

Scaling up and down: movement ecology for microorganisms

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HIGHLIGHTS

- Our mechanistic understanding of the machinery that powers microbial motility has advanced considerably alongside mounting evidence from the ecological literature that dispersal plays a key role in structuring patterns of microbial biodiversity.
- Despite the parallel developments in these fields, they have focused largely on microbial movement at different scales, hindering the cross-scale integration from individual motility behavior to the dynamics of populations and communities.
- Movement ecology is a recent framework that could provide a means to integrate across these different perspectives to better understand microbial movement and explicitly identify the fundamental features of movement.
- Empirical studies using novel techniques have revealed important ways that microorganisms can sense and move through different environments, unlocking the potential to study microbial motility at different scales from a movement ecology perspective.

ABSTRACT

Movement is critical for the fitness of organisms, both large and small. It dictates how individuals acquire resources, evade predators, exchange genetic material, and respond to stressful environments. Movement also influences ecological and evolutionary dynamics at scales beyond the individual organism. However, the links between individual motility and the processes that generate and maintain microbial diversity are poorly understood. Movement ecology is a framework linking the physiological and behavioral properties of individuals to movement patterns across scales of space, time, and biological organization. By synthesizing insights from cell biology, ecology, and evolution, we expand theory from movement ecology to predict the causes and consequences of microbial movements from small to large scales.

MICROBIAL MOVEMENTS ACROSS SCALES

Movement (see Glossary) is a fundamental aspect of life [1]. Among microorganisms, movement allows cells to encounter new resources [2], evade predators and parasites [3,4], exchange genetic material [5,6], form complex multicellular biofilms [7,8], and track favorable environmental conditions [9]. Because movement is essential, many different strategies have evolved that allow microbes to successfully navigate their environments. For example, internal energy stores in the cell power swimming **motility** in aqueous environments and swarming, twitching, and gliding along surfaces [2], while body size, attachment to particles, associations with hosts, and engagement in dormancy can promote passive movements [10]. Despite such detailed knowledge about the strategies and molecular mechanisms underlying movement at the individual level, it remains a challenge to scale these individual-level mechanisms up to understand patterns and processes in microbial **populations** and **communities**.

Microorganisms are thought to have the highest movement capacities among all of life on earth [11–13]. However, this perspective is disconnected from the movement of individual cells. Instead, views on microbial movement are often informed by **biogeographic** patterns like **dispersal** ranges, which result from a multi-generational sequence of individual reproduction events and cellular movements [9,14,15]. Consequently, there is a chasm between the mechanistic understanding of individual movements and the collective dispersal patterns that emerge from individual-level processes [16]. For example, the “run-and-tumble” motility strategy explains how chemotaxis lets individuals track favorable **environmental gradients** in spatially heterogeneous habitats, but it is not clear how this motility strategy aligns with our broader understanding of the ecological and evolutionary effects of habitat-informed movement on populations and communities [17]. An integrative perspective to microbial movement must

link between individuals and the net dispersal that emerges from the collective actions of those individuals. Closing this gap requires integration across scales of space, time, and biological organization, which will open new opportunities to examine how individual traits influence eco-evolutionary dynamics across scales and environments.

Movement ecology may provide a way to resolve this problem of scale mismatch. It is a multi-scale framework that links individual-level movement behaviors with emergent properties at higher levels of organization, such as populations and communities [16,18]. Most often applied to macro-organisms (i.e., plants and animals), movement ecology emphasizes four main mechanisms governing organismal movement: *locomotion* (i.e., how organisms move), the *internal state* of the organism (i.e., the factors that motivate or allow movement), *navigation* capacities (i.e., whether organisms can directionally orient their movements), and the *environmental* context (e.g., fluid flows, abiotic stresses, biotic constraints) of movement decisions [16]. Movement ecology proposes that individual movement paths depend on the interplay among these mechanisms and can be characterized by different movement phases (e.g., random searching, rest, tracking) that accumulate over the individual's lifetime (Fig. 1). From these four fundamental mechanisms, the collective movements of individuals lead to population level patterns of dispersal. By examining interactions among movement mechanisms there is an opportunity to unify insights into the movement strategies of microorganisms, but it is necessary to account for the unique features of microbial life to complete the integration between individual, population, and community scales.

