Defect Unbinding in Active Nematics

Suraj Shankar, Sriram Ramaswamy, M. Cristina Marchetti, and Mark J. Bowick

Phys. Rev. Lett. **121**, 108002 — Published 7 September 2018

DOI: 10.1103/PhysRevLett.121.108002

Defect unbinding in active nematics

Suraj Shankar[a,b],[*] Sriram Ramaswamy[b,c],[†] M. Cristina Marchetti[a,b],[‡] and Mark J. Bowick[a,b§]
[a] *Physics Department and Syracuse Soft and Living Matter Program, Syracuse University, Syracuse, NY 13244, USA.*
[b] *Kavli Institute for Theoretical Physics, University of California, Santa Barbara, CA 93106, USA.*
[c] *Centre for Condensed Matter Theory, Department of Physics, Indian Institute of Science, Bangalore 560012, India.*
(Dated: August 3, 2018)

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 non-equilibrium 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 re-entrant 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.

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 line-like 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 point-like 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 2d 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 spatio-temporal 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 comet-like 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.

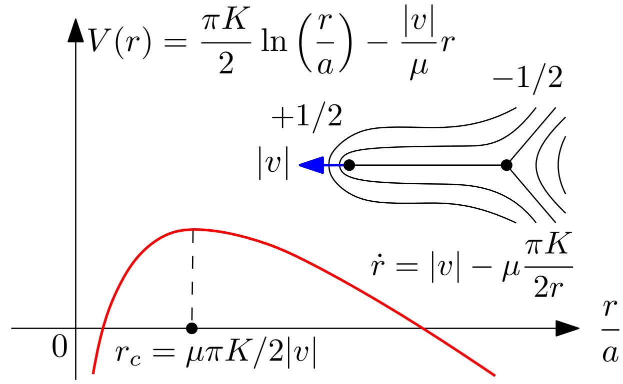

FIG. 1: Potential $V(r)$ for a neutral defect pair for the configuration in which the direction of motility of the +1/2 disclination points away from the −1/2 and is held fixed. This naïve picture suggests that incipient active defect pairs have an exponentially small, but finite, rate to overcome the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

In this paper 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 Berezenskii-Kosterlitz-Thouless (BKT) transition in $2d$ 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 re-entrant isotropic-nematic-isotropic sequence [55] 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]

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

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 $V(r_c) = (\pi K/2)\left[\ln\left(\pi\mu K/(2|v|a)\right) - 1\right]$ 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 $2d$ nematic liquid crystal written in terms of the flow velocity $\mathbf{u}$ and the tensor order parameter $Q_{\mu\nu} = S(2n_\mu n_\nu - \delta_{\mu\nu})$, 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 [39],

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

where $\mathcal{D}_t = \partial_t + \mathbf{u}\cdot\boldsymbol{\nabla} - [\cdot,\boldsymbol{\Omega}]$ is the comoving and corotational derivative with the vorticity tensor $\Omega_{\mu\nu} = (\nabla_\mu u_\nu - \nabla_\nu u_\mu)/2$. 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 SI. 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 $-\Gamma\mathbf{u} + \boldsymbol{\nabla}\cdot\boldsymbol{\sigma}^a = \mathbf{0}$, 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 [40, 41]. 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 $\mathbf{e}_i = a\boldsymbol{\nabla}\cdot\mathbf{Q}(\mathbf{r}_i^+)$ (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. [42] to treat multi-defect configurations. An isolated $+1/2$ defect has a non-vanishing 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 doesn't, due to its three-fold symmetry ($\mathbf{u}(\mathbf{r}_i^-) = \mathbf{0}$) [56]. We show that the resulting positional dynamics of the defects, including both motility and passive interactions (for a derivation, see SI) [57], is given by

