

Defect Unbinding in Active Nematics

Suraj Shankar,^{1,2,*} Sriram Ramaswamy,^{2,3,†} M. Cristina Marchetti,^{1,2,‡} and Mark J. Bowick^{1,2,§}

¹*Physics Department and Syracuse Soft and Living Matter Program, Syracuse University, Syracuse, New York 13244, USA*

²*Kavli Institute for Theoretical Physics, University of California, Santa Barbara, California 93106, USA*

³*Centre for Condensed Matter Theory, Department of Physics, Indian Institute of Science, Bangalore 560 012, India*

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We formulate the statistical dynamics of topological defects in the active nematic phase, formed in two dimensions by a collection of self-driven particles on a substrate. An important consequence of the nonequilibrium drive is the spontaneous motility of strength $+1/2$ disclinations. Starting from the hydrodynamic equations of active nematics, we derive an interacting particle description of defects that includes active torques. We show that activity, within perturbation theory, lowers the defect-unbinding transition temperature, determining a critical line in the temperature-activity plane that separates the quasi-long-range ordered (nematic) and disordered (isotropic) phases. Below a critical activity, defects remain bound as rotational noise decorrelates the directed dynamics of $+1/2$ defects, stabilizing the quasi-long-range ordered nematic state. This activity threshold vanishes at low temperature, leading to a reentrant transition. At large enough activity, active forces always exceed thermal ones and the perturbative result fails, suggesting that in this regime activity will always disorder the system. Crucially, rotational diffusion being a two-dimensional phenomenon, defect unbinding cannot be described by a simplified one-dimensional model.

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Liquid crystals exhibit remarkable orientationally ordered phases, the simplest being the nematic phase in which particles macroscopically align along a single preferred orientation, without a head-tail distinction. The name nematic itself comes from $\nu\eta\mu\alpha$, meaning thread, for the linelike topological defects (disclinations) that are inevitably produced in quenches from the high-temperature disordered phase to the nematic phase [1–4]. In two dimensions (2D), though, disclinations are pointlike defects, and so may be thought of as localized particles. The nematic pattern around a disclination is a distinctive fingerprint of the spontaneous symmetry breaking that characterizes nematic order and distinguishes the elementary defects from, say, integer strength vortices in two-dimensional spin systems. The nematic director rotates through a half-integer multiple of 2π as one circumnavigates a defect. Thus, the lowest-energy defects are referred to as carrying strength $\pm 1/2$. In two dimensional equilibrium nematics the entropic unbinding of such point disclinations drives the nematic to isotropic (NI) transition [5–8].

In recent years there has been much focus on nematics composed of elongated units that are self-driven—hence *active* nematics [9,10]. Examples include collections of living cells [11–17], synthetic systems built of cellular extracts [18–20], and vibrated granular rods [21]. Active nematics exhibit complex spatiotemporal dynamics, accompanied by spontaneous defect proliferation. Much progress has been made in understanding the properties of the ordered phase [9,22–26], but a complete theory of order,

fluctuations, defects and phase transitions of active nematics still eludes us. Although the nematic itself has no net polarity, the director pattern around a strength $+1/2$ defect has a local cometlike geometric polarity (Fig. 1). In an active system this renders $+1/2$ defects motile [21,27] with a self-propelling speed proportional to activity [27]. Both experiments [14,18–20,28–30] and simulations [27,31–37] have shown that motile defects play a key role in driving self-sustained active flows.

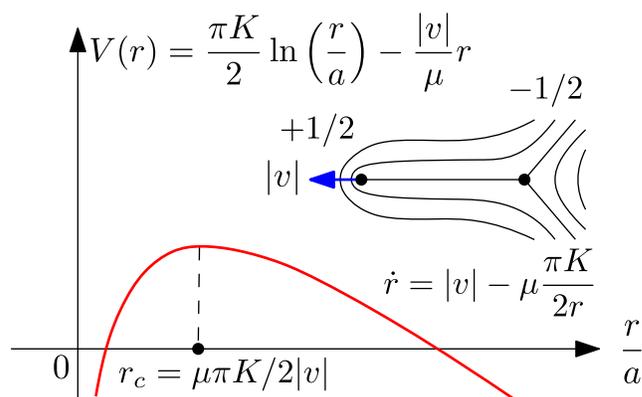


FIG. 1. Potential $V(r)$ for a neutral defect pair for the configuration in which the direction of motility of the $+1/2$ disclination points away from the $-1/2$ and is held fixed. This naïve picture suggests that incipient active defect pairs have an exponentially small, but finite, rate to overcome the barrier at low temperature, and hence always unbind.

