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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

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

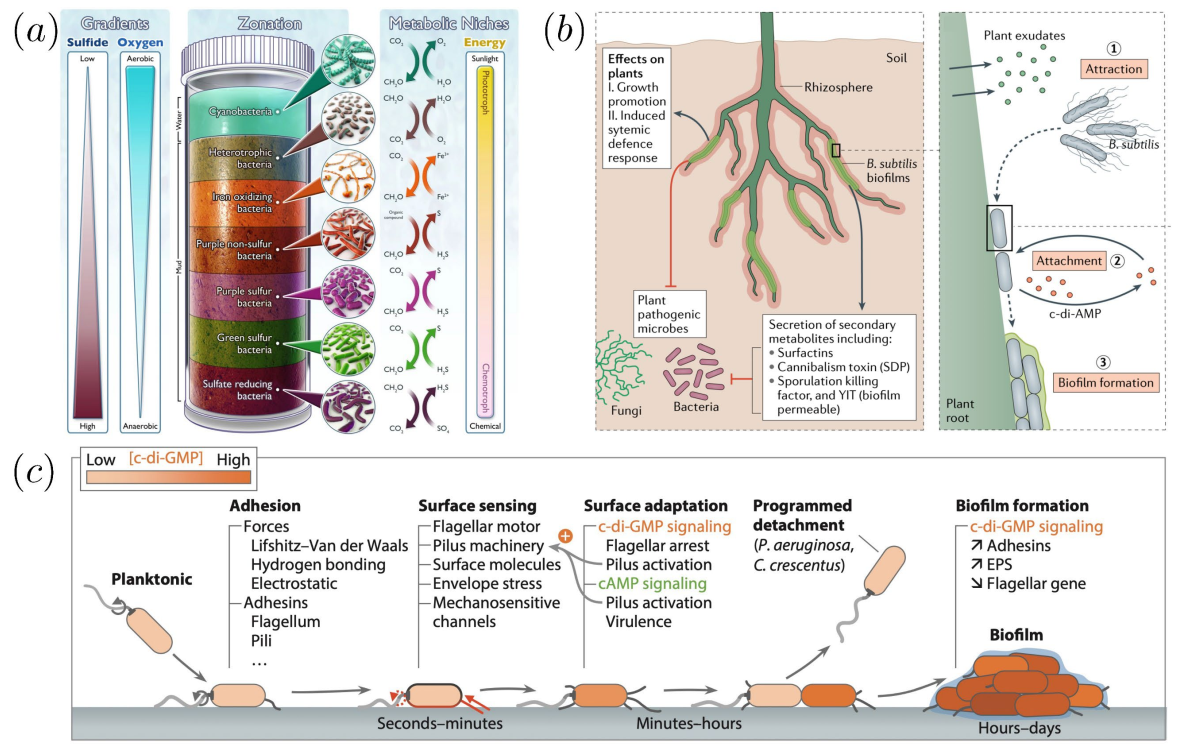

Figure 1: Bacterial ecosystems in the soil. **(a)** Winogradsky column: biogeochemical cycles in the cross-section of a pond (courtesy of HHMI BioInteractive). **(b)** Motility and chemotaxis toward exudates allows *B. subtilis* colonization of the plant roots (Republished with permission (13)). **(c)** 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

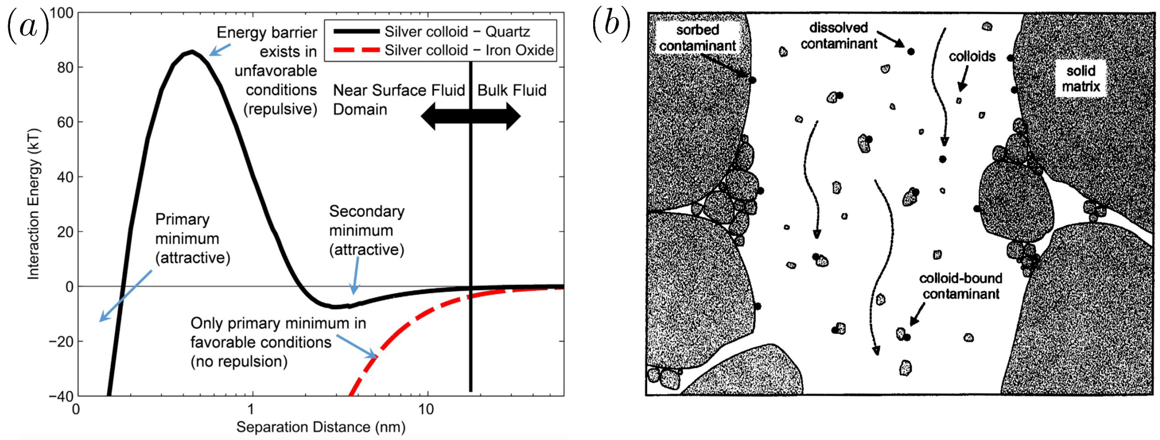

Figure 2: Colloid and contaminant transport in subsurface flows. **(a)** DLVO interactions describe the interactions between the colloids and surrounding surfaces (Republished with permission (137)). (**b)** Colloids can facilitate the spreading of contaminants (courtesy of (104)). A pdf file for all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

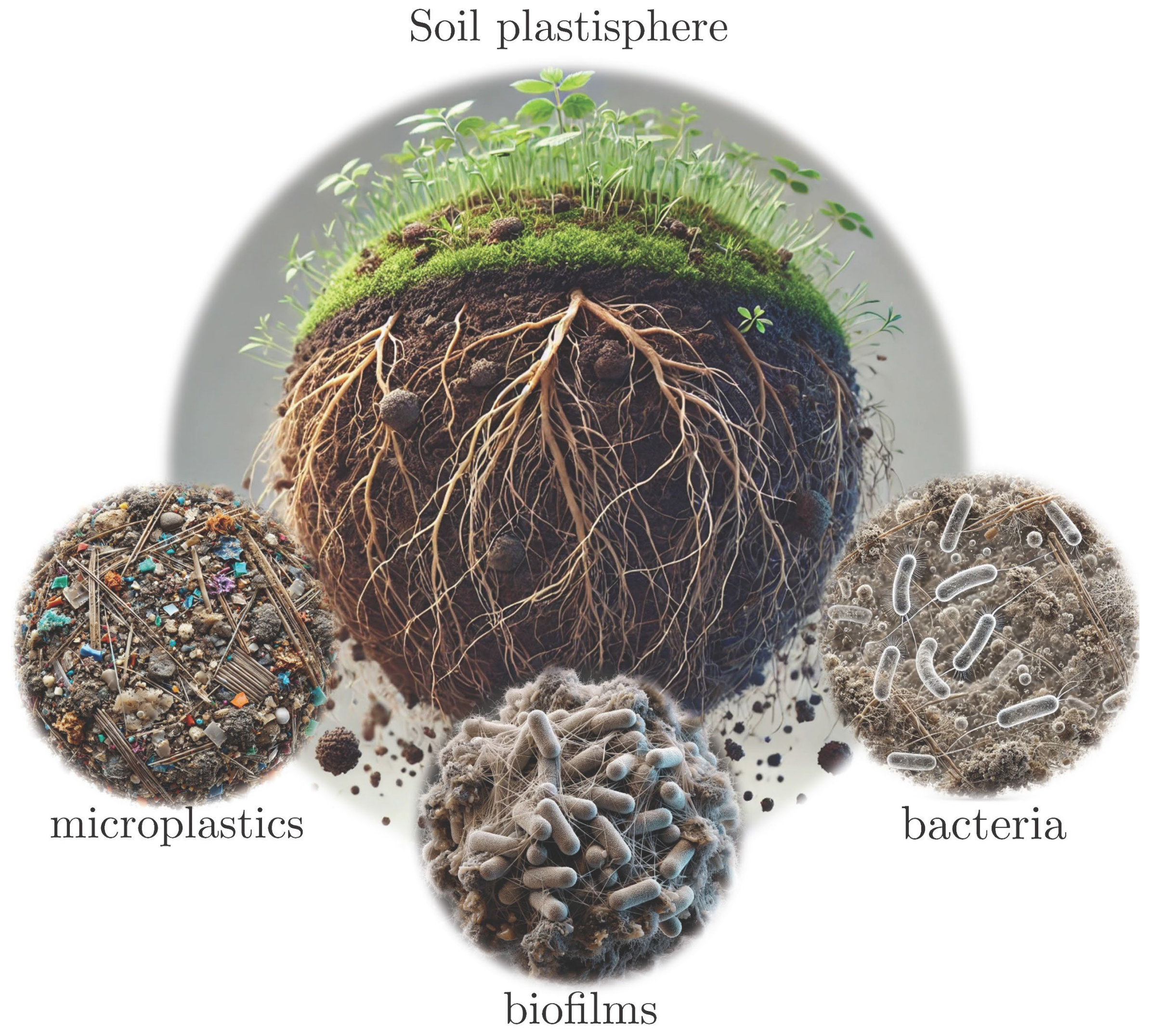

Figure 3: The microbial interactions with the microplastics could potentially disrupt the global biogeochemical cycles, pointing at the urgent need to advance our fundamental understanding of the processes in the soil plastisphere. A pdf file for all figures in this paper can be downloaded here.