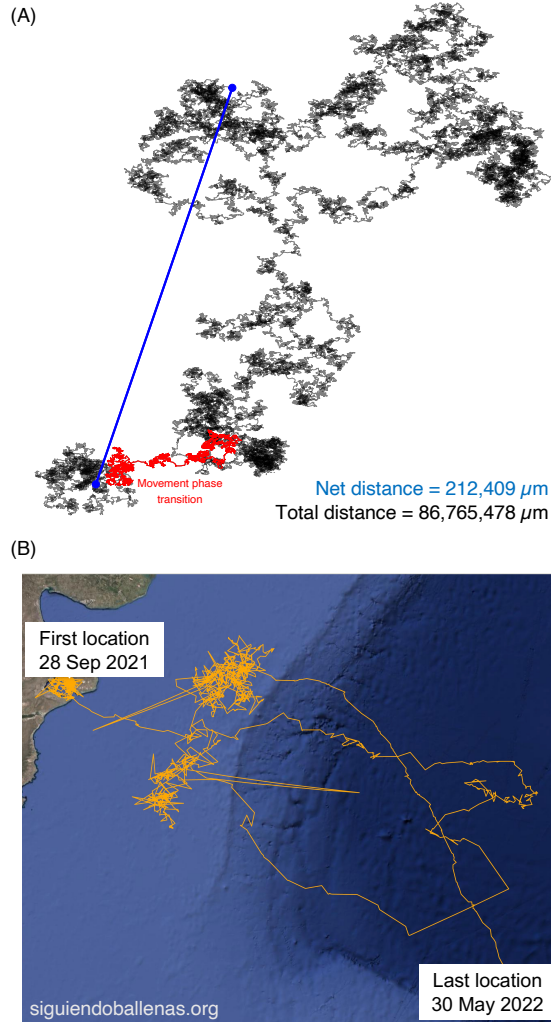


Figure 1. A movement ecology perspective provides a unified approach to studying movement patterns, spanning microorganisms to macroorganisms. (A) This line is a trace of a random walk, without chemotaxis, but the movement pattern demonstrates important features of movement. The net displacement distance (blue) is much smaller than the total distance traveled (black). This reflects the deep sinuosity of the random walk. Even with a flat movement kernel, random walks can exhibit spatial clusters of movements that the individual transitions between, denoting movement phases (outlined in red). (B) Compare the movements of the random walk with the movements of a Southern Right Whale (*Eubalaena australis*) in the Southern Atlantic Ocean off the coast of Argentina. Outlined in orange is the movement pattern of Centaura, a mother with calf, between 28 September 2021 and 30 May 2022. The whale is navigating a different ecosystem, with different locomotive strategies and complex sensory abilities. Despite these differences, we can see spatial clusters of movements interspersed with longer-distance movements, perhaps due to different behaviors underlying movement decisions (e.g., feeding). Data obtained from <https://siguiendoballenas.org> on 6 Jun 2022. The approach we outline can be used to link the study of microbial movement with the study of larger organisms across broad spatial scales.

A MOVEMENT ECOLOGY FOR MICROORGANISMS

Building on the four mechanisms of movement ecology, we develop a general framework adapted for microorganisms to understand why microbes move the way they do in different environments. We consider the correlated traits and life-history features of microorganisms that distinguish their movement behaviors from the movements of macro-organisms, such as smaller body size, shorter generation times, and the propensity for prolonged **dormancy** and reduced metabolism.

Locomotion – active versus passive movement:

A major distinction between movement approaches is whether the microbial cell has the molecular structures to power active locomotion. Active movement can be accomplished through a variety of mechanisms, such as swimming or swarming via flagella [2,9], twitching via pili [19], or gliding via secretion systems [20,21], which can generate a range of movement patterns [22]. For example, rod-shaped bacteria (e.g., *E. coli*, *Bacillus*) can rotate bundles of flagella to generate thrust through an aqueous environment. Molecular mechanisms can reverse the direction of flagellar motors, causing reorientation of the cell body and subsequent forward motion occurs in a new direction [23]. This mixture of runs interspersed with reorientations (i.e., “run-and-tumble” strategy) is common in swimming bacteria [9]. In contrast, helical cells do not need flagella and can rotate their bodies through environments due to their corkscrew body shape [24]. On surfaces, twitching motility relies not on flagella, but instead on the extension, adhesion, and retraction of pili, which can reorient cells upon detachment of pili from a surface [19], while gliding employs a range of mechanisms to move across slightly drier surfaces [20]. These mechanisms affect travel in profound ways. For example, speed varies by orders of

magnitude (Box 1), ranging from $\sim 1000 \mu\text{m/s}$ in *Ovobacter propellens*, which is powered by 400 flagella [25], to $\sim 1 \mu\text{m/s}$ in *Neisseria gonorrhoeae*, which employs twitching motility (Fig. 2) [26]. Some gliding mechanisms are even slower: *Myxococcus xanthus* travels at roughly five body lengths per minute [20]. The structural variation in motility apparatuses likely reflects different costs and benefits that constrain cellular movements [2].

