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Invited Commentary

THE SOIL PLASTISPHERE: THE NEXUS OF MICROPLASTICS, BACTERIA, AND BIOFILMS

Amir A. Pahlavan

Department of Mechanical Engineering and Materials Science, Yale University, New Haven, Connecticut, USA

Correspondence to:
Amir A. Pahlavan,
amir.pahlavan@yale.edu

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ABSTRACT

Bacteria are one of the oldest life forms on Earth, dating back to more than 3.5 billion years ago. They control the global cycling of carbon, nitrogen, and oxygen. They provide plants, fungi and other organisms with the necessary nutrients and elements. They help us digest our food, protect us against pathogens, and even affect our behavior. Microplastics, however, have disrupted the bacterial ecosystems across the globe, from the soil to the oceans. Microplastics are tiny plastic particles formed as a result of the breakdown of the consumer products and plastic waste. Due to their stability and persistence, they can travel long distances in the soil and subsurface environments, ultimately making their way to the water resources, rivers, and oceans. In this journey, they interact with bacteria and other micro/macro-organisms, become ingested or colonized, and act as carriers for contaminants and pathogens. How and whether bacteria adapt to these new microplastic-rich ecosystems are open questions with far-reaching implications for the health of our planet and us. Therefore, there is an urgent need for improving our fundamental understanding of bacterial interactions with the microplastics in complex environments. In this commentary, we focus on the nexus of bacteria, biofilms, and microplastics, also known as the "plastisphere", and discuss the challenges and opportunities.

KEYWORDS

Microplastics, Biofilms, Bacterial ecosystems, Plastisphere

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1. BACTERIAL ECOSYSTEMS IN SOIL

1.1. Element and Nutrient Cycling

Bacteria are essential to virtually all biogeochemical cycles on Earth (67, 183, 195). Their remarkable metabolic diversity and adaptability enables them to thrive in almost every environment on the planet (125). They can be aerobic (requiring oxygen), anaerobic (surviving without oxygen), phototrophic (using light as energy source), or chemotrophic (using chemical reactions for energy) (103). They are the key drivers in cycling of carbon, sulfur, nutrients, and nitrogen fixation, making atmospheric nitrogen accessible to plants (67, 118). Cyanobacteria, one of the oldest photosynthetic organisms, are believed