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

REFERENCES

1. Adadevoh, J. S. T., Ramsburg, C. A., Ford, R. M. (2018). Chemotaxis increases the retention of bacteria in porous media with residual NAPL entrapment. *Environmental Science & Technology*, 52(13):7289–7295. https://doi.org/10.1021/acs.est.8b01172
2. Adadevoh, J. S. T., Triolo, S., Ramsburg, C. A., Ford, R. M. (2016). Chemotaxis increases the residence time of bacteria in granular media containing distributed contaminant sources. *Environmental Science & Technology*, 50(1):181–187. https://doi.org/10.1021/acs.est.5b03956

3. Adler, J. (1969). Chemoreceptors in Bacteria: Studies of chemotaxis reveal systems that detect attractants independently of their metabolism. Science, 166(3913), 1588–1597. https://doi.org/10.1126/science.166.3913.1588
4. Al Harraq, A., Bharti, B. (2022). Microplastics through the lens of colloid science. *ACS Environmental Au*, 2(1):3–10. https://doi.org/10.1021/acsenvironau.1c00016
5. Al Harraq, A., Brahana, P. J., Arcemont, O., et al. (2022). Effects of weathering on microplastic dispersibility and pollutant uptake capacity. *ACS Environmental Au*, 2(6):549–555. https://doi.org/10.1021/acsenvironau.2c00036
6. Alcolombri, U., Peaudecerf, F. J., Fernandez, V. I., et al. (2021). Sinking enhances the degradation of organic particles by marine bacteria. *Nature Geoscience*, 14(10):775–780. https://doi.org/10.1038/s41561-021-00817-x
7. Alimi, O. S., Farner Budarz, J., Hernandez, L. M., Tufenkji, N. (2018). Microplastics and nanoplastics in aquatic environments: Aggregation, deposition, and enhanced contaminant transport. *Environmental Science & Technology*, 52(4):1704–1724. https://doi.org/10.1021/acs.est.7b05559
8. Alipour, M., Li, Y., Liu, H., Pahlavan, A. (2024). Diffusiophoretic transport of colloids in porous media. *arXiv*. https://arxiv.org/abs/2411.14712
9. Allen, R. J., & Waclaw, B. (2018). Bacterial growth: a statistical physicist's guide. *Reports on Progress in Physics*, 82(1):016601. https://doi.org/10.1088/1361-6633/aae546
10. Amaral-Zettler, L. A., Zettler, E. R., & Mincer, T. J. (2020). Ecology of the plastisphere. *Nature Reviews Microbiology*, 18(3):139–151. https://doi.org/10.1038/s41579-019-0308-0
11. Anderson, J. L. (1989). Colloid transport by interfacial forces. *Annual Review of Fluid Mechanics*, 21(Volume 21, 1989):61–99. https://doi.org/10.1146/annurev.fl.21.010189.000425
12. Aralappanavar, V. K., Mukhopadhyay, R., Yu, Y., Liu, J., Bhatnagar, A., et al (2024). Effects of microplastics on soil microorganisms and microbial functions in nutrients and carbon cycling –a review. *Science of The Total Environment*, 924:171435. https://doi.org/10.1016/j.scitotenv.2024.171435
13. Arnaouteli, S., Bamford, N. C., Stanley-Wall, N. R., e al (2021). Bacillus subtilis biofilm formation and social interactions. *Nature Reviews Microbiology*, 19(9):600–614. https://doi.org/10.1038/s41579-021-00540-9
14. Ault, J. T. and Shin, S. (2024). Physicochemical hydrodynamics of particle diffusiophoresis driven by chemical gradients. *Annual Review of Fluid Mechanics*. Under Review. https://doi.org/10.1146/annurev-fluid-030424-110950
15. Berg, H. (1975). Chemotaxis in bacteria. *Annual review of biophysics and bioengineering*, 4(00):119—136. https://doi.org/10.1146/annurev.bb.04.060175.001003
16. Berg, H. C., Purcell, E. M. (1977). Physics of chemoreception. *Biophysical Journal*, 20(2):193– 219. https://doi.org/10.1016/s0006-3495(77)85544-6
17. Beroz, F., Yan, J., Meir, Y., et al. (2018). Verticalization of bacterial biofilms. *Nature Physics*, 14(9):954–960. https://doi.org/10.1038/s41567-018-0170-4
18. Bhattacharjee, T., Amchin, D. B., Ott, J. A., et al. (2021). Chemotactic migration of bacteria in porous media. *Biophysical Journal*, 120(16):3483–3497. https://doi.org/10.1016/j.bpj.2021.05.012
19. Bhattacharjee, T. and Datta, S. S. (2019). Bacterial hopping and trapping in porous media. *Nature Communications*, 10(1):2075. https://doi.org/10.1038/s41467-019-10115-1
20. Bian, X., Kim, C., and Karniadakis, G. E. (2016). 111 years of brownian motion. *Soft Matter*, 12:6331–6346. https://doi.org/10.1039/C6SM01153E
21. Bizmark, N., Schneider, J., Priestley, R. D., and Datta, S. S. (2020). Multiscale dynamics of colloidal deposition and erosion in porous media. *Science Advances*, 6(46):eabc2530. https://doi.org/10.1126/sciadv.abc2530
22. Boots, B., Russell, C. W., and Green, D. S. (2019). Effects of microplastics in soil ecosystems: Above and below ground. *Environmental Science & Technology*, 53(19):11496–11506. https://doi.org/10.1021/acs.est.9b03304
23. Bordoloi, A. D., Scheidweiler, D., Dentz, M., et al. (2022). Structure induced laminar vortices control anomalous dispersion in porous media. *Nature Communications*, 13(1):3820. https://doi.org/10.1038/s41467-022-31552-5
24. Borrelle, S. B., Ringma, J., Law, K. Let al. (2020). Predicted growth in plastic waste exceeds efforts to mitigate plastic pollution. *Science*, 369(6510):1515–1518. https://doi.org/10.1126/science.aba3656
25. Borrelle, S. B., Rochman, C. M., Liboiron, M., et al. (2017). Why we need an international agreement on marine plastic pollution. *Proceedings of the National Academy of Sciences*, 114(38):9994–9997. https://doi.org/10.1073/pnas.1714450114
26. Bradford, S. A., Bettahar, M., Simunek, J., and van Genuchten, M. T. (2004). Straining and attachment of colloids in physically heterogeneous porous media. *Vadose Zone Journal*, 3(2):384–394. https://doi.org/10.2136/vzj2004.0384
27. Bradford, S. A., Morales, V. L., Zhang, W., et al. (2013). Transport and fate of microbial pathogens in agricultural settings. *Critical Reviews in Environmental Science and Technology*, 43(8):775–893.