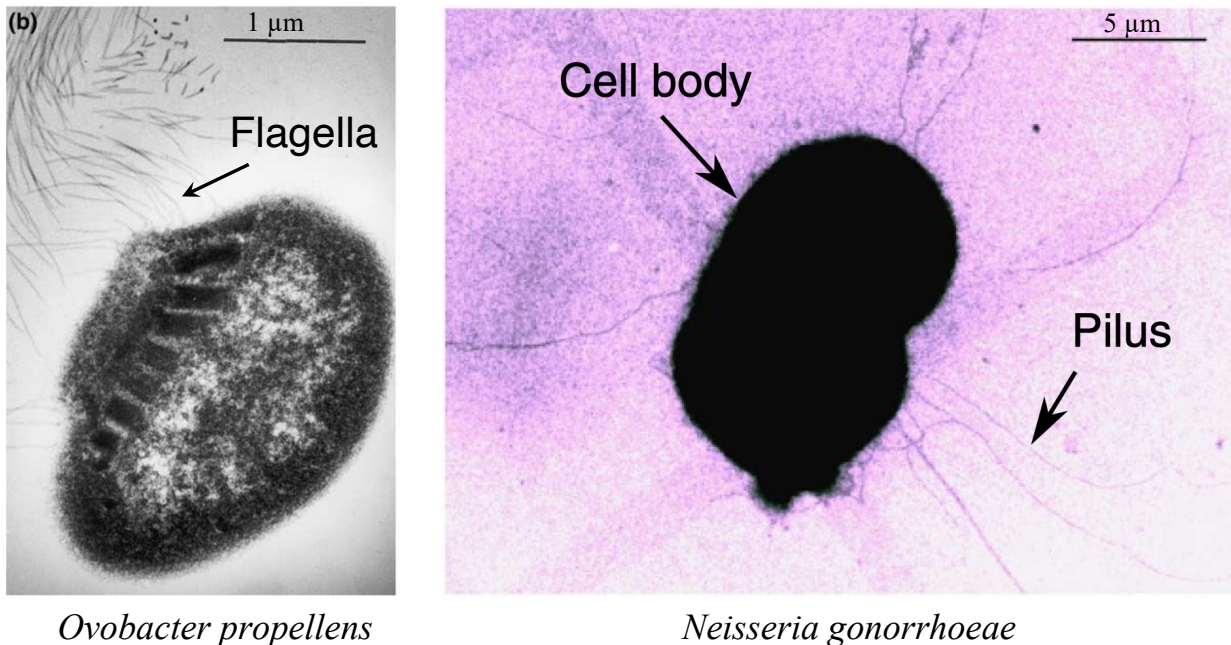


Figure 2. A comparison of two bacterial approaches to motility. (A) *Ovobacter propellens* relies on roughly 400 flagella to power its motility ($\sim 1000 \mu\text{m/s}$). (B) In contrast, *Neisseria gonorrhoeae* uses several pili to undertake twitching motility, resulting in substantially slower movements ($\sim 1 \mu\text{m/s}$). These two organisms move at drastically different speeds, evidenced by their differential structural investments and the costs to maintain them over evolutionary time. Figure of *O. propellens* from reference [25]. Figure of *N. gonorrhoeae* from reference [79].

Microorganisms can also move passively through the landscape. Passive movement may occur instead of, or in addition to, active movement, and could counteract active movements, making them less energetically efficient. Microbes have evolved a range of morphological structures that promote passive movement. For example, many microorganisms are capable of

long-range dispersal owing to small body sizes, buoyant structures [27], and life-history strategies including dormancy [28], host- or microbial-associations [29,30], and ballistosporic discharge [31]. Long-range dispersal can be further aided by the fact that microorganisms suspended in the atmosphere often have mean residence times of around one week [32], which can contribute to global-scale dispersal when attached to dust particles [33].

