Trends in **Microbiology**

CellPress

Opinion

Scaling up and down: movement ecology for microorganisms

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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 higher organizational levels, such as populations and communities. 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.

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]. Many different strategies have evolved that allow microbes to successfully navigate their environments. For example, internal energy powers swimming **motility** in aqueous environments, as well as swarming, twitching, and gliding along surfaces [2,10], while body size, attachment to particles, associations with hosts, and engagement in **dormancy** can promote passive movements [11]. Despite detailed knowledge of 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 [12–14]. However, this perspective is disconnected from the movement of individual cells. Instead, views on microbial movement are often informed by **biogeographic** patterns, which result from a multigenerational sequence of individual reproduction events and cellular movements [9,15,16]. Consequently, there is a disconnect between the mechanistic understanding of individual movements and the collective **dispersal** patterns that emerge from individual-level processes [17]. An integrative perspective on 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 and time, and across different levels of biological organization.

Movement ecology provides a way to resolve the problem of scale mismatch [17,18]. Most often applied to macro-organisms (i.e., plants and animals), movement ecology emphasizes four main components 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

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.

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decisions [17]. Movement ecology proposes that individual movement paths depend on the interplay of these components and can be characterized by different movement phases (e.g., random searching, rest, tracking) that accumulate over the individual's lifetime (Figure 1). From these fundamental components, the collective movements of individuals lead to population-level patterns of dispersal.

A movement ecology for microorganisms

Building on the four components 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 traits and life-history features of microorganisms that distinguish their movement from 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., *Escherichia 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 from a surface [19]. Gliding uses 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 ~1000 µm/s in *Ovobacter propellens*, which is powered by 400 flagella [25], to ~1 µm/s in *Neisseria gonorrhoeae*, which uses twitching motility (Figure 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 [2,10].

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], 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, 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 *O. 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)

Net distance = 212 409 μm
Total distance = 86 765 478 μm

interactions ranging from mutualistic to parasitic.

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

(B)

Figure 1. A movement ecology perspective provides a unified approach to studying movement patterns, spanning microorganisms to macro-organisms. (A) This line is a trace of a simulated random walk for the species *Ovobacter propellens* (speed = 1000 μm/s), without chemotaxis. The simple process demonstrates important features of

(Figure legend continued at the bottom of the next page.)
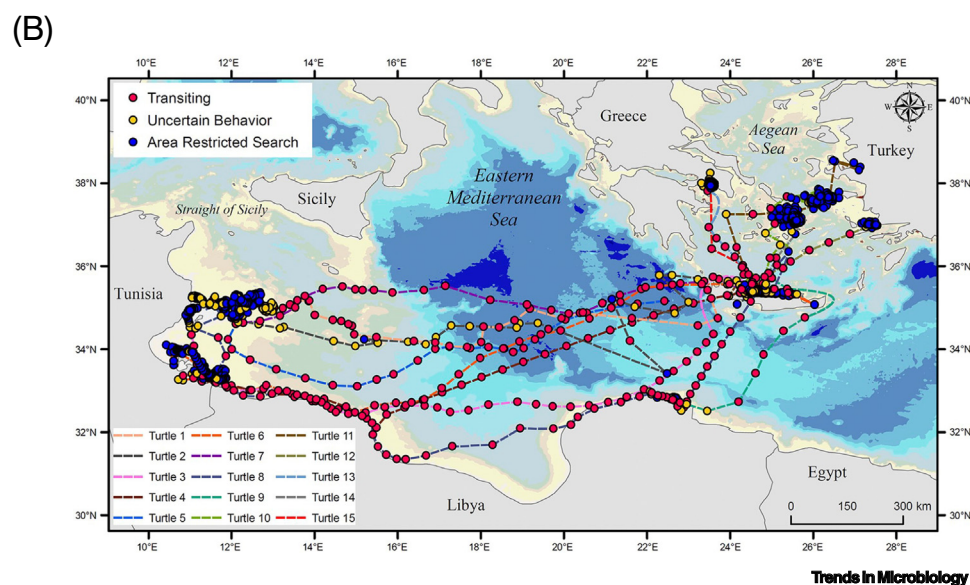
a cell may be unable to power the machinery due to energetic limitations. Indeed, genomic evidence suggests that motility is often lost during nutrient limitations [34], and laboratory experiments have shown that motility can be especially costly during starvation [9], sometimes provoking a reduction 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., 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, shortening movement distances in the absence of survival mechanisms like dormancy. For instance, anaerobic gut-associated taxa are strongly dependent on the host as a vector, unable to survive oxygenated conditions. This metabolic 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 and costly 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). Like foraging behaviors and sensory cues that guide animal movements (e.g., sight, smell), taxis allows active movements to be nonrandomly 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, 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

