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Stochastic dynamics of chemotactic colonies with logistic growth

RICCARDO BEN ALÌ ZINATI¹(a)(b) (b), CHARLIE DUCLUT²(b) (b), SAEED MAHDISOLTANI^{3,4}(b) (b), ANDREA GAMBASSI⁵ (b) and RAMIN GOLESTANIAN^{4,3} (b)

¹ Sorbonne Université & CNRS, Laboratoire de Physique Théorique de la Matière Condensée, LPTMC F-75005, Paris, France

² Max-Planck-Institut für Physik komplexer Systeme - D-01187 Dresden, Germany

³ Rudolf Peierls Centre for Theoretical Physics, University of Oxford - Oxford OX1 3PU, UK

⁴ Max Planck Institute for Dynamics and Self-Organization (MPIDS) - D-37077 Göttingen, Germany

⁵ SISSA – International School for Advanced Studies & INFN - via Bonomea 265, I-34136 Trieste, Italy

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Abstract – The interplay between cellular growth and cell-cell signaling is essential for the aggregation and proliferation of bacterial colonies, as well as for the self-organization of cell tissues. To investigate this interplay, we focus here on the collective properties of dividing chemotactic cell colonies by studying their long-time and large-scale dynamics through a renormalization group (RG) approach. The RG analysis reveals that a relevant but unconventional chemotactic interaction —corresponding to a polarity-induced mechanism— is generated by fluctuations at macroscopic scales, even when an underlying mechanism is absent at the microscopic level. This emerges from the interplay of the well-known Keller-Segel (KS) chemotactic nonlinearity and cell birth and death processes. At one-loop order, we find no stable fixed point of the RG flow equations. We discuss a connection between the dynamics investigated here and the celebrated Kardar-Parisi-Zhang (KPZ) equation with long-range correlated noise, which points at the existence of a strong-coupling, nonperturbative fixed point.

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Introduction. - The pervasiveness of emergent selforganization in living systems shows how local interactions among individuals underpin global structures whose size can significantly exceed the microscopic scale set by each unit. Chemotaxis, namely the ability of cells and synthetic particles to direct their motion according to the spatial gradient of some chemical signals, is one of the primary mechanisms for such self-organization in many biological processes, e.g., immune response and cancer metastasis. Phenomenological models describing chemotaxis as a directed motion guided by the chemical gradients [1] and undergoing stochastic fluctuations [2-5] have proven useful in studying chemotactic aggregation (collapse) of bacteria [6,7], the collective behavior of synthetically active colloids and enzymes [8–12], as well as the interplay between birth and death processes among the living individuals of a colony [13,14].

A thorough investigation of the emergent properties of active systems can occasionally be achieved via a bottomup approach and by coarse-graining the microscopic dynamics of individual particles. Nevertheless, it is known that such a direct coarse-graining may not necessarily expose all the interaction terms that turn out to be relevant for describing the macroscopic dynamics of the system. To obtain a sound macroscopic description of the possibly emerging collective dynamics, one generally relies on statistical and field-theoretical techniques, such as the renormalization group (RG). These dictate the structure of the relevant interactions that are compatible with the symmetry and conservation laws of the system under investigation [15,16]. Such approaches have been successfully utilized in characterizing the dynamical properties of a wide range of biological and synthetic systems [17–24].

In the present work, we investigate the collective behavior of chemotactic particles undergoing birth and death processes by dynamic renormalization group theory. We find that an unconventional chemotactic coupling, previously studied in the context of polarity-induced chemotaxis [22], is generated at mesoscopic scales upon coarse-graining the dynamics, even when the underlying polarity mechanism is not explicitly present at the singleparticle level. We therefore extend the analysis presented in ref. [13], where the polarity-induced chemotactic term

^(a)E-mail: riccardo.baz@pm.me (corresponding author)

^(b)These authors contributed equally to this work.

was neglected, leading to a theory not closed under renormalization. The extended model presents a critical point separating a homogeneous phase with constant density from a collapsed phase characterized by aggregation and nonuniform particle density. At that critical point, in the framework of a perturbative dimensional expansion, we find that the RG flow exhibits a runaway behavior, with no real-valued stable RG fixed points in the vicinity of the upper critical dimension. However we highlight a connection between our model and the celebrated Kardar-Parisi-Zhang (KPZ) equation with long-range correlated noise [25], which suggests a possible explanation for the runaway behavior in terms of the existence of a strongcoupling fixed point which is beyond the reach of our analysis.

