

Stochastic Pairwise Forces Enhance Tracer Diffusion in Nonmotile Active Matter

Henry Alston^{1,2}, Raphaël Voituriez,^{3,4} and Thibault Bertrand¹

¹*Department of Mathematics, Imperial College London, South Kensington, London SW7 2AZ, United Kingdom*

²*Laboratoire de Physique, École Normale Supérieure, CNRS, PSL Université, Sorbonne Université, Université de Paris, 75005 Paris, France*

³*Laboratoire Jean Perrin, UMR8237 CNRS, Sorbonne Université, 75005 Paris, France*

⁴*Laboratoire de Physique Théorique de la Matière Condensée, UMR7600 CNRS, Sorbonne Université, 75005 Paris, France*



(Received 27 August 2025; accepted 5 February 2026; published 27 March 2026)

Stochasticity is a defining feature of the pairwise forces governing interactions in biological systems—from molecular motors to cell-cell adhesion—yet its consequences on large-scale dynamics remain poorly understood. Here, we show that reciprocal but randomly fluctuating interactions between particles create active suspensions that can enhance the diffusion of an external tracer particle, even in the absence of self-propulsion or nonreciprocity. Starting from a lattice model with pairwise dynamics that minimally break detailed balance, we derive a coarse-grained dynamical theory for spatiotemporal density fluctuations and reveal an elevated effective temperature at short wavelengths. We then compute the self-diffusion coefficient of a tracer particle weakly coupled to our active fluid, demonstrating that purely reciprocal stochastic interactions provide a distinct and generic route to enhanced diffusivity in dense nonequilibrium suspensions.

DOI: [10.1103/yxch-hpbv](https://doi.org/10.1103/yxch-hpbv)

For systems at thermodynamic equilibrium, the diffusion of a tracer is expected to slow, not surge, in denser suspensions of particles [1–3]. However, intuition from equilibrium thermodynamics routinely fails to describe the phenomena displayed in active systems [4–9]. These systems are driven far-from-equilibrium by the local consumption of energy [10–14] allowing microscopic dynamics breaking detailed balance: the simplest example is particle self-propulsion in motile active matter [15–18].

Diffusive tracers in nonequilibrium systems remain a central model for understanding transport, organization, and signaling dynamics in living matter [19–22]. The transport properties of tracers in baths of self-propelling particles have received much attention: polystyrene micron-scale beads suspended in a soap film containing motile bacteria such as *Escherichia coli* [23] or microswimmers such as *Chlamydomonas reinhardtii* [24] demonstrate transient ballistic (superdiffusive) motion. This was motivated by an effective force-dipole acting on the tracer with a finite correlation time arising due to the persistent motion of the microorganisms [23] and hydrodynamic effects [24]. Moreover, tracers with anisotropic

shape demonstrate persistent motion [25,26] and anomalous diffusion at long times [27].

Analytical formulations for the tracer dynamics can be derived through a separation of timescales argument between tracer and suspension dynamics (see Ref. [28] for a review) or assuming weak tracer-suspension couplings [29–31]. The latter approach was recently employed to detail the enhanced tracer diffusion observed in binary mixtures of particles with nonreciprocal interactions [32]. While nonreciprocity provides an alternative route to making matter active [33–39], the proposed mechanism underlying this diffusion enhancement is familiar: the formation of two-particle dimers in the suspension exhibiting transient ballistic motion [32,40].

Importantly, systems can be made active without the persistent motion of individual particles (as in self-propulsion) or particle pairs (as in nonreciprocity). Indeed, stochastic reciprocal forces provide an example [41], and recent experimental works have demonstrated how they endow dense clusters with heightened response to external forces [42–45] and help direct growth during morphogenetic processes [46–48]. They have recently also been shown to drive nontrivial diffusion properties: the bacterium *Neisseria meningitidis* exhibits enhanced self-diffusion in dense aggregates due to (intermittent) pili-mediated interactions [42]. Naturally, the underlying mechanism must deviate from the active systems discussed above as the bacteria's mean-squared displacements do not exhibit transient ballistic scaling [42,49], suggesting an alternative route to activity-enhanced diffusion of passive tracers.