In this Letter we precisely map the dynamics of active defects onto that of a mixture of motile (+1/2) and passive (-1/2) particles with interaction forces and aligning torques, putting on firm ground previous purely phenomenological models [19,27,38]. A key new result is the derivation of the angular dynamics of the +1/2 defects. Treating activity as a small parameter, we then construct and solve the defect Fokker-Planck equation and show that activity weakens the logarithmic attraction between opposite-charge defects. As a result, increasing activity past a threshold drives a nonequilibrium NI phase transition to a phase of unbound defects, much like the Berezinskii-Kosterlitz-Thouless (BKT) transition in two-dimensional spin systems [5–7] and passive nematics [8]. Rotational diffusion (D_R) of the +1/2 defect is suppressed at low noise, where self-propulsion directly drives unbinding with a threshold that vanishes as D_R goes to zero. This yields a reentrant isotropic-nematic-isotropic sequence [39] as a function of temperature at fixed activity. Our effective equations for defect dynamics also provide a simple model capable of quantifying the dynamics of interacting active defects in confined geometries.

The proof of the existence of a low-activity quasi-long-range ordered active nematic in 2D [22,26] is an important result because a naïve argument suggests otherwise. In an equilibrium nematic, two $\pm 1/2$ defects at a distance r experience an attractive interaction $V_0(r) = (\pi K/2) \ln(r/a)$, with K a Frank elastic constant and a the size of the defect core. Hence, neglecting inertia, they are drawn towards each other according to $\dot{r} = -\mu \partial_r V_0$, with μ a defect mobility. One could then argue that the dynamics of a suitably oriented $\pm 1/2$ defect pair in an active nematic is governed by relaxation in an effective potential [27]

$$\dot{r} = -\mu \partial_r V, \quad V(r) = \frac{\pi K}{2} \ln\left(\frac{r}{a}\right) - \frac{|v|}{\mu} r, \quad (1)$$

where $|v|$ is the self-propelling speed with which the +1/2 disclination is moving away from the -1/2 disclination (see Fig. 1). The resulting barrier $V(r_c) = (\pi K/2) \{\ln[\pi \mu K / (2|v|a)] - 1\}$ at distance $r_c = \pi \mu K / (2|v|)$ is finite, which means that the defect pair is always unbound, and active nematic order thus destroyed, at any nonzero temperature (Fig. 1). As activity is increased, more and more defect pairs will be liberated [18,27,31] suggesting that nematic order would be completely destroyed by the swarming disordered cores, much like driven vortices in superconducting films can destroy superconductivity. Here we show that this heuristic argument fails because rotational noise, by disrupting the directed motion of the +1/2 defects, counterintuitively restores the ordered nematic phase.

We begin with the hydrodynamics of a two-dimensional nematic liquid crystal written in terms of the flow velocity

\mathbf{u} and the tensor order parameter $Q_{\mu\nu} = S(2\hat{n}_\mu\hat{n}_\nu - \delta_{\mu\nu})$, where S is the scalar order parameter and $\hat{\mathbf{n}}$ is the director field. We ignore density fluctuations, although we expect this restriction could be dropped without qualitatively changing the results. The \mathbf{Q} equation is as for passive nematics [40],

$$\gamma \mathcal{D}_t \mathbf{Q} = [a_2 - a_4 \text{tr}(\mathbf{Q}^2)] \mathbf{Q} + K \nabla^2 \mathbf{Q}, \quad (2)$$

where $\mathcal{D}_t = \partial_t + \mathbf{u} \cdot \nabla - [\cdot, \boldsymbol{\Omega}]$ is the comoving and corotational derivative with the vorticity tensor $\boldsymbol{\Omega}_{\mu\nu} = (\nabla_\mu u_\nu - \nabla_\nu u_\mu)/2$. Only the relaxational part of the dynamics is retained in Eq. (2), with γ a rotational viscosity, K a Frank elastic constant and a_2, a_4 the parameters that set the mean-field NI transition at $a_2 = 0$. A treatment including various flow alignment terms is given in the Supplemental Material [41]. At equilibrium, the homogeneous ordered state for $a_2 > 0$ has $S_0 = \sqrt{a_2/(2a_4)}$ and an elastic coherence length $\xi = \sqrt{K/a_2}$. For an isolated static $\pm 1/2$ defect in equilibrium, the director $\hat{\mathbf{n}}(\varphi) = (\cos(\varphi/2), \pm \sin(\varphi/2))$ rotates by $\pm \pi$ with the azimuthal angle φ , and S vanishes at the core of the defect, assuming its bulk value on length scales larger than the defect core size $a \sim \xi$. Activity enters in the force balance equation, which, ignoring inertia and in-plane viscous dissipation, is given by $-\Gamma \mathbf{u} + \nabla \cdot \boldsymbol{\sigma}^a = \mathbf{0}$, where Γ is the friction with the substrate and $\boldsymbol{\sigma}^a = \alpha \mathbf{Q}$ is the active stress tensor that captures the internal forces generated by active units [42,43]. We neglect elastic and Ericksen stresses as they are higher order in gradients. The system is extensile for $\alpha < 0$ and contractile for $\alpha > 0$. For a +1/2 disclination, the active backflow at its core gives rise to a self-propulsion speed $\sim |\alpha|/(\Gamma a)$ [27,38].

