LETTER

REPLY TO BAVEYE AND DARNAULT: Useful models are simple and extendable

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> Model building is the art of selecting those aspects of a process that are relevant to the question being asked.
>
> John H. Holland (1)

Baveye and Darnault (2) contend that our model (3) is too simple and that we should have considered more intricate biofilm distributions and other microbes than bacteria. We were surprised by these comments. All models can be made more complex, such that the observation that the world is "not that simple" relative to a given model is an empty truism. The very goal of a model is to seek simplicity to increase understanding. One can also always propose alternative parameterizations or extensions to any model. However, in their suggestions, Baveye and Darnault (2) have misunderstood key aspects of our model and, moreover, it is not clear that their proposed extensions would provide interesting or contradictory results. Here, we discuss our model in light of the comments made with the hope that this encourages primary research rather than further speculation.

Our paper (3) uses experiments and models to resolve how two biofilm patches interact with one another via flow, assuming the competing biofilms have a uniform thickness and extend for equal length in the direction of flow. We do not explicitly assume that "continuous" biofilms coat the entirety of the pore space; but rather, we use a one-dimensional model to simulate a discrete biofilm patch, which eliminates the need to make arbitrary assumptions about the geometry of the pore space and how different genotypes are initialized within it. Consistent with this model, we motivated our study with a Stokes flow simulation that illustrates how a discrete biofilm patch within a single pore throat perturbs the flow.

Our model, although simple, is representative of many porous environments where bacteria are observed in discrete patches. In porous environments, these surface-attached cells are often called biofilms; however, in the soil literature they sometimes are not and this can depend on one's definition of a biofilm (4–9). Regardless of their name, however, groups of surface-attached cells growing in a pore space are expected to locally perturb flow, as predicted by our model (3). In addition, we want to emphasize that our model is aimed at capturing how bacterial growth diverts flow from one pore to another at the microscopic pore scale, and we do not think that models that parameterize the permeability reduction caused by biofilms at the macroscopic, Darcy scale (8, 10) provide a useful benchmark for the present study.

In summary, our contribution develops a framework to understand how flow affects bacterial competition and evolution in porous environments. It is clear that many diverse processes shape the composition of microbial communities and there are a number of possible extensions to our work. However, our model's purpose was not to provide comprehensive representation of all of these, but rather to provide a deeper intuition of one of them.

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