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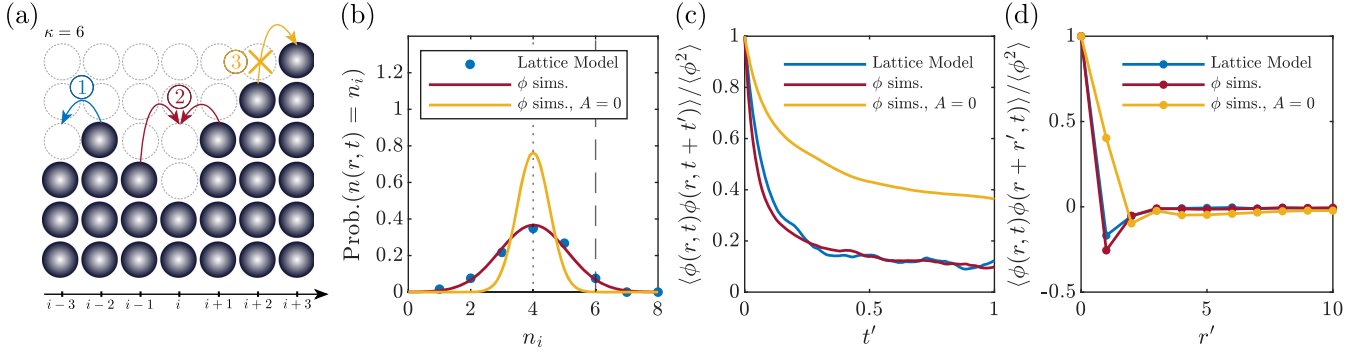


FIG. 1. Lattice model and continuum description. (a) Schematic of the present lattice model where particles ① diffuse to neighboring sites and ② interact over two sites by hopping to the center of mass, while ③ partial exclusion ensures slowed rates onto crowded sites and enforces a finite carrying capacity, enforced here as $\kappa = 6$ (dashed gray line). We then set $\bar{n} = 4$ (dotted gray line) and compare the spatial and temporal correlation functions in simulations of the two dynamics (discrete lattice model and continuous field dynamics). We find quantitative agreement between (b) the distribution of particle numbers, (c) the relaxation time of the two-time correlation function, and (d) the relaxation length for the two-space correlation function. Note that we set the lattice spacing to be equal to $a = 1$.

In this Letter, we demonstrate that stochastic reciprocal forces can create active suspensions where tracer diffusion is larger in denser phases. Starting from a lattice model, we derive a linear field theory describing nonequilibrium density fluctuations due to pairwise dynamics between particles that break detailed balance (but conserve center of mass) and drive liquid-gas phase separation. These dynamics capture the essential features of particle fluctuations in dense suspensions with isotropic active stresses arising from fluctuating interactions such as pili binding-unbinding or ATP-driven actin-myosin turnover in cell monolayers. We then calculate the self-diffusion coefficient of a passive tracer weakly coupled to this fluctuating field, quantifying how the active interactions in the suspension enhance tracer diffusion.

Lattice model with minimal detailed-balance breaking attractive interactions—We consider a lattice model of the partial exclusion process [50,51] on a periodic domain $\mathcal{L}$ with spacing a , augmented with detailed-balance breaking pairwise dynamics bringing particles together while conserving center of mass. These additional dynamics serve to minimally model stochastic attractive interactions.

Let $n_i(t)$ denote the particle number at site i and define the state $\mathbf{n} = \{n_i\}_{i \in \mathcal{L}}$. The model dynamics are then defined as follows: ① Particles at site i jump to site $i \pm 1$ with rate $\alpha_{i,\pm 1}(\mathbf{n}) = D_r n_i (1 - n_{i \pm 1} / \kappa)$, where D_r^{-1} sets the typical timescale associated with the diffusive motion and κ is the carrying capacity at each site, assumed to be constant throughout the system; ② Two particles at sites $\{i-1, i+1\}$ simultaneously hop to site i with rate $\beta_i(\mathbf{n}) = k_r n_{i-1} n_{i+1} \max[0, 1 - n_i / (\kappa - 1)]$, where the partial exclusion due to the carrying capacity takes into account the $+2$ increase in particle number.