movement. The net displacement distance (blue) is much smaller than the total distance traveled (black). This reflects the deep sinuosity of the random walk. (B) The movements of 15 loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. Points indicate the daily location estimate for an individual turtle, with lines connecting each turtle's path. A switching state-space model identified different behaviors underlying movement, including foraging (blue points) and transitions between sites (red points). Compared to microorganisms undergoing random walks, the turtles are navigating a different ecosystem, with different locomotive strategies and complex sensory abilities, but these movement trajectories can be analyzed with similar tools from a movement ecology perspective. Panel B reproduced with permission from [60].

Box 1. A primer on dispersal kernels

The dispersal kernel is the distribution of movement distances that an individual microorganism is likely to move. The summation of individual kernels helps to quantify the net population-level movement [77]. This aggregation is important for making connections with ecological and evolutionary theory developed at higher levels of biological organization. Total distance traveled by an individual cell is typically much longer than its overall displacement from its starting point per unit time, especially if movement includes backtracking (i.e., large turning angles) (see Figure 1 in main text). 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 [89]. To link with existing theory, we focus on how individual distances traveled scale up to overall net displacement at the population level.

Individual cells move at a range of speeds, spanning orders of magnitude (e.g., <1–1000 μm s^{-1}) [90]. 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 0–2π. For populations of 1000 individuals, there was a wide range of distances that individuals and populations were displaced after a single day of movement (Figure I). These simulations assume unlimited cellular energy, no rest, no hydrological flow, and no chemotaxis, but nevertheless reveal dispersal kernels with wide variances, long tails, and means that span roughly four orders of magnitude. These conditions also align with conditions obtainable in microfluidic devices [54,82]. In general, net distances traveled per day might range from ~1 μm to nearly a meter (Figure I). The faster the speed, the wider the variance in distance traveled (note the log scale on the x-axis in the figure). When these values are placed in the context of more general ecological and evolutionary theories, we might predict different outcomes for species with low dispersal rates versus those with high dispersal rates.
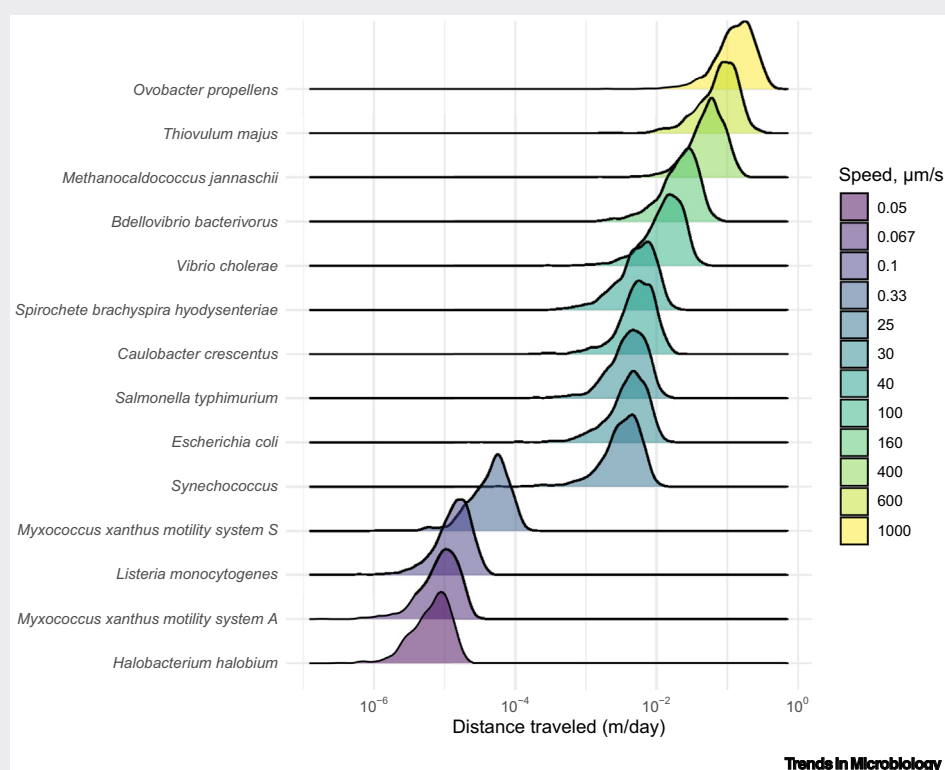
Figure I. Movement distributions (dispersal kernels) for microorganisms with different movement speeds. The distribution of movements in a simulated population of 1000 individual cells undergoing a random walk. For each taxon presented here, estimates of movement rates were obtained from Table 4-8 in [90]. For each individual in the population, we simulated 1 day of movement at its estimated speed, then computed the net distance traveled to estimate the population dispersal kernel for a given day. Higher movement speeds can lead to higher mean distances traveled, but also wider distributions of individual movements because in a random walk (absent chemotaxis or prevailing currents), individuals can diverge widely in their directions of movement.
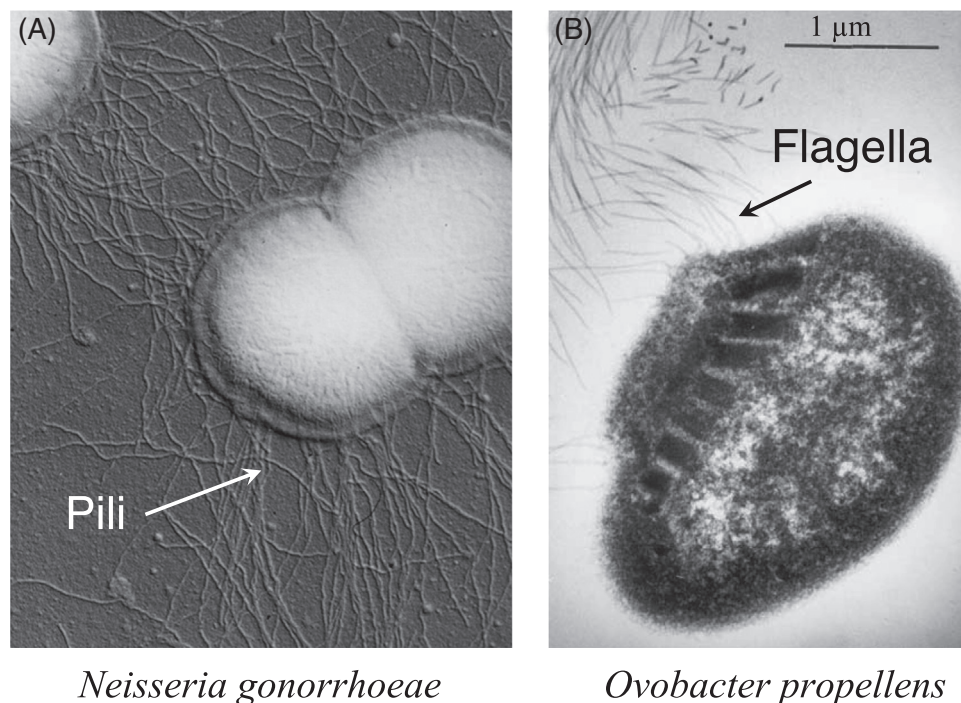
Neisseria gonorrhoeae   *Ovobacter propellens*

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Figure 2. A comparison of two bacterial approaches to motility. (A) *Neisseria gonorrhoeae* uses several pili to undertake twitching motility, resulting in slow movements (~1 μm/s). (B) In contrast, *Ovobacter propellens* relies on roughly 400 flagella to power its much faster swimming motility (~1000 μm/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 *N. gonorrhoeae* reproduced with permission from [93]. Figure of *O. propellens* reproduced with permission from [25].

