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A *particularly* useful system to study the ecology of microbes

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They may represent just a *particular* system, but particles have great potential to become a preferred model system to address fundamental questions in microbial ecology. Guided by our Crystal Ball, we thus launch into the treacherous territory of predictions . . .

Particles of organic matter are a fundamental feature of a wide range of environments and our appreciation for their functions will continue to grow. Particles made of biofilms have long been studied in wastewater systems, where they appear as ‘flocs’ or ‘granules’ that harbor different species of microbes with complementary metabolic functions – the end product of one species’ metabolism is substrate for another. Particles are ubiquitous in natural aquatic environments, where they are produced through aggregation of algal remnants and other detritus. For bacteria, these ‘marine snow’ particles represent important nutrient hotspots that shape their spatial ecology and the prevalence of specific traits (e.g., swimming or attachment), and act as scaffolds for the assembly of multi-species communities that collectively degrade the particles. When considered over ocean scales, these minute communities play a major role in the global carbon cycle, by tuning the rate of particle turnover and thus the vertical flux of carbon associated with the particles’ sinking. This process, called the ‘biological pump’, is responsible for vast amounts of carbon sinking to the ocean floor and remaining sequestered for centuries. Biofilm-laden particles or granule-like biofilms can also be found in tidal ponds, where they often combine sulfate reducers and sulfide oxidizers, as well as in deep marine sediments, where they form consortia of archaea and bacteria that act symbiotically to oxidize methane.

Microbial communities on particles will provide us with an ideal system to study the interplay between community assembly, microbial physiology and ecological interactions. Because they are often hotspots in a nutritional desert – such as in the ocean – particles attract and harbor a wide range of species, sampling colonists from the surrounding environment with a range of metabolic functions that differ in rates and efficiency. The ensuing assembly of the particle-bound community is a self-organizing process controlled by microbial metabolism as well as by ecological interactions and dispersal abilities. Metabolic trade-offs may determine the order of colonization and the kinetics of particle degradation, for example if fast-but-wasteful metabolizers grab all the goodies, leaving only recalcitrant crumbs to the slow-but-efficient metabolizers. Competitive, exploitative, or cooperative interactions between particle-dwellers can have a large influence on particle dynamics and function. Successful particle colonizers may be those that, despite having lower metabolic rates, are capable of claiming space by forming biofilms or thwarting competitors by producing antibiotics. Along the same line, because particles are often made of complex carbohydrates that require extracellular enzymes to digest, interactions between enzyme producers and cheaters can modulate the relative abundance of degraders, affecting the rates of particle turnover and the biological pump.

The study of community self-assembly on particles will help answer fundamental questions about the allocation of metabolic functions among species. By revealing the structure of self-assembled communities we can assess the contribution of specialists, each performing a certain limited function, versus generalists, with a wide spectrum of metabolic capabilities. We will also learn whether different species in a community are redundant, complementary or orthogonal in their functional potential. These answers will ultimately help us understand how the interplay between community ecology and metabolism impacts the functional properties of the multi-species collective.

Particles will become a powerful model to study microbial spatial ecology. Ecologists are well aware of the importance of a landscape’s spatial structure in driving species interactions and composition, but classical techniques in microbial ecology – such as growth in batch cultures and chemostats – have largely ignored this spatial element. However, real microbial environments are heterogeneous, and often this heterogeneity is not ancillary, but fundamental. In soil, grains and pores are physically and chemically different, providing a great many niches. In the gut, topography is complex and gradients abound. Even in the ocean, which one may intuitively expect to be well-mixed, myriad point sources, such as dying microorganisms and particles, create strong heterogeneity. How do microbes ‘forage’ in such a heterogeneous landscape? What underpins their choice to swim or not to swim, to attach or not to attach, and when to leave a particle to seek a new one? These are fundamental questions underpinning spatial behavior that in ecology find their conceptual framework in optimal foraging theory: can we develop an optimal foraging theory for microbes, accounting for the energetics of their spatial behaviors and physiological strategies to predict which sets of traits are optimal for a given resource landscape?

Particles will become a new paradigm in the study of biofilms. The colonization of particles by matrix-producing species is a biofilm inside-out. Traditional biofilms, grown on inert substrates, derive their nutrients from the overlying fluid and expand outwards to maximize access to nutrients or avoid choking. By contrast, for particle-associated biofilms, the particle itself is the nutrient source and biofilms dig away the ground beneath their feet when they eat. As a consequence, biofilms on particles will strive to retain nutrients and their own enzymes used to degrade them, which otherwise diffuse away into the bulk, rather than trying to be ‘permeable’ to nutrients diffusing in from the outside. In this type of inside-out biofilms dispersal from the outer layers may be an adaptive strategy, not only allowing individuals to find new particles, but also preventing the particle-biofilm interface from becoming anoxic.

We will ultimately be able to answer quantitatively one of the most important questions of all: does it all just average out? What are the macroscopic effects of microbes on particles, including effects on particle degradation rates and the efficiency of the biological pump? Can we ignore ecological interactions and simply focus on enzyme kinetics? Our initial work on degradation suggests this not to be the case: even for the simplest case – one nutrient, one bacterial species – processes are surprisingly non-linear. We foresee that studying the interactions at the scale of the microbes and of the particles will yield fundamental principles that allow us to ‘scale up’ and better predict the macroscale consequences of microbial degradation processes.

When paired with the modern toolkit comprising molecular approaches, nanoscale chemical analyses and real-time imaging, the particle model system will greatly contribute to develop an integrative community ecology for microbes. At the same time, this approach will yield new insights into the ecological strategies of microbes in heterogeneous landscapes and will pave the way to more robust approaches to predict and engineer microbial consortia. Particles are well-suited to address these questions because they can be readily obtained or fabricated with high replication for systematic experimentation. Particles are conducive to sampling for molecular and chemical analysis, as well as direct imaging to unveil spatial and temporal dynamics.

Looking into our Crystal Ball tells us that we should get back to work and look into our particles instead. Just like they harbor important resources for microbes, particles harbor many secrets about the fundamental principles of how microbial communities work. We see in the Crystal Ball a future in which scientists and engineers with a wide range of complementary skills will have developed the tools to study and the concepts to understand life on particles, as one blueprint for life at the microscale.