Note that as $n_i \leq \kappa$ the rates introduced above are always non-negative. The breaking of detailed balance is evident: the probability that a pair of particles hop together in the

next dt time units is $\mathcal{O}(dt)$, whereas the reverse event (two diffusive hops apart) happens with probability $\mathcal{O}(dt^2)$. Finally, the choice of partial exclusion prevents the unphysical collapse of all particles onto a single site. A schematic of these hopping rules is provided in Fig. 1(a).

Our choice of lattice hopping rules captures, at a most minimal level, pairwise dynamics due to intermittent attractive forces: particle pairs diffuse apart before hopping together stochastically in a manner that breaks detailed balance [41]. These forces were previously studied in an off-lattice, particle-based model in Ref. [52]: the (deterministic) density dynamics were shown to pertain to the nonequilibrium phase separation field theory Active Model B+. Our current approach provides an exact microscopic derivation of the stochastic terms appearing in the field theory: we will show these dynamics break fluctuation-dissipation at the linear level, leading to nonequilibrium corrections to the self-diffusion of a tracer particle to linear order.

Dynamical description for the particle number fluctuations—We now coarse-grain the dynamics of the lattice model following the approach of Ref. [53]. We remark here that while providing accurate results for a range of models, the coarse-graining procedure was shown to provide spurious phase separation results for asymmetric interaction kernels [54]. Therefore, we compare our results below to numerical simulations to identify when our dynamics suitably capture those of our lattice model.

Following Ref. [53], we derive a Langevin equation for the particle number field through the construction of a Martin-Siggia-Rose dynamical action. The procedure involves identifying the action $\mathcal{S}[\mathbf{n}(t), \tilde{\mathbf{n}}(t)]$ from which the path probability for the process can be evaluated as

$$\mathbb{P}[\mathbf{n}(t)] = \frac{1}{Z} \int \mathcal{D}\tilde{\mathbf{n}} e^{-\mathcal{S}[\mathbf{n}(t), \tilde{\mathbf{n}}(t)]}, \quad (1)$$

where $\mathbf{n}(t) = \{n_i(t)\}_{i \in \mathcal{L}}$, $\tilde{\mathbf{n}} = \{\tilde{n}_i(t)\}_{i \in \mathcal{L}}$, $\mathcal{D}\tilde{\mathbf{n}} = \prod_{i \in \mathcal{L}} d\tilde{n}_i$, and Z normalizes the distribution. The action can be determined (see full details in Supplemental Material [55]) and takes the form

$$\mathcal{S}(\mathbf{n}, \tilde{\mathbf{n}}) = \sum_{i \in \mathcal{L}} \int dt \left[\tilde{n}_i \partial_t n_i - \sum_{\nu=\pm 1} \alpha_{i,\nu} (e^{\tilde{n}_{i+\nu} - \tilde{n}_i} - 1) - \beta_i (e^{-\nabla^2 \tilde{n}_i} - 1) \right]. \quad (2)$$

To derive an equation for $\partial_t n_i$, we then rewrite all nonlocal terms as local terms (site i in the summand) using gradient (Taylor) expansions, then expand the exponential terms involving the conjugate fields. We then follow the same approach taken for other lattice models with simultaneous particle hopping and fix the lattice spacing to 1 [56,57] and make the (*a priori* uncontrolled) assumption that we can discard higher-order gradient terms on the basis that they are dominated by leading-order terms. This assumption is valid when considering long-wavelength fluctuations, and this will be the focus of the work below. In the current Letter, we only seek to capture the particle number fluctuations $\phi(x, t) \equiv n(x, t) - \bar{n}$, such that, under the assumption that $\phi \ll \bar{n}$, we only need to keep leading-order terms in ϕ (see the End Matter for a discussion of the nonlinear dynamics).