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]. Taxic behavior is an important link between individual-level movements and the collective movements of the population.

Environmental context – physical and biotic factors
Microbes live in environments that vary widely in their fluid properties (e.g., oceans, guts, soils, intracellular). Strong physical environmental flows can quickly overcome the forces of active movement, leading to predominantly planktonic lifestyles guided by passive movement [47]. If fluid flows displace microbes from their optimal habitats, active machinery could be necessary to maintain position. Pulsed environments, such as guts, may favor microbial traits like dormancy, which can 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 [52]. 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 locomotion [24]. Movement along surfaces requires a thin fluid layer, such as in swarming, a collective form of motility whereby differentiated phenotypes quickly

expand outward [53]. Swimming can also be modified by hydrodynamic forces associated with nearby surfaces, even in the absence of pressure or chemical gradients [54]. On surfaces without sufficient fluid for active motility, movement relies on passive vectors, like wind [11].

Animals 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 [55]. But microbes that are horizontally transmitted between hosts must possess traits that allow them to survive both on hosts and in the environment [56]. Consequently, the environment may retain or eliminate microbial cells that could potentially colonize new hosts, altering patterns of microbial movement within and across generations.

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 integration across scales. By considering interactions among the four fundamental components of movement (locomotion, internal conditions, navigation capacity, and environment), the framework treats motility in a broader ecoevolutionary context, providing a common interface between individual-level motility and processes occurring at larger scales of space and biological organization [18].

Individual movement is typically recorded as a time series of spatial coordinates or a series of movement metrics that describe the movement trajectory. The sequences of step lengths (i.e., the distance traveled per time step) and turning angles (i.e., the change in direction between successive displacements) provide useful information for understanding phases of movement [57,58]. For example, organisms may move long distances to search for resources and then remain relatively stationary while consuming them. It is possible to fit statistical models, such as hidden Markov models (HMMs) or state-space models (SSMs), to detect these different phases in movement data (e.g., Figure 1B) and predict transitions between them [57,59,60]. Different distributions of step lengths and turning angles may be associated with each movement phase and statistical models can relate them to different environmental covariates to predict transition probabilities [57].

Appropriate microbial movement data could be generated, for example, in a microfluidic chamber [54,61]. These data can be used to fit HMMs or SSMs that identify environmental or physical features (e.g., temperature, chemicals) that trigger transitions between movement phases (e.g., searching vs. uptake in chemotaxis). Parameters can then be compared across microbial taxa and with data from macro-organisms (see Figure I in Box 2) [62]. Furthermore, because individual movement often depends on nearby individuals (e.g., via quorum sensing), statistical models can also incorporate temporal correlations in the turning angles and step lengths among individuals to understand social aspects of movement behavior [63,64]. By fitting statistical models to microbial movement data, biologists can more explicitly probe the causes and consequences of different motility strategies by investigating the four components of the movement ecology framework. Experiments that incorporate multiple individuals or species may be important for understanding how interactions among individuals and their environments influence movement at population and community levels (Box 2).

By recasting population and community movement parameters as distributions of individual movements (with means and variances), the study of microbial motility can intersect in novel ways with ecological and evolutionary dynamics [18,65]. 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 [66,67], population synchrony and stability [68–70], as well as community assembly and dynamics [71,72]. A substantial body of work on microbial communities and biogeography has revealed a central role for movement in understanding spatial patterns of biodiversity alongside biotic and abiotic constraints on species persistence [73–77]. For example, dispersal must be sufficient for individuals to colonize a suitable habitat, but extremely high dispersal can result in species establishing in unfavorable environments [78,79]. However, few, if any, of these frameworks distinguish between the different types of microbial motility. Nor is it clear how our knowledge of variance in individual movement properties can strengthen inferences of the role of movement at population and community levels.

