

Universal Law for the Dispersal of Motile Microorganisms in Porous Media

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Dispersal is essential to the plethora of motile microorganisms living in porous environments, yet how it relates to movement patterns and pore space structure remains largely unknown. Here we investigate numerically the long-time dispersal of a run-and-tumble microorganism that remains trapped at solid surfaces and escapes from them by tumbling. We find that dispersal and mean run time are connected by a universal relation, that applies for a variety of porous microstructures and swimming strategies. We explain how this generic dependence originates in the invariance of the mean free path with respect to the movement pattern, and we discuss the optimal strategy that maximizes dispersal. Finally, we extend our approach to microorganisms moving along the surface. Our results provide a general framework to quantify dispersal that works across the vast diversity of movement patterns and porous media.

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Among the 10^{30} prokaryotes that populate the Earth, a majority live in oceanic and terrestrial subsurfaces, made of sediments, soil, or rocks [1,2]. With myriad of bacteria also inhabiting higher organisms [3], porous media is a widespread habitat for microbial life [4,5]. The strategies microorganisms adopt to navigate their environment impact their ability to access resources [6], invade new areas [7,8], and ultimately contribute to determine their survival [9]. Therefore, establishing how navigation strategies regulate dispersal in relation to the physical environment is key to understand the ecological success of many species of bacteria. Additionally, predicting bacterial dispersal is important because it plays a crucial role in infections [10], food contamination by pathogens [11], targeted drug-delivery in tumors [12], rhizosphere enhancement for plant growth [13], and the bioremediation of porous aquifers [14].

Understanding the dispersal of motile microorganisms poses at least two challenges. The first is the existence of a vast parameter space. Bacteria generally swim in random walks where nearly straight runs are punctuated by reorientation events, which exist in several types and define a repertoire of swimming strategies [15–19]. The diversity of porous microstructures, from rocks to tissues and body gels, is no less daunting, with pores widely varying in morphology and spanning micrometers to millimeters in size [4]. In spite of a recent surge of research on both non-tumbling [20–23] and tumbling microorganisms [24–33], most of the parameter space remains unexplored. The

second challenge is that little generic finding has emerged. The one exception is the existence, across different systems, of an optimal persistence time at which dispersal is maximal [25,27–30,32,34], yet there is no overarching principle to predict this maximum. In this context, an intriguing proposition put forward by Mattingly [35,36] is that the microstructure can be “largely forgotten,” in the sense that only a small set of features is relevant. How general this finding is, however, remains unknown, because it was reached for a specific microstructure and swimming strategy. Overall, it is unclear how knowledge gained in idealized porous media mostly used to date—typically arrangements of spheres or disks—can be transferred to the great diversity of microstructures found in the natural world.

In this work, we show that the dispersal of motile microorganisms in porous media has a universal character.

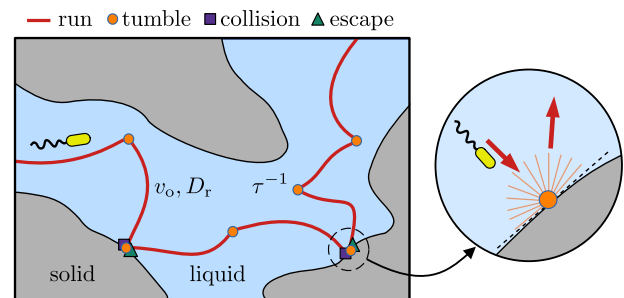


FIG. 1. Model of run-and-tumble microorganism in a porous medium (see text for parameter definition). After a collision with the surface, the microorganism escapes by tumbling, with a direction randomly sampled in the available half-space (orange rays in the inset).