A dynamical equation for ϕ describing Gaussian fluctuations about the mean-field fixed point can be identified from the action: the $\mathcal{O}(\bar{n})$ terms contributing to the deterministic dynamics and $\mathcal{O}(\bar{n}^2)$ terms to stochastic terms. The resulting dynamics is given by

$$\partial_t \phi = D_0 \partial_x^2 \phi - \gamma \partial_x^4 \phi + \sqrt{2D_1} \partial_x \Lambda + \sqrt{A} \partial_x^2 \xi, \quad (3)$$

where crucially γ , D_0 , D_1 , and A are all derived in terms of the microscopic jump rates and exclusion factors with the coefficients for the deterministic terms given by

$$D_0 = D_r - k_r \left(2\bar{n} - \frac{3\bar{n}^2}{\kappa - 1} \right) \quad (4a)$$

$$\gamma = \frac{1}{12} \left[-D_r + k_r \left(14\bar{n} - \frac{15\bar{n}^2}{\kappa - 1} \right) \right]. \quad (4b)$$

Neglecting higher-order terms is valid when modeling small wave number dynamics: our effective field theory captures the essential collective physics at large scales. When calculating observables below, we impose a minimum wavelength (UV cutoff) to avoid divergences at higher Fourier modes q . This cutoff is set to $q_{\max} = \sqrt{12}$ to avoid unphysical divergences in the limit $k_r = 0$. The stochastic terms $\Lambda(x, t)$ and $\xi(x, t)$ are zero-mean, unit variance Gaussian white noise processes and have coefficients

$$D_1 = D_r \bar{n} \left(1 - \frac{\bar{n}}{\kappa} \right) \quad \text{and} \quad A = k_r \bar{n}^2 \left(1 - \frac{\bar{n}}{\kappa - 1} \right). \quad (5)$$

While the dynamics are written here in one dimension, the extension to higher dimensions is trivial due to the orthogonal nature of the lattice dynamics. These dynamics also exhibit phase separation: D_0 can be negative for some range of $\bar{n} < \kappa$ for sufficiently large k_r , indicating the presence of a spinodal instability (as captured in the off-lattice model of Ref. [52]). We consider densities $\bar{n}$ above this range such that $D_0(\bar{n}) > 0$ and the linearized dynamics are stable.

We compare the particle number fluctuations in the lattice model to those described by Eq. (3) through numerical simulations, comparing the spatial and temporal correlation functions [61]. The results are given in Figs. 1(b)–1(d): we find quantitative agreement in the temporal and spatial relaxation of fluctuations. Interestingly, the spatial correlations in panel (d) show a depletion at a distance of one lattice site, compared to the equilibrium picture for attractive interactions (in yellow). This arises due to the stochastic nature of the interactions and represents a nonequilibrium feature of our model. We remark here that D_1 can be interpreted with a thermal temperature, T : the self-diffusion coefficient of an isolated particle in the lattice model is D_r (for unit lattice spacing), setting the temperature through an Einstein relation. With this in mind, we identify $D_1 = \mu_\phi T$, the product of the field motility, $\mu_\phi = \bar{n}(1 - \bar{n}/\kappa)$, and the temperature.

The noise term of Eq. (3) with coefficient $\propto \sqrt{A}$ vanishes when $k_r = 0$: it captures the stochastic nature of the attractive interactions. It is crucial for agreement between lattice and field dynamics, as demonstrated in Figs. 1(b)–1(d). The noise appears under a Laplacian operator: such noise terms have been identified previously in the study of hyperuniform systems [63] whereby interactions conserving the center of mass drive the suppression of low wave number (large-scale) density fluctuations [56,64,65]. This long-range order was recently argued to arise from dynamical active stresses in $d = 2$ dimensions [66]. The connection with the current Letter is immediate: in a linearized description of the particle number fluctuations, stochastic isotropic active stresses—modeled as white noise—give rise to the noise ξ that appears in Eq. (3). Results from Ref. [57] imply that any stochastic hopping dynamics conserving center of mass but not the moment $\int dx x^2 n(x, t)$ would generate a noise term akin to the $\propto \sqrt{A}$ term appearing here through the mean-field coarse-graining performed here.

