Review Article | Published: 25 July 2016

Spatial structure, cooperation and competition in biofilms

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Nature Reviews Microbiology 14, 589–600 (2016) | Download Citation

Abstract

Bacteria often live within matrix-embedded communities, termed biofilms, which are now understood to be a major mode of microbial life. The study of biofilms has revealed their vast complexity both in terms of resident species composition and phenotypic diversity. Despite this complexity, theoretical and exper work in the past decade has identified common principles for understanding microbial biofilms. In th Review, we discuss how the spatial arrangement of genotypes within a community influences the coo

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and competitive cell–cell interactions that define biofilm form and function. Furthermore, we argue that a perspective rooted in ecology and evolution is fundamental to progress in microbiology.

Key points

- Bacteria often exist in biofilms, which are surface-adhering or free-floating groups of cells that are bound together by a secreted polymer matrix. These microbial collectives are important for bacterial occupation of diverse ecological niches, they contribute to biogeochemical cycling, and they cause disease in multicellular organisms.

- Within biofilms, bacteria interact with each other closely through cooperative phenotypes, such as the production of digestive enzymes, and antagonistic phenotypes, such as the expression of type V or type VI secretion systems. The evolutionary dynamics of these social phenotypes depend on their costs and their effects on other cells.

- Many bacterial social phenotypes involve the secretion of products that affect neighbours in a distance-dependent manner. As a result, interaction networks within biofilms are largely determined by the spatial structure of the biofilms — that is, the arrangement in space of different clones, strains and species.

- When biofilms are segregated into clonal clusters, the neighbourhood of a given cell mostly contains clonemates, and natural selection often favours the secretion of compounds that benefit all recipient cells. However, when different strains and species are spatially mixed within biofilms, cells primarily interact with other genotypes and antagonistic behaviour is often favoured. Under certain circumstances, between-species commensalism or mutualism can also evolve and remain stable against cheating.

- Cooperative and antagonistic phenotypes fall under the control of sophisticated sensory mechanisms, such as competition sensing and quorum sensing, that evolved to help account for the variation in exposure to other strains and species in space and time. These regulatory mechanisms help to reduce the marginal costs of social phenotypes, maximize their fitness impacts and ensure that the correct recipient cells are targeted.

- Both cooperative and antagonistic behaviours feed back onto population spatial structure by locally altering the growth rates of other cells and thus changing local biofilm composition.

- Many bacteria and unicellular eukaryotes have evolved strategies for actively altering biofilm population structure, either through selective adhesion that spatially assorts the biofilm into groups that contain one or more specific genotypes or through the secretion of extracellular matrix components that spatially organize biofilm-dwelling cells.

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Acknowledgements

The authors are grateful to A. Persat, A. Stacy, D. Cornforth, N. Oliveira, W. Kim, S. Diggle and two anonymous reviewers for providing comments on the manuscript. P. Singh and R. Hartmann provided invaluable help in the preparation of figure 4d. Work in the contributing laboratories was supported by European Research Council grant 242670 (K.R.F.), The Max Planck Society (K.D.), the Human Frontier Science Program (K.D.) and the Alexander von Humboldt Foundation (C.D.N.).

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Competing interests

The authors declare no competing financial interests.

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Glossary

Microbiota

The community of microorganisms that live in association with a particular host organism (for example, the gut microbiota) or abiotic environment (for example, the soil microbiota).

Social phenotypes

Phenotypes that exert an effect (either positive or negative) on the reproductive output of other individuals and which evolved, in part, because of this fitness effect that they exert.

Type VI secretion system

(T6SS). A mechanism for killing neighbouring cells by the extension of a phage-tail-derived structure to putatively puncture adjacent cells and deliver toxic effectors.

Dispersal

The process by which cells depart from a community, either individually or collectively. Dispersal can be active, in response to stresses such as nutrient limitation, or passive, owing to biofilm erosion by fluid flow.

Genetic drift

A change in allele frequency in a population due to random sampling of organisms across generations (for example, due to stochasticity in reproductive success).

Public goods

Substances that are secreted into the extracellular space that provide a benefit to other cells in the vicinity.

Cheating mutants

Genotypes that gain a relative fitness advantage by receiving the benefits of an evolved cooperative trait of other genotypes, such as a public good, without contributing to the cooperative interaction themselves.

Ecological productivity

The total biomass produced by a strain or species in a given environmental setting

Antibiotics

Molecules that are produced by various microorganisms and act as toxins against other microorganisms; some antibiotics have been co-opted as pharmaceuticals for the treatment of microbial infections.

Bacteriocins

Antibiotics that are produced by bacteria and specifically target other bacteria. Bacteriocins often occur as toxin–antitoxin pairs that are encoded on the same plasmid or in the same genomic neighbourhood.

Contact-dependent inhibition

A mechanism of inhibiting the growth of neighbouring cells by the extension of a helical structure to contact target cells and deliver toxic effector molecules.

Syntrophic relationships

Interactions in which one species benefits by using the product of another as a nutrient source; the producing species may in turn benefit from the removal of this product.

Flocculation

Aggregation of yeast cells to form large multicellular groups that precipitate from liquid cultures and exhibit heightened stress tolerance.

Greenbeard gene

A gene (or a set of closely linked genes) that is responsible for both an identifying phenotypic trait and a cooperative behaviour that targets that identifying trait, ensuring that the greenbeard gene bearer preferentially benefits other bearers of the greenbeard gene.

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Publication history

Published

25 July 2016

DOI

https://doi.org/10.1038/nrmicro.2016.84

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