



## And yet they move: microbial movement in soil habitats

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Movement of organisms plays a crucial role in microbial ecology, yet little is known about how, when and at what speeds soil microorganisms move. Literature offers conflicting lines of evidence, even regarding whether single-celled organisms can move at all under typical soil conditions. We review the literature on microbial movement in the context of soil physicochemical complexity, to establish its likelihood and its prerequisite conditions. Our focus is on movement at the spatial and temporal scales relevant for microbiota ( $\mu\text{m}$  to  $\text{cm}$ , seconds to days), with particular attention to bacteria and fungi. We synthesize experimental data for bacteria to show that unicellular movement can occur in moderately moist soils, although it is suppressed under dry conditions. By integrating current knowledge of microbial physiology and soil physics, we propose underlying mechanisms that may overcome the challenging conditions of soil, including non-flagellar surface movements (pili, in particular) and the role of biosurfactants. Our energetic analysis also shows that movement is possible, even under moderately oligotrophic conditions. Movement modes are entirely different for filamentous microorganisms like fungi, however, which are not restricted by water connectivity, grow much slower than prokaryotic movement, and must contend with the great tortuosity of the soil habitat. However, once a fungal network is established, cytoplasmic streaming can translocate resources and even the entire fungal cytoplasm at speeds comparable to bacteria ( $5 \mu\text{m/s}$ ). Fungal hyphae also provide physical connections and favorable conditions to support prokaryotic movement along their surfaces. Hitchhiking, in which one organism is transported by the movement and energy of another, is also likely to be important in soil. A diverse array of movement possibilities emerges from our analysis, suggesting that soil microorganisms may be much more mobile than often appreciated. These also indicate substantial implications of movement for the ecology and ecological functions of soil microbiota. However, many key unknowns remain to be addressed and hypotheses experimentally tested, and we propose an ambitious roadmap to a comprehensive understanding of microbial movement in soil, and its relevance for biogeochemical cycling.

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