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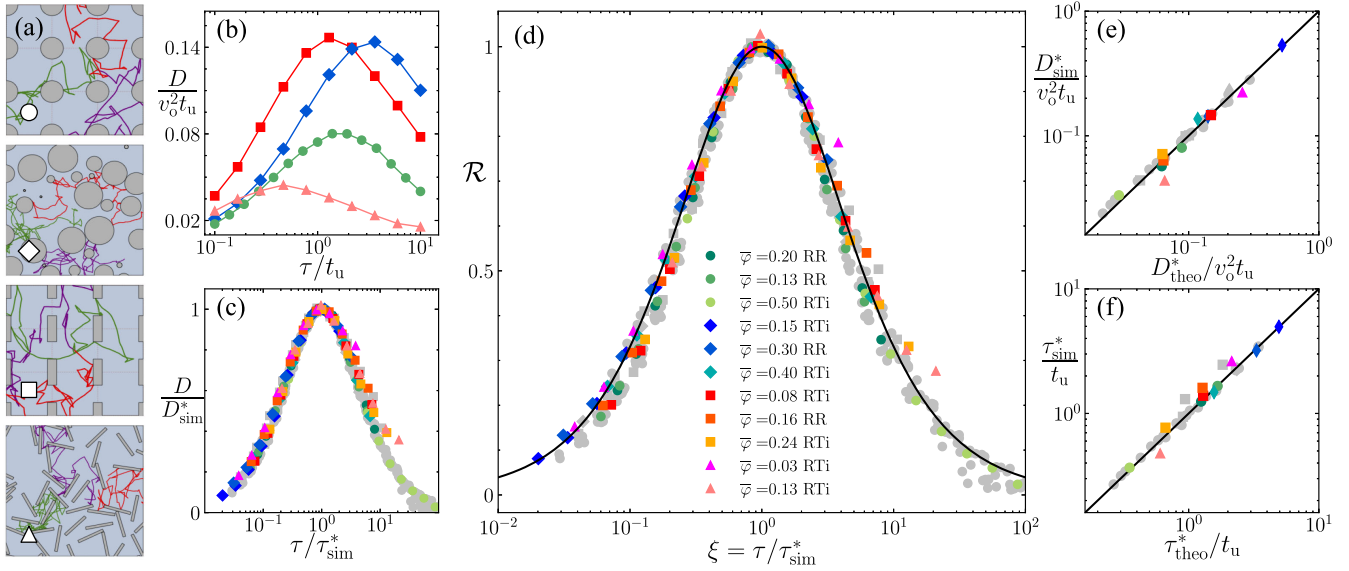


FIG. 2. Diffusivity of a run-and-tumble microorganism in porous media. (a) Simulated motion within different microstructures: ordered disks (Circle), disordered polydisperse disks (Diamond), ordered rectangles (Square), and disordered rods (Triangle), with solid fractions $\bar{\varphi} = 1 - \varphi = 0.25, 0.3, 0.24$, and 0.13 respectively. (b) Diffusivity as a function of the mean run time for four systems. The timescale t_u depends on the microstructure [41]. (c) Diffusivity curves rescaled by the value and time of their maximum. Gray points show additional data, detailed in Table I of the Supplemental Material [41], including different microstructures, swimming strategies, rotational diffusivities, solid fractions between 0.01 and 0.5 , and a model with partial trapping. (d) The modified diffusivity ratio \mathcal{R} for all investigated models collapses on a universal curve (black line), defined by Eq. (5). The legend applies across panels (b)–(f). Here $D_r = 0.1 t_u^{-1}$. (e),(f) Comparison between simulations (y axis) and theory (x axis) for (e) the maximum diffusivity D^* and (f) the optimal mean run time τ^* .

We study a run-and-tumble microorganism, which stops moving upon encountering a solid surface but can escape from it by tumbling. We find numerically that, across diverse microstructures and swimming strategies, the dispersal is related to the mean run time by a universal dependence, that we derive in an analytical model. We explain why one can forget almost everything about the porous medium when predicting the microorganism diffusivity. The key insight is the invariance of the mean free path [37,38]. As a result, what matters for dispersal is only the ratio between the accessible volume and the amount of interface. Besides, we show that the dispersal law is also relevant for microorganisms moving along surfaces. Our results demonstrates that, despite the diversity of porous structures and motion patterns in natural systems, dispersal can be understood within a common and remarkably simple framework.

We consider a run-and-tumble (RT) microorganism moving in a porous medium (Fig. 1). It has velocity v_o , is subject to rotational diffusion with coefficient D_r , and tumbles with rate τ^{-1} , with a distribution of reorientation angles that is nonchiral but otherwise arbitrary. The model includes as particular cases two swimming strategies: run-reverse (RR), where reorientation events involve perfect reversal of swimming direction, and RT with isotropic reorientation (RTi). We assume the simplest behavior at the surface [39]: the microorganism has vanishing velocity

there, but at each tumble, it can escape with a probability η^{-1} and a direction uniformly distributed in the free half-space (Fig. 1 inset). Dispersal is characterized by the diffusivity $D = \lim_{t \rightarrow \infty} M(t)/2dt$, with $M(t)$ the mean-square displacement at time t and d the space dimension. We performed agent-based simulations [40] to determine the diffusivity as a function of the mean run time τ in different porous environments, both ordered and disordered [Fig. 2(a)]. We found that, for all environments and swimming strategies tested, there is an optimal run time τ^* for which the diffusivity D reaches a maximum [Fig. 2(b)]. Moreover, when rescaled by the diffusivity maximum D^* and by the optimal mean run time τ^* , all the data collapse onto a master curve. We now explain this universal behavior.