https://doi.org/10.1080/10643389.2012.710449

28. Bradford, S. A., Yates, S. R., Bettahar, M., and Simunek, J. (2002). Physical factors affecting the transport and fate of colloids in saturated porous media. *Water Resources Research*, 38(12):1327. https://doi.org/10.1029/2002WR001340
29. Bravo, P., Ng, S. L., MacGillivray, K. A., et al. (2023). Vertical growth dynamics of biofilms. *Proceedings of the National Academy of Sciences*, 120(11):e2214211120. https://doi.org/10.1073/pnas.2214211120
30. Brown, R. (1828). XXVII. a brief account of microscopical observations made in the months of June, July and August 1827, on the particles contained in the pollen of plants; and on the general existence of active molecules in organic and inorganic bodies. *The Philosophical Magazine*, 4(21):161–173. https://doi.org/10.1080/14786442808674769
31. Camesano, T. A. and Logan, B. E. (1998). Influence of fluid velocity and cell concentration on the transport of motile and nonmotile bacteria in porous media. *Environmental Science & Technology*, 32(11):1699–1708.
32. Carniello, V., Peterson, B. W., van der Mei, H. C., and Busscher, H. J. (2018). Physico-chemistry from initial bacterial adhesion to surface-programmed biofilm growth. *Advances in Colloid and Interface Science*, 261:1–14. https://doi.org/10.1016/j.cis.2018.10.005
33. Carrel, M., Morales, V. L., Beltran, M. A., et al. (2018a). Biofilms in 3d porous media: Delineating the influence of the pore network geometry, flow and mass transfer on biofilm development. *Water Research*, 134:280–291. https://www.sciencedirect.com/science/article/pii/S0043135418300733
34. Carrel, M., Morales, V. L., Dentz, M., et al. (2018b). Pore-scale hydrodynamics in a progressively bioclogged three-dimensional porous medium: 3-D particle tracking experiments and stochastic transport modeling. *Water Resources Research*, 54(3):2183– 2198. https://doi.org/10.1002/2017WR021726
35. Ceriotti, G., Borisov, S. M., Berg, J. S., and de Anna, P. (2022). Morphology and size of bacterial colonies control anoxic microenvironment formation in porous media. *Environmental Science & Technology*, 56(23):17471–17480. https://doi.org/10.1021/acs.est.2c05842
36. Chai, L., Zaburdaev, V., and Kolter, R. (2024). How bacteria actively use passive physics to make biofilms. *Proceedings of the National Academy of Sciences*, 121(40):e2403842121. https://doi.org/10.1073/pnas.2403842121
37. Chajwa, R., Flaum, E., Bidle, K. D., et al. (2024). Hidden comet tails of marine snow impede ocean-based carbon sequestration. *Science*, 386(6718):eadl5767. https://doi.org/10.1126/science.adl5767
38. Choi, O. and Hu, Z. (2008). Size dependent and reactive oxygen species related nanosilver toxicity to nitrifying bacteria. *Environmental Science & Technology*, 42(12):4583–4588. https://doi.org/10.1021/es703238h
39. Chopra, P., Quint, D., Gopinathan, A., and Liu, B. (2022). Geometric effects induce anomalous size-dependent active transport in structured environments. *Phys. Rev. Fluids*, 7:L071101. https://doi.org/10.1103/PhysRevFluids.7.L071101
40. Claessen, D., Rozen, D. E., Kuipers, O. P., et al. (2014). Bacterial solutions to multicellularity: a tale of biofilms, filaments and fruiting bodies. *Nature Reviews Microbiology*, 12(2):115–124. https://doi.org/10.1038/nrmicro3178
41. Coyte, K. Z., Tabuteau, H., Gaffney, E. A., et al. (2017). Microbial competition in porous environments can select against rapid biofilm growth. *Proceedings of the National Academy of Sciences*, 114(2):E161–E170. https://doi.org/10.1073/pnas.1525228113
42. Cramer, A., Benard, P., Zarebanadkouki, M., et al. (2023). Microplastic induces soil water repellency and limits capillary flow. *Vadose Zone Journal*, 22(1):e20215. http://dx.doi.org/10.1002/vzj2.20215
43. Cremer, J., Honda, T., Tang, Y., et al. (2019). Chemotaxis as a navigation strategy to boost range expansion. *Nature*, 575(7784):658–663. https://doi.org/10.1038/s41586-019-1733-y
44. Creppy, A., Clément, E., Douarche, C., et al. (2019). Effect of motility on the transport of bacteria populations through a porous medium. *Phys. Rev. Fluids*, 4:013102. https://doi.org/10.1103/PhysRevFluids.4.013102
45. Crossman, J., Hurley, R. R., Futter, M., and Nizzetto, L. (2020). Transfer and transport of microplastics from biosolids to agricultural soils and the wider environment. *Science of The Total Environment*, 724:138334. https://doi.org/10.1016/j.scitotenv.2020.138334
46. Croze, O. A., Ferguson, G. P., Cates, M. E., and Poon, W. C. K. (2011). Migration of chemotactic bacteria in soft agar: Role of gel concentration. *Biophysical Journal*, 101(3):525–534. https://doi.org/10.1016/j.bpj.2011.06.023
47. Cryan, J. F. and Dinan, T. G. (2012). Mind-altering microorganisms: the impact of the gut microbiota on brain and behaviour. *Nature Reviews Neuroscience*, 13(10):701–712. https://doi.org/10.1038/nrn3346
48. Davit, Y., Byrne, H., Osborne, J., et al. (2013). Hydrodynamic dispersion within porous biofilms. *Phys. Rev. E*, 87:012718. https://doi.org/10.1103/PhysRevE.87.012718
49. de Anna, P., Pahlavan, A. A., Yawata, Y., et al. (2021). Chemotaxis under flow disorder shapes microbial dispersion in porous media. *Nature Physics*, 17(1):68–73. https://doi.org/10.1038/s41567-020-1002-x