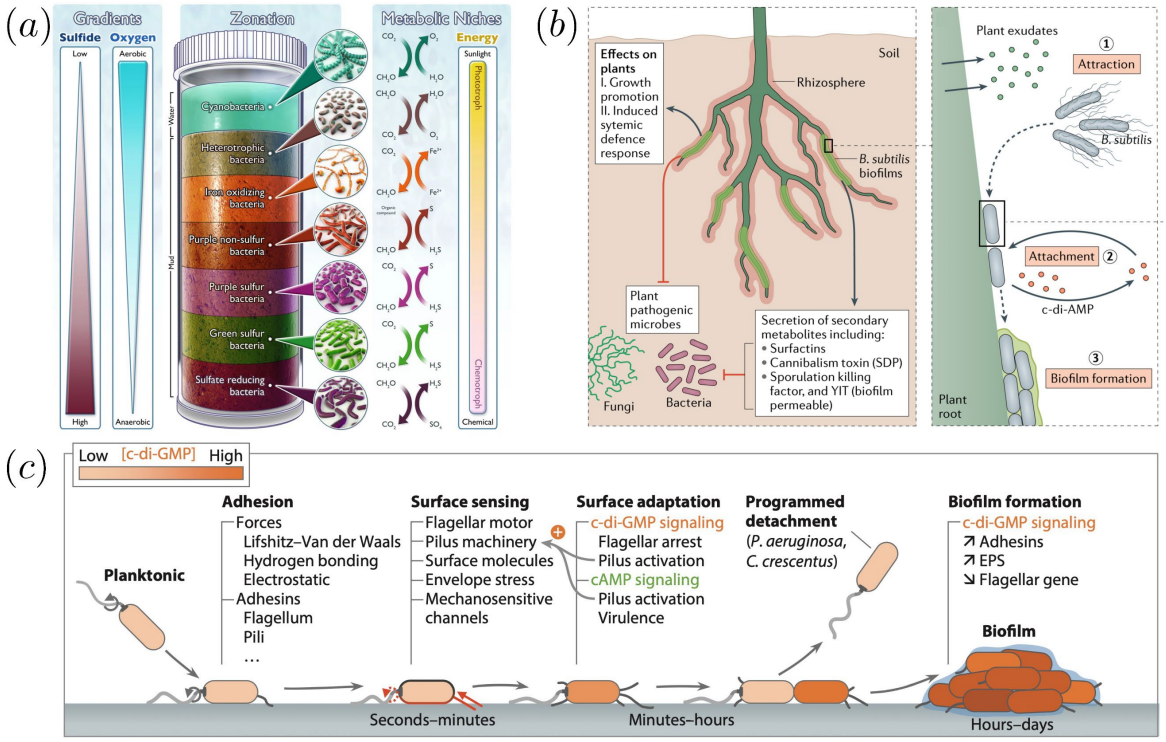


Figure 1: Bacterial ecosystems in the soil. **(a)** Winogradsky column: biogeochemical cycles in the cross-section of a pond (courtesy of HHMI BioInteractive). **(b)** Motility and chemotaxis toward exudates allows *B. subtilis* colonization of the plant roots (Republished with permission (13)). **(c)** Surface attachment and biofilm growth is modulated by the mechanosensing (Republished with permission (114)). A pdf file for all figures in this paper can be downloaded here.

to have played a major role in the Great Oxygenation Event 2.4 billion years ago, and still contribute to the global oxygen production (92, 185). Many bacteria form mutualistic relationships with other organisms, playing an essential role in their survival and health; for instance, our gut bacteria help us digest our food, aid our immune system, defend us against the pathogenic bacteria, and even control our mood (47, 139).

Most bacterial biomass resides in the soil and ocean sediments, with substantial populations also in the open oceans and inside other organisms (71). In soil, aerobic species reside near the surface and anaerobic species colonize the deeper, less oxygenated zones. This vertical stratification of the microbial communities is important for the element cycling, as different bacteria facilitate distinct biochemical transformations (157) (**Fig. 1a**). The aerobic bacteria such as Bacillus spp. and Pseudomonas spp. facilitate organic matter decomposition and nitrification, providing the plants with nitrogen. The anaerobic bacteria such as Clostridium spp. and Methanogens convert nitrates to nitrogen gas and produce methane. These processes affect both the soil, plant health, and greenhouse gas emissions (63, 81, 146, 184, 201).

1.1. Bacterial motility and chemotaxis

In nutrient-rich environments, bacterial motility does not offer an advantage as it incurs energetic cost, which can otherwise be invested into growth and reproduction (136). However, even nutrient-rich environments can experience fluctuations and uncertainties. For instance, the rhizosphere, i.e., the soil region surrounding plant roots is rich in sugars and amino acids providing a hotspot for microbial activity; however, environmental factors, including flows due to rainfall and irrigation, and differences across plant species expose bacterial communities in the rhizosphere to chemical and mechanical stresses (118, 121, 158) (**Fig. 1b**).

Bacteria, therefore, need to adapt to their dynamic and complex environments (144). Motility allows them to explore, foraging for nutrients and new territories (65, 113). Motile bacteria can also adapt their swimming behavior to follow chemical gradients, for instance toward root exudates, in a process known as chemotaxis (3, 15, 16, 158, 163, 188, 198). While the molecular machinery of bacterial chemotaxis is very well understood (124, 196, 209), its ecological functions have remained mostly unknown (101). Chemotaxis allows the bacteria to find nutrients in resource-limited environments, explore new territories, and adapt to and thrive in dynamic and heterogeneous habitats (1, 2, 43, 46, 49, 72, 74, 120, 163, 181, 212).