The +1/2 disclination has a local geometric polarization $\mathbf{e}_i = a \nabla \cdot \mathbf{Q}(\mathbf{r}_i^+)$ (evaluated at the core of the defect), defined here to be dimensionless. Note that \mathbf{e}_i is *not* a unit vector. Our treatment does not require the mode expansion used in Ref. [44] to treat multidefect configurations. An isolated +1/2 defect has a nonvanishing flow velocity at its core ($\mathbf{u}(\mathbf{r}_i^+) = v \mathbf{e}_i$, $v = \alpha S_0 / \Gamma a$), while the -1/2 defect does not, due to its threefold symmetry ($\mathbf{u}(\mathbf{r}_i^-) = \mathbf{0}$) [45]. We show that the resulting positional dynamics of the defects, including both motility and passive interactions (for a derivation, see the Supplemental Material [41]) [46], is given by

$$\dot{\mathbf{r}}_i^+ = v \mathbf{e}_i - \mu \nabla_i \mathcal{U} + \sqrt{2\mu T} \boldsymbol{\xi}_i(t), \quad (3a)$$

$$\dot{\mathbf{r}}_i^- = -\mu \nabla_i \mathcal{U} + \sqrt{2\mu T} \boldsymbol{\xi}_i(t), \quad (3b)$$

where $\mu \propto 1/\gamma$ is a defect mobility, $\boldsymbol{\xi}_i(t)$ Gaussian white noise, and

$$\mathcal{U} = -2\pi K \sum_{i \neq j} q_i q_j \ln \left| \frac{\mathbf{r}_i - \mathbf{r}_j}{a} \right| \quad (4)$$

is the Coulomb interaction between defects, with $q_i = \pm 1/2$ the strength of the i th defect. The elastic constant K includes corrections from hydrodynamic flows linear in activity which can destabilize the nematic state even in the absence of topological defects [47,48]. Here we take $K > 0$ (permitted in a domain of parameter space [47,48]) to guarantee an elastically stable nematic. Note that $v \propto \alpha$ can be of either sign. The translational noise strength T arises from thermal or active noise in the \mathbf{Q} equation [Eq. (2)]. A more sophisticated calculation (see the Supplemental Material [41]) gives logarithmic corrections to the defect mobility μ [49–52]. The important feature of activity is that it elevates the geometric structural polarity of the $+1/2$ disclination to a *dynamical* degree of freedom, one that drives motion. In turn, \mathbf{e}_i also has its own dynamics, which is, in principle, contained in the \mathbf{Q} equation. Neglecting noise for now and using the quasistatic approximation in a frame comoving with the $+1/2$ defect, i.e., $[\partial_t \mathbf{Q}]_{\mathbf{r}_i^+(t)} = \mathbf{0}$, we have $\dot{\mathbf{e}}_i(t) = a[\mathbf{v}_i(t) \cdot \nabla] \nabla \cdot \mathbf{Q}(\mathbf{r}_i^+(t))$, where $\mathbf{v}_i = v\mathbf{e}_i - \mu \nabla_i \mathcal{U}$ is the deterministic part of $\dot{\mathbf{r}}_i^+$ [Eq. (3a)]. Our approximation neglects elastic torques on \mathbf{e}_i due to smooth director distortions, shown to be unimportant for the dynamics of neutral pairs [53,54] (a more detailed justification and comparison with previous work is given in the Supplemental Material [41]). Assuming a dilute gas of slowly moving defects, we perturbatively expand Eq. (2) about the equilibrium defect configuration and solve for \mathbf{Q} . Using this solution, we evaluate $\nabla \nabla \cdot \mathbf{Q}$ at the core of the defect to obtain (for details, see the Supplemental Material [41])

$$\dot{\mathbf{e}}_i = -\frac{5\gamma}{8K} [\mathbf{v}_i \cdot (\mathbf{v}_i - v\mathbf{e}_i)] \mathbf{e}_i - \frac{v\gamma}{8K} (\mathbf{v}_i \times \mathbf{e}_i) \boldsymbol{\epsilon} \cdot \mathbf{e}_i, \quad (5)$$

where $\boldsymbol{\epsilon}$ is the two-dimensional Levi-Civita tensor. Since \mathbf{e}_i is not a unit vector, its deterministic dynamics has a term along \mathbf{e}_i fixing its preferred magnitude and one transverse to it aligning the polarization to the force.

To elucidate the nature of the torques on the polarization, we write $\mathbf{e}_i = |\mathbf{e}_i|(\cos \theta_i, \sin \theta_i)$ and decompose the elastic force acting on the i th defect ($\mathbf{F}_i = -\nabla_i \mathcal{U}$) as $\mathbf{F}_i = |\mathbf{F}_i|(\cos \psi_i, \sin \psi_i)$. For the defect orientation θ_i , Eq. (5) then reduces to

$$\partial_t \theta_i = v \frac{\mu\gamma}{8K} |\mathbf{F}_i| |\mathbf{e}_i| \sin(\theta_i - \psi_i). \quad (6)$$