Minimal model of diffusivity and Cauchy universality—We propose a simple model of microbial dispersal in a porous medium, whose main approximation is to discard the complex correlations between microorganism trajectory and microstructure. Specifically, we assume that encounters with solid surfaces occur along the trajectory as a Poissonian process with rate T^{-1} and can therefore be treated as a second type of tumble [33]. We then derive the diffusivity of the microorganism as [41]

$$D = \frac{T}{T + \tau_s D'_r + \bar{\alpha} \tau^{-1} + \bar{\beta} T^{-1}} K(\bar{\varphi}). \quad (1)$$

Here, $\tau_s = \eta\tau$ is the mean time spent at the surface after an encounter, $D_r' \equiv (d-1)D_r$, $\bar{\alpha} \equiv 1 - \alpha$, $\bar{\beta} \equiv 1 - \beta$, and $\bar{\varphi} \equiv 1 - \varphi$. $\alpha \equiv \langle \cos \theta_t \rangle$ is the mean cosine of the reorientation angle θ_t —henceforth called “correlation” for short—induced by a tumble [47], and β is similarly the “correlation” of reorientation induced by an encounter with the surface. $K(\bar{\varphi})$ is a correction factor that depends on the porosity φ and the microstructure. Each of the three factors in Eq. (1) encapsulates one physical effect governing dispersal. The first factor is the fraction ν of time spent moving. The second factor captures the three independent processes—rotational diffusion, tumbles, and surface encounters—responsible for orientational decorrelation, whose rates are additive. Finally, the third factor accounts for the excluded volume and correlation of the microstructure. $K(\bar{\varphi})$ is chosen so that the diffusivity is correct in the limit of Brownian motion [48]; $K(\bar{\varphi})$ is known in several microstructures [42,49,50] and, at low solid fraction $\bar{\varphi}$, $K(\bar{\varphi}) = 1 - \bar{\varphi}/(d-1) + \mathcal{O}(\bar{\varphi}^2)$ holds for arbitrary material [41]. To complete the model, one then needs only to specify the mean time \mathcal{T} between two surface encounters.

The surface encounter time \mathcal{T} has a surprisingly simple expression. Since velocity is constant in modulus, $v_o\mathcal{T}$ is the mean free path $\langle L \rangle$, defined as the trajectory length between two successive contacts with the surface. The mean free path possesses an invariance property, also called Cauchy universality [51], which states that it is equal to the mean chord length l_c of the medium, giving

$$v_o\mathcal{T} = \langle L \rangle = l_c = \sigma_d \frac{\Omega}{\partial\Omega} = \sigma_d \frac{\varphi}{\mathcal{S}}, \quad (2)$$

with $\sigma_d = \pi$ and 4 for $d = 2$ and 3, respectively, Ω the volume of porous space, $\partial\Omega$ the amount of solid interface, and \mathcal{S} the specific surface of the material. First written for ballistic motion [50,52,53], Eq. (2) actually holds true in more general conditions [51,54], that are still under investigation [55], but include random motion with reorientation events that may be anisotropic, inhomogeneous, or even non-Poissonian [37,38,56]. Cauchy universality is thus applicable to our generic run-and-tumble motion.

Diffusivity master curve and maximum—Knowing that the encounter time \mathcal{T} is a purely geometric quantity independent of the mean run time τ , Eq. (1) gives

$$\frac{D}{D^*} = \frac{(2+c)\xi}{1+c\xi+\xi^2}, \quad \xi \equiv \frac{\tau}{\tau^*}, \quad (3)$$

where ξ is a rescaled mean run time. The diffusivity reaches a maximum D^* at the mean run time τ^* , with

$$D^* = \sqrt{ab}K(\bar{\varphi})/(2+c)\bar{\alpha}d, \quad \tau^* = \sqrt{ab}, \quad (4)$$

and $a \equiv \mathcal{T}/\eta$, $b \equiv \bar{\alpha}/(D_r + \bar{\beta}/\mathcal{T})$, and $c \equiv (a+b)/\sqrt{ab}$. The dependence of D/D^* on c can be entirely accounted

for by introducing the modified diffusivity ratio

$$\mathcal{R} \equiv 4 \left[2 - c + (2+c) \frac{D^*}{D} \right]^{-1} = \frac{4\xi}{(1+\xi)^2}, \quad (5)$$

which is a function of ξ only. For the 38 parameter combinations tested, that differ in swimming strategy, rotational diffusion, porosity, or morphology of the medium, the diffusivity values from simulations collapse [57], without any free parameter, on the master curve $\mathcal{R}(\xi)$ from Eq. (5) [Fig. 2(d)]. Additionally, the simulation results for D^* and τ^* also align closely with the theoretical predictions from Eq. (4) [Figs. 2(e) and 2(f)].