1.2. Biofilm formation and growth

Motility, however, makes individual bacteria vulnerable to threats as they explore their environment. This is perhaps why the majority of the bacteria exist in the form of surface-attached communities encased in extracellular polymeric substances (EPS) known as biofilms (70, 71). Biofilms are typically composed of polysaccharides, proteins, and DNA, creating a sticky matrix that attaches the bacteria to surfaces. They protect the bacteria from external fluctuations and stresses, making them less susceptible to antibiotics, and more stable environments for bacteria to grow (69).

Both motile and immotile bacteria can form biofilms depending on the environmental and biological factors. Motile bacteria go through different stages, including reversible and irreversible attachment, before they attach to a surface and become immotile (**Fig. 1c**). This transition can happen in nutrient-rich environments, where bacterial motility does not offer a benefit, or when the bacteria are exposed to mechanical/chemical stresses, including low nutrient availability, low pH, oxidative stress, high osmolarity, or exposure to antibiotics, where biofilm formation could provide stability, allowing the bacteria to share resources to survive.

Bacterial attachment to surfaces begins with reversible, weak interactions between the bacterial cell surface and the substrate. These initial interactions are often mediated by Derjaguin–Landau–Verwey–Overbeek theory (DLVO) and hydrophobic interactions (32). The strength and duration of initial attachment are influenced by the chemical composition and roughness of the surface, the ionic strength and pH of the surrounding environment, and the presence of nutrients that could facilitate bacterial growth. Some bacteria use flagella or pili, i.e., hair-like appendages, to enhance initial attachment (114). In motile bacteria, flagella allow cells to reach surfaces actively, often moving against flows or along gradients. Flagella can also help bacterial cells stick to surfaces, as they sometimes act like hooks.

Once bacteria make initial contact, they begin to strengthen their attachment, making it more permanent. Contact with a surface can trigger genetic changes in bacteria, activating genes involved in adhesion and biofilm formation, including secondary messenger c-di-GMP (114, 152). Bacteria also use quorum sensing—a cell-to-cell communication system based on signaling molecules—to detect when enough cells are present to collectively activate genes associated with biofilm formation (114, 152). This transition to irreversible surface attachment involves the secretion of extracellular polymeric substances (EPS), which act as adhesives and create a more permanent bond with the surface.

The surface-attached bacteria then grow and form micro-colonies, which gradually coalesce and form 3D microbial communities (17, 60, 83). The biofilm's architecture is determined by the mechanical and chemical constraints while enabling efficient resource sharing and protection against external stresses (197, 214). Mature biofilms can release planktonic (free-swimming) cells in response to environmental signals. This dispersal allows bacteria to colonize new areas, spreading the biofilm to other surfaces (180, 202) (**Fig. 1c**).

2. COLLOID TRANSPORT IN SUBSURFACE FLOWS

2.1. Natural Colloids

The word "colloid" originates from the Greek word *kolla*, meaning "glue", introduced by Thomas Graham in 1861 (78). Graham used colloid to describe substances that, like glue, formed stable, non-crystallizing dispersions in water. The use of colloidal dispersions by humans, however, dates back thousands of years