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

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

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

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

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 [43, 44]. Here we take $K > 0$ (permitted in a domain of parameter space [43, 44]) 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 SI) gives logarithmic corrections to the defect mobility μ [45–48]. 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 $\dot{\mathbf{e}}_i(t) = a[\mathbf{v}_i(t)\cdot\boldsymbol{\nabla}]\boldsymbol{\nabla}\cdot\mathbf{Q}(\mathbf{r}_i^+(t))$, where $\mathbf{v}_i = v\mathbf{e}_i - \mu\boldsymbol{\nabla}_i\mathcal{U}$ 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 [49, 50] (a more detailed justification and comparison is given in the SI). 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 $\boldsymbol{\nabla}\boldsymbol{\nabla}\cdot\mathbf{Q}$ at the core of the defect to obtain (for details, see SI)

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

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 ($\mathbf{F}_i = -\boldsymbol{\nabla}_i\mathcal{U}$) 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 [51, 52], but here it arises naturally from the active dynamics of a $2d$ 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 *anti-alignment* of polarization and force (Fig. 2). The equations obtained 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 Fig. 2a-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 $1d$ 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 (Fig. 2c-d) that are stable against transverse deflections of either polarization. As shown, aster-like structures are favored in an extensile system while vortex-like structures are favored in a contractile one, as seen in confined fibroblasts [53].

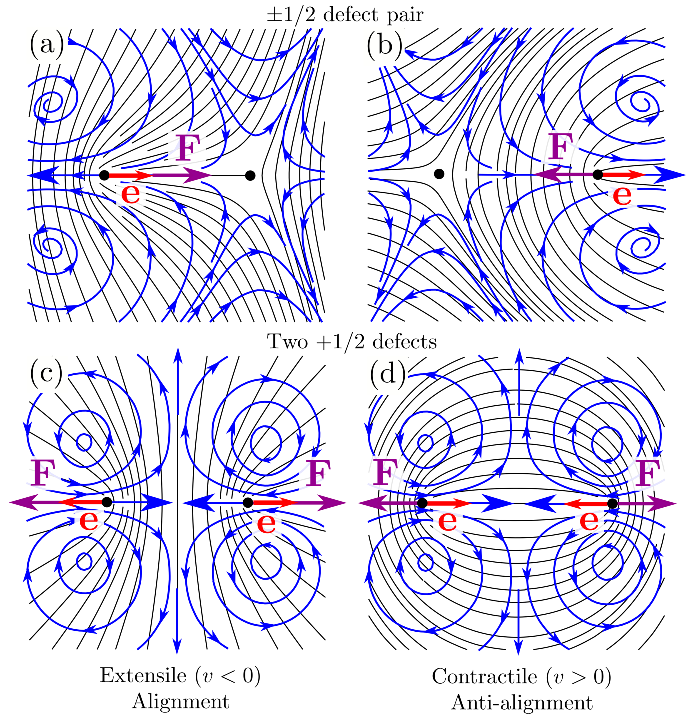

FIG. 2: Configurations of defect pairs whose orientations, for an imposed fixed separation, are stable to transverse fluctuations of the $+1/2$ polarization(s). The active backflow is shown in blue and the director configuration in black. The polarization and force on each $+1/2$ defect is shown in red and in purple respectively. The top row shows a neutral $\pm1/2$ 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 aster-like structure when (c) extensile ($v < 0$) and a vortex-like structure when (d) contractile ($v > 0$).

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

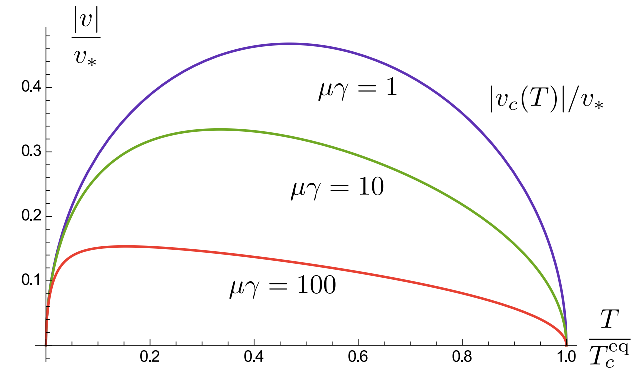

FIG. 3: Phase boundary in the $|v| - T$ plane (Eq. 11) for different values of $\mu\gamma$. The region enclosed by the curve $|v_c(T)|$ for a given $\mu\gamma$ corresponds to the ordered nematic.