We believe that the form of the dynamics in Eq. (3) extend beyond the lattice model studied, in principle describing (to leading order in deterministic and stochastic terms) symmetric particle number fluctuations in systems subject to thermal and active interaction-mediated (center-of-mass conserving) fluctuations. We confirm that the last term in Eq. (3) is sufficient to drive a departure from

equilibrium: recalling $D_1 = \mu_\phi T$, we write the dynamics in Fourier space as

$$\partial_t \tilde{\phi}(q, t) = [-D_0 q^2 - \gamma q^4] \tilde{\phi} + \sqrt{\mu_\phi} \eta(q, t), \quad (6a)$$

$$\langle \eta(q, t) \eta(q', t') \rangle = [2Tq^2 + A'q^4] \delta(q + q') \delta(t - t'). \quad (6b)$$

The dynamics for the Fourier mode q are exactly of *Model B* form (in the Gaussian approximation) with the effective temperature $T_{\text{eff}}(q) = T + A'q^2/2$ [58] where $A' = A/\mu_\phi$. The q dependence here indicates that each mode $\tilde{\phi}(q)$ is at equilibrium with its own thermal reservoir at temperature $T_{\text{eff}}(q)$, and linearity implies there is no heat flow between modes. However, we cannot simply describe the field dynamics for the full system through a global rescaling of the temperature, indicating a genuine departure from equilibrium fluctuation dynamics. This contrasts with the top-down derivations for active systems such as Active Model B [67] and B+ [8,9,68], where higher-order deterministic terms maintain a departure from equilibrium. For the off-lattice model of [52], we concluded the intermittent attractive forces drive AMB+ density fluctuations: here, a formal treatment of the stochastic pairwise dynamics demands a stochastic term to capture the departure from equilibrium. Previous work has considered such q -dependent noise in active field theories in the context of self-propelled particles [8,69,70], but we provide here an alternative motivation in the context of nonmotile active systems describing pili-mediated aggregates and confluent cell tissues.

Self-diffusion coefficient of tracer particle coupled to field dynamics Eq. (3) in d dimensions—Employing this dynamical description, we consider the effect of stochastic interactions on the diffusivity of an external, Brownian tracer particle (at temperature T) at position $\mathbf{y}(t)$, which we reciprocally couple to the dynamical field ϕ . Note that we assume a separation of length scales: the tracer size is assumed to be much smaller than the length scale of relaxation of the field $\phi(\mathbf{r}, t)$. As a consequence, the tracer only feels the local gradient of the field. The following calculation captures the transport properties of our active suspension (diffusion of an external tracer), rather than the random motion of the suspension particles themselves.

As a starting point, we consider the field dynamics from before but now written in d dimensions. Upon coupling to the tracer, the dynamics takes the following form:

$$\begin{aligned} \partial_t \phi(\mathbf{r}, t) = & D_0 \nabla^2 \phi - \gamma \nabla^4 \phi + h \nabla^2 \delta(\mathbf{y}) \\ & + \sqrt{2D_1} \nabla \cdot \mathbf{A}(\mathbf{r}, t) + \sqrt{A} \nabla^2 \xi(\mathbf{r}, t) \end{aligned} \quad (7a)$$

$$\dot{\mathbf{y}}(t) = -h \nabla \phi(\mathbf{y}, t) + \sqrt{2D_y} \boldsymbol{\eta}_y(t). \quad (7b)$$

The form of the tracer-field coupling can be argued through employing the exact formulation from Dean [59] as in Ref. [31] (see details in Supplemental Material [55]).

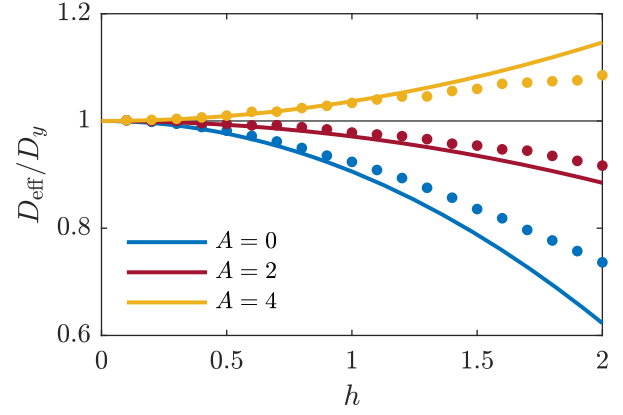


FIG. 2. Range of validity for tracer self-diffusion coefficient result. We compare results from simulations of Eqs. (7a) and (7b) (black dots) to our analytic result Eq. (9) for the self-diffusion coefficient of the tracer particle. We find accurate agreement up to $h = 1$ and confirm the observation that sufficiently strong interaction fluctuations can enhance the diffusion of the tracer. Parameter values are $D_0 = \gamma = D_1 = 1$.