Internal organismal state – energy reserves

Movement is affected by the internal state of an individual, which can be influenced by nutrient limitation, sensing of predators, viruses, or stressful abiotic conditions. Active movement is costly and could lead to the depletion of energy stores with implications for survival and growth in new habitats. For example, the high swimming speeds of *Ovobacter propellens* are powered by rotating the flagellar filaments in excess of 10,000 rotations per second [22]. Thus, even if the structures for active movement are in place, a cell may be unable to power the machinery due to energetic limitations. Indeed, genomic evidence suggests that motility is often lost during nutrient limitations [34], and lab experiments have shown that motility can be especially costly during starvation [9], sometimes provoking a reduction in swimming cells [35]. In the deep biosphere, extreme energy limitation has eliminated motility in some cases [36]. One reason for this might be because, for slower growing cells, motility costs make up a larger portion of the cell's **energy budget** [9]. Starvation can also modify cell sizes, and smaller cells may be less energetically efficient at swimming due to the relationships between nutrient uptake, drag forces, and flagellar motor power requirements [37]. These energetic costs tend to increase with the viscosity of the environment [38], but could be alleviated or exacerbated in the face of strong passive movements.

Even passive movements can be shaped by internal organismal states. For example, **genome streamlining** and metabolic strategies that reduce energetic costs (e.g., growth suspension or dormancy) are often correlated with broad spatial distributions of certain microbial taxa [39–41]. This pattern suggests that energetic traits could be important for promoting passive dispersal across generations, thereby increasing range size. Metabolic constraints may also limit the environments in which cells can acquire energy for maintenance, creating barriers to dispersal in the absence of dormancy. For instance, anaerobic gut-associated taxa are strongly dependent on the host as a vector, unable to survive oxygenated conditions. This environmental constraint limits passive movement capacity, but many gut microorganisms are capable of producing dormant spores that do not allocate energy to reproduction and survive harsh conditions [42–45]. In environments that disfavor dormancy, however, complex sporulation pathways like that of *Bacillus subtilis* are quick to decay [46]. Thus, the internal states of microorganisms (metabolic, genomic, and energetic) can have implications for both active and passive movement patterns.

Navigation capacities – taxis

Many microorganisms have sensory capacities that allow them to track favorable environmental conditions through space (i.e., taxis). Similar to foraging behaviors and sensory cues that guide animal movements (e.g., sight, smell), taxis allows active movements to be non-randomly directed along environmental gradients (e.g., light, chemical concentration, temperature, magnetic fields). Sensory cues may be the direct targets of bacterial motility (e.g., carbon substrates) or they may be indirectly associated with favorable environments. The sensory machinery is energetically costly [9,29], but helps individuals reach reproductively favorable

habitats [47], including motile hosts that emit chemical signals [48]. For example, marine bacteria and archaea exhibit strong chemotaxis towards phytoplankton-produced organic matter, helping them find resource hotspots in the open ocean [49].

Taxis may also be a density-dependent mechanism mediated by **quorum sensing**, which relies on the production, transmission, and reception of cell-cell signaling molecules. In high-density environments, such as guts or fertile soils, quorum sensing can leverage the multiple independent search paths of individual bacteria to find suitable microhabitats, from which they can produce signals that allow nearby cells to navigate along the signal gradient. For example, the secretion of Autoinducer-2 by *E. coli* can provide a gradient that other neighboring conspecific cells can follow via chemotaxis [50]. The production of quorum sensing molecules then can synchronize cell movements, and rapidly reorient individual movement pathways, transitioning from a gradient-seeking random walk to a directed walk up a signaling gradient. In soils, *B. subtilis* followed a gradient of quorum sensing molecules to localize on the tips of plant roots [51]. Thus, taxis behavior is an important link between individual-level movements and the collective movements of the population. Examining the environmental or signaling gradients that coordinate movement among individuals is therefore a critical feature in understanding the distribution of movements at larger organization levels.

Physical factors – fluid versus static vectors

Microbes live in environments that vary widely in their fluid properties. From current-dominated rivers and oceans, to static environments in soils or within plants (e.g., leaf endophytes, rhizobia in roots), to the periodic flushing of the gastrointestinal tract, many microbes are at the mercy of current and flow. Strong physical environmental flows can quickly overcome the forces of active

movement, leading to predominantly planktonic lifestyles guided by passive movement [47]. Alternatively, if fluid flows displace microbes from their optimal habitats, active machinery could be necessary to maintain position. Some environments, such as guts, may favor microbial traits like dormancy that promote **colonization** by improving survival through low-pH environments and between hosts [42]. The fluidity of the environment can also modify how individuals perceive other features, such as spatial heterogeneity and chemical gradients.