Active backflows tend to align the defect polarization with the force acting on the defect. A similar alignment kernel has been used previously to phenomenologically model flocking and jamming in cellular systems [55,56], but here it arises naturally from the active dynamics of a two-dimensional nematic. Importantly, here the torque is controlled by activity ($v \propto \alpha$). An extensile system ($v \propto \alpha < 0$) favors *alignment* of the polarization with the force, while a contractile system ($v \propto \alpha > 0$) favors *antialignment* of polarization and force (Fig. 2). The equations obtained

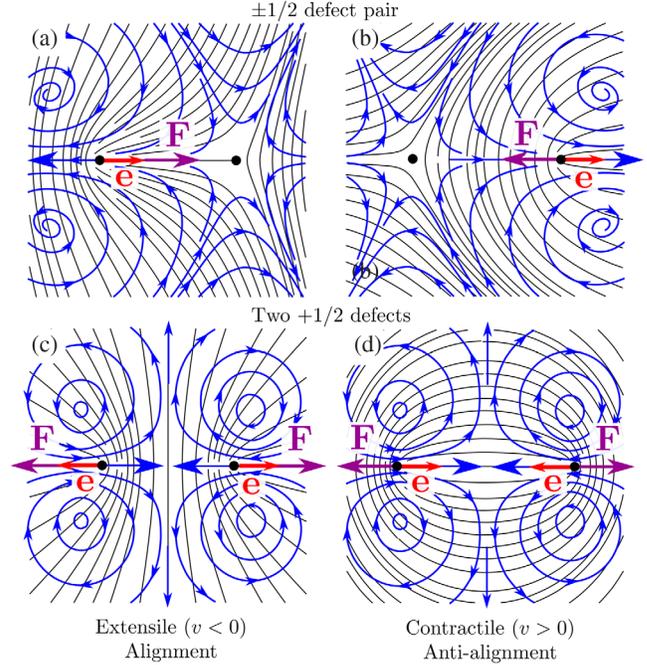


FIG. 2. Configurations of defect pairs whose orientations, for an imposed fixed separation, are stable to transverse fluctuations of the $+1/2$ polarization(s). The active backflow is shown in blue and the director configuration in black. The polarization and force on each $+1/2$ defect is shown in red and in purple, respectively. The top row shows a neutral $\pm 1/2$ defect pair orientationally stable for (a) extensile ($v < 0$) and (b) contractile ($v > 0$) systems. Similarly, in the bottom row we have a pair of $+1/2$ defects that are orientationally stable. The far field nematic texture for these two-defect configurations has an asterlike structure when (c) extensile ($v < 0$) and a vortexlike structure when (d) contractile ($v > 0$).

here also predict patterns for four $+1/2$ defects on a sphere as obtained in Ref. [19].

For configurations in which the $+1/2$ is running *away* from the $-1/2$ in an isolated neutral defect pair, the active aligning torque [Eq. (6)] stabilizes the $+1/2$ defect polarization against transverse fluctuations [see Figs. 2(a)–2(b)], irrespective of the sign of activity. Hence activity not only renders the $+1/2$ defect motile, but enhances the persistence of defect motion through the torques, favoring the unbinding of defect pairs. This feature breaks the symmetry between pair creation and annihilation events for both extensile and contractile systems and justifies the one-dimensional cartoon in Fig. 1. As we will see below, however, the stochastic part of the defect dynamics (neglected so far) can disrupt these configurations, preventing unbinding. We finally remark that one can also obtain configurations for pairs of $+1/2$ disclinations [Figs. 2(c)–2(d)] that are stable against transverse deflections of either polarization. As shown, in the far-field of these two-defect configurations, asterlike structures are favored in an extensile system while vortexlike structures are favored in a contractile one, as seen in confined fibroblasts [57].

The stochastic part of the dynamics of \mathbf{e}_i also derives from noise in the dynamics of \mathbf{Q} , but a full calculation is challenging and beyond the scope of the present work. In the limit of low activity, we assume that the noise statistics can be inferred from the known equilibrium joint probability distribution of \mathbf{r}_i^\pm and \mathbf{e}_i ,

$$P_{\text{eq}}^{2N} = \frac{1}{Z_{2N}} e^{-\mathcal{U}/T} \prod_{i=1}^N \left(\frac{K}{2\pi T} e^{-K|\mathbf{e}_i|^2/2T} \right), \quad (7)$$

where Z_{2N} is the Coulomb gas partition function and $K|\mathbf{e}_i|^2/2$ is the simplest contribution to the defect core energy [58]. This results in

$$\dot{\mathbf{e}}_i = \frac{5\mu\gamma}{8K} [\nabla_i \mathcal{U} \cdot (\mathbf{v}\mathbf{e}_i - \mu \nabla_i \mathcal{U})] \mathbf{e}_i + \frac{v\mu\gamma}{8K} (\nabla_i \mathcal{U} \times \mathbf{e}_i) \boldsymbol{\epsilon} \cdot \mathbf{e}_i - \sqrt{2D_R} \boldsymbol{\epsilon} \cdot \mathbf{e}_i \eta_i(t) + \boldsymbol{\nu}_i(t), \quad (8)$$