Analytical frameworks for calculating statistics of the tracer particle's motion have been considered previously [29–31]. Here, we consider field dynamics augmented with stochastic terms breaking fluctuation-dissipation through gradient terms [71]: a full rederivation in this case is given in Supplemental Material [55]. The result for the self-diffusion coefficient is then calculated from the long-time mean-squared displacement as follows:

$$D_{\text{eff}} = \lim_{t \rightarrow \infty} \frac{\langle |\mathbf{y}(t) - \mathbf{y}(0)|^2 \rangle}{2dt}. \quad (8)$$

The final result for the coupled dynamics of Eqs. (7a) and (7b) to quadratic order in h takes the form

$$\frac{D_{\text{eff}}}{D_y} - 1 = -\frac{h^2}{d} \int \frac{d^d \mathbf{q}}{(2\pi)^d} \frac{\mu_\phi T_{\text{eff}}(\mathbf{q}) + [2 - D_y^{-1} \mu_\phi T_{\text{eff}}(\mathbf{q})] \Delta(\mathbf{q})}{\Delta(\mathbf{q}) [D_y + \Delta(\mathbf{q})]^2}, \quad (9)$$

where D_0 is taken to be positive and we have defined $\Delta(\mathbf{q}) = D_0 + \gamma |\mathbf{q}|^2$ and recall the definition $\mu_\phi T_{\text{eff}}(\mathbf{q}) = D_1 + (A/2) |\mathbf{q}|^2$. We explore the range of validity of this perturbative result by comparing it to numerical simulations of Eqs. (7a) and (7b). We set all coefficients to 1 and impose a (UV) cutoff for the Fourier modes of $q_{\text{max}} = 2\pi$, which implicitly models a unit lattice spacing. The numerical method is detailed in Supplemental Material [55], and the results are given in Fig. 2, where we find a good agreement for $h < 1$.

From this analytic result, we draw two important conclusions. First, $A > 0$ does not generically lead to increased tracer self-diffusion: if $(-1 + D_0 + \gamma q_{\text{max}}^2) < 0$ then the correction due to $A > 0$ is negative (leading to $D_{\text{eff}}/D_y < 1$

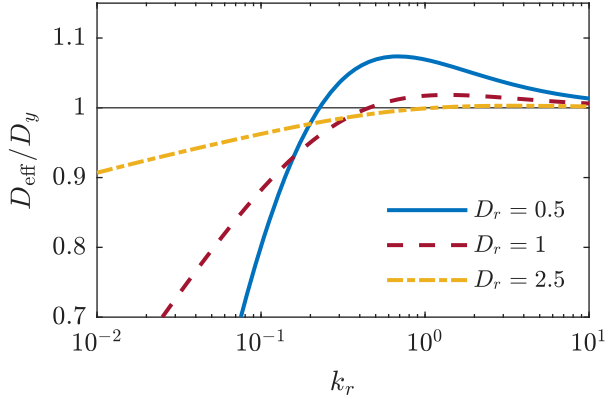


FIG. 3. Connecting tracer diffusivity enhancement to microscopic hopping rates. We plot the analytic result Eq. (9) where the constants are evaluated using the expressions for the particle model with $\bar{n} = 4$ and $\kappa = 6$ as in Fig. 1 and $h = 0.5$. We observe a range for the interaction rate k_r in which the diffusion of the tracer particle is enhanced, including a finite k_r that maximizes this effect.

for all values of h). More strikingly, in the case where D_0 and γ are such that this correction is positive, sufficiently large $A > 0$ can enhance the self-diffusion of the tracer above its bare diffusion coefficient $D_{\text{eff}} > D_y$. This is a truly nonequilibrium consequence of our model: studies of field dynamics satisfying fluctuation-dissipation universally report a decrease in tracer self-diffusion upon weak (reciprocal) coupling to the field. The case where the coupling is not reciprocal (i.e., the case where the field does not feel the force of the particle) can exhibit increases in the self-diffusion of the tracer upon coupling [29]. The reciprocal coupling thus ensures that the particle must overcome a self-trapping effect it generates by locally deforming the field, making diffusion enhancement a nontrivial observation. The enhancement in diffusion also persists in the limit $D_y = 0$ due to the final term in the numerator. Here, we demonstrate how nonequilibrium fluctuations, driven by microscopic reciprocal interactions breaking detailed balance, can drive an enhancement in the transport properties of the tracer. We remark here that we can also consider the effective motility κ_{eff} of a tracer being dragged with some force $\mathbf{f}$, defined as $\kappa_{\text{eff}}(\mathbf{f}) = \lim_{t \rightarrow \infty} (\langle \mathbf{y}(t) \rangle / \mathbf{f}t)$. However, we show in Supplemental Material [55] that the effective motility is unaffected by A : it is identical to that of Model B in the Gaussian approximation, as studied in Ref. [29].