Stochastic chemotactic model with growth. -

Stochastic Keller-Segel model. A corpuscular description of the dynamics of the mobile chemotactic particles is obtained by considering n particles moving in a d-dimensional space, coupled according to the stochastic Langevin equation $\dot{\mathbf{r}}_i = \mu_1 \nabla \Phi(\mathbf{r}_i, t) + \boldsymbol{\xi}_i$, where $\mathbf{r}_i(t)$ describes the position of particle i, which undergoes an overdamped motion. The trajectory of each particle is biased by gradients of the chemical concentration field Φ according to the Keller-Segel (KS) model [1]; in addition, particles are subject to Gaussian white noises $\boldsymbol{\xi}_i$ with vanishing mean and correlations $\langle \xi_{i,\alpha}(t)\xi_{j,\beta}(t')\rangle = 2D\delta_{ij}\delta_{\alpha\beta}\delta(t-t')$, where D is the noise strength, $i, j = 1, \ldots, n$ are particle indices, and α, β indicate Cartesian coordinates.

As we are interested in the large-scale behavior of the colony, it is convenient to move from a microscopic description, to a coarser one involving a smoothly varying version $C(\mathbf{r}, t)$ of the particle density $\sum_{i=1}^{n} \delta^{d}(\mathbf{r} - \mathbf{r}_{i})$. To include the important fluctuations in the dynamics of the chemotactic colony [2,26], we go beyond a mean-field description following the Dean-Kawasaki approach [27,28], which yields a stochastic field theory for the density distribution of chemotactic particles [22,29]. The resulting Langevin dynamics describing the colony of chemotactic particles is given by [29]

$$\partial_t C = D\nabla^2 C - \mu_1 \nabla \cdot (C\nabla\Phi) + \nabla \cdot \boldsymbol{\xi}^{\text{con}}.$$
 (1)

This equation describes the stochastic evolution of the particle density with diffusion coefficient D and with KS chemotactic current $\mu_1 C \nabla \Phi$ [1]. The multiplicative noise field $\boldsymbol{\xi}^{\text{con}}$, which arises from the individual noises $\boldsymbol{\xi}_i$, has a vanishing mean and correlations $\langle \xi_{\alpha}^{\text{con}}(\mathbf{r},t)\xi_{\beta}^{\text{con}}(\mathbf{r}',t')\rangle = 2DC(\mathbf{r},t)\delta_{\alpha\beta}\delta^d(\mathbf{r}-\mathbf{r}')\delta(t-t').$

We assume that the particles release chemicals at constant rate. Under the assumption that the diffusion of chemicals is sufficiently fast compared to the particles' dynamics, the chemical field Φ instantaneously reaches the steady-state profile with $\partial_t \Phi(\mathbf{r}, t) \simeq 0$ corresponding to a given $C(\mathbf{r}, t)$ and is governed by the screened Poisson equation

$$\left(-\nabla^2 + \kappa^2\right)\Phi(\mathbf{r}, t) = C(\mathbf{r}, t),\tag{2}$$

where κ^{-1} is an effective screening length determined by the diffusive spread of the chemical signals before their degradation occurs.

Nonlinear birth and death processes. The combined effect of the cell birth and death processes and their long-range chemotactic interactions are essential to understand the macroscopic properties of growing cell colonies. As discussed in ref. [13], in order to account for birth and decay processes in the coarse-grained description of self-chemotactic systems, we phenomenologically extend the Langevin equation (1) by considering i) the cell division process $A \rightarrow 2A$ with rate β_d , and ii) the cell death/coagulation process $2A \rightarrow A$ with rate β_c . Utilizing a system-size expansion [30,31], one can encode these microscopic processes into a Langevin description for the particle density within a system of volume Ω , which is valid in the limit of a large number of particles and reads

$$\partial_t C|_{\text{growth}} = \lambda C (C_0 - C) + \xi^{\text{nc}}.$$
 (3)