At a more mechanistic level, the physical medium constrains the types of microbial movement that can occur. Aqueous environments allow swimming, but active movement cannot occur without a fluid. In viscous fluids like mucous in the gut, helical cell bodies are particularly adept at using rotational locomotive mechanisms [24]. Movement along surfaces requires a thin fluid layer, such as in swarming, a collective form of locomotion whereby differentiated phenotypes quickly move in an outward expansion [52]. Fluid layers also allow passive movement via diffusion along the surface, which may be counteracted by the formation of biofilms. On surfaces without sufficient fluid for active motility, movement relies on passive vectors, like wind [10].

Animal vectors can direct the movements of their associated **symbionts** and free-living microorganisms through more complex forms of connectivity. For example, social behaviors can promote host-to-host **transmission** in ways that bypass the environment altogether [53]. But microbes that are horizontally transmitted between hosts must possess traits that allow them to survive both on hosts and in the environment [54]. Consequently, the environment may retain or eliminate microbial cells that could potentially colonize new hosts, altering patterns of microbial movement within and across generations. Thus, the mode of transmission between hosts and the

favorability of the external environment are likely to matter for understanding the movement of host-associated microbes.

MOVEMENT ECOLOGY: THEORY AND DATA ACROSS SCALES

Movement ecology is an established framework that may be useful for studying long-standing challenges in microbiology related to integrations across scales. By considering interactions among the four fundamental aspects of movement (locomotion, internal conditions, navigation capacity, and external conditions), the framework treats motility in a broader eco-evolutionary context, providing a common interface between individual-level motility and processes occurring at larger scales of space and biological organization [18]. Critical to making this connection is to understand how interactions among individuals and their environments influence the aggregation of movements into population-level movements, especially with respect to how these factors control the mean and variance of the population movement distribution (Box 2). Approaching motility from a movement ecology perspective connects to a broad array of theory on spatial population dynamics [55], and could shed new light on empirical approaches from the lab and field [56,57], such as microfluidic devices [58] and novel host-microbe imaging techniques [59].

Once population-level movement is characterized as a distribution of individual movements, the study of microbial motility can intersect in novel ways with ecological and evolutionary dynamics (Box 3). That is, movement is no longer characterized by a single value for the whole population (or community), but instead by means and variances. This more quantitative characterization can help understand how different motility strategies govern eco-evolutionary processes in microbial populations and communities. A promising outlook is to integrate the collective motility of microorganisms into existing ecological or evolutionary

theory to better understand how microbial movements influence range expansions [60,61], population synchrony and stability [62,63], as well as community assembly and dynamics [64,65]. But integrating movement distributions with existing theory can also help understand the origins and maintenance of different motility strategies that may be overlooked by theoreticians. There is much to be gained at the interface of microbiological studies of motility and eco-evolutionary perspectives on microbial movement [66]. Movement ecology outlines an explicit framework to improve the transferability across these fields and stimulate important new research.

CONCLUDING REMARKS

We argue that movement ecology provides a strong foundation for the study of microbial movements. By explicitly considering the internal and external states of organisms, their locomotive machinery, and the environmental context, the study of motility can be integrated into existing concepts of movement from the broader ecological and evolutionary literature. Furthermore, this conceptual integration can promote the examination of novel questions about the origins, maintenance, and implications of microbial movements in more complex systems, spanning scales of space, time, and biological organization (see Outstanding Questions). Future work at the intersection of these fields could focus on several fronts. First, the quantification of movement distributions under different environmental and intracellular contexts. Second, the development of new theory. Third, the empirical testing of theory through lab experiments (e.g., via novel imaging tools), or in larger, more complex experiments that take advantage of increased detection and monitoring capabilities to track microbial movements in situ.

OUTSTANDING QUESTIONS

1. What are the typical movement patterns and distributions of diverse microbial taxa?
2. How dependent are microbial movement distributions on locomotive machinery, internal states, and external environments? Do these factors have generalizable effects on microbial movements at the individual or population levels?
3. How do differences among individuals in their movement behaviors alter our understanding of microbial population dynamics, stability, and functioning?
4. Can differences among microbial taxa in their movement strategies influence patterns of diversity by altering species interactions, coexistence, and community-level dynamics?
5. Does existing theory adequately explain the evolution of microbial movement strategies? Or does novel theory need to be developed to understand microbial systems?
6. What are the human implications of microbial movement? Can we refine the role of microorganisms in human health, agriculture, and epidemiology by focusing on movement distributions?