50. de Souza Machado, A. A., Kloas, W., Zarfl, C., et al. (2018a). Microplastics as an emerging threat to terrestrial ecosystems. *Global Change Biology*, 24(4):1405–1416. https://doi.org/10.1111/gcb.14020
51. de Souza Machado, A. A., Lau, C. W., Kloas, W., et al. (2019). Microplastics can change soil properties and affect plant performance. *Environmental Science & Technology*, 53(10):6044–6052. https://doi.org/10.1021/acs.est.9b01339
52. de Souza Machado, A. A., Lau, C. W., Till, J., et al. (2018b). Impacts of microplastics on the soil biophysical environment. *Environmental Science & Technology*, 52(17):9656–9665. https://doi.org/10.1021/acs.est.8b02212
53. Dehkharghani, A., Waisbord, N., Dunkel, J., and Guasto, J. S. (2019). Bacterial scattering in microfluidic crystal flows reveals giant active taylor–aris dispersion. *Proceedings of the National Academy of Sciences*, 116(23):11119–11124. https://doi.org/10.1073/pnas.1819613116
54. Delarue, M., Hartung, J., Schreck, C., et al. (2016). Self-driven jamming in growing microbial populations. *Nature Physics*, 12(8):762–766. https://doi.org/10.1038/nphys3741
55. Dentz, M., Creppy, A., Douarche, C., et al. (2022). Dispersion of motile bacteria in a porous medium. *Journal of Fluid Mechanics*, 946:A33. https://doi.org/10.1017/jfm.2022.596
56. Dentz, M., Hidalgo, J. J., and Lester, D. (2023). Mixing in porous media: Concepts and approaches across scales. *Transport in Porous Media*, 146(1):5–53. https://doi.org/10.1007/s11242-022-01852-x
57. Dentz, M., Le Borgne, T., Englert, A., and Bijeljic, B. (2011). Mixing, spreading and reaction in heterogeneous media: A brief review. *Journal of Contaminant Hydrology*, 120-121:1–17. https://doi.org/10.1016/j.jconhyd.2010.05.002
58. Dervaux, J., Magniez, J. C., and Libchaber, A. (2014). On growth and form of Bacillus subtilis biofilms. *Interface Focus*, 4(6):20130051. https://doi.org/10.1098/rsfs.2013.0051
59. Dissanayake, P. D., Kim, S., Sarkar, B., et al. (2022). Effects of microplastics on the terrestrial environment: A critical review. *Environmental Research*, 209:112734. https://doi.org/10.1016/j.envres.2022.112734
60. Drescher, K., Dunkel, J., Nadell, C. D., et al. (2016). Architectural transitions in vibrio cholerae biofilms at single-cell resolution. *Proceedings of the National Academy of Sciences*, 113(14):E2066–E2072. https://doi.org/10.1073/pnas.1601702113
61. Drescher, K., Shen, Y., Bassler, B. L., and Stone, H. A. (2013). Biofilm streamers cause catastrophic disruption of flow with consequences for environmental and medical systems. *Proceedings of the National Academy of Sciences*, 110(11):4345–4350. https://doi.org/10.1073/pnas.1300321110
62. Ducklow, H. (2001). Upper ocean carbon export and the biological pump. *Oceanography*. 14(4):50–58, https://doi.org/10.5670/oceanog.2001.06
63. Ebrahimi, A. and Or, D. (2015). Hydration and diffusion processes shape microbial community organization and function in model soil aggregates. *Water Resources Research*, 51(12):9804–9827. http://dx.doi.org/10.1002/2015WR017565
64. Einstein, A. (1905) On the movement of small particles suspended in stationary liquids required by the molecular-kinetic theory of heat. *Annals of Physics*, 322, 549560. http://dx.doi.org/10.1002/andp.19053220806
65. Elgeti, J., Winkler, R. G., and Gompper, G. (2015). Physics of microswimmers—single particle motion and collective behavior: a review. *Reports on Progress in Physics*, 78(5):056601. https://doi.org/10.1088/0034-4885/78/5/056601
66. Elias, S. and Banin, E. (2012). Multi-species biofilms: living with friendly neighbors. *FEMS Micro- biology Reviews*, 36(5):990–1004. https://doi.org/10.1111/j.1574-6976.2012.00325.x
67. Falkowski, P. G., Fenchel, T., and Delong, E. F. (2008). The microbial engines that drive earth’s biogeochemical cycles. *Science*, 320(5879):1034–1039. https://doi.org/10.1126/science.1153213
68. Fei, C., Mao, S., Yan, J., et al. (2020). Nonuniform growth and surface friction determine bacterial biofilm morphology on soft substrates. *Proceedings of the National Academy of Sciences*, 117(14):7622–7632. https://doi.org/10.1073/pnas.1919607117
69. Flemming, H.-C., van Hullebusch, E. D., Neu, T. R., et al (2023). The biofilm matrix: multitasking in a shared space. *Nature Reviews Microbiology*, 21(2):70–86. https://doi.org/10.1038/s41579-022-00791-0
70. Flemming, H.-C., Wingender, J., Szewzyk, U., et al. (2016). Biofilms: an emergent form of bacterial life. *Nature Reviews Microbiology*, 14(9):563–575. https://doi.org/10.1038/nrmicro.2016.94
71. Flemming, H.-C. and Wuertz, S. (2019). Bacteria and archaea on earth and their abundance in biofilms. *Nature Reviews Microbiology*, 17(4):247–260. https://doi.org/10.1038/s41579-019-0158-9
72. Ford, R. M. and Harvey, R. W. (2007). Role of chemotaxis in the transport of bacteria through saturated porous media. *Advances in Water Resources*, 30(6):1608–1617. https://doi.org/10.1016/j.advwatres.2006.05.019
73. Ganesh, A., Alipour, M., and Pahlavan, A. (2024). Bacterial chemotaxis toward ephemeral nutrient sources. Unpublished manuscript. *arXiv*.

74. Gao, B., Wang, X., and Ford, R. M. (2023). Chemotaxis along local chemical gradients enhanced bacteria dispersion and PAH bioavailability in a heterogenous porous medium. *Science of The Total Environment*, 859:160004. https://doi.org/10.1016/j.scitotenv.2022.160004
75. Ge, Y., Schimel, J. P., and Holden, P. A. (2011). Evidence for negative effects of TiO_2 and ZnO nanoparticles on soil bacterial communities. *Environmental Science & Technology*, 45(4):1659–1664. https://doi.org/10.1021/es103040t
76. Glotzer, S. C. and Solomon, M. J. (2007). Anisotropy of building blocks and their assembly into complex structures. *Nature Materials*, 6(8):557–562. https://doi.org/10.1038/nmat1949
77. Gniewek, P., Schreck, C. F., and Hallatschek, O. (2019). Biomechanical feedback strengthens jammed cellular packings. *Physical Review Letters*, 122:208102. https://journals.aps.org/prl/abstract/10.1103/PhysRevLett.122.208102
78. Graham, T. (1861). X. Liquid diffusion applied to analysis. *Philosophical Transactions of the Royal Society of London*, 151:183–224.
79. Grolimund, D., Elimelech, M., Borkovec, M., et al. (1998). Transport of in situ mobilized colloidal particles in packed soil columns. *Environmental Science & Technology*, 32(22):3562–3569. https://doi.org/10.1021/es980356z
80. Hallatschek, O., Datta, S. S., Drescher, K., et al. (2023). Proliferating active matter. *Nature Reviews Physics*, 5(7):407–419. https://doi.org/10.1038/s42254-023-00593-0
81. Hartmann, M. and Six, J. (2023). Soil structure and microbiome functions in agroecosystems. *Nature Reviews Earth & Environment*, 4(1):4–18. https://doi.org/10.1038/s43017-022-00366-w
82. Hartmann, R., Jeckel, H., Jelli, E., Singh, P. K., Vaidya, S., et al (2021). Quantitative image analysis of microbial communities with biofilmq. *Nature Microbiology*, 6(2):151–156. https://doi.org/10.1038/s41564-020-00817-4
83. Hartmann, R., Singh, P. K., Pearce, P., et al. (2019). Emergence of three-dimensional order and structure in growing biofilms. *Nature Physics*, 15(3):251–256. https://doi.org/10.1038/s41567-018-0356-9
84. Hassanpourfard, M., Ghosh, R., Thundat, T., and Kumar, A. (2016). Dynamics of bacterial streamers induced clogging in microfluidic devices. *Lab Chip*, 16:4091–4096. https://doi.org/10.1039/C6LC01055E
85. He, S., Jia, M., Xiang, Y., et al. (2022). Biofilm on microplastics in aqueous environment: Physicochemical properties and environmental implications. *Journal of Hazardous Materials*, 424:127286. https://doi.org/10.1016/j.jhazmat.2021.127286
86. Heyman, J., Lester, D. R., Turuban, R., et al. (2020). Stretching and folding sustain microscale chemical gradients in porous media. *Proceedings of the National Academy of Sciences*, 117(24):13359–13365. https://doi.org/10.1073/pnas.2002858117
87. Hibbing, M. E., Fuqua, C., Parsek, M. R., and Peterson, S. B. (2010). Bacterial competition: surviving and thriving in the microbial jungle. *Nature Reviews Microbiology*, 8(1):15–25. https://doi.org/10.1038/nrmicro2259
88. Hickl, V. and Juarez, G. (2022). Tubulation and dispersion of oil by bacterial growth on droplets. *Soft Matter*, 18:7217–7228. https://doi.org/10.1039/d2sm00813k
89. Hickl, V., Pamu, H. H., and Juarez, G. (2023). Hydrodynamic treadmill reveals reduced rising speeds of oil droplets deformed by marine bacteria. *Environmental Science & Technology*, 57(37):14082– 14089. https://doi.org/10.1021/acs.est.3c04902
90. Hobley, L., Harkins, C., MacPhee, C. E., and Stanley-Wall, N. R. (2015). Giving structure to the biofilm matrix: an overview of individual strategies and emerging common themes. *FEMS Microbiology Reviews*, 39(5):649–669. https://doi.org/10.1093/femsre/fuv015
91. Huang, W. and Xia, X. (2024). Element cycling with micro(nano)plastics. *Science*, 385(6712):933– 935. https://doi.org/10.1126/science.adk9505
92. Huisman, J., Codd, G. A., Paerl, H. W., et al. (2018). Cyanobacterial blooms. *Nature Reviews Microbiology*, 16(8):471–483. https://doi.org/10.1038/s41579-018-0040-1
93. Jeckel, H. and Drescher, K. (2021). Advances and opportunities in image analysis of bacterial cells and communities. *FEMS Microbiology Reviews*, 45(4):fuaa062. https://doi.org/10.1093/femsre/fuaa062
94. Jin, C. and Sengupta, A. (2024). Microbes in porous environments: from active interactions to emergent feedback. *Biophysical Reviews*, 16(2):173–188. https://doi.org/10.1007/s12551-024-01185-7
95. Johnson, P. R., Sun, N., and Elimelech, M. (1996). Colloid transport in geochemically heterogeneous porous media: Modeling and measurements. *Environmental Science & Technology*, 30(11):3284– 3293. https://doi.org/10.1021/es960053+
96. Jotkar, M., de Anna, P., Dentz, M., and Cueto-Felgueroso, L. (2024). The impact of diffusiophoresis on hydrodynamic dispersion and filtration in porous media. *Journal of Fluid Mechanics*, 991:A8. http://dx.doi.org/10.1017/jfm.2024.546
97. Kamaly, N., Yameen, B., Wu, J., and Farokhzad, O. C. (2016). Degradable controlled-release polymers and polymeric nanoparticles: Mechanisms of controlling drug release. *Chemical Reviews*, 116(4):2602–2663. https://doi.org/10.1021/acs.chemrev.5b00346