Here, the subscript "growth" indicates that only the contributions from cell growth and death processes are accounted for in this equation. We have introduced the growth coefficient $\lambda = \beta_c \Omega$, the carrying capacity $C_0 = (1 + \beta_d / \beta_c) / \Omega$, and the nonconserving multiplicative noise $\xi^{\rm nc}$ with correlations

$$\langle \xi^{\rm nc}(\boldsymbol{r},t)\xi^{\rm nc}(\boldsymbol{r}',t')\rangle = \lambda C(C_0 - 2/\Omega + C)\delta^d(\boldsymbol{r} - \boldsymbol{r}')\delta(t - t').$$
(4)

Since we are interested in the dynamics in the asymptotic large-scale and long-time regime, the specific form of the microscopic processes that led to eq. (3) is irrelevant, provided that C_0 is a stable steady state of the growth process. It is worth mentioning that the Langevin description (3) breaks down close to the absorbing state $(C_0 \rightarrow 0)$, as suggested by the fact that, correspondingly, the noise correlations may become negative, leading to a Langevin dynamics with an ill-defined imaginary noise. Close to the absorbing state, one thus needs to make use of alternative descriptions of the growth processes that are exact at low densities [32,33]. In the following, we focus on the case in which the particle density is sufficiently large to be far from the absorbing state and such that the description given by eq. (4) is accurate.

Dynamics of density fluctuations. Provided the chemotactic colony is considered sufficiently far from the absorbing state of the dynamics, we expand the particle density C around the constant carrying capacity C_0 as $C(\mathbf{r},t) = C_0 + \rho(\mathbf{r},t)$, where $\rho \ll C_0$, and subsequently focus on the dynamics of the density-fluctuation field ρ . The chemical concentration Φ may also be expanded around a spatially uniform concentration Φ_0 according to $\Phi(\mathbf{r},t) = \Phi_0 + \phi(\mathbf{r},t)$, where ϕ represents the chemical fluctuations that induce chemotactic interactions among the particles [34]. As a result, eq. (2) relating the chemical concentration and particle density fields can be decomposed as $(-\nabla^2 + \kappa^2)\Phi_0 = C_0$ and $(-\nabla^2 + \kappa^2)\phi = \rho(\mathbf{r}, t)$, where the first equation admits the uniform solution $\Phi_0 = \kappa^{-2}C_0$. Accordingly, the background chemical concentration Φ_0 is maintained by the uniform part of the particle density C_0 , whereas the chemical fluctuation field $\phi(\mathbf{r}, t)$ is induced by the particle fluctuations, $\rho(\mathbf{r}, t)$. In the limit in which the chemical signals do not degrade considerably within the system size and are therefore capable of mediating interactions among distant particles [8,34], the chemical fluctuation ϕ is given by the Poisson-like equation

$$-\nabla^2 \phi(\mathbf{r}, t) = \rho(\mathbf{r}, t). \tag{5}$$

As we discuss below, focusing on particle and chemical fluctuations ρ and ϕ also renders the noise terms in the dynamics additive [13,22].

Chemotactic model with growth. Let us consider the coarse-grained model of chemotaxis that also accounts for birth and decay processes. Combining eqs. (1) and (3), the stochastic Langevin equation for the density fluctuations ρ reads

$$(\tau\partial_t - D\nabla^2 + \sigma)\rho = -\lambda\rho^2 - \mu_1\nabla(\rho\nabla\phi) - \mu_2\nabla^2(\nabla\phi)^2 + \zeta.$$
(6)

The linear term $\sigma = (\lambda - \mu_1)C_0$ introduces a length scale $\xi = \sqrt{D/\sigma}$ over which density fluctuations remain correlated. Such correlation length diverges when the control parameter σ approaches its critical value σ_c . This critical point σ_c demarks the transition between a dilute, homogeneous phase for $\sigma > \sigma_c$, and a dense, collapsed one for $\sigma < \sigma_c$ [22]. In the absence of nonlinearities, the critical value $\sigma_{c,0} = 0$ is achieved when the linear part of the chemotactic aggregation term $\mu_1 C_0$ balances the linear decay contribution $C_0\lambda$. In the presence of nonlinearities, this critical value will be shifted, with a non-universal fluctuation-induced shift that depends on microscopic details. Note also that we have introduced the time-scale parameter τ since it eventually acquires a non-trivial renormalization.