Relation to the microscopic jump rates—Finally, we relate our result Eq. (9) to our lattice model to interpret the diffusion enhancement in terms of microscopic timescales: the results are plotted in Fig. 3. We identify three regimes: for $D_r \gg k_r$, the detailed-balance breaking lattice dynamics are unimportant and the result mirrors that of Refs. [29,30] conserved equilibrium field dynamics. For $D_r \ll k_r$, the timescales for the tracer and field dynamics are widely separated: in this limit, only the k_r terms are important in

the field dynamics, thus it sets the timescale for $\partial_t \phi$; the dynamics for the tracer do not scale with k_r . In this case, $D_{\text{eff}} \rightarrow D_y$ as $k_r \rightarrow \infty$ as argued previously for fast field dynamics [29,30].

In Fig. 3, we see tracer diffusion enhancement requires similar interaction and diffusion rates and is optimized for finite interaction rates, reminiscent of stochastic resonance [72–74]. This enhancement strongly resembles a particle coupled nonreciprocally to the field: tracer diffusive enhancement is observed when the field does not deform due to the presence of the particle (so-called passive rather than active tracers [29]). This is also optimized for a finite relaxation time of the field dynamics. We propose that the nonequilibrium stochastic term ($\propto \sqrt{A}$) may combat the deformation of the field due to the tracer, thus preventing local trapping.

Discussion and conclusion—We have demonstrated that a minimal example of attractive, reciprocal, and detailed-balance-breaking pairwise interactions are sufficient to drive nonequilibrium fluctuations in particle number. After a mean-field coarse-graining procedure, we confirmed that the derived dynamics for the particle number fluctuations quantitatively capture those of the underlying model when the system is dense. Moreover, the general form of our continuum description Eq. (3) describes a broad class of nonmotile active systems: we consider only the minimal ingredients of diffusion augmented with center-of-mass conserving stochastic interactions [56,64] breaking detailed balance. Our equation also arises from a hydrodynamic description of active systems with fluctuating isotropic stresses [66] modeling type-IV pili-mediated interactions between *Neisseria meningitidis* [42–45] and dynamical cell-cell tensions driven by actin-myosin turnover in embryonic cell tissues in zebrafish [46–48].

We then calculated the self-diffusion coefficient for a tracer particle coupled to the fluctuating field dynamics, deriving an analytic expression to quadratic order in the coupling strength h (which we compared to results from numerical simulations, concluding on good agreement up to $h \approx 1$). We illustrated how coupling to the field can enhance the diffusive motion of the tracer, an effect that is inimitable for passive scalar field dynamics with reciprocal tracer-field couplings [29,30]. Our results extend straightforwardly to other models of center-of-mass conserving dynamics: most notably, Eq. (9) gives the self-diffusion coefficient of a tracer coupled to the COMCon model [56], a model exhibiting hyperuniformity. We demonstrate in Supplemental Material [55] how the timescale of the lattice dynamics sets the tracer diffusion coefficient and can induce an enhancement of tracer diffusion, quantifying for the first time this nonequilibrium feature of the model. Our results thus point toward center-of-mass conserving fluctuations (modeling, for instance, active stochastic pairwise forces between agents) as a generic route for enhancing transport properties in complex systems and an

alternative mechanism to particle self-propulsion in motile active matter.

Acknowledgments—The authors are grateful to Vincent Démery, Julien Tailleur, Paul C. Bressloff, Sunghan Ro, and Emir Sezik for interesting discussions. H. A. was supported by a Roth PhD scholarship funded by the Department of Mathematics at Imperial College London.

Data availability—The data that support the findings of this article are openly available [75].