98. Kanti Sen, T. and Khilar, K. C. (2006). Review on subsurface colloids and colloid-associated contaminant transport in saturated porous media. *Advances in Colloid and Interface Science*, 119(2):71–96. https://doi.org/10.1016/j.cis.2005.09.001
99. Karimi, A., Karig, D., Kumar, A., and Ardekani, A. M. (2015). Interplay of physical mechanisms and biofilm processes: review of microfluidic methods. *Lab Chip*, 15:23–42. https://doi.org/10.1039/C4LC01095G
100. Karimifard, S., Li, X., Elowsky, C., and Li, Y. (2021). Modeling the impact of evolving biofilms on flow in porous media inside a microfluidic channel. *Water Research*, 188:116536. https://doi.org/10.1016/j.watres.2020.116536
101. Keegstra, J. M., Carrara, F., and Stocker, R. (2022). The ecological roles of bacterial chemotaxis. *Nature Reviews Microbiology*, 20(8):491–504. https://doi.org/10.1038/s41579-022-00709-w
102. Keller, A. S., Jimenez-Martinez, J., and Mitrano, D. M. (2020). Transport of nano- and microplastic through unsaturated porous media from sewage sludge application. *Environmental Science & Technology*, 54(2):911–920. https://doi.org/10.1021/acs.est.9b06483
103. Kleber, M., Bourg, I. C., Coward, E. K., et al. (2021). Dynamic interactions at the mineral–organic matter interface. *Nature Reviews Earth & Environment*, 2(6):402–421. https://doi.org/10.1038/s43017-021-00162-y
104. Kretzschmar, R., Borkovec, M., Grolimund, D., and Elimelech, M. (1999). Mobile Subsurface Colloids and Their Role in Contaminant Transport. *Advances in Agronomy*, volume 66, pages 121–193. *Academic Press*. http://dx.doi.org/10.1016/s0065-2113(08)60427-7
105. Krsmanovic, M., Biswas, D., Ali, H., et al. (2021). Hydro-dynamics and surface properties influence biofilm proliferation. *Advances in Colloid and Interface Science*, 288:102336. https://doi.org/10.1016/j.cis.2020.102336
106. Kumar, M., Guasto, J. S., and Ardekani, A. M. (2022). Transport of complex and active fluids in porous media). *Journal of Rheology*, 66(2):375–397. https://doi.org/10.1122/8.0000389
107. Kurz, D. L., Secchi, E., Carrillo, F. J., et al. (2022). Competition between growth and shear stress drives intermittency in preferential flow paths in porous medium biofilms. *Proceedings of the National Academy of Sciences*, 119(30):e2122202119. https://doi.org/10.1073/pnas.2122202119
108. Kurz, D. L., Secchi, E., Stocker, R., and Jimenez-Martinez, J. (2023). Morphogenesis of biofilms in porous media and control on hydrodynamics. *Environmental Science & Technology*, 57(14):5666– 5677. https://doi.org/10.1021/acs.est.2c08890
109. Kurzthaler, C., Mandal, S., Bhattacharjee, T., et al. (2021). A geometric criterion for the optimal spreading of active polymers in porous media. *Nature Communications*, 12(1):7088. https://doi.org/10.1038/s41467-021-26942-0
110. Laganenka, L., Colin, R., and Sourjik, V. (2016). Chemotaxis towards autoinducer 2 mediates autoaggregation in escherichia coli. *Nature Communications*, 7(1):12984. https://doi.org/10.1038/ncomms12984
111. Laganenka, L., Lee, J.-W., Malfertheiner, L., et al (2023). Chemotaxis and autoinducer-2 signaling mediate colonization and contribute to co-existence of escherichia coli strains in the murine gut. *Nature Microbiology*, 8(2):204–217. https://doi.org/10.1038/s41564-022-01286-7
112. Langeslay, B. and Juarez, G. (2023). Microdomains and stress distributions in bacterial monolayers on curved interfaces. *Soft Matter*, 19:3605–3613. https://doi.org/10.1039/D2SM01498J
113. Lauga, E. (2016). Bacterial hydrodynamics. *Annual Review of Fluid Mechanics*, 48(Volume 48, 2016):105–130. https://doi.org/10.1146/annurev-fluid-122414-034606
114. Laventie, B.-J. and Jenal, U. (2020). Surface sensing and adaptation in bacteria. *Annual Review of Microbiology*, 74(Volume 74, 2020):735–760. https://doi.org/10.1146/annurev-micro-012120-063427
115. Le Borgne, T., Dentz, M., and Villermaux, E. (2013). Stretching, coalescence, and mixing in porous media. *Physical Review Letters*, 110:204501. https://journals.aps.org/prl/abstract/10.1103/PhysRevLett.110.204501
116. Lee, S. H., Secchi, E., and Kang, P. K. (2023). Rapid formation of bioaggregates and morphology transition to biofilm streamers induced by pore-throat flows. *Proceedings of the National Academy of Sciences*, 120(14):e2204466120. https://doi.org/10.1073/pnas.2204466120
117. Liu, S., Wu, J., Sun, L., et al. (2023a). Analysis and study of the migration pattern of microplastic particles in saturated porous media pavement. *Science of The Total Environment*, 861:160613. https://doi.org/10.1016/j.scitotenv.2022.160613
118. Liu, Y., Xu, Z., Chen, L., et al. (2023b). Root colonization by beneficial rhizobacteria. *FEMS Microbiology Reviews*, 48(1):fuad066. https://doi.org/10.1093/femsre/fuad066
119. Lohrmann, C. and Holm, C. (2023). A novel model for biofilm initiation in porous media flow. *Soft Matter*, 19:6920–6928. https://doi.org/10.1039/D3SM00575E
120. Long, T. and Ford, R. M. (2009). Enhanced transverse migration of bacteria by chemotaxis in a porous t-sensor. *Environmental Science & Technology*, 43(5):1546–1552. https://doi.org/10.1021/es802558j
121. Lugtenberg, B. and Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology*, 63(Volume 63, 2009):541–556. https://doi.org/10.1146/annurev.micro.62.081307.162918
122. Luo, E., Leu, A. O., Eppley, J. M., Karl, D. M., and DeLong, E. F. (2022). Diversity and origins of bacterial and

archaeal viruses on sinking particles reaching the abyssal ocean. *The ISME Journal*, 16(6):1627–1635. https://doi.org/10.1038/s41396-022-01202-1

