual dynamics and reconstructed the genealogy of the colony. Along each lineage, the fluorescence of cells fluctuated in time, with a correlation time of about twice the division time. To explain the dynamics of the colony, we considered a simple and very general model of siderophore exchange between adjacent cells. With the measured parameters, our model can be used to make concrete, testable predictions with no free parameters on the distribution and fluctuations of siderophores in the colony. These predictions were quantitatively confirmed by data collected from 10 micro-colonies. Our findings suggest that a spatial mechanism of reciprocity (similar to a tit-for-tat strategy) may promote cooperation by allowing producers to exchange public goods with their exclusive and immediate neighborhood.

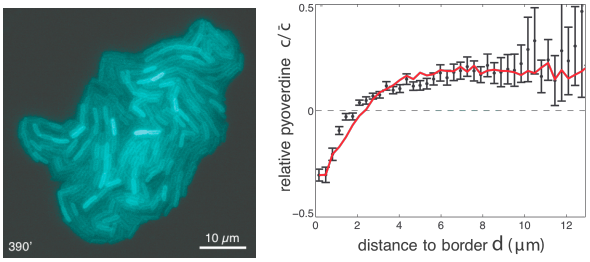

Fig 1: Pyoverdine (siderophore) distribution in a monoclonal micro-colony (left) and its spatial gradient (right)

III. Conclusion

The exchange mechanism observed between adjacent cells is similar to paracrine signaling in eukaryotic tissues. The further observation of a spatial gradient in a growing micro-colony suggests an analogy between biofilm formation and tissue development. Altogether, these aspects emphasize the growing recognition that bacterial colonies might share many more similarities with multicellular organisms than previously assumed.

References

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* desprat@ens.fr
Acknowledgements: This work was funded by ANR JCJC and CNRS.
[1]Laboratoire de Physique Statistique (UMR8550), Ecole Normale Superieure,
[2]Biotechnologie et Signalisation Cellulaire (UMR 7242), Universite de Strasbourg-CNRS, ESBS