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Diffusion limited mutualism

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Microbes trade diffusible molecules to survive and maintain complex ecological functions. Physicists have substantially advanced our understanding of microbial populations, primarily relying on the evolutionary game theory. Game theory however was developed for higher organisms and cannot easily describe microbial cooperation, which involves the exchange of small, highly diffusible molecules. We formulated and solved a model that accurately represents the physics of diffusion in microbial colonies. In particular, we discovered a general approach that eliminates metabolite diffusion and recasts population dynamics in the traditional game theory framework, but with renormalized parameters. We applied this approach to the problem of two-way cross-feeding, a common interaction motif in the microbial world that is the subject of several experimental studies. Naively one would assume that nutrient diffusion should facilitate mutualistic interactions in microbial colonies. Indeed, because microbes are not completely mixed inside a colony, different species tend to form small domains, and diffusion should facilitate the exchange of the nutrients between the two cross-feeding species. We, however, find that nutrient diffusion reduces the strength of mutualism and leads to a phase transition that makes mutualism impossible. We analytically compute the critical diffusivity at which mutualism is lost and find the universality class of the phase transition. The distance to this phase transition controls the size of the domains formed by the species, a quantity of prime interest in empirical studies. Finally, we show that the differences in public good diffusivities affect mutualism only in the presence of nonlinearities in the public good dynamics. In particular, fitness nonlinearities suppress mutualism and favor the species producing nutrients that diffuse more slowly.