energy [54]. This results in

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

where we have written $\mathbf{v}_i$ in terms of the force $-\boldsymbol{\nabla}_i\mathcal{U}$. 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 SI)

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

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 $\pm1/2$ 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 $\langle\mathbf{ee}\rangle$ and neglecting all higher order moments in $\mathbf{e}$ (see SI). Integrating over the polarization, we obtain the steady-state defect pair density at large distances to have an equilibrium-like form $\rho_{ss}(\mathbf{r}) \propto e^{-\mathcal{U}_{\mathrm{eff}}(\mathbf{r})/T}$ with an effective pair potential $\mathcal{U}_{\mathrm{eff}}(\mathbf{r}) \simeq (\pi K_{\mathrm{eff}}/2)\ln(r/a)$ where, to leading order in activity,

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

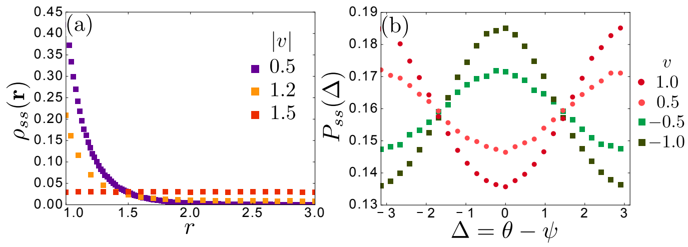

FIG. 4: Steady-state statistics for a $\pm1/2$ defect pair in a periodic box of size $L = 50a$ ($T/T_c^{\mathrm{eq}} = 0.51$, all other parameters are unity). (a) The pair separation distribution $\rho_{ss}(\mathbf{r})$ for low ($|v| = 0.5, 1.2$, bound phase) and high ($|v| = 1.5$, unbound phase) activity, 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 (□) and contractile (◯) systems.

Hence, for large pair separation, the defect interaction is weakened by activity. A small activity reduces the entropic BKT transition temperature $T_c^{\mathrm{eq}} = \pi K/8$ to $T_c(v) = \pi K_{\mathrm{eff}}(v)/8$. Inverting this equation for small $|v|$, we obtain the phase boundary below which the ordered nematic is stable,

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

with $\tilde{T} = T/T_c^{\mathrm{eq}}$ and $v_* = \mu T_c^{\mathrm{eq}}/\ell_R$. As shown in Fig. 3, this implies re-entrant behavior as a function of T. If the rotational diffusivity D_R has a non-thermal part D_R^a, then there is a nonzero activity threshold $\sim\sqrt{D_R^a}$ for unbinding as $T \to 0$ and no re-entrance at low activity. If D_R^a is large enough then re-entrance is abolished altogether. For $|v| > |v_c(T)|$, the effective pair potential $\mathcal{U}_{\mathrm{eff}}$ 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 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 $1d$ 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

$2d$ active nematic, we have derived the statistical dynamics of its topological defects as a noisy mixture of motile and non-motile 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 re-entrant 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.

We thank Ananyo Maitra and Mike Cates for insightful comments. This work was supported by the National Science Foundation at Syracuse University through awards DMR-1609208 (MCM & SS) and DGE-1068780 (MCM) and at KITP under Grant PHY-1748958. MCM, MJB & SS thank the Syracuse Soft and Living Matter Program for support. All authors thank the Simons Foundation for support and the KITP for hospitality in the course of this work. SR acknowledges the support of the Tata Education and Development Trust, and a J C Bose Fellowship of the Science & Engineering Research Board, India.

* sushanka@syr.edu
† sriram@iisc.ac.in
‡ mcmarche@syr.edu
§ bowick@kitp.ucsb.edu

[1] Pierre Gilles De Gennes and Jacques Prost. *The physics of liquid crystals*. Clarendon Press, Oxford, 1993.