BOX 1: A PRIMER ON DISPERSAL KERNELS

The dispersal kernel is the distribution of movement distances that an individual microorganism is likely to move (Fig. I). It helps quantify the net population-level effects of movement. This aggregation is important for making connections with ecological and evolutionary theory developed at higher levels of biological organization. An important distinction to make is the difference between total distance traveled by an individual cell and its overall displacement from its starting point per unit time (Fig. 1). Cells can be displaced by traveling, at minimum, the exact movement distance (if they travel in a straight line), or they may travel a much larger total distance than net displacement distance if the path is sinuous and involves backtracking. These movement patterns can be categorized as true dispersal (a net displacement prior to reproduction), migration (back-and-forth movements in a lifetime), station-keeping (movement required to maintain spatial location), and nomadism (wandering movements with no consistent home/destination) [18]. Ecological and evolutionary frameworks have typically focused on the overall net displacement of individuals, ignoring the route taken [67]. Thus, to link with existing theory, we will focus on how individual distances traveled scale up to overall net displacement at the population level.

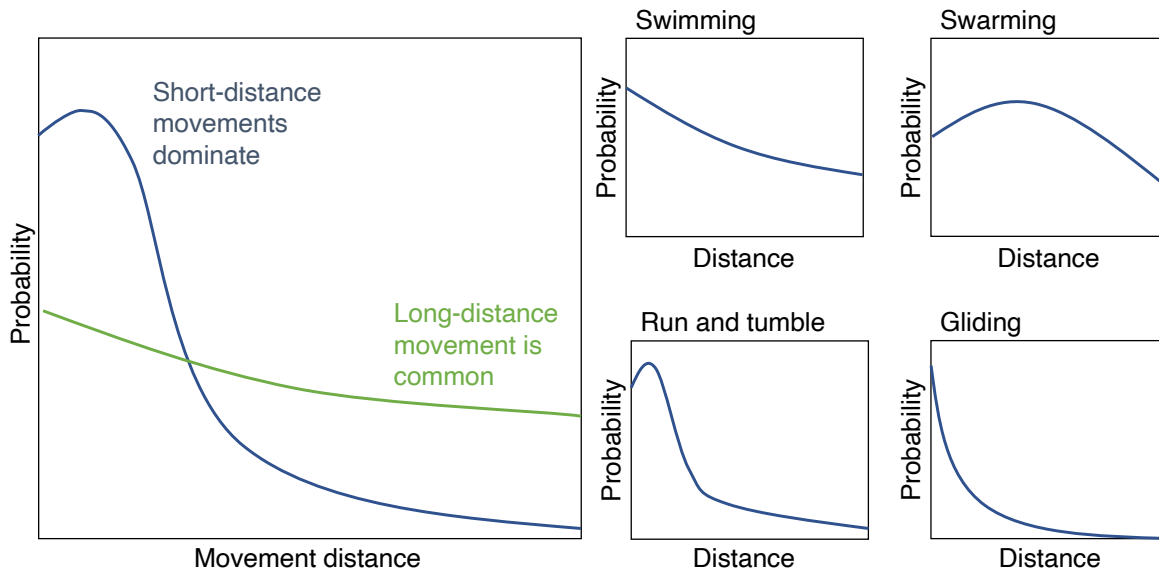


Figure I. Examples of how different movement strategies may influence the distribution of movements in a population. Swimming may lead to a high frequency of long-distance movement events. Swarming may shift the mode of the movement distribution as individuals move in the same direction. Run and tumble approaches could lead to many back-movements that cluster around an intermediate distance, with a few long-distance dispersers representing individuals who encountered toxic cues. And gliding motility, which represents a much slower process, could lead to a steep distribution, with most individuals somewhat clustered at near the starting point and only a few individuals moving a long distance.

Individual cells move at a range of speeds, spanning orders of magnitude (e.g., $\sim 1-1000 \mu\text{m s}^{-1}$) [68]. The population-level implications of this variation can be seen through heuristic models of individual random walks, where the distance traveled per second is uniformly distributed between 0 and the maximum speed, and the reorientation angle is randomly drawn from a uniform distribution spanning $0-2\pi$. For populations of 1000 individuals, the Euclidean distance displaced from the starting point after a single day varies widely (Fig. II), assuming unlimited cellular energy and no rest. Swimming motility leads to a much larger net displacements than twitching motility, where cells move approximately $1 \mu\text{m s}^{-1}$ and change orientation sporadically. In general, distances traveled per day might range from $\sim 100 \mu\text{m}$ to

nearly a meter (Fig. II). The faster the speed, the wider the variance in distance traveled (note the log-scale on the x-axis in the figure).