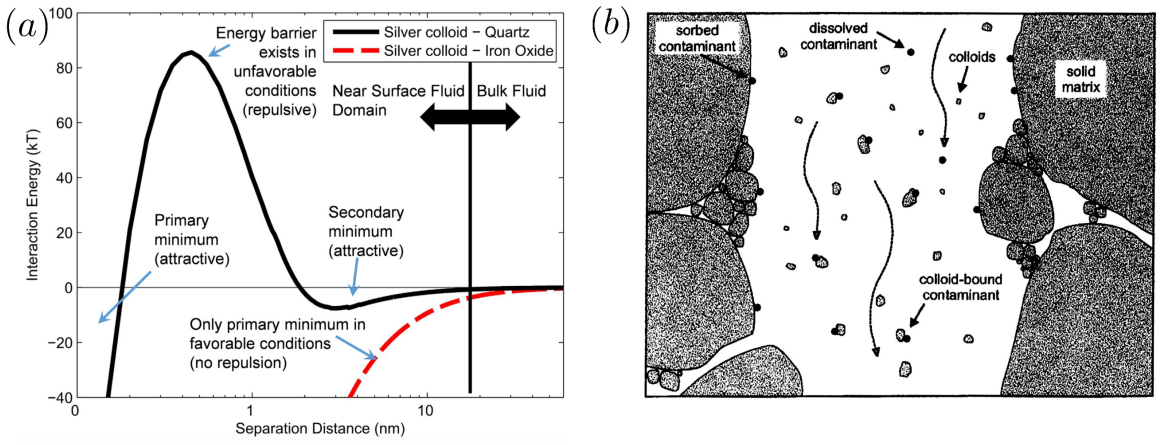


Figure 2: Colloid and contaminant transport in subsurface flows. **(a)** DLVO interactions describe the interactions between the colloids and surrounding surfaces (Republished with permission (137)). **(b)** Colloids can facilitate the spreading of contaminants (courtesy of (104)). A pdf file for all figures in this paper can be downloaded here.

as evidenced by the artifacts left behind by the ancient civilizations. Colloids are small enough to move randomly due to thermal fluctuations as first reported by Robert Brown in 1827 (30), and formalized by Bachelier, Einstein, Smoluchowski, and Perrin almost a century later (20, 64). Their works demonstrated that Brownian motion is indirect evidence for the existence of atoms and molecules. The colloidal stability reported by Graham was explained in the 1940s by Derjaguin, Landau, Verwey, and Overbeek to originate from the balance between van der Waals attraction and electrostatic repulsion, which prevents the aggregation of the colloidal particles (175) (**Fig. 2a**).

Colloids are abundant in nature in the form of minerals and organic matter. Natural colloids are typically charged and can adsorb ions and organic molecules. They can therefore act as carrier vehicles for contaminants such as pesticides, heavy metals, and nutrients (104, 135). Rainfall or irrigation mobilize these colloids, facilitating the transport of contaminants over large distances to the water resources (**Fig. 2b**). Early attempts of describing colloidal transport in subsurface flows relied on filtration models that were originally developed to explain the filtration of particles by sand filters. This theory quantifies the retention of colloidal particles based on particle size, pore size, flow conditions, and DLVO-type interactions. The filtration models were later adapted to describe colloid transport in subsurface flows, accounting for attachment-detachment dynamics, pore-scale variability, reactive transport processes, heterogeneous surface interactions, as well as dynamic and intermittent flows (21, 26, 28, 79, 95, 104, 134, 151, 176, 204, 205, 210). Coupled colloid-contaminant transport models further allowed predicting the colloid-mediated spreading of contaminants (98).

2.2. Synthetic colloids

The field of colloidal science developed significantly in the decades following the development of the DLVO theory. The food, cosmetics, and pharmaceutical industries utilized the colloid science to improve the product stability, texture, and longevity. Engineers, physicists, and chemists combined forces to design self-assembling colloids using programmable interactions to fabricate photonic crystals, metamaterials, and stimuli-responsive drug delivery carriers (76, 97). Colloids have also been used as analogs for atoms and molecules in studying phase transitions, crystallization, defect dynamics, melting, and glass formation.

However, the introduction of synthetic colloids, including nanoparticles (e.g. silver nanoparticles, titanium dioxide, carbon nanotubes, and Nano zero-valent iron (nZVI) for remediation) and microplastics into soils and water bodies through agricultural runoff, industrial waste, and consumer products has led to growing concerns regarding their toxicity, persistence, and potential to disrupt ecosystems (123, 203). Unlike natural colloids, synthetic colloids often have coatings or surface functionalities that alter their reactivity, mobility, persistence, and ecological impact. Similar to their natural counterparts, synthetic

colloids can also act as contaminant carrier vehicles. Their stability and persistence can lead to the transport of contaminants over much longer distances, influencing ecosystems, biogeochemical cycles, and bioaccumulating through food webs (12, 59, 91, 126, 165, 221). For instance, silver nanoparticles can be harmful to microbial communities, altering their growth and enzymatic activity that are crucial for nutrient and element cycling (38, 75, 143 ,155); zinc oxide (ZnO) nanoparticles can inhibit root elongation and affect plant nutrient uptake, impacting overall plant health (123). Microplastics can alter soil texture, water retention, and aeration, influencing the root growth and microbial populations, and impacting crop yield and soil fertility over time (42, 50-52, 167). These effects need to be contrasted with those of natural colloids such as clay and organic matter, which contribute to soil aggregation by forming stable micro-aggregates that improve the soil structure.