The diffusivity maximum occurs because diffusivity increases as $D \sim \tau$ for short runs and decreases as $D \sim (\eta\tau)^{-1}$ for long runs, since then most time is spent at the surface waiting to escape. The optimal mean run time exhibits two regimes. When rotational diffusion is strong ($D_r\mathcal{T} \gg 1$), $\tau^* \simeq \sqrt{\bar{\alpha}\mathcal{T}/D_r\eta}$ is the harmonic mean between the surface encounter time and the rotational diffusion time, a trade-off between the two processes driving the orientation decorrelation. When rotational diffusion is negligible ($D_r\mathcal{T} \ll 1$), $\tau^* \simeq \mathcal{T}\sqrt{\bar{\alpha}/\eta\bar{\beta}}$ is controlled by the surface encounter time. Here, the optimal mean run length $v_o\tau^*$ is dictated by the mean free path $l_c = v_o\mathcal{T}$, since it realizes the best compromise between efficient transport in porous space and the penalty of being blocked at the surface.

Multimodal motion and surface sliding—In addition to trapping at the wall studied so far (and extended to partial trapping in the Supplemental Material [41]), a relevant class of surface behaviors involves sliding, wherein a microorganism encountering the solid moves with velocity v_o along the surface. Motion then becomes multimodal. To understand the implications, we first investigate the diffusivity of a bimodal process where two modes $m = 1$ and 2 alternate. Mode m is characterized by a Liouvillian \mathcal{L}_m , which governs the Fokker-Planck equation $\partial_t p_m = \mathcal{L}_m p_m$ for the distribution $p_m(\theta, t)$ of the angle θ describing the microorganism orientation (we took $d = 2$ for simplicity). In particular, motion that includes rotational diffusion and tumbles with rate τ_m^{-1} and a turning angle distribution h_m yields $\mathcal{L}_m = D_{r,m}\partial_{\theta\theta} - \tau_m^{-1}(1 - h_m \otimes)$, where \otimes denotes convolution. A transition from mode m to m' occurs at rate μ_m and induces a reorientation specified by the distribution of turning angle h_m with correlation β_m .

Using an exact formalism based on Fourier and Laplace transforms [41], the diffusivity of a bimodal process is

$$D = \nu_1 D_1(\mu_1, \beta_1^e) + \nu_2 D_2(\mu_2, \beta_2^e) + (\beta_1 + \beta_2)C. \quad (6)$$

Here, $\nu_m = \tau_m/(\tau_m + \tau_{m'})$ is the fraction of time spent in mode m . $D_m(\mu, \beta) \equiv \frac{1}{2} \sum_{l=\pm 1} [-\mathcal{L}_m(l) + \mu_m \bar{\beta}]^{-1}$, with $\mathcal{L}_m(l)$ the Fourier series of $\mathcal{L}_m(\theta)$, is the diffusivity for a process involving motion in mode m , but interrupted with rate μ by

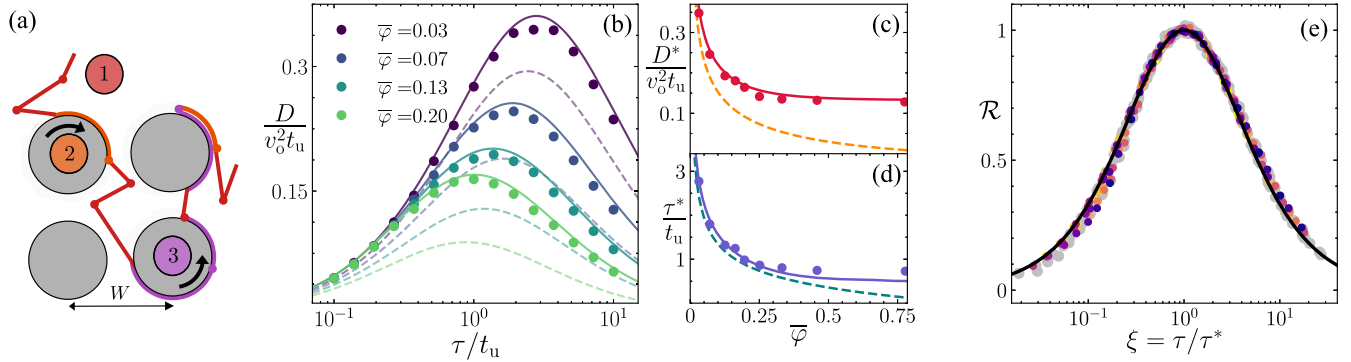


FIG. 3. Run-and-tumble with sliding along surface. (a) The porous medium consists of disks on a square lattice with spacing W . The microorganism moves through porous space (mode 1) or along obstacle surfaces (modes 2 and 3). It aligns with walls upon collision and when tumbling at the surface, escapes with probability $1/2$ and reverses with probability $1/4$. (b) Diffusivity as a function of mean run time, comparing numerical data (points) and a model (solid line). Dashed lines show diffusivity without sliding. Time unit is $t_u = W/v_o$. (c),(d) Diffusivity maximum D^* and optimal mean run time τ^* as a function of solid fraction, with and without surface sliding (continuous and dashed lines respectively). Circles show simulation data. (e) The modified diffusivity ratios \mathcal{R} for various solid fractions ($\bar{\varphi} = 0.08\text{--}0.69$) and swimming strategies collapse on the master curve, Eq. (5) (black line). Gray circles show additional data for sliding without surface reversals, sliding on ordered rectangles, and sliding in disordered environments. The 37 datasets are detailed in Table II of the Supplemental Material [41].