Intraspecific movement heterogeneity may also have important evolutionary implications. Movement can modify rates of gene flow [80], or movement can evolve if it is regulated by traits that have a heritable genetic component [81]. Novel theory and experiments could shed light on how different motility strategies arise in particular abiotic and biotic environments. For example, the evolution of motility strategies may be partly explained by interactions with competing species. New tools, such as microfluidic devices [54,82] and dynamic microbial imaging techniques [61,83], can provide detailed data on microbial movements that can test previously untestable theoretical predictions [84]. Microfluidic landscapes with varying spatial structure can be engineered to closely align with metapopulation and metacommunity theories to incorporate different types of movement based on species composition. In turn, as more microbial movement data become available, ecological and evolutionary theory could take inspiration from the unique features of microorganisms to understand how their movement diverges from plants and animals.

Aspects of movement, like other ecological and evolutionary processes, are expected to change across spatial and temporal scales [85]. There are two key components of scale: grain (i.e., the

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Box 2. Linking individual to population movement

Links between individual- and population-level movements arise through simple summation or through the emergence of more complex behaviors (e.g., swarming, biofilm formation, stalk formation). The distributions of step lengths and turning angles per time in the population are important properties that depend on whether the collective movements of individuals are unidirectional, migratory, foraging-based/taxic, or stochastic (Figure I). The shapes of these distributions at the population level depend on the interactions among individuals and their movement trajectories [65], which may be strongly affected by movement components such as chemotaxis and both biotic and abiotic environmental factors [91].

To understand the effects of these movement components on population-level movement, we can analyze how movement distributions change with population density. For example, microfluidic devices with dynamic imaging can be used to track the movements of individual bacteria in highly controlled settings [82]. Inoculating chambers with different bacterial densities and parameterizing step length and turning angle distributions across a gradient of population size can provide information on how the distribution of movements (or the dispersal kernel) changes as more individuals are moving and interacting with one another and the environment. The sensitivity of the distribution to various population-level features could shed light on the relative importance of biotic interactions versus environmental properties on movement, especially if experiments are conducted along environmental gradients.

Analyzing movement 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 dispersal 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 [92]. This heterogeneity could lead to a broader, flatter dispersal kernel when scaling up to the population. Characterizing dispersal kernels associated with different motility strategies and microbial taxa is likely to be informative for understanding the role of movement in different ecosystems.
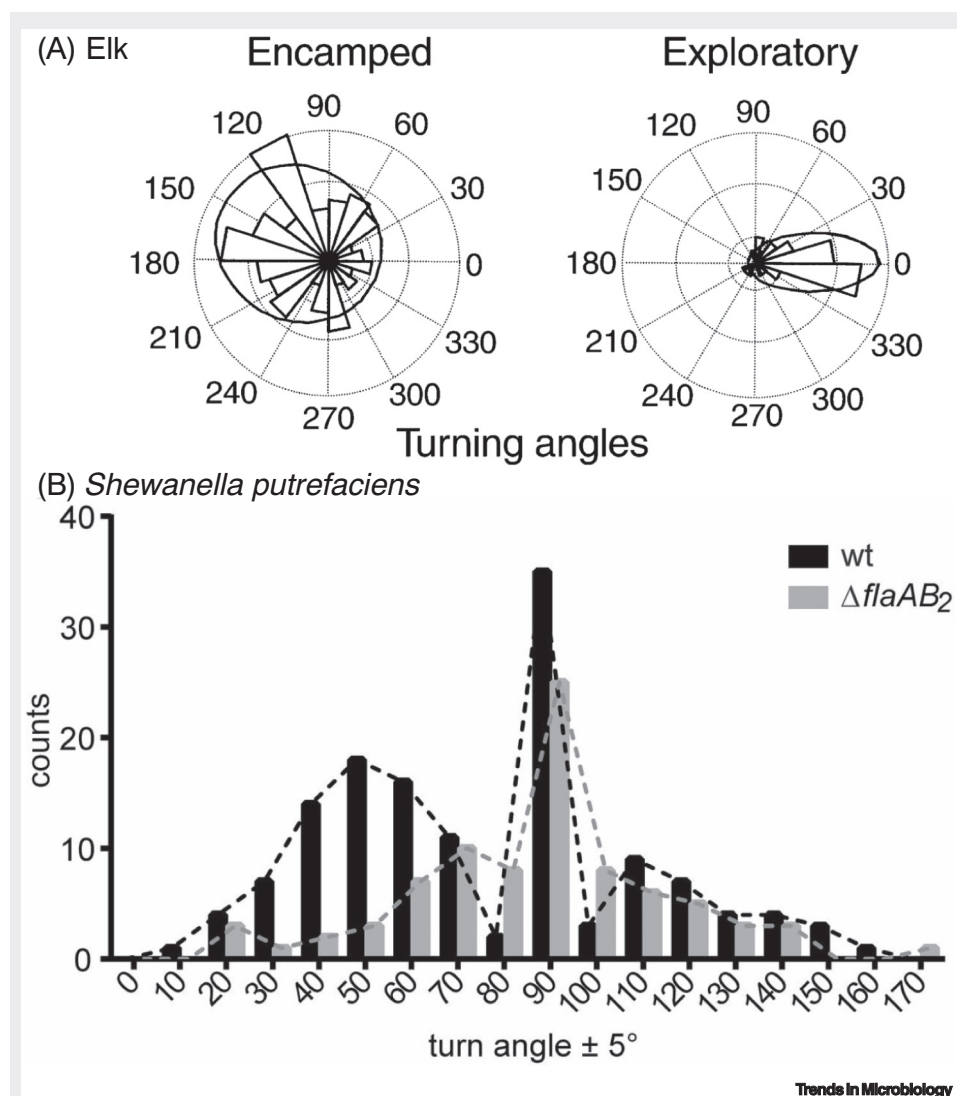
Figure I. Turning angle distributions provide common currency. (A) The distribution of turning angles for cow elk (*Cervus elaphus*) in Elk Island National Park, Alberta. Turning angle distributions differ for different movement phases. In the 'Encamped' phase, turning angles are wider and more broadly distributed, consistent with local foraging in a given area. In the 'Exploratory' phase, turning angles are much narrower, consistent with animals traversing broad stretches of space with little backtracking. (B) Turning angle distributions for *Shewanella putrefaciens*. In this figure, the wild-type strain containing multiple secondary flagellar filaments is contrasted with a knockout strain ($\Delta flaAB_2$) that contains only polar flagella. In effect, the mutant strain can move only via a 'run-reverse-flick' strategy, which allows for efficient movement at 90° turning angles, but strongly reduces the turns at smaller angles that the wild-type strain frequently uses. Panel A reproduced with permission from [59] and panel B reproduced with permission from [94].