3. THE PLASTISPHERE: CHALLENGES AND OPPORTUNITIES

The rate of plastic production is overtaking the rate of global carbon emissions (25). This observation together with the fact that there is a time-lag between the plastic production and realizing its effects across different ecosystems highlight the urgency of the need for improving our fundamental understanding of the processes at play in the plastisphere, their consequences, and ways to predict and mitigate them (24, 168).

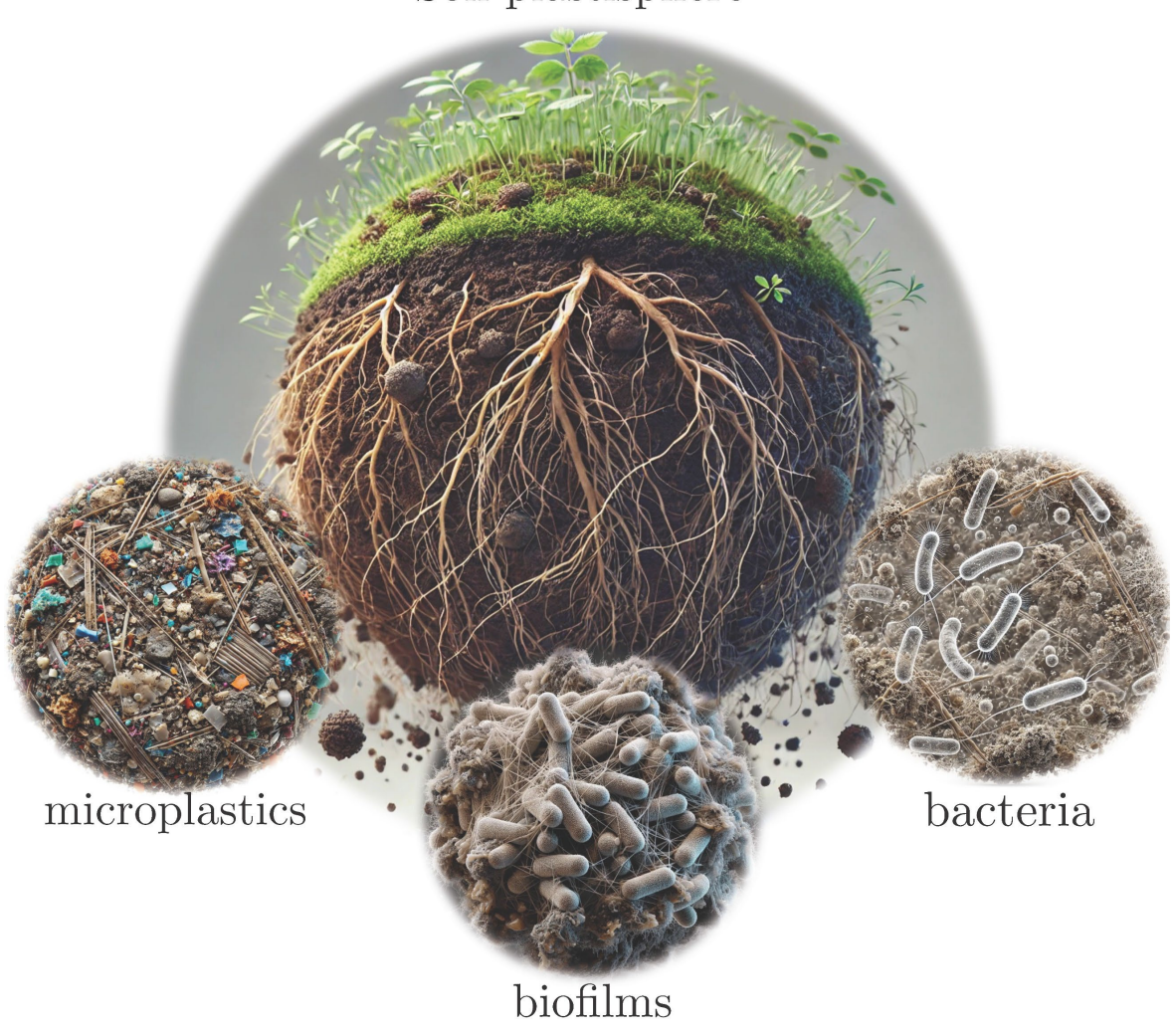


Figure 3: The microbial interactions with the microplastics could potentially disrupt the global biogeochemical cycles, pointing at the urgent need to advance our fundamental understanding of the processes in the soil plastisphere. A pdf file for all figures in this paper can be downloaded here.

The plastisphere is a dynamic environment shaped by the interplay between microplastics and bacteria (10) (**Fig. 3**). In soil, flows, chemical gradients, and confinement modulate the evolution of the plastisphere. Flows due to irrigation, rain, or other groundwater sources can transport the microplastics and bacteria. Microplastic properties, including their hydrophobicity and surface chemistry as well as their stability and persistence offer an advantage for microbial colonization over the natural colloids, which degrade much faster (4, 5, 7, 12, 22, 45, 59, 85, 117, 126, 153, 154, 166, 168, 178, 211, 219).

Microplastic Transport: Chemical gradients are ubiquitous in the subsurface environments, from contaminants to reactive sites, pesticides, industrial wastes, and natural salinity gradients in the coastal zones (56, 57, 86, 115, 169, 208). These chemical gradients could drive the **phoretic migration** of colloids and microplastics (11, 14, 128, 191). Recent studies have demonstrated that the phoretic migration could lead to significant changes in the macroscopic transport and dispersion of colloids (8, 96, 150). Therefore, the coupled transport of microplastics and contaminants needs to be revisited to account for these non-equilibrium interactions. Incorporating these effects together with the DLVO interactions with the solid surfaces, hydrodynamic/steric interactions, rheological effects at higher colloid concentrations, as well as permeability evolution due to intermittent deposition, clogging and erosion events will lead to more realistic and predictive models for the transport of microplastics and contaminants.