reorientation events of correlation β . The effective correlation $\beta_m^e \equiv (\beta_1 \beta_2 / 2) \sum_{l=\pm 1} [1 - \mathcal{L}_m(l) / \mu_m']^{-1}$ characterizes the reorientation occurring between an escape from mode m and a return to mode m . The correction C is given by $C^{-1} \equiv (\mu_1 + \mu_2) ([\mu_1 \mu_2 \mathcal{D}_1(0) \mathcal{D}_2(0)]^{-1} - \beta_1 \beta_2)$ where $\mathcal{D}_m(0) \equiv \mathcal{D}_m(0, \cdot)$ is the diffusivity in pure mode m . The first two terms in Eq. (6) are the weighted averages of interrupted unimodal diffusivities, because each mode m is interrupted with rate μ_m by the other, and these interruptions induce a reorientation with effective correlation β_m^e . Yet, Eq. (6) also includes an additional correction term whenever some degree of correlation is retained, on average, when switching the mode ($\beta_1 + \beta_2 \neq 0$).

As a specific case coupling bulk and surface motion, we consider a square lattice of disks and assume that tumbles at the surface can induce either escapes or reversals along the surface. Since sliding around obstacles can be clockwise or counterclockwise, the process is now trimodal [Fig. 3(a)]. The formalism can be extended [41] and yields a formula analogous to Eq. (6). The predicted diffusivity is in agreement with simulation data [Fig. 3(b)]. At high solid fraction $\bar{\varphi}$, the maximum D^* vanishes in case of wall trapping, whereas for sliding it can display nonmonotonic behavior or reach a plateau [Fig. 3(c)], where displacement becomes surface dominated. The optimal run times with sliding and trapping remain comparable up to $\bar{\varphi} \approx 0.4$, which suggests that environments with distinct surface properties may nevertheless lead to similar optimal strategies.

Finally, we show that the universal law of dispersal is also relevant to multimodal motions. Because analytical approaches become too complex, we resort to numerical simulations to explore several variations in surface

behaviors and environments. These include sliding on disks without surface reversals, sliding on rectangles with reversals at corners, as well as monodisperse ordered disks and several types of polydisperse disordered disks. Taking c as a free parameter in Eq. (5), all scenarios considered lead to a collapse on the master curve $\mathcal{R}(\xi)$ [Fig. 3(e)]. This indicates that the law of dispersal, demonstrated above for trapping at surfaces, also extends to a variety of surface behaviors that involve sliding.

In spite of its apparent broad applicability, the law of dispersal is not without exception. Finding a generic criterium for failure is a challenge, but one requirement is indicated by the following counterexample. Assume a microorganism that moves amid ordered rectangular obstacles, slides along surfaces, and escapes at every corner with direction unchanged. Because motion is essentially ballistic and tumbles are not any more needed for escape, dispersal is highest for $\tau \rightarrow \infty$, and there is no maximum at finite run time. One necessary condition for collapse is thus the existence of a trade-off that penalizes both short and long run times.

Discussion—Though applied to a RT microorganism, the model is applicable to nontumbling motion. For an active Brownian particle (ABP) with vanishing surface velocity and which escapes by rotational diffusion [58], Eq. (3) for diffusivity still holds, with $\xi = \tau_p / \tau_p^*$ and $\tau_p \equiv 1/D_r'$ the persistence time [41]. For all natural porous environments where surface trapping is a good approximation, such as rocks, soils, gels, and tissues [26,59], all having irregular boundaries, the diffusivity given by Eqs. (3)–(5) is remarkably generic. To predict long-time dispersal, most properties of the microstructure [50] are irrelevant: only the mean chord length matters.

The connection between dispersal and Cauchy universality sheds new light on some previous findings. The idea of a generic dispersal in porous media was suggested by Mattingly [35,36] from the study of a specific system [60]. His prediction, recovered as a particular case of Eq. (1), was obtained by homogenization. Our derivation from a minimal model explains why the result is widely applicable. Besides, for RT polymers in a disordered medium, Ref. [27] concluded that the “size of the pores, not their shape, matters” while for ABPs in a periodic medium, Ref. [23] identified the “effective mean free path as the critical length scale governing cell transport.” Both statements follow from the Cauchy universality embodied in Eq. (2). Finally, the reverse-when-stuck strategy was shown numerically to outperform other swimming patterns [30]. Equation (1) allows one to generalize this conclusion. The optimal pattern for an organism with surface sensing ability involves ballistic runs and escape immediately after collision in a direction parallel—not normal—to the surface [61].

