

# Microbial competition and evolution in natural porous environments: Not that simple

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In their recent article, Coyte et al. (1) use an innovative combination of microfluidic experiments, mechanistic models, and game theory to study the impact of physical microenvironments on the activity of bacteria in porous media. The authors find that hydrodynamics can profoundly affect how bacteria compete and evolve in these systems. They indicate that this conclusion could in principle have important implications for the management of a range of engineered and natural porous media. However, two aspects of the research significantly limit its relevance to practical applications, especially in soils and sediments.

The first aspect is the premise that bacterial growth in porous media occurs within biofilms that cover pore walls uniformly. This assumption underlies the model used by Coyte et al. (1), and has clearly motivated the design of their experiments. However, biofilms are far from ubiquitous in natural porous media. In the pore space of unsaturated soils, where many bacteria live, such biofilms are typically not observed (2, 3). In saturated fine- to medium-textured porous media, numerous microscopic observations indicate that biofilms are the exception rather than the rule. Indeed, even when severe bioclogging occurs in such systems, bacterial cells are not located in continuous biofilms but instead aggregate preferentially at pore necks (4, 5). Various modeling efforts have shown conclusively that to describe the occasionally pronounced effects of bacteria on the hydrodynamics of saturated porous media, approaches assuming the presence of continuous biofilms are not satisfactory, even when biofilms are considered to be permeable, and models need to

invoke the development of plugs of low permeability, obstructing the lumen of pores (6, 7). It is possible that Coyte et al.'s (1) conclusions would still stand upon consideration of such plugs, but this will need to be checked.

The second aspect that decreases the appeal of Coyte et al.'s (1) results in practice is the fact that, even though their research claims to be related to microbial competition, it involves only bacteria. In real porous media, other microorganisms are unavoidably present (8) and may affect not only the competition and evolution of bacteria directly, but also the hydrodynamics of the pore space. Growing fungal hyphae (9) may transport bacteria (and archaea) from one portion of the pore space to another, as well as partially clog pores. Hydrodynamics may have a sizeable effect on the dynamics of protozoan predators (10), predatory bacteria, or viral particles (phages), all ubiquitous in natural porous media and directly influencing the fate of bacterial populations.

In this context, Coyte et al.'s (1) research should be viewed as the exploration of one scenario, among several plausible ones, to account for the competition or evolution of bacteria in porous media. Their results, in particular related to the application of game theory, are interesting, but do not settle the many questions associated with what determines the level of microbial biodiversity found in subsurface environments. A complete description will require the development of more realistic models, and additional data associated with the physical, chemical, and microbial characteristics of microenvironments in real porous media.

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