Bacterial Interception: Motile bacteria can escape the flow streamlines, exploring their environment in search of nutrients and new territories. They spend more time near surfaces due to hydrodynamic and steric interactions, leading to their anomalous dispersion through porous media (31, 39, 44, 53, 55, 94, 109, 177). Their larger residence time near surfaces could lead to their interception by the faster moving microplastics. Alternatively, swimming bacteria might intercept the larger microplastics. Bacteria swimming near flowing microplastics experience a shear flow near the microplastic surface, leading to their reorientation and potential capture (129, 172, 187, 194). Further, microplastics can adsorb nutrients or other chemicals and contaminants, and act as traveling beacons, leading to the chemotactic migration of bacteria toward their plumes and their potential colonization (73, 101, 163, 164, 179, 199, 200, 217). There is a need for improving our fundamental understanding of how the interplay between flow shear near surfaces, confinement, and chemotaxis governs the colonization of microplastics by the motile bacteria.

Biofilm Formation and Growth: When bacteria intercept the microplastics, they can transition to become surface-attached and form biofilms. The biofilms formed on microplastics could travel much longer distances than those formed on natural colloids, interacting with distinct microbial communities and forming multispecies biofilm colonies (41, 66, 87, 161, 182, 193), and potentially acting as carrier vectors for pathogens (27, 211, 222). Some of these communities develop distinct features such as antibiotic resistance (223). Conversely, the growth of the sticky biofilm matrix on the microplastics could lead to their trapping or aggregation. Further, biofilms in soil, subsurface flows, or even wastewater treatment facilities could act as natural filters for the microplastics, preventing their spread (102, 156).