To conclude, we found that the dispersal of motile microorganisms within porous media is governed by a generic law, whose universality originates in the invariance of the mean free path [Eq. (2)]. Cauchy universality has been shown to govern wave propagation through scattering media [62,63] and residence time of bacteria in microstructures [64]. It also implies that, whatever the diversity of motion patterns and porous media, microbial dispersal can be understood within a unified framework. Future research may assess the effect of non-Poissonian processes for tumble and trapping [26,65], and characterize anisotropic dispersal induced by external fields, flows [66], or symmetry-breaking microstructures [67]. Finally, given the analogy between random motions and polymer chains, one may wonder about the implications of Cauchy invariance for polymers in porous media and nanocomposites [68–70].

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- [1] W. B. Whitman, D. C. Coleman, and W. J. Wiebe, Prokaryotes: The unseen majority, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 6578 (1998).
 - [2] J. Kallmeyer, R. Pockalny, R. R. Adhikari, D. C. Smith, and S. D’Hondt, Global distribution of microbial abundance and biomass in subseafloor sediment, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 16213 (2012).
 - [3] R. Sender, S. Fuchs, and R. Milo, Revised estimates for the number of human and bacteria cells in the body, *PLoS Biol.* **14**, e1002533 (2016).

- [4] C. Jin and A. Sengupta, Microbes in porous environments: From active interactions to emergent feedback, *Biophys. Rev.* **16**, 173 (2024).
- [5] D. Shrestha, J. Ou, A. Rogers, A. Jereb, D. Okyere, J. Chen, and Y. Wang, Bacterial mobility and motility in porous media mimicked by microspheres, *Colloids Surf. B* **222**, 113128 (2023).
- [6] N. W. Frankel, W. Pontius, Y. S. Dufour, J. Long, L. Hernandez-Nunez, and T. Emonet, Adaptability of non-genetic diversity in bacterial chemotaxis, *eLife* **3**, e03526 (2014).
- [7] A. Finkelshtein, D. Roth, E. B. Jacob, and C. J. Ingham, Bacterial swarms recruit cargo bacteria to pave the way in toxic environments, *mBio* **6**, e00074 (2015).
- [8] H. M. Kurkjian, M. Javad Akbari, and B. Momeni, The impact of interactions on invasion and colonization resistance in microbial communities, *PLoS Comput. Biol.* **17**, e1008643 (2021).
- [9] K. Z. Coyte, H. Tabuteau, E. A. Gaffney, K. R. Foster, and W. M. Durham, Microbial competition in porous environments can select against rapid biofilm growth, *Proc. Natl. Acad. Sci. U.S.A.* **114**, E161 (2016).
- [10] K. Zegadło, M. Gieroń, P. Żarnowiec, K. Durlik-Popińska, B. Kręcis, W. Kaca, and G. Czerwonka, Bacterial motility and its role in skin and wound infections, *Int. J. Mol. Sci.* **24**, 1707 (2023).
- [11] D. Ribet and P. Cossart, How bacterial pathogens colonize their hosts and invade deeper tissues, *Microbes Infect.* **17**, 173 (2015).
- [12] K. H. Gupta, C. Nowicki, E. F. Giurini, A. L. Marzo, and A. Zloza, Bacterial-based cancer therapy (BBCT): Recent advances, current challenges, and future prospects for cancer immunotherapy, *Vaccines* **9**, 1497 (2021).
- [13] S. Compant, C. Clément, and A. Sessitsch, Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization, *Soil Biol. Biochem.* **42**, 669 (2010).
- [14] T. R. Ginn, B. D. Wood, K. E. Nelson, T. D. Scheibe, E. M. Murphy, and T. P. Clement, Processes in microbial transport in the natural subsurface, *Adv. Water Resour.* **25**, 1017 (2002).
- [15] M. Grognot and K. M. Taute, More than propellers: How flagella shape bacterial motility behaviors, *Curr. Opin. Microbiol.* **61**, 73 (2021).
- [16] R. Stocker, Reverse and flick: Hybrid locomotion in bacteria, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 2635 (2011).
- [17] K. F. Jarrell and M. J. McBride, The surprisingly diverse ways that prokaryotes move, *Nat. Rev. Microbiol.* **6**, 466 (2008).
- [18] E. Lauga and T. R. Powers, The hydrodynamics of swimming microorganisms, *Rep. Prog. Phys.* **72**, 096601 (2009).
- [19] B. Herzog and R. Wirth, Swimming behavior of selected species of Archaea, *Appl. Environ. Microbiol.* **78**, 1670 (2012).
- [20] A. Morin, D. Lopes Cardozo, V. Chikkadi, and D. Bartolo, Diffusion, subdiffusion, and localization of active colloids in random post lattices, *Phys. Rev. E* **96**, 042611 (2017).
- [21] M. Brun-Cosme-Bruny, E. Bertin, B. Coasne, P. Peyla, and S. Rafaï, Effective diffusivity of microswimmers in a crowded environment, *J. Chem. Phys.* **150**, 104901 (2019).