where we have written \mathbf{v}_i in terms of the force $-\nabla_i \mathcal{U}$. Smooth director phase fluctuations can be shown to generate rotational noise [first term in the second line of Eq. (8)] that changes the direction of \mathbf{e}_i , while keeping $|\mathbf{e}_i|$ fixed. Here $\eta_i(t)$ is unit white noise and $D_R = \mu T / \ell_R^2$ is the rotational diffusivity of the $+1/2$ defect, with $\ell_R \sim a$. The properties of the longitudinal component $\boldsymbol{\nu}_i(t)$ of the noise are determined by requiring that the probability distribution of the defect gas relaxes to the corresponding equilibrium form where (for one Frank constant) defect position and polarization are decoupled in the absence of activity (i.e., for $v = 0$), with the result (see Supplemental Material [41])

$$\langle \boldsymbol{\nu}_i(t) \boldsymbol{\nu}_j(t') \rangle = \mathbf{1} \delta_{ij} T \frac{5\mu^2\gamma}{4} \frac{|\nabla_i \mathcal{U}|^2}{K^2} \delta(t - t'). \quad (9)$$

No summation on repeated indices is implied. As written, the noise has no stochastic ambiguity and is independent of any thermodynamic parameters, involving only the defect mobility μ and rotational viscosity γ , as it should.

To study defect unbinding, we now examine the dynamics of an isolated $\pm 1/2$ defect pair governed by coupled Langevin equations for the pair separation $\mathbf{r} = \mathbf{r}^+ - \mathbf{r}^-$ [obtained from Eqs. (3a), (3b)] and the $+1/2$ polarization \mathbf{e} [Eq. (8)]. We derive and solve the corresponding Fokker-Planck equation for the steady state distribution, perturbatively in activity by using an isotropic closure for $\langle \mathbf{e}\mathbf{e} \rangle$ and neglecting all higher order moments in \mathbf{e} (see Supplemental Material [41]). Integrating over the polarization, we obtain the steady-state defect pair density at large distances to have an equilibrium like form $\rho_{ss}(\mathbf{r}) \propto e^{-\mathcal{U}_{\text{eff}}(\mathbf{r})/T}$ with an effective pair potential $\mathcal{U}_{\text{eff}}(\mathbf{r}) \simeq (\pi K_{\text{eff}}/2) \ln(r/a)$ where, to leading order in activity,

$$K_{\text{eff}}(v) = K - \frac{v^2}{2\mu D_R} \left(1 + \mu\gamma \frac{3T}{4K} \right) + \mathcal{O}(v^4). \quad (10)$$

Hence, for large pair separation, the defect interaction is weakened by activity. A small activity reduces the entropic

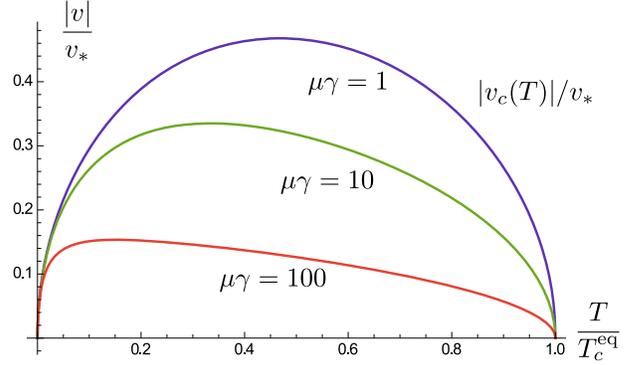


FIG. 3. Phase boundary in the $|v| - T$ plane [Eq. (11)] for different values of $\mu\gamma$. The region enclosed by the curve $|v_c(T)|$ for a given $\mu\gamma$ corresponds to the ordered nematic.

BKT transition temperature $T_c^{\text{eq}} = \pi K/8$ to $T_c(v) = \pi K_{\text{eff}}(v)/8$. Inverting this equation for small $|v|$, we obtain the phase boundary below which the ordered nematic is stable,

$$\frac{|v_c(T)|}{v_*} = \sqrt{\frac{16\tilde{T}(1-\tilde{T})}{\pi[1 + (3\pi/32)\mu\gamma\tilde{T}]}}, \quad (11)$$

with $\tilde{T} = T/T_c^{\text{eq}}$ and $v_* = \mu T_c^{\text{eq}}/\ell_R$. As shown in Fig. 3, this implies reentrant behavior as a function of T . If the rotational diffusivity D_R has a nonthermal part D_R^a , then there is a nonzero activity threshold $\sim \sqrt{D_R^a}$ for unbinding as $T \rightarrow 0$ and no reentrance at low activity. If D_R^a is large enough then reentrance is abolished altogether. For $|v| > |v_c(T)|$, the effective pair potential \mathcal{U}_{eff} develops a maximum as in Fig. 1, thereby implying that incipient defect pairs unbind for arbitrarily small temperature. The physical picture is then quite clear. At low activity, rotational diffusion randomizes the orientation of the $+1/2$ disclination and makes its motion less persistent, allowing the defect pair to remain bound. It is in this way that noise