Much of our understanding of biofilm formation and growth is due to lab studies on bacterial colonies on agar plates (70, 127). These studies have significantly improved our understanding of the inner workings of biofilms, the genes involved, their microscopic packing, mechanical and rheological properties, and morphological evolution (13, 17, 29, 36, 40, 58, 60, 68, 69, 90, 141, 142, 145, 152, 159, 170, 189, 215, 218). In their natural habitats, however, bacteria experience dynamic and heterogeneous flows, chemical gradients, and confinement (54, 71, 80, 101, 131, 156). The interplay between flows and confinement can lead to the formation of a new category of biofilms, known as **streamers** (173, 174). These biofilm streamers form due to the mechanical shear stress, and act as catching nets, trapping more bacteria, growing to clog the pore spaces, redirect the flow, and lead to intermittent channeling and rupturing, creating a dynamic, **living poroelastic medium** (61, 105, 107, 108, 116). The heterogeneous and permeable nature of the biofilms formed in subsurface flows further impacts the transport and mixing of solutes, nutrients and antibiotics (33, 34, 48, 100, 130, 147).

In the oceans, microplastics can disrupt the biological pump, i.e., the vertical flux of sedimenting organic matter known as **marine snow**, which plays an important role in carbon cycling in the oceans (37, 62,

192, 206). Bacterial interception and colonization of these sedimenting particles could impact their sedimentation and degradation rate, and therefore whether or not they make it to the abyss (6, 122, 190). Microplastics provide novel surfaces for the bacteria to colonize, potentially competing with the marine snow particles (4, 7). Microplastics can also be incorporated into the marine snow, leading to their chemical heterogeneity, and impacting their microbial communities.

Recent progress on experimental and computational techniques allow us to tackle the above listed challenges. On the experimental side, microfluidics and 3D porous media offer platforms for observing the dynamics of bacteria and microplastics over multiple lengths and timescales (18, 19, 23, 49, 84, 99, 106, 148, 171, 179, 181, 186, 207, 216). Confocal microscopy together with machine learning allows imaging and extracting the orientation and packing structure of the biofilms and their evolution (82, 83, 93, 162). For instance, recent works have demonstrated how the morphology of bacterial colonies formed on the surface of oil drops influences their rate of consumption (88, 89, 160). The special chemistry of microplastics could potentially lead to novel morphologies with implications for the development of antibiotic resistance (59, 85, 178, 223). On the modeling and simulation side, agent based as well as continuum models have advanced our understanding of how the interplay between mechanical interactions and growth shapes the evolution of biofilms (9, 54, 77, 112, 119, 132, 145, 213, 220). These models need to be further developed to couple the bacterial growth to nutrient concentration, quorum sensing, secondary signaling molecules, and oxygen concentration (35, 80, 110, 111, 133, 138, 181). These models can also shed light on how phenotypic patterning emerges in biofilms, and whether the parallels with morphogenesis of eukaryotic cells can offer insights for our understanding of biofilm growth and evolution (197).

The porous media community is perfectly situated to tackle these fundamental, interdisciplinary and consequential questions. The decades of knowledge in the areas of scalar, colloid, and contaminant transport in subsurface flows are perfect starting points for understanding the microplastic transport. Predictive models for the coupled evolution of microplastics, bacteria, and biofilms require advancing our fundamental understanding of these processes at the pore-scale. How bacterial motility and chemotaxis influences their interception of microplastics, how and when this initial encounter leads to colonization and biofilm formation, how background flows and chemical gradients modulate this process, and how the transport of biofilm-coated microplastics differs from that of natural colloids or uncoated microplastics are immediate questions that can be addressed, advancing our fundamental understanding of the soil plastisphere.

STATEMENTS AND DECLARATIONS

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Conflicts of Interest

There are no conflicts of interest to declare.

ORCID ID

1st author  https://orcid.org/0000-0003-3505-9718

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