- [22] T. Jakuszeit, O. A. Croze, and S. Bell, Diffusion of active particles in a complex environment: Role of surface scattering, *Phys. Rev. E* **99**, 012610 (2019).
- [23] A. Dehkharghani, N. Waisbord, and J. S. Guasto, Self-transport of swimming bacteria is impaired by porous microstructure, *Commun. Phys.* **6**, 18 (2023).
- [24] K. J. Duffy, P. T. Cummings, and R. M. Ford, Random walk calculations for bacterial migration in porous media, *Biophys. J.* **68**, 800 (1995).
- [25] N. A. Licata, B. Mohari, C. Fuqua, and S. Setayeshgar, Diffusion of Bacterial cells in porous media, *Biophys. J.* **110**, 247 (2016).
- [26] T. Bhattacharjee and S. S. Datta, Bacterial hopping and trapping in porous media, *Nat. Commun.* **10**, 2075 (2019).
- [27] C. Kurzthaler, S. Mandal, T. Bhattacharjee, H. Löwen, S. S. Datta, and H. A. Stone, A geometric criterion for the optimal spreading of active polymers in porous media, *Nat. Commun.* **12**, 7088 (2021).
- [28] E. Irani, Z. Mokhtari, and A. Zippelius, Dynamics of bacteria scanning a porous environment, *Phys. Rev. Lett.* **128**, 144501 (2022).
- [29] P. Rizkallah, A. Sarracino, O. Bénichou, and P. Illien, Microscopic theory for the diffusion of an active particle in a crowded environment, *Phys. Rev. Lett.* **128**, 038001 (2022).
- [30] C. Lohrmann and C. Holm, Optimal motility strategies for self-propelled agents to explore porous media, *Phys. Rev. E* **108**, 054401 (2023).
- [31] D. Saintillan, Dispersion of run-and-tumble microswimmers through disordered media, *Phys. Rev. E* **108**, 064608 (2023).
- [32] T. Pietrangeli, C. Ybert, C. Cottin-Bizonne, and F. Detcheverry, Optimal run-and-tumble in slit-like confinement, *Phys. Rev. Res.* **6**, 023028 (2024).
- [33] T. Jakuszeit and O. A. Croze, Role of tumbling in bacterial scattering at convex obstacles, *Phys. Rev. E* **109**, 044405 (2024).
- [34] T. Bertrand, Y. Zhao, O. Bénichou, J. Tailleur, and R. Voituriez, Optimized diffusion of run-and-tumble particles in crowded environments, *Phys. Rev. Lett.* **120**, 198103 (2018).
- [35] H. H. Mattingly, Bacterial diffusion in disordered media, by forgetting the media, [arXiv:2311.10612](https://arxiv.org/abs/2311.10612).
- [36] H. H. Mattingly, Coarse-graining bacterial diffusion in disordered media to surface states, *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2407313122 (2025).
- [37] J. N. Bardsley and A. Dubi, Average transport path length in scattering media, *SIAM J. Appl. Math.* **40**, 71 (1981).
- [38] S. Blanco and R. Fournier, An invariance property of diffusive random walks, *Europhys. Lett.* **61**, 168 (2003).
- [39] G. Junot, T. Darnige, A. Lindner, V. A. Martinez, J. Arlt, A. Dawson, W. C. K. Poon, H. Auradou, and E. Clément, Run-to-tumble variability controls the surface residence times of *E. coli* bacteria, *Phys. Rev. Lett.* **128**, 248101 (2022).
- [40] R. Foffi and A. Meligrana, MicrobeAgents.jl: V0.5.2, Zenodo, 2025.
- [41] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/PhysRevLett.134.188303> for derivation of all results, details of simulations and additional data. See also Refs. [42–46] therein.
- [42] I. L. Novak, F. Gao, P. Kraikivski, and B. M. Slepchenko, Diffusion amid random overlapping obstacles: Similarities, invariants, approximations, *J. Chem. Phys.* **134**, 154104 (2011).
- [43] P. Lovely and F. Dahlquist, Statistical measures of bacterial motility and chemotaxis, *J. Theor. Biol.* **50**, 477 (1975).
- [44] J. Taktikos, H. Stark, and V. Zaburdaev, How the motility pattern of bacteria affects their dispersal and chemotaxis, *PLoS One* **8**, e81936 (2013).
- [45] F. Detcheverry, Unimodal and bimodal random motions of independent exponential steps, *Eur. Phys. J. E* **37**, 114 (2014).
- [46] I. L. Novak, P. Kraikivski, and B. M. Slepchenko, Diffusion in cytoplasm: Effects of excluded volume due to internal membranes and cytoskeletal structures, *Biophys. J.* **97**, 758 (2009).
- [47] $\alpha = 0$ for RTi and -1 for RR.
- [48] Brownian motion is recovered in the limit $\tau \rightarrow 0$ and $v_0 \rightarrow \infty$ while keeping $v_0^2 \tau$ finite.
- [49] M. Mangeat, T. Guérin, and D. S. Dean, Effective diffusivity of Brownian particles in a two dimensional square lattice of hard disks, *J. Chem. Phys.* **152**, 234109 (2020).
- [50] S. Torquato, *Random Heterogeneous Materials* (Springer, New York, 2002).
- [51] R. Artuso and D. J. Zamora, Cauchy universality and random billiards, *Phys. Rev. Res.* **6**, L032029 (2024).
- [52] A. Santaló, *Introduction to Integral Geometry* (Hermann, Paris 1953).
- [53] N. Chernov, Entropy, Lyapunov exponents, and mean free path for billiards, *J. Stat. Phys.* **88**, 1 (1997).
- [54] P. Shukla and D. Thongjaomayum, Surprising variants of Cauchy's formula for mean chord length, *Phys. Rev. E* **100**, 050103(R) (2019).
- [55] D. J. Zamora and R. Artuso, Exploring run-and-tumble movement in confined settings through simulation, *J. Chem. Phys.* **161**, 114107 (2024).
- [56] A. Mazzolo, C. de Mulatier, and A. Zoia, Cauchy's formulas for random walks in bounded domains, *J. Math. Phys. (N.Y.)* **55**, 083308 (2014).
- [57] Equation [3] includes a dependence on the c parameter but because c varies over a limited range of values across different simulations, an approximate collapse is seen for D/D^* in Fig. 2(c).
- [58] E. Q. Z. Moen, K. S. Olsen, J. Rønning, and L. Angheluta, Trapping of active Brownian and run-and-tumble particles: A first-passage time approach, *Phys. Rev. Res.* **4**, 043012 (2022).
- [59] T. Bhattacharjee and S. S. Datta, Confinement and activity regulate bacterial motion in porous media, *Soft Matter* **15**, 9920 (2019).
- [60] Specifically, the system considered involves a single type of RT motion—ballistic runs and isotropic tumbles—within a specific porous medium—randomly placed overlapping disks.
- [61] Taking $\tau_s = 0$ in Eq. (1) maximizes the first term, while the second is largest for ballistic motion and $\bar{\beta}$ small.
- [62] R. Pierrat, P. Ambichl, S. Gigan, A. Haber, R. Carminati, and S. Rotter, Invariance property of wave scattering through disordered media, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 17765 (2014).