123. Ma, X., Geiser-Lee, J., Deng, Y., and Kolmakov, A. (2010). Interactions between engineered nanoparticles (ENPS) and plants: Phytotoxicity, uptake and accumulation. *Science of The Total Environment*, 408(16):3053–3061. https://doi.org/10.1016/j.scitotenv.2010.03.031
124. Macnab, R. M. and Koshland, D. E. (1972). The gradient-sensing mechanism in bacterial chemotaxis. *Proceedings of the National Academy of Sciences*, 69(9):2509–2512. https://doi.org/10.1073/pnas.69.9.2509
125. Magnabosco, C., Husain, F., Paoletti, M. M., et al (2024). Toward a natural history of microbial life. *Annual Review of Earth and Planetary Sciences*, 52(Volume 52, 2024):85–108. http://dx.doi.org/10.1146/annurev-earth-031621-070542
126. Maguire, L. W. and Gardner, C. M. (2023). Fate and transport of biological microcontaminants bound to microplastics in the soil environment. *Science of The Total Environment*, 892:164439. https://doi.org/10.1016/j.scitotenv.2023.164439
127. Maier, B. (2021). How physical interactions shape bacterial biofilms. *Annual Review of Biophysics*, 50(Volume 50, 2021):401–417. https://doi.org/10.1146/annurev-biophys-062920-063646
128. Marbach, S. and Bocquet, L. (2019). Osmosis, from molecular insights to large-scale applications. *Chemical Society Reviews*, 48:3102–3144. https://doi.org/10.1039/C8CS00420J
129. Marcos, Fu, H. C., Powers, T. R., and Stocker, R. (2012). Bacterial rheotaxis. *Proceedings of the National Academy of Sciences*, 109(13):4780–4785. https://doi.org/10.1073/pnas.1120955109
130. Markale, I., Carrel, M., Kurz, D. L., et al. (2023). Internal biofilm heterogeneities enhance solute mixing and chemical reactions in porous media. *Environmental Science & Technology*, 57(21):8065–8074. https://doi.org/10.1021/acs.est.2c09082
131. Martínez-Calvo, A., Bhattacharjee, T., Bay, R. K., et al. (2022). Morphological instability and roughening of growing 3D bacterial colonies. *Proceedings of the National Academy of Sciences*, 119(43):e2208019119. https://doi.org/10.1073/pnas.2208019119
132. Mattei, M. R., Frunzo, L., D'Acunto, B., et al. (2018). Continuum and discrete approach in modeling biofilm development and structure: a review. *Journal of Mathematical Biology*, 76(4):945–1003. https://doi.org/10.1007/s00285-017-1165-y
133. Mattingly, H. H. and Emonet, T. (2022). Collective behavior and nongenetic inheritance allow bacterial populations to adapt to changing environments. *Proceedings of the National Academy of Sciences*, 119(26):e2117377119. https://doi.org/10.1073/pnas.2117377119
134. McCarthy, J. F. and McKay, L. D. (2004). Colloid transport in the subsurface: Past, present, and future challenges. *Vadose Zone Journal*, 3(2):326–337. https://doi.org/10.2136/vzj2004.0326
135. McCarthy, J. F. and Zachara, J. M. (1989). Subsurface transport of contaminants. *Environmental Science & Technology*, 23(5):496–502. https://digitalcommons.unl.edu/usdoepub/175?utm_source=digitalcommons.unl.edu%2Fusdoepub%2F175&utm_medium=PDF&utm_campaign=PDFCoverPages
136. Mitchell, J. G. (2002). The energetics and scaling of search strategies in bacteria. *The American Naturalist*, 160(6):727–740. PMID: 18707461. https://doi.org/10.1086/343874
137. Molnar, I. L., Johnson, W. P., Gerhard, J. I., Willson, C. S., and O'Carroll, D. M. (2015). Predicting colloid transport through saturated porous media: A critical review. *Water Resources Research*, 51(9):6804–6845. https://doi.org/10.1002/2015WR017318
138. Moore-Ott, J. A., Chiu, S., Amchin, D. B., Bhattacharjee, T., and Datta, S. S. (2022). A biophysical threshold for biofilm formation. *eLife*, 11:e76380. https://doi.org/10.7554/eLife.76380
139. Motta, J.-P., Wallace, J. L., Buret, A., et al. (2021). Gastrointestinal biofilms in health and disease. *Nature Reviews Gastroenterology & Hepatology*, 18(5):314–334. https://doi.org/10.1038/s41575-020-00397-y
140. Mukherjee, S. and Bassler, B. L. (2019). Bacterial quorum sensing in complex and dynamically changing environments. *Nature Reviews Microbiology*, 17(6):371–382. https://doi.org/10.1038/s41579-019-0186-5
141. Nadell, C. D., Drescher, K., and Foster, K. R. (2016). Spatial structure, cooperation and competition in biofilms. *Nature Reviews Microbiology*, 14(9):589–600. https://doi.org/10.1038/nrmicro.2016.84
142. Nadezhdin, E., Murphy, N., Dalchau, N., et al. (2020). Stochastic pulsing of gene expression enables the generation of spatial patterns in bacillus subtilis biofilms. *Nature Communications*, 11(1):950. https://doi.org/10.1038/s41467-020-14431-9
143. Navarro, E., Baun, A., Behra, R., e al. (2008). Environmental behavior and ecotoxicity of engineered nanoparticles to algae, plants, and fungi. *Ecotoxicology*, 17(5):372–386. https://doi.org/10.1007/s10646-008-0214-0
144. Nguyen, J., Fernandez, V., Pontrelli, S., e al. (2021). A distinct growth physiology enhances bacterial growth under rapid nutrient fluctuations. *Nature Communications*, 12(1):3662. https://doi.org/10.1038/s41467-021-23439-8
145. Nijjer, J., Li, C., Kothari, M., et al. (2023). Biofilms as self-shaping growing nematics. *Nature Physics*,