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End Matter

The full nonlinear equation for $\partial_t n(x, t)$ can be derived from Eq. (2). The resulting dynamics to fourth order in gradients for the deterministic terms and with the leading-order stochastic terms from above takes the form

$$\begin{aligned} \partial_t n(x, t) = & \partial_x [D_0(n) \partial_x n - \gamma(n) \partial_x^3 n \\ & + \lambda(n) (\partial_x n)^3 + \zeta(n) \partial_x n \partial_x^2 n] \\ & + \partial_x \left[\sqrt{2D_1(n)} \Lambda(x, t) \right] + \partial_x^2 \left[\sqrt{A(n)} \eta(x, t) \right] \\ & + \mathcal{O}(\partial_x^6), \end{aligned} \quad (\text{A1})$$

where we have defined

$$D_0(n) = D_r - k_r \left(2n - \frac{3n^2}{\kappa - 1} \right) \quad (\text{A2a})$$

$$\gamma(n) = \frac{1}{12} \left[-D_r + k_r \left(14n - \frac{15n^2}{(\kappa - 1)} \right) \right] \quad (\text{A2b})$$

$$\lambda(n) = -\frac{k_r}{2(\kappa - 1)} \quad (\text{A2c})$$

$$\zeta(n) = \frac{k_r}{2} + \frac{3k_r n}{2(\kappa - 1)} \quad (\text{A2d})$$

$$D_1(n) = D_r n \left(1 - \frac{n}{\kappa} \right) \quad (\text{A2e})$$

$$A(n) = k_r n^2 \left(1 - \frac{n}{\kappa - 1} \right). \quad (\text{A2f})$$

Upon linearizing by writing $\phi(x, t) = n(x, t) - \bar{n}$ where $\bar{n}$ is the average number of particles per site and assuming $\phi \ll \bar{n}$, we derive the deterministic field dynamics given by Eq. (3).

This full nonlinear equation deserves several remarks. First, we note that extending the lattice model to higher dimensions results in orthogonal dynamics. As such, the parallel dynamical description of the lattice model in higher dimensions is simply an additive sum of dynamics of the form of Eq. (A1). One may look to classify these dynamics in relation to active field theories for nonequilibrium phase

separating systems, connecting to either Active Model B or B+. However, the orthogonality of the dynamics imply a broken rotational symmetry to fourth order in gradient: terms like $\nabla n \nabla^2 n$ do not appear because terms of the form $\partial_x n \partial_x^2 n$ are absent and so on. Crucially, this implies that the dynamics belong to neither class. Also, no distinction between these two field theories can be established in dimension $d = 1$ as they are equivalent dynamically (they can be mapped onto one another after an integration by parts).

Second, we note that the dynamics are linearly unstable for moderate densities $\bar{n}$ at sufficiently large k_r . As such, the nonlinear dynamics here describe nonequilibrium phase separation. In principle, the phase equilibria expressed by these dynamics can be calculated using the framework of Solon *et al.* [76]: the key idea there is to identify an effective free energy for the nonequilibrium current and then extremize it as one would do for passive systems through a generalized common tangent construction.

The final remark is that the deterministic dynamics here are equivalent to a mean-field description of the lattice dynamics. As such, it is not known *a priori* how accurately the phase equilibria predicted by these dynamics (through, for instance, the method of [76]) capture those of the underlying lattice model. Indeed, mean-field dynamics have been shown to make inaccurate predictions for phase equilibria in systems with asymmetric interaction kernels. In the current Letter, we work instead with the linearized dynamics for ϕ where we assume that the dynamics are linearized about a large value of the mean density $\bar{n}$, namely a dense homogeneous state. This is sufficient to conclude on the tracer dynamics in dense systems and deep in the bulk of the liquid phase of a liquid-gas phase separated system. We demonstrate good agreement between the lattice model and the linearized dynamics and further motivate the analysis with the fact that the ϕ dynamics take a general form, which describe density fluctuations in a broad class of systems with detailed-balance breaking reciprocal pairwise forces. We recall here that in a previous work [52], intermittent attractive forces were studied in an off-lattice, particle-based model: a full nonlinear description for the field would allow for extending such analysis to the model of Ref. [52], an open problem that we hope to address in future work.