In addition to the KS chemotactic nonlinearity $\mu_1 \nabla \cdot (\rho \nabla \phi)$, in eq. (6) we have also introduced a second chemotactic nonlinearity $\mu_2 \nabla^2 (\nabla \phi)^2$; this unconventional interaction is a relevant coupling in the macroscopic dynamics, and, as has been shown in ref. [22], it gives rise to novel large-scale phenomena such as superdiffusion and non-Poissonian number fluctuations in the absence of nonlinear growth processes. The μ_2 coupling may arise from the polarity effects in the microscopic dynamics of chemotactic particles, and therefore this term is referred to as the *polarity-induced chemotaxis* [22]. As will become clear below, even if this term is not present in the single-particle dynamics of eq. (6), the polarity-induced coupling is effectively generated in the macroscopic dynamics upon coarsegraining and it is as relevant (in the RG sense) as the KS nonlinear term $\propto \mu_1$ and the nonlinear growth term $\propto \lambda$. In this respect, the present analysis extends the model of ref. [13] by incorporating the effective polarity-induced coupling in the chemotactic dynamics.

Finally, the noise term $\zeta = \xi^{\text{nc}} + \nabla \cdot \boldsymbol{\xi}^{\text{con}}$ in eq. (6) is Gaussian and combines an additive and a multiplicative part. As long as the system evolves far from the absorbing state, the expansion $C = C_0 + \rho$ allows us to discard the multiplicative part of the noise ζ , as it is also RG irrelevant [22]. The remaining additive noise has correlations given by

$$\langle \zeta(\mathbf{r},t)\zeta(\mathbf{r}',t')\rangle = 2(\mathcal{D}_0 - \mathcal{D}_2\nabla^2)\delta^d(\mathbf{r} - \mathbf{r}')\delta(t-t'), \quad (7)$$

where the conserving part $\mathcal{D}_2 = DC_0$ comes from the stochastic KS equation (1), whereas the nonconserving part $\mathcal{D}_0 = \lambda C_0^2$ comes from the expansion¹ of the stochastic growth equation (3).

To conclude this section, let us analyse the symmetries of the stochastic chemotaxis model with growth. The Langevin equation (6) possesses a trivial ϕ -shift symmetry and a more subtle pseudo-Galilean symmetry. The ϕ -shift symmetry is a direct consequence of the fact that the dynamics considered here is only sensitive to the gradients of the chemical field ϕ , which makes the Langevin equation trivially invariant under the shift $\phi \rightarrow \phi' = \phi + \text{const.}$ The pseudo-Galilean symmetry expresses the invariance of the dynamics under the transformation [22]

$$\phi'(\mathbf{r},t) = \phi(\mathbf{r} + t(\mu_1 - 2\mu_2)\mathbf{v}/\tau, t) - \mathbf{v} \cdot \mathbf{r}, \qquad (8a)$$

$$\rho'(\mathbf{r},t) = \rho(\mathbf{r} + t(\mu_1 - 2\mu_2)\mathbf{v}/\tau, t), \tag{8b}$$

where \mathbf{v} is an arbitrary *d*-dimensional boost vector. As we discuss below, this symmetry enforces an identity between critical exponents. Moreover, in the absence of the $\lambda \rho^2$ term, eq. (6) reduces to the number-conserving chemotaxis model considered in ref. [22]. In that case, the pseudo-Galilean symmetry, accompanied by the nonrenormalization of the noise term, is such that the dynamical scaling exponents can be determined exactly. In the present case of chemotactic dynamics with logistic growth, namely eq. (6), even if an exact exponent identity holds as a consequence of the pseudo-Galilean transformation (8)(see eq. (13)), the noise term \mathcal{D}_0 acquires a non-trivial renormalization due to the presence of λ . As a consequence, the critical exponents are no longer known exactly, but we describe in the following how they can be calculated by using RG techniques.

Renormalization group analysis. – Transforming eq. (6) in Fourier space² we obtain

$$\rho(\hat{k}) = G_0(\hat{k})\zeta(\hat{k}) + G_0(\hat{k}) \int_{\hat{k}_1} V_0(\mathbf{k}, \mathbf{k}_1)\rho(\hat{k}_1)\rho(\hat{k}-\hat{k}_1), \quad (9)$$

¹We have neglected the term $2/\Omega$ compared to C_0 in eq. (4), which is consistent with the assumption of being far from an absorbing state and of considering large populations, such that $\Omega \gg 1$.