19(12):1936–1944. https://doi.org/10.1038/s41567-023-02221-1

146. Or, D., Smets, B. F., Wraith, J. M., e al. (2007). Physical constraints affecting bacterial habitats and activity in unsaturated porous media –a review. *Advances in Water Resources*, 30(6):1505–1527. https://doi.org/10.1016/j.advwatres.2006.05.025
147. Ostvar, S., Iltis, G., Davit, Y., et al. (2018). Investigating the influence of flow rate on biofilm growth in three dimensions using microimaging. *Advances in Water Resources*, 117:1–13. https://doi.org/10.1016/j.advwatres.2018.03.018
148. Papadopoulos, C., Larue, A. E., Toulouze, Cet al. (2024). A versatile micromodel technology to explore biofilm development in porous media flows. *Lab on a Chip*, 24:254–271. https://doi.org/10.1039/D3LC00293D
149. Papenfort, K. and Bassler, B. L. (2016). Quorum sensing signal–response systems in gram-negative bacteria. *Nature Reviews Microbiology*, 14(9):576–588. https://doi.org/10.1038/nrmicro.2016.89
150. Park, S. W., Lee, J., Yoon, H., and Shin, S. (2021). Microfluidic investigation of salinity-induced oil recovery in porous media during chemical flooding. *Energy & Fuels*, 35(6):4885–4892. https://doi.org/10.1021/acs.energyfuels.0c04320
151. Patino, J. E., Johnson, W. P., and Morales, V. L. (2023). Relating mechanistic fate with spatial positioning for colloid transport in surface heterogeneous porous media. *Journal of Colloid and Interface Science*, 641:666–674. https://doi.org/10.1016/j.jcis.2023.03.005
152. Persat, A., Nadell, C. D., Kim, M. K., et al. (2015). The mechanical world of bacteria. *Cell*, 161(5):988–997. https://doi.org/10.1016/j.cell.2015.05.005
153. Pete, A. J., Brahana, P. J., Bello, M., et al. (2023). Biofilm formation influences the wettability and settling of microplastics. *Environmental Science & Technology Letters*, 10(2):159–164. https://doi.org/10.1021/acs.estlett.2c00728
154. Petersen, F. and Hubbart, J. A. (2021). The occurrence and transport of microplastics: The state of the science. *Science of The Total Environment*, 758:143936. https://doi.org/10.1016/j.scitotenv.2020.143936
155. Petosa, A. R., Jaisi, D. P., Quevedo, I. R., et al. (2010). Aggregation and deposition of engineered nanomaterials in aquatic environments: Role of physicochemical interactions. *Environmental Science & Technology*, 44(17):6532–6549. https://doi.org/10.1021/es100598h
156. Philipp, L.-A., Bühler, K., Ulber, R., and Gescher, J. (2024). Beneficial applications of biofilms. *Nature Reviews Microbiology*, 22(5):276–290. https://doi.org/10.1038/s41579-023-00985-0
157. Philippot, L., Chenu, C., Kappler, A., et al. (2024). The interplay between microbial communities and soil properties. *Nature Reviews Microbiology*, 22(4):226–239. https://doi.org/10.1038/s41579-023-00980-5
158. Philippot, L., Raaijmakers, J. M., Lemanceau, P., and van der Putten, W. H. (2013). Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology*, 11(11):789–799. https://doi.org/10.1038/nrmicro3109
159. Pokhrel, A. R., Steinbach, G., Krueger, A., et al (2024). The biophysical basis of bacterial colony growth. *Nature Physics*, 20(9):1509–1517. https://doi.org/10.1038/s41567-024-02572-3
160. Prasad, M., Obana, N., Lin, S. Z., et al. (2023). Alcanivorax borkumensis biofilms enhance oil degradation by interfacial tubulation. *Science*, 381(6659):748–753. https://doi.org/10.1126/science.adf3345
161. Qian, P.-Y., Cheng, A., Wang, R., and Zhang, R. (2022). Marine biofilms: diversity, interactions and biofouling. *Nature Reviews Microbiology*, 20(11):671–684. https://doi.org/10.1038/s41579-022-00744-7
162. Qin, B., Fei, C., Bridges, A. A., et al. (2020). Cell position fates and collective fountain flow in bacterial biofilms revealed by light-sheet microscopy. *Science*, 369(6499):71–77. https://doi.org/10.1126/science.abb8501
163. Raina, J.-B., Fernandez, V., Lambert, B., et al. (2019). The role of microbial motility and chemotaxis in symbiosis. *Nature Reviews Microbiology*, 17(5):284–294. https://doi.org/10.1038/s41579-019-0182-9
164. Raina, J.-B., Lambert, B. S., Parks, D. H., et al. (2022). Chemotaxis shapes the microscale organization of the ocean's microbiome. *Nature*, 605(7908):132–138. https://doi.org/10.1038/s41586-022-04614-3
165. Ren, Z., Gui, X., Xu, X., e al. (2021). Microplastics in the soil-groundwater environment: Aging, migration, and co-transport of contaminants–a critical review. *Journal of Hazardous Materials*, 419:126455. https://doi.org/10.1016/j.jhazmat.2021.126455
166. Rillig, M. C. and Lehmann, A. (2020). Microplastic in terrestrial ecosystems. *Science*, 368(6498):1430–1431. https://doi.org/10.1126/science.abb5979
167. Rillig, M. C., Ziersch, L., and Hempel, S. (2017). Microplastic transport in soil by earthworms. *Scientific Reports*, 7(1):1362. https://doi.org/10.1038/s41598-017-01594-7
168. Rochman, C. M. (2018). Microplastics research—from sink to source. *Science*, 360(6384):28–29. https://doi.org/10.1126/science.aar7734
169. Rolle, M. and Le Borgne, T. (2019). Mixing and reactive fronts in the subsurface. *Reviews in Mineralogy and Geochemistry*, 85(1):111–142. https://doi.org/10.2138/rmg.2018.85.5
170. Rooney, L. M., Amos, W. B., Hoskisson, P. A., and McConnell, G. (2020). Intra-colony channels in e. coli function as a nutrient uptake system. *The ISME Journal*, 14(10):2461–2473. https://pubmed.ncbi.nlm.nih.gov/32555430/

171. Rusconi, R., Garren, M., and Stocker, R. (2014a). Microfluidics expanding the frontiers of microbial ecology. *Annual Review of Biophysics*, 43(Volume 43, 2014):65–91. https://doi.org/10.1146/annurev-biophys-051013-022916
172. Rusconi, R., Guasto, J. S., and Stocker, R. (2014b). Bacterial transport suppressed by fluid shear. *Nature Physics*, 10(3):212–217. https://doi.org/10.1038/nphys2883
173. Rusconi, R., Lecuyer, S., Autrusson, N., et al. (2011). Secondary flow as a mechanism for the formation of biofilm streamers. *Biophysical Journal*, 100(6):1392–1399. https://doi.org/10.1016/j.bpj.2011.01.065
174. Rusconi, R., Lecuyer, S., Guglielmini, L., and Stone, H. A. (2010). Laminar flow around corners triggers the formation of biofilm streamers. *Journal of The Royal Society Interface*, 7(50):1293– 1299. https://doi.org/10.1098/rsif.2010.0096
175. Russel, W. B., Russel, W., Saville, D. A., and Schowalter, W. R. (1991). *Colloidal dispersions*. Cambridge University Press. https://books.google.de/books/about/Colloidal_Dispersions.html?id=3shp8Kl6YoUC&redir_esc=y
176. Ryan, J. N. and Elimelech, M. (1996). Colloid mobilization and transport in groundwater. *Colloids and Surfaces A: Physicochemical and Engineering Aspects*, 107:1–56. https://doi.org/10.1016/0927-7757(95)03384-X
177. Saintillan, D. (2023). Dispersion of run-and-tumble microswimmers through disordered media. *Phys. Rev. E*, 108:064608. https://doi.org/10.1103/PhysRevE.108.064608
178. Sajjad, M., Huang, Q., Khan, S., et al. (2022). Microplastics in the soil environment: A critical review. *Environmental Technology & Innovation*, 27:102408. https://doi.org/10.1016/j.eti.2022.102408
179. Salek, M. M., Carrara, F., Zhou, J., et al. (2024). Multiscale porosity microfluidics to study bacterial transport in heterogeneous chemical landscapes. *Advanced Science*, 11(20):2310121. https://doi.org/10.1002/advs.202310121
180. Sauer, K., Stoodley, P., Goeres, D. M., et al. (2022). The biofilm life cycle: expanding the conceptual model of biofilm formation. *Nature Reviews Microbiology*, 20(10):608–620. https://doi.org/10.1038/s41579-022-00767-0
181. Scheidweiler, D., Bordoloi, A. D., Jiao, W., et al. (2024). Spatial structure, chemotaxis and quorum sensing shape bacterial biomass accumulation in complex porous media. *Nature Communications*, 15(1):191. https://doi.org/10.1038/s41467-023-44267-y
182. Scheidweiler, D., Peter, H., Pramateftaki, P., et al. (2019). Unraveling the biophysical underpinnings to the success of multispecies biofilms in porous environments. *The ISME Journal*, 13(7):1700–1710. https://doi.org/10.1038/s41396-019-0381-4
183. Schimel, J. and Schaeffer, S. M. (2012). Microbial control over carbon cycling in soil. *Frontiers in Microbiology*, 3. https://doi.org/10.3389/fmicb.2012.00348
184. Schimel, J. P. (2018). Life in dry soils: Effects of drought on soil microbial communities and processes. *Annual Review of Ecology, Evolution, and Systematics*, 49(Volume 49, 2018):409–432. http://dx.doi.org/10.1146/annurev-ecolsys-110617-062614
185. Schirrmeister, B. E., Gugger, M., and Donoghue, P. C. J. (2015). Cyanobacteria and the great oxidation event: evidence from genes and fossils. *Palaeontology*, 58(5):769–785. https://doi.org/10.1111/pala.12178
186. Secchi, E., Savorana, G., Vitale, A., et al. (2022). The structural role of bacterial eDNA in the formation of biofilm streamers. *Proceedings of the National Academy of Sciences*, 119(12):e2113723119. https://doi.org/10.1073/pnas.2113723119
187. Secchi, E., Vitale, A., Miño, G. L., et al. (2020). The effect of flow on swimming bacteria controls the initial colonization of curved surfaces. *Nature Communications*, 11(1):2851. https://doi.org/10.1038/s41467-020-16620-y
188. Segall, J. E., Block, S. M., and Berg, H. C. (1986). Temporal comparisons in bacterial chemotaxis. *Proceedings of the National Academy of Sciences*, 83(23):8987–8991. https://doi.org/10.1073/pnas.83.23.8987
189. Seminara, A., Angelini, T. E., Wilking, J. N., et al. (2012). Osmotic spreading of bacillus subtilis biofilms driven by an extracellular matrix. *Proceedings of the National Academy of Sciences*, 109(4):1116–1121. https://doi.org/10.1073/pnas.1109261108
190. Seymour, J. R., Amin, S. A., Raina, J.-B., and Stocker, R. (2017). Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships. *Nature Microbiology*, 2(7):17065. https://doi.org/10.1038/nmicrobiol.2017.65
191. Shim, S. (2022). Diffusiophoresis, diffusioosmosis, and microfluidics: Surface-flow-driven phenomena in the presence of flow. *Chemical Reviews*, 122(7):6986–7009. https://doi.org/10.1021/acs.chemrev.1c00571
192. Siegel, D. A., DeVries, T., Cetinic, I., and Bisson, K. M. (2023). Quantifying the ocean's biological pump and its carbon cycle impacts on global scales. *Annual Review of Marine Science*, 15(Volume 15, 2023):329–356. https://doi.org/10.1146/annurev-marine-040722-115226