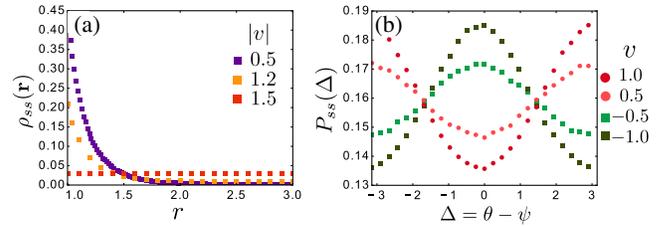


FIG. 4. Steady-state statistics for a $\pm 1/2$ defect pair in a periodic box of size $L = 50a$ ($T/T_c^{\text{eq}} = 0.51$, all other parameters are unity). (a) The pair separation distribution $\rho_{ss}(\mathbf{r})$ for low ($|v| = 0.5, 1.2$, bound phase) and high ($|v| = 1.5$, unbound phase) activity, suggesting that Eq. (11) which gives $|v_c| \simeq 2.06$, overestimates the unbinding threshold. (b) The distribution of the relative angle ($\Delta = \theta - \psi$) between the polarization \mathbf{e} and the force \mathbf{F} on the $+1/2$ defect for extensile (square) and contractile (circle) systems.

counterintuitively stabilizes the ordered nematic phase. At higher activity, the active torques compete with rotational diffusion, but ultimately enhance the persistent nature of defect motion. In this case rotational noise becomes irrelevant and we recover the scenario sketched in Fig. 1. The simple one dimensional model predicts defect unbinding self-consistently if the persistence length of the $+1/2$ disclination ($|v|/D_R$) is greater than the position of the barrier in the potential [$r_c = K/(|v|\gamma)$]. Equating the two lengths, we obtain the same threshold scaling as in Eq. (11) at low T . We have verified this scenario by numerically integrating Eqs. (3) and (8) for either sign of v , as shown in Fig. 4.

In summary, starting from the equations of motion of a two-dimensional active nematic, we have derived the statistical dynamics of its topological defects as a noisy mixture of motile and nonmotile particles. Through a Fokker-Planck approach, we show perturbatively that the rotational diffusion of $+1/2$ defects allows the nematic phase to survive defect proliferation below an activity threshold. We identify, for small activity, the temperature-activity locus of a BKT-like active-nematic-isotropic transition, and provide arguments suggesting that defects are unbound at any nonzero temperature above a critical activity, and that a reentrant disordered phase arises at low temperature. Venturing beyond the present perturbative approach and taking many-defect features, such as screening, into account are clearly the immediate challenges.

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*sushanka@syr.edu

†sriram@iisc.ac.in

‡Present address: Department of Physics, University of California, Santa Barbara, California 93106, USA
mcmarche@syr.edu