²Here we use the following convention: $f(\mathbf{x}, t) = \int_{\hat{k}} f(\mathbf{k}, \omega) \mathrm{e}^{-\mathrm{i}\omega t + \mathrm{i}\mathbf{k}\cdot\mathbf{x}}$ with shorthand notation $\hat{k} \equiv (\mathbf{k}, \omega)$ and $\int_{\hat{k}} \equiv \int \mathrm{d}^d \mathbf{k} \, \mathrm{d}\omega/(2\pi)^{d+1}$.

where $G_0(\hat{k}) \equiv (-i\tau\omega + Dk^2 + \sigma)^{-1}$ is the bare propagator, a scaling function. The three critical exponents z, χ and $\tilde{\chi}$ while the nonlinearities $\mu_{1,2}$ and λ enter via the the vertex are in principle independent; however, the pseudo-Galilean function $V_0(\mathbf{k}, \mathbf{k}_1)$, which upon symmetrization $\mathbf{k}_1 \leftrightarrow \mathbf{k} - \mathbf{k}_1$ \mathbf{k}_1 , reads

$$V_{0}(\mathbf{k}, \mathbf{k}_{1}) = -\lambda - \mu_{2} \frac{\mathbf{k}_{1} \cdot (\mathbf{k} - \mathbf{k}_{1})k^{2}}{(\mathbf{k} - \mathbf{k}_{1})^{2}k_{1}^{2}} + \frac{1}{2}\mu_{1} \left[\frac{\mathbf{k} \cdot \mathbf{k}_{1}}{k_{1}^{2}} + \frac{\mathbf{k} \cdot (\mathbf{k} - \mathbf{k}_{1})}{(\mathbf{k} - \mathbf{k}_{1})^{2}} \right].$$
(10)

We then denote the bare correlation function (spectral function) $N_0(\hat{k}) = 2\mathcal{D}_0|G_0(\hat{k})|^2$. Note that we have discarded the conserving part of the noise correlations (7)proportional to \mathcal{D}_2 , as it is irrelevant in the RG sense. In view of setting the perturbative expansion, it is convenient to introduce the following diagrammatic representation [25, 35]:

$$G_0(\hat{k}) = \rightarrow$$
, $V_0(\mathbf{k}, \mathbf{k}_1) = -\langle , N_0(\hat{k}) = \rightarrow \circ \leftarrow$. (11)

The integral equation (9) is then solved perturbatively in the vertex V_0 : the one-loop corrections to the bare quantities (11) are schematically given by

$$\begin{split} G(\hat{k}) &= & \rightarrow + 4 \not \longrightarrow, \\ V(\mathbf{k}, \mathbf{k}_1) &= - \not \leftarrow + 4 - \not \bigcirc , \\ N(\hat{k}) &= \rightarrow \odot \leftarrow + 2 \not \longrightarrow \leftarrow, \end{split}$$

where the prefactors in front of each one-loop contribution account for all the possible noise contractions (the corresponding explicit expressions are given in the Supplementary Material Supplementarymaterial.pdf (SM)). The renormalization group procedure can then be set by first integrating out fluctuations within the momentum shell $\Lambda e^{-\ell} \leq |\mathbf{k}| \leq \Lambda$, where Λ represents the momentum cutoff (set, e.g., by the inverse particle size). This momentum integration is followed by a rescaling back to the original cutoff Λ , a rescaling of the fields according to $\rho \to \rho' = e^{\ell \chi} \rho$, $\eta \to \eta' = e^{-\ell \tilde{\chi}} \eta$, and a temporal rescaling $t \to t' = e^{\ell z} t$. The roughness exponent χ , the dynamical exponent z, and the exponent $\tilde{\chi}$, characterize the scaling behavior of the critical system in the macroscopic limit. For instance, the long-time and large-scale particle density correlations assume the scaling form [15,25]

$$\langle \rho(\mathbf{x},t)\rho(\mathbf{x}',t)\rangle \sim |\mathbf{x}'-\mathbf{x}|^{2\chi}F\left(\frac{|t'-t|}{|\mathbf{x}'-\mathbf{x}|^{z}}\right),$$
 (12)

where F is a scaling function.