193. Sivadon, P., Barnier, C., Urios, L., and Grimaud, R. (2019). Biofilm formation as a microbial strategy to assimilate particulate substrates. *Environmental Microbiology Reports*, 11(6):749–764. https://doi.org/10.1111/1758-2229.12785
194. Słomka, J., Alcolombri, U., Secchi, E., et al I. (2020). Encounter rates between bacteria and small sinking particles. *New Journal of Physics*, 22(4):043016. https://doi.org/10.1088/1367-2630/ab73c9
195. Sokol, N. W., Slessarev, E., Marschmann, G. L., et al (2022). Life and death in the soil microbiome: how ecological processes influence biogeochemistry. *Nature Reviews Microbiology*, 20(7):415–430. https://doi.org/10.1038/s41579-022-00695-z
196. Sourjik, V. and Wingreen, N. S. (2012). Responding to chemical gradients: bacterial chemotaxis. *Current Opinion in Cell Biology*, 24(2):262–268. https://doi.org/10.1016/j.ceb.2011.11.008
197. Squyres, G. R. and Newman, D. K. (2024). Biofilms as more than the sum of their parts: lessons from developmental biology. *Current Opinion in Microbiology*, 82:102537. https://doi.org/10.1016/j.mib.2024.102537
198. Stehnach, M. R., Henshaw, R. J., Floge, S. A., and Guasto, J. S. (2023). Multiplexed microfluidic screening of bacterial chemotaxis. *eLife*, 12:e85348. https://doi.org/10.7554/eLife.85348
199. Stocker, R. (2012). Marine microbes see a sea of gradients. *Science*, 338(6107):628–633. https://doi.org/10.1126/science.1208929
200. Stocker, R., Seymour, J. R., Samadani, A., et al. (2008). Rapid chemotactic response enables marine bacteria to exploit ephemeral microscale nutrient patches. *Proceedings of the National Academy of Sciences*, 105(11):4209–4214. https://doi.org/10.1073/pnas.0709765105
201. Tecon, R. and Or, D. (2017). Biophysical processes supporting the diversity of microbial life in soil. *FEMS Microbiology Reviews*, 41(5):599–623. https://doi.org/10.1093/femsre/fux039
202. Teschler, J. K., Nadell, C. D., Drescher, K., and Yildiz, F. H. (2022). Mechanisms underlying vibrio cholerae biofilm formation and dispersion. *Annual Review of Microbiology*, 76(Volume 76, 2022):503–532. https://doi.org/10.1146/annurev-micro-111021-053553
203. Tratnyek, P. G. and Johnson, R. L. (2006). Nanotechnologies for environmental cleanup. *Nano Today*, 1(2):44–48. https://doi.org/10.1016/S1748-0132(06)70048-2
204. Tufenkji, N. and Elimelech, M. (2004). Deviation from the classical colloid filtration theory in the presence of repulsive DLVO interactions. *Langmuir*, 20(25):10818–10828. https://doi.org/10.1021/la0486638
205. Tufenkji, N. and Elimelech, M. (2005). Breakdown of colloid filtration theory: Role of the secondary energy minimum and surface charge heterogeneities. *Langmuir*, 21(3):841–852. https://doi.org/10.1021/la048102g
206. Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Progress in Oceanography*, 130:205–248. http://dx.doi.org/10.1016/j.pocean.2014.08.005
207. Ugolini, G. S., Wang, M., Secchi, E., et al. (2024). Microfluidic approaches in microbial ecology. *Lab on a Chip*, 24:1394–1418. https://doi.org/10.1039/D3LC00784G
208. Valocchi, A. J., Bolster, D., and Werth, C. J. (2019). Mixing-limited reactions in porous media. *Transport in Porous Media*, 130(1):157–182. https://doi.org/10.1007/s11242-018-1204-1
209. Wadhams, G. H. and Armitage, J. P. (2004). Making sense of it all: bacterial chemotaxis. *Nature Reviews Molecular Cell Biology*, 5(12):1024–1037. https://doi.org/10.1038/nrm1524
210. Wang, C., Wang, R., Huo, Z., Xie, E., and Dahlke, H. E. (2020). Colloid transport through soil and other porous media under transient flow conditions—a review. *WIREs Water*, 7(4):e1439. https://doi.org/10.1002/wat2.1439
211. Wang, J., Guo, X., and Xue, J. (2021). Biofilm-developed microplastics as vectors of pollutants in aquatic environments. *Environmental Science & Technology*, 55(19):12780–12790. https://doi.org/10.1021/acs.est.1c04466
212. Wang, M. and Ford, R. M. (2009). Transverse bacterial migration induced by chemotaxis in a packed column with structured physical heterogeneity. *Environmental Science & Technology*, 43(15):5921– 5927. https://doi.org/10.1021/es901001t
213. Weady, S., Palmer, B., Lamson, A., et al J. (2024). Mechanics and morphology of proliferating cell collectives with self-inhibiting growth. *Phys. Rev. Lett.*, 133:158402. https://doi.org/10.1103/PhysRevLett.133.158402
214. Wei, G. and Yang, J. Q. (2023). Microfluidic investigation of the impacts of flow fluctuations on the development of Pseudomonas putida biofilms. *NPJ Biofilms and Microbiomes*, 9(1):73. https://doi.org/10.1038/s41522-023-00442-z
215. Wilking, J. N., Zaburdaev, V., Volder, M. D., et al. (2013). Liquid transport facilitated by channels in bacillus subtilis biofilms. *Proceedings of the National Academy of Sciences*, 110(3):848–852. https://doi.org/10.1073/pnas.1216376110
216. Wu, H. and Schwartz, D. K. (2020). Nanoparticle tracking to probe transport in porous media. *Accounts of Chemical Research*, 53(10):2130–2139. https://doi.org/10.1021/acs.accounts.0c00408

217. Xie, H., Chen, J., Feng, L., et al. (2021). Chemotaxis-selective colonization of mangrove rhizosphere microbes on nine different microplastics. *Science of The Total Environment*, 752:142223. https://doi.org/10.1016/j.scitotenv.2020.142223
218. Yan, J., Nadell, C. D., Stone, H. A., et al. (2017). Extracellular-matrix- mediated osmotic pressure drives vibrio cholerae biofilm expansion and cheater exclusion. *Nature Communications*, 8(1):327. https://doi.org/10.1038/s41467-017-00401-1
219. Yang, L., Zhang, Y., Kang, S., et al. (2021). Microplastics in soil: A review on methods, occurrence, sources, and potential risk. *Science of The Total Environment*, 780:146546. https://doi.org/10.1016/j.scitotenv.2021.146546
220. You, Z., Pearce, D. J. G., and Giomi, L. (2021). Confinement-induced self-organization in growing bacterial colonies. *Science Advances*, 7(4):eabc8685. https://doi.org/10.1126/sciadv.abc8685
221. Yu, Y., Zhang, L., Zhuang, Z., et al (2024). Nanoplastics in soil plastisphere: Occurrence, bio-interactions and environmental risks. *Nano Today*, 58:102409. https://doi.org/10.1016/j.nantod.2024.102409
222. Zettler, E. R., Mincer, T. J., and Amaral-Zettler, L. A. (2013). Life in the “plastisphere”: Microbial communities on plastic marine debris. *Environmental Science & Technology*, 47(13):7137–7146. https://doi.org/10.1021/es401288x
223. Zhu, D., Ma, J., Li, G., Rillig, M. C., and Zhu, Y.-G. (2021). Soil plastispheres as hotspots of antibiotic resistance genes and potential pathogens. *The ISME Journal*, 16(2):521–532. https://doi.org/10.1038/s41396-021-01103-9