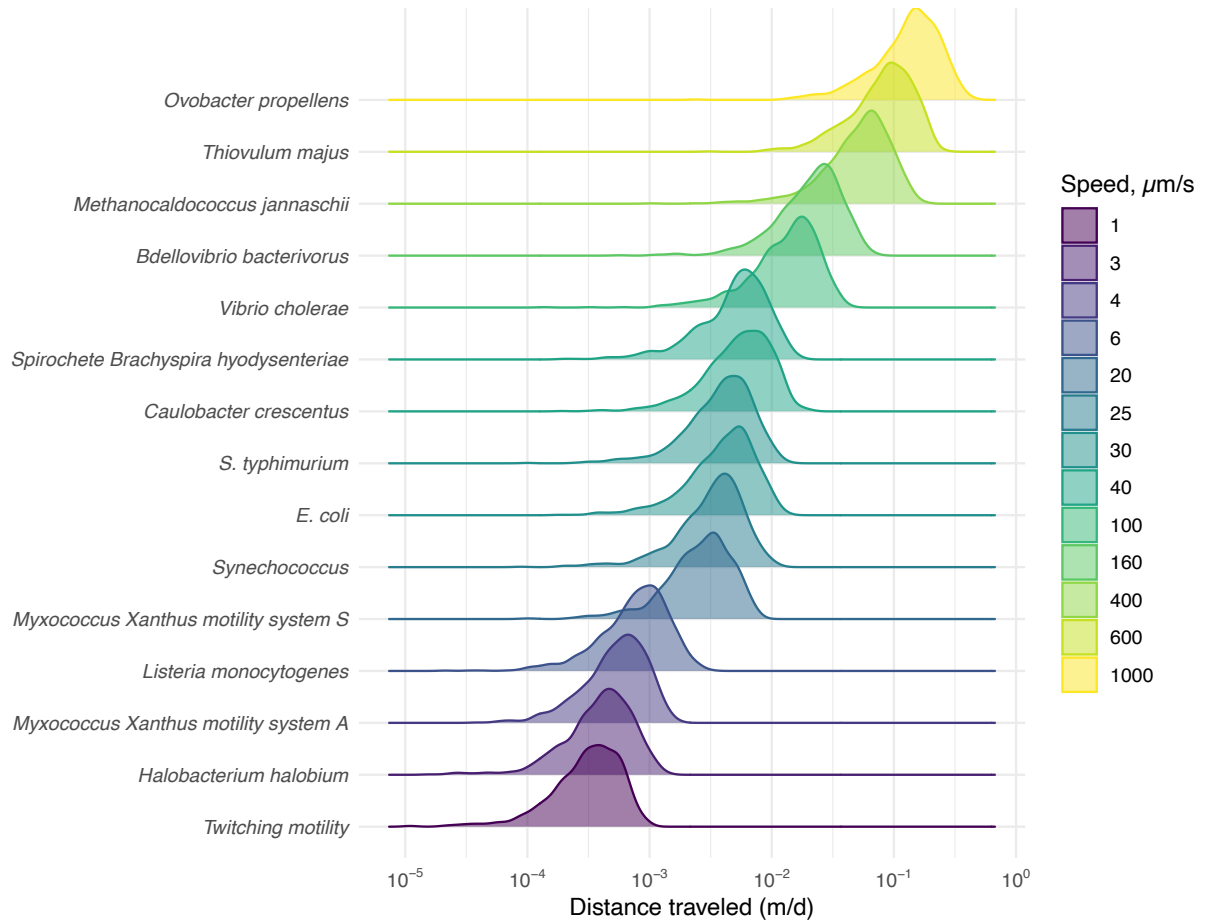


Figure II. Movement distributions (dispersal kernels) for microorganisms with different movement speeds. The distribution of movements in a population of 1000 individual cells undergoing a random walk. Higher movement speeds can lead to a higher mean distance traveled, but also a wider distribution of individual movements as individuals can diverge widely in their directions of movement. Movement distributions are the result of a single day of constant movement.

BOX 2: SCALING UP TO POPULATION DYNAMICS

Individual movements can scale up to populations through simple summation or through the emergence of more complex behaviors (e.g., swarming, biofilm formation, stalk formation). The distribution of movement distances per time in the population is an important property that depends on whether the collective movements of individuals are unidirectional, migratory, foraging-based/taxic, or stochastic (Box 1). The shape of this distribution depends on the individual-to-population scaling of movement [69], which may be strongly affected by whether cells can sense environmental gradients, the dynamic nature of the environment, and the types of biotic interactions among individuals. Due to the potentially large number of individuals in a population, long-distance movements may be more likely to occur due to increased sampling from the long tail of the dispersal kernel [70].