[2] Isaac Chuang, Ruth Durrer, Neil Turok, and Bernard Yurke. Cosmology in the laboratory: Defect dynamics in liquid crystals. *Science*, 251(4999):1336–1342, 1991.

[3] Mark J Bowick, L Chandar, Eric A Schiff, and Ajit M Srivastava. The cosmological kibble mechanism in the laboratory: string formation in liquid crystals. *Science*, 263(5149):943–945, 1994.

[4] Grigory E Volovik. *The universe in a helium droplet*, volume 117. Clarendon Press, 2003.

[5] VL Berezinskii. Destruction of long-range order in one-dimensional and two-dimensional systems having a continuous symmetry group i. classical systems. *Soviet Journal of Experimental and Theoretical Physics*, 32:493, 1971 [ZhETF 59, 907 (1971)].

[6] John Michael Kosterlitz and David James Thouless. Ordering, metastability and phase transitions in two-dimensional systems. *Journal of Physics C: Solid State Physics*, 6(7):1181, 1973.

[7] JM Kosterlitz. The critical properties of the two-dimensional xy model. *Journal of Physics C: Solid State Physics*, 7(6):1046, 1974.

[8] DL Stein. Kosterlitz-thouless phase transitions in two-dimensional liquid crystals. *Physical Review B*, 18(5): 2397, 1978.

[9] Sriram Ramaswamy, R Aditi Simha, and John Toner. Active nematics on a substrate: Giant number fluctuations and long-time tails. *EPL (Europhysics Letters)*, 62 (2):196, 2003.

[10] Aphrodite Ahmadi, M Cristina Marchetti, and Tanniemola B Liverpool. Hydrodynamics of isotropic and liquid crystalline active polymer solutions. *Physical Review E*, 74(6):061913, 2006.

[11] H Gruler, U Dewald, and M Eberhardt. Nematic liquid crystals formed by living amoeboid cells. *The European Physical Journal B-Condensed Matter and Complex Systems*, 11(1):187–192, 1999.

[12] R Kemkemer, D Kling, D Kaufmann, and H Gruler. Elastic properties of nematoid arrangements formed by amoeboid cells. *The European Physical Journal E*, 1(2-3):215–225, 2000.

[13] Guillaume Duclos, Simon Garcia, HG Yevick, and P Silberzan. Perfect nematic order in confined monolayers of spindle-shaped cells. *Soft matter*, 10(14):2346–2353, 2014.

[14] Shuang Zhou, Andrey Sokolov, Oleg D. Lavrentovich, and Igor S. Aranson. Living liquid crystals. *Proceedings of the National Academy of Sciences*, 111(4):1265–1270, 2014.

[15] Daiki Nishiguchi, Ken H Nagai, Hugues Chaté, and Masaki Sano. Long-range nematic order and anomalous fluctuations in suspensions of swimming filamentous bacteria. *Physical Review E*, 95(2):020601, 2017.

[16] Kyogo Kawaguchi, Ryoichiro Kageyama, and Masaki Sano. Topological defects control collective dynamics in neural progenitor cell cultures. *Nature*, 545(7654):327, 2017.

[17] Thuan Beng Saw, Amin Doostmohammadi, Vincent Nier, Leyla Kocgozlu, Sumesh Thampi, Yusuke Toyama, Philippe Marcq, Chwee Teck Lim, Julia M Yeomans, and Benoit Ladoux. Topological defects in epithelia govern cell death and extrusion. *Nature*, 544(7649):212, 2017.

[18] Tim Sanchez, Daniel TN Chen, Stephen J DeCamp, Michael Heymann, and Zvonimir Dogic. Spontaneous motion in hierarchically assembled active matter. *Nature*, 491(7424):431–434, 2012.

[19] Felix C Keber, Etienne Loiseau, Tim Sanchez, Stephen J DeCamp, Luca Giomi, Mark J Bowick, M Cristina Marchetti, Zvonimir Dogic, and Andreas R Bausch. Topology and dynamics of active nematic vesicles. *Science*, 345(6201):1135–1139, 2014.