resolution at which the phenomenon is observed) and extent (i.e., the spatial or temporal range of observations). Aligning the scale of the research question with the scale of data is critical for detecting the movement process of interest. At fine spatial grains and small extents, individual movements are more readily detectable and relate to individual interactions and movement decisions that drive ecological and evolutionary processes. Fine-scale studies have shown that spatial population structure can exhibit dynamic patterning through traveling waves [9] and that

chemotaxis can lead to rapid expansion of range edges [67]. At coarser grains and broader extents, individual movements can average out. However, it may be possible to use tracer studies (e.g., using fluorescently labeled cells) to reveal the shapes of dispersal kernels for different taxa in different environments [86]. Some taxa may serve as useful biological tracers due to their ability to form dormant resting stages, enabling quantitative estimates of dispersal rates [87].

Scaling of movement across time may help to explain the origins of spatiotemporal patterns of biodiversity over longer durations and at coarser resolutions through the processes of evolutionary diversification, community succession, and local adaptation. By considering spatial context, it is also possible to explore how movement relates to broad scale patterns of microbial biogeography. For example, estimates of movement from phylogeographic data suggest that microbial lineages may spread across the globe at rates ranging from about 0.04 km^2 $year^{-1}$ in the terrestrial subsurface to >1000 km^2 $year^{-1}$ in human-associated taxa [15,16]. These estimates align well with the isolation of these habitats and demonstrate that genomic signatures of evolutionary divergence can reveal insight into microbial movements over long timescales. Thus, there is much to be gained at the interface of microbiological studies of motility and ecoevolutionary perspectives on microbial movement [88]. Movement ecology outlines an explicit framework to improve the transferability across these fields and stimulate important new research.

Concluding remarks

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 their sensing abilities, 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 laboratory 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*.

Declaration of interests

No interests are declared.

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