Scaling up from individuals to populations depends on the differences in orientation of individual movements. For example, strong and consistent responses to environmental gradients can entrain populations if all individuals track the same cues [9], or engage in quorum sensing. If all individuals travel in the same direction and take a direct path, the movement kernel can have reduced variance. Population-level entrainment is also likely to occur with strong environmental vectors of passive movement. If all individuals get swept up in the same currents, they are more likely to move in the same direction for similar distances. However, when movement is not governed by sensory processes and the environment is somewhat static, individual movements can be highly variable in distance and direction. Considerable variation in movement phenotypes among individuals can be detected in microbial populations [71]. This heterogeneity could lead to a broader, flatter dispersal kernel when scaling up to the population.

BOX 3: ECO-EVOLUTIONARY IMPLICATIONS OF MOVEMENT DISTRIBUTIONS

Movement is fundamental in evolutionary ecology, but it is traditionally simplified to a single mean value. However, individual microorganisms can use the same motility strategy but differ in their internal/external states, causing different movement patterns that alter the scaling of movement up to the population level (Box 2) [18,69]. Spatial population structure can exhibit dynamic patterning through traveling waves [9], and chemotaxis can lead to rapid expansion of range edges [61]. Connections between these microbiological studies and the broader study of range size and expansion may be important for extending existing theory to microorganisms and for generating new hypotheses about how populations spread in a spatial context [60,72]. In addition to affecting spatial patterns, intraspecific movement heterogeneity may have important implications for evolutionary dynamics [73,74], by modifying gene flow or through the evolution of motility itself if intraspecific motility differences have a heritable genetic component.

A substantial body of work has attempted to understand the assembly, structure, and dynamics of multi-species microbial assemblages and biogeography [75–78]. Movement plays a central role in understanding spatial patterns of biodiversity, but has largely focused on how dispersal, abiotic constraints, and biotic interactions influence species persistence and coexistence. However, little, if any, of these frameworks distinguish clearly between the different types of microbial motility. Nor is it clear how our knowledge of individual motility can strengthen inferences of the role of movement at population- and community levels.

Integrating motility with eco-evolutionary models of dispersal would be a fruitful outcome for both fields. Novel theory and experiments on motility in multi-species assemblages could shed light on how intra- and interspecific properties influence motility and species coexistence. For example, the evolution of interesting motility strategies may be explained, in

part, due to interactions with competing species. We argue that ecological and evolutionary theory could take inspiration from the unique features of microbial movement, which often diverge from the typical movement strategies of plants and animals. An explicit consideration of individual-level movement patterns could also reveal new insights into the ways that microbial systems are structured by refining the characterization of microbial movement alongside other microbial traits. This integration would also strengthen research at the intersection of movement ecology, microbiology, and novel molecular techniques.

GLOSSARY

Biogeography: the description of species abundances and geographic ranges and the ecological and evolutionary processes that cause them to change over space and time

Colonization: the arrival and subsequent establishment of a population in a new habitat

Community: a collection of multiple individuals of multiple species in the same place at the same time

Dispersal: the one-time translocation of an organism from location of birth to location of reproduction

Dormancy: a reversible state of reduced metabolic activity that buffers against stressful environments at the cost of delayed reproduction

Energy budget: the allocation of assimilated energy into various processes, including reproduction, cellular maintenance, and movement

Environmental gradient: a gradual change in an important feature of the external ecosystem that can potentially alter the structure and dynamics of biological entities

Genome streamlining: the evolutionary process by which the genome becomes leaner through the elimination of redundant or superfluous genes that are not essential to maintaining viable populations

Motility: a broad term for the movement of an individual microorganism due to swimming, gliding, or twitching mechanisms

Movement: the process by which an individual organism changes its spatial location

Movement ecology: a framework to integrate the four key mechanisms of movement: locomotion, internal states, external states, and navigation capacities

Population: a collection of multiple individuals of the same species in a given location at the same time

Quorum sensing: the process of bacterial cell-to-cell signaling that relies on the production, transmission, and detection of extracellular signaling molecules that initiates a collective response

Symbiont: an organism, which may range from mutualistic to parasitic, that is dependent on a host for at least part of its life cycle

Transmission: the process by which a symbiont is transferred between hosts, typically vertically (parent-to-offspring) or horizontally (indirectly via the environment)

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