[20] Perry W Ellis, Daniel JG Pearce, Ya-Wen Chang, Guillermo Goldsztein, Luca Giomi, and Alberto Fernandez-Nieves. Curvature-induced defect unbinding and dynamics in active nematic toroids. *Nature Physics*, 14(1):85, 2018.

[21] Vijay Narayan, Sriram Ramaswamy, and Narayanan Menon. Long-lived giant number fluctuations in a swarming granular nematic. *Science*, 317(5834):105–108, 2007 (Also see Supporting Information, page 4).

[22] Shradha Mishra, R Aditi Simha, and Sriram Ramaswamy. A dynamic renormalization group study of active nematics. *Journal of Statistical Mechanics: Theory and Experiment*, 2010(02):P02003, 2010.

[23] Eric Bertin, Hugues Chaté, Francesco Ginelli, Shradha Mishra, Anton Peshkov, and Sriram Ramaswamy. Mesoscopic theory for fluctuating active nematics. *New journal of physics*, 15(8):085032, 2013.

[24] Xia-qing Shi, Hugues Chaté, and Yu-qiang Ma. Instabil-

ities and chaos in a kinetic equation for active nematics. *New Journal of Physics*, 16(3):035003, 2014.

[25] Sandrine Ngo, Anton Peshkov, Igor S Aranson, Eric Bertin, Francesco Ginelli, and Hugues Chaté. Large-scale chaos and fluctuations in active nematics. *Physical review letters*, 113(3):038302, 2014.

[26] Suraj Shankar, Sriram Ramaswamy, and M Cristina Marchetti. Low-noise phase of a two-dimensional active nematic system. *Physical Review E*, 97(1):012707, 2018.

[27] Luca Giomi, Mark J Bowick, Xu Ma, and M Cristina Marchetti. Defect annihilation and proliferation in active nematics. *Physical review letters*, 110(22):228101, 2013.

[28] Pau Guillamat, Jordi Ignés-Mullol, Suraj Shankar, M Cristina Marchetti, and Francesc Sagués. Probing the shear viscosity of an active nematic film. *Physical Review E*, 94(6):060602, 2016.

[29] Pau Guillamat, Jordi Ignés-Mullol, and Francesc Sagués. Control of active liquid crystals with a magnetic field. *Proceedings of the National Academy of Sciences*, 113 (20):5498–5502, 2016.

[30] Pau Guillamat, Jordi Ignés-Mullol, and Francesc Sagués. Taming active turbulence with patterned soft interfaces. *Nature communications*, 8(1):564, 2017.

[31] Sumesh P Thampi, Ramin Golestanian, and Julia M Yeomans. Velocity correlations in an active nematic. *Physical review letters*, 111(11):118101, 2013.

[32] Xia-qing Shi and Yu-qiang Ma. Topological structure dynamics revealing collective evolution in active nematics. *Nature communications*, 4:3013, 2013.

[33] Luca Giomi, Mark J Bowick, Prashant Mishra, Rastko Sknepnek, and M Cristina Marchetti. Defect dynamics in active nematics. *Phil. Trans. R. Soc. A*, 372(2029): 20130365, 2014.

[34] Sumesh P Thampi, Ramin Golestanian, and Julia M Yeomans. Instabilities and topological defects in active nematics. *EPL (Europhysics Letters)*, 105(1):18001, 2014.

[35] Sumesh P Thampi, Ramin Golestanian, and Julia M Yeomans. Vorticity, defects and correlations in active turbulence. *Phil. Trans. R. Soc. A*, 372(2029):20130366, 2014.

[36] Tong Gao, Robert Blackwell, Matthew A Glaser, Meredith D Betterton, and Michael J Shelley. Multiscale polar theory of microtubule and motor-protein assemblies. *Physical review letters*, 114(4):048101, 2015.

[37] Luca Giomi. Geometry and topology of turbulence in active nematics. *Physical Review X*, 5(3):031003, 2015.