§bowick@kitp.ucsb.edu

- [1] P. G. De Gennes and J. Prost, *The Physics of Liquid Crystals* (Clarendon Press, Oxford, 1993).
- [2] I. Chuang, R. Durrer, N. Turok, and B. Yurke, Cosmology in the laboratory: Defect dynamics in liquid crystals, *Science* **251**, 1336 (1991).
- [3] M. J. Bowick, L. Chandar, E. A. Schiff, and A. M. Srivastava, The cosmological kibble mechanism in the laboratory: String formation in liquid crystals, *Science* **263**, 943 (1994).
- [4] G. E. Volovik, *The Universe in a Helium Droplet* (Clarendon Press, Oxford, 2003), Vol. 117.
- [5] V. L. Berezinskii, Destruction of long-range order in one-dimensional and two-dimensional systems having a continuous symmetry group I. Classical systems, *Zh. Eksp. Teor. Fiz.* **59**, 907 (1971) [*Sov. J. Exper. Theor. Phys.* **32**, 493 (1971)]; Destruction of long-range order in one-dimensional and two-dimensional systems possessing a continuous symmetry group. II. Quantum Systems, *Zh. Eksp. Teor. Fiz.* **61**, 1144 (1971) [*Sov. J. Exper. Theor. Phys.* **34**, 610 (1972)].
- [6] J. M. Kosterlitz and D. J. Thouless, Ordering, metastability and phase transitions in two-dimensional systems, *J. Phys. C* **6**, 1181 (1973).
- [7] J. M. Kosterlitz, The critical properties of the two-dimensional xy model, *J. Phys. C* **7**, 1046 (1974).
- [8] D. L. Stein, Kosterlitz-thouless phase transitions in two-dimensional liquid crystals, *Phys. Rev. B* **18**, 2397 (1978).
- [9] S. Ramaswamy, R. Aditi Simha, and J. Toner, Active nematics on a substrate: Giant number fluctuations and long-time tails, *Europhys. Lett.* **62**, 196 (2003).
- [10] A. Ahmadi, M. Cristina Marchetti, and T. B. Liverpool, Hydrodynamics of isotropic and liquid crystalline active polymer solutions, *Phys. Rev. E* **74**, 061913 (2006).
- [11] H. Gruler, U. Dewald, and M. Eberhardt, Nematic liquid crystals formed by living amoeboid cells, *Eur. Phys. J. B* **11**, 187 (1999).
- [12] R. Kemkemer, D. Kling, D. Kaufmann, and H. Gruler, Elastic properties of nematoid arrangements formed by amoeboid cells, *Eur. Phys. J. E* **1**, 215 (2000).
- [13] G. Duclos, S. Garcia, H. G. Yevick, and P. Silberzan, Perfect nematic order in confined monolayers of spindle-shaped cells, *Soft Matter* **10**, 2346 (2014).
- [14] S. Zhou, A. Sokolov, O. D. Lavrentovich, and I. S. Aranson, Living liquid crystals, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 1265 (2014).
- [15] D. Nishiguchi, K. H. Nagai, H. Chaté, and M. Sano, Long-range nematic order and anomalous fluctuations in suspensions of swimming filamentous bacteria, *Phys. Rev. E* **95**, 020601 (2017).
- [16] K. Kawaguchi, R. Kageyama, and M. Sano, Topological defects control collective dynamics in neural progenitor cell cultures, *Nature (London)* **545**, 327 (2017).
- [17] T. B. Saw, A. Doostmohammadi, V. Nier, L. Kocgozlu, S. Thampi, Y. Toyama, P. Marcq, C. T. Lim, J. M. Yeomans, and B. Ladoux, Topological defects in epithelia govern cell death and extrusion, *Nature (London)* **544**, 212 (2017).
- [18] T. Sanchez, D. T. N. Chen, S. J. DeCamp, M. Heymann, and Z. Dogic, Spontaneous motion in hierarchically assembled active matter, *Nature (London)* **491**, 431 (2012).
- [19] F. C. Keber, E. Loiseau, T. Sanchez, S. J. DeCamp, L. Giomi, M. J. Bowick, M. C. Marchetti, Z. Dogic, and A. R. Bausch, Topology and dynamics of active nematic vesicles, *Science* **345**, 1135 (2014).
- [20] P. W. Ellis, D. J. G. Pearce, Y.-W. Chang, G. Goldsztein, L. Giomi, and A. Fernandez-Nieves, Curvature-induced defect unbinding and dynamics in active nematic toroids, *Nat. Phys.* **14**, 85 (2018).
- [21] V. Narayan, S. Ramaswamy, and N. Menon, Long-lived giant number fluctuations in a swarming granular nematic, *Science* **317**, 105 (2007) (Also see Supplemental Material