The exponent $\tilde{\chi}$ determines the scaling properties of the response function R of the system to an external force $h(\mathbf{x}', t')$. Namely, by defining $R(\mathbf{x}, t, \mathbf{x}', t') =$ $\delta \langle \rho(\mathbf{x},t) \rangle / \delta h(\mathbf{x}',t') |_{h=0}$, we have $R(\mathbf{x},t,\mathbf{x}',t') \sim |\mathbf{x}' - \mathbf{x}'|_{h=0}$ $\mathbf{x}^{|\chi+\tilde{\chi}}H(|t'-t|/|\mathbf{x}'-\mathbf{x}|^z)$ in the asymptotic limit, with H

symmetry (8) enforces the exact exponent identity [22]

$$z + \chi = 0. \tag{13}$$

Furthermore, we note that for systems relaxing to an equilibrium configuration (which is not the case here), the fluctuation-dissipation theorem provides a relation between response function and correlation function [36], which implies the exponent identity $2\chi - z = \chi + \tilde{\chi}$. This identity is broken³ for the critical dynamics of eq. (6).

We obtain the RG functions in the limit $\ell \to 0$ and through a dimensional expansion in the parameter $\varepsilon =$ $d_c - d \ll 1$ around the upper critical dimension $d_c = 6$. On defining the rescaled variables $\bar{\lambda}^2 = \lambda^2 K_d \Lambda^{-\varepsilon} \mathcal{D}_0 / (D^3 \tau)$ and $\bar{\mu}_{1,2}^2 = \mu_{1,2}^2 K_d \Lambda^{-\varepsilon} \mathcal{D}_0 / (D^3 \tau)$, where $K_d \equiv S_d / (2\pi)^d$ with S_d the area of a unit sphere in d dimensions, we obtain the following RG flow equations:

$$\frac{\partial_{\ell} \mathcal{D}_{0}}{\mathcal{D}_{0}} = d + z + 2\tilde{\chi} + \bar{\lambda}^{2}, \qquad (14a)$$

$$\frac{\partial_{\ell} D}{D} = d + z + \chi + \tilde{\chi} - 2 - \frac{25}{48}\bar{\mu}_{1}^{2} - \frac{15}{8}\bar{\mu}_{1}\bar{\mu}_{2}$$

$$- \frac{1}{16}\bar{\mu}_{1}\bar{\lambda} + \frac{53}{24}\bar{\mu}_{2}\bar{\lambda} + \frac{2}{3}\bar{\lambda}^{2}, \qquad (14b)$$

$$\partial_{\ell}\tau = (d + \chi + \tilde{\chi})\tau - \frac{5}{6}\bar{\mu}_{1}\bar{\lambda} + \bar{\lambda}^{2}, \qquad (14c)$$

$$\partial_{\ell}\bar{\mu}_{1} = (d + z + 2\chi + \tilde{\chi})\,\bar{\mu}_{1} - \frac{l}{8}\bar{\mu}_{1}^{2}\bar{\lambda} + \frac{11}{6}\bar{\mu}_{1}\bar{\mu}_{2}\bar{\lambda} + \frac{1}{2}\bar{\mu}_{2}^{2}\bar{\lambda} + \bar{\mu}_{1}\bar{\lambda}^{2} - 2\bar{\mu}_{2}\bar{\lambda}^{2}, \qquad (14d)$$

$$\partial_{\ell}\bar{\mu}_{2} = (d + z + 2\chi + \tilde{\chi})\,\bar{\mu}_{2} - \frac{1}{48}\bar{\mu}_{1}^{2}\bar{\lambda} \\ + \frac{1}{12}\bar{\mu}_{1}\bar{\mu}_{2}\bar{\lambda} + \frac{1}{4}\bar{\mu}_{2}^{2}\bar{\lambda}\,, \qquad (14e)$$

$$\partial_{\ell}\bar{\lambda} = (d+z+2\chi+\tilde{\chi})\bar{\lambda} + \frac{35}{16}\bar{\mu}_{1}^{2}\bar{\lambda} + \frac{5}{4}\bar{\mu}_{1}\bar{\mu}_{2}\bar{\lambda} + \frac{5}{12}\bar{\mu}_{2}^{2}\bar{\lambda} - 6\bar{\mu}_{1}\bar{\lambda}^{2} - \frac{4}{3}\bar{\mu}_{2}\bar{\lambda}^{2} + 4\bar{\lambda}^{3}.$$
(14f)

By taking the logarithm of the definition of $\bar{\mu}_{1,2}$ and λ , differentiating with respect to ℓ , and taking advantage of eq. (14), we obtain the following closed flow equations for arbitrary χ , $\tilde{\chi}$ and z,

$$\partial_{\ell}\bar{\lambda} = \frac{1