[38] LM Pismen. Dynamics of defects in an active nematic layer. *Physical Review E*, 88(5):050502, 2013.

[39] Antony N Beris and Brian J Edwards. *Thermodynamics of flowing systems: with internal microstructure*. Number 36. Oxford University Press on Demand, 1994.

[40] Sriram Ramaswamy. The mechanics and statistics of active matter. *Annual Review of Condensed Matter Physics*, 1(1):323–345, 2010.

[41] M Cristina Marchetti, Jean-François Joanny, Sriram Ramaswamy, Tanniemola B Liverpool, Jacques Prost, Madan Rao, and R Aditi Simha. Hydrodynamics of soft active matter. *Reviews of Modern Physics*, 85(3):1143, 2013.

[42] Dario Cortese, Jens Eggers, and Tanniemola B Liverpool. Pair creation, motion, and annihilation of topological defects in two-dimensional nematic liquid crystals. *Physical Review E*, 97(2):022704, 2018.

[43] Pragya Srivastava, Prashant Mishra, and M Cristina Marchetti. Negative stiffness and modulated states in active nematics. *Soft Matter*, 12(39):8214–8225, 2016.

[44] Ananyo Maitra, Pragya Srivastava, M Cristina Marchetti, Juho S Lintuvuori, Sriram Ramaswamy, and Martin Lenz. A nonequilibrium force can stabilize 2d active nematics. *Proceedings of the National Academy of Sciences*, page 201720607, 2018.

[45] LM Pismen and JD Rodriguez. Mobility of singularities in the dissipative ginzburg-landau equation. *Physical Review A*, 42(4):2471, 1990.

[46] G Ryskin and M Kremenetsky. Drag force on a line defect moving through an otherwise undisturbed field: Disclination line in a nematic liquid crystal. *Physical review letters*, 67(12):1574, 1991.

[47] Colin Denniston. Disclination dynamics in nematic liquid crystals. *Physical Review B*, 54(9):6272, 1996.

[48] Len M Pismen. *Vortices in nonlinear fields: from liquid crystals to superfluids, from non-equilibrium patterns to cosmic strings*, volume 100. Oxford University Press, 1999.

[49] Arthur J Vromans and Luca Giomi. Orientational properties of nematic disclinations. *Soft matter*, 12(30):6490–6495, 2016.

[50] Xingzhou Tang and Jonathan V Selinger. Orientation of topological defects in 2d nematic liquid crystals. *Soft matter*, 13(32):5481–5490, 2017.

[51] Balint Szabo, GJ Szöllösi, B Gönci, Zs Jurányi, David Selmeczi, and Tamás Vicsek. Phase transition in the collective migration of tissue cells: experiment and model. *Physical Review E*, 74(6):061908, 2006.

[52] Silke Henkes, Yaouen Fily, and M Cristina Marchetti. Active jamming: Self-propelled soft particles at high density. *Physical Review E*, 84(4):040301, 2011.

[53] Guillaume Duclos, Christoph Erlenkämper, Jean-François Joanny, and Pascal Silberzan. Topological defects in confined populations of spindle-shaped cells. *Nature Physics*, 13(1):58, 2017.

[54] Paul M Chaikin and Tom C Lubensky. *Principles of condensed matter physics*. Cambridge university press, 2000.

[55] A. Maitra and M. Cates, personal communication.

[56] Including a “second” active force $\sim \alpha' \mathbf{Q} \cdot (\boldsymbol{\nabla} \cdot \mathbf{Q})$ does not affect the ballistic motion of the $+1/2$ defect [44].

[57] 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 $\dot{\mathbf{r}}_i^{\pm} \sim \alpha \boldsymbol{\sigma}_3 \cdot \boldsymbol{\nabla}_i \sum_{j \neq i} q_j \ln |(\mathbf{r}_i - \mathbf{r}_j)/a|$, where $\boldsymbol{\sigma}_3$ 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 $\boldsymbol{\nabla}_i \mathcal{U}$.