- at http://science.sciencemag.org/content/suppl/2007/07/05/317.5834.105.DC1?_ga=2.179103332.1326147887.1535141063-1731216484.1511393993, page 4).
- [22] S. Mishra, R. A. Simha, and S. Ramaswamy, A dynamic renormalization group study of active nematics, *J. Stat. Mech.* **2010**, P02003.
- [23] E. Bertin, H. Chaté, F. Ginelli, S. Mishra, A. Peshkov, and S. Ramaswamy, Mesoscopic theory for fluctuating active nematics, *New J. Phys.* **15**, 085032 (2013).
- [24] X.-q. Shi, H. Chaté, and Y.-q. Ma, Instabilities and chaos in a kinetic equation for active nematics, *New J. Phys.* **16**, 035003 (2014).
- [25] S. Ngo, A. Peshkov, I. S. Aranson, E. Bertin, F. Ginelli, and H. Chaté, Large-Scale Chaos and Fluctuations in Active Nematics, *Phys. Rev. Lett.* **113**, 038302 (2014).
- [26] S. Shankar, S. Ramaswamy, and M. C. Marchetti, Low-noise phase of a two-dimensional active nematic system, *Phys. Rev. E* **97**, 012707 (2018).
- [27] L. Giomi, M. J. Bowick, X. Ma, and M. C. Marchetti, Defect Annihilation and Proliferation in Active Nematics. *Phys. Rev. Lett.* **110**, 228101 (2013).
- [28] P. Guillamat, J. Ignés-Mullol, S. Shankar, M. C. Marchetti, and F. Sagués, Probing the shear viscosity of an active nematic film, *Phys. Rev. E* **94**, 060602 (2016).
- [29] P. Guillamat, J. Ignés-Mullol, and F. Sagués, Control of active liquid crystals with a magnetic field, *Proc. Natl. Acad. Sci. U.S.A.* **113**, 5498 (2016).
- [30] P. Guillamat, J. Ignés-Mullol, and F. Sagués, Taming active turbulence with patterned soft interfaces, *Nat. Commun.* **8**, 564 (2017).
- [31] S. P. Thampi, R. Golestanian, and J. M. Yeomans, Velocity Correlations in an Active Nematic, *Phys. Rev. Lett.* **111**, 118101 (2013).
- [32] X.-q. Shi and Y.-q. Ma, Topological structure dynamics revealing collective evolution in active nematics, *Nat. Commun.* **4**, 3013 (2013).
- [33] L. Giomi, M. J. Bowick, P. Mishra, R. Sknepnek, and M. C. Marchetti, Defect dynamics in active nematics, *Phil. Trans. R. Soc. A* **372**, 20130365 (2014).
- [34] S. P. Thampi, R. Golestanian, and J. M. Yeomans, Instabilities and topological defects in active nematics, *Europhys. Lett.* **105**, 18001 (2014).
- [35] S. P. Thampi, R. Golestanian, and J. M. Yeomans, Vorticity, defects and correlations in active turbulence, *Phil. Trans. R. Soc. A* **372**, 20130366 (2014).
- [36] T. Gao, R. Blackwell, M. A. Glaser, M. D. Betterton, and M. J. Shelley, Multiscale Polar Theory of Microtubule and Motor-Protein Assemblies, *Phys. Rev. Lett.* **114**, 048101 (2015).
- [37] L. Giomi, Geometry and Topology of Turbulence in Active Nematics, *Phys. Rev. X* **5**, 031003 (2015).
- [38] L. M. Pismen, Dynamics of defects in an active nematic layer, *Phys. Rev. E* **88**, 050502 (2013).
- [39] A. Maitra and M. Cates (private communication).
- [40] A. N. Beris and B. J. Edwards, *Thermodynamics of Flowing Systems: With Internal Microstructure*, No. 36 (Oxford University Press on Demand, Oxford, 1994).
- [41] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/PhysRevLett.121.108002> for a derivation and discussion.
- [42] S. Ramaswamy, The mechanics and statistics of active matter, *Annu. Rev. Condens. Matter Phys.* **1**, 323 (2010).
- [43] M. C. Marchetti, J.-F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. A. Simha, Hydrodynamics of soft active matter, *Rev. Mod. Phys.* **85**, 1143 (2013).
- [44] D. Cortese, J. Eggers, and T. B. Liverpool, Pair creation, motion, and annihilation of topological defects in two-dimensional nematic liquid crystals, *Phys. Rev. E* **97**, 022704 (2018).
- [45] Including a “second” active force $\sim \alpha' \mathbf{Q} \cdot (\nabla \cdot \mathbf{Q})$ does not affect the ballistic motion of the $+1/2$ defect [48].
- [46] Apart from the motility of the $+1/2$ defect, both charge disclinations are also entrained by active flows generated by other defects. This leads to $\dot{\mathbf{r}}_i^\pm \sim \alpha \sigma_3 \cdot \nabla_i \sum_{j \neq i} q_j \ln |(\mathbf{r}_i - \mathbf{r}_j)/a|$, where σ_3 is a Pauli matrix, and provides an anisotropic active correction to bend and splay elasticity. Including fluctuations, this term is $\sim \mathcal{O}(r_{ij}^{-1-\eta})$ [26], where r_{ij} is the distance between two defects and $\eta = T/(2\pi K)$, so it is subdominant to the passive interaction $\nabla_i \mathcal{U}$.
- [47] P. Srivastava, P. Mishra, and M. C. Marchetti, Negative stiffness and modulated states in active nematics, *Soft Matter* **12**, 8214 (2016).
- [48] A. Maitra, P. Srivastava, M. C. Marchetti, J. S. Lintuvuori, S. Ramaswamy, and M. Lenz, A nonequilibrium force can stabilize 2D active nematics, *Proc. Natl. Acad. Sci. U.S.A.* **115**, 6934 (2018).
- [49] L. M. Pismen and J. D. Rodriguez, Mobility of singularities in the dissipative Ginzburg-Landau equation, *Phys. Rev. A* **42**, 2471 (1990).
- [50] G. Ryskin and M. Kremenetsky, Drag Force on a Line Defect Moving through an Otherwise Undisturbed Field: Disclination Line in a Nematic Liquid Crystal, *Phys. Rev. Lett.* **67**, 1574 (1991).
- [51] C. Denniston, Disclination dynamics in nematic liquid crystals, *Phys. Rev. B* **54**, 6272 (1996).
- [52] L. M. Pismen, *Vortices in Nonlinear Fields: From Liquid Crystals to Superfluids, from Non-Equilibrium Patterns to Cosmic Strings* (Oxford University Press, New York, 1999).
- [53] A. J. Vromans and L. Giomi, Orientational properties of nematic disclinations, *Soft Matter* **12**, 6490 (2016).
- [54] X. Tang and J. V. Selinger, Orientation of topological defects in 2d nematic liquid crystals, *Soft Matter* **13**, 5481 (2017).
- [55] B. Szabo, G. J. Szöllösi, B. Gönci, Z. Jurányi, D. Selmeczi, and T. Vicsek, Phase transition in the collective migration of tissue cells: experiment and model, *Phys. Rev. E* **74**, 061908 (2006).
- [56] S. Henkes, Y. Fily, and M. C. Marchetti, Active jamming: Self-propelled soft particles at high density, *Phys. Rev. E* **84**, 040301 (2011).
- [57] G. Duclos, C. Erlenkämper, J.-F. Joanny, and P. Silberzan, Topological defects in confined populations of spindle-shaped cells, *Nat. Phys.* **13**, 58 (2017).
- [58] P. M. Chaikin and T. C. Lubensky, *Principles of Condensed Matter Physics* (Cambridge University Press, Cambridge, England, 2000).