- [63] R. Savo, R. Pierrat, U. Najar, R. Carminati, S. Rotter, and S. Gigan, Observation of mean path length invariance in light-scattering media, *Science* **358**, 765 (2017).
- [64] G. Frangipane, G. Vizsnyiczai, C. Maggi, R. Savo, A. Sciortino, S. Gigan, and R. Di Leonardo, Invariance properties of bacterial random walks in complex structures, *Nat. Commun.* **10**, 2442 (2019).
- [65] F. Detcheverry, Non-Poissonian run-and-turn motions, *Europhys. Lett.* **111**, 60002 (2015).
- [66] P. de Anna, A.A. Pahlavan, Y. Yawata, R. Stocker, and R. Juanes, Chemotaxis under flow disorder shapes microbial dispersion in porous media, *Nat. Phys.* **17**, 68 (2021).
- [67] F.Q. Potiguar, G.A. Farias, and W.P. Ferreira, Self-propelled particle transport in regular arrays of rigid asymmetric obstacles, *Phys. Rev. E* **90**, 012307 (2014).
- [68] S.K. Kumar, V. Ganesan, and R.A. Riggleman, Perspective: Outstanding theoretical questions in polymer-nanoparticle hybrids, *J. Chem. Phys.* **147**, 020901 (2017).
- [69] J. Jancar, J. Douglas, F. Starr, S. Kumar, P. Cassagnau, A. Lesser, S. Sternstein, and M. Buehler, Current issues in research on structure–property relationships in polymer nanocomposites, *Polymer* **51**, 3321 (2010).
- [70] Q. Zeng, A. Yu, and G. Lu, Multiscale modeling and simulation of polymer nanocomposites, *Prog. Polym. Sci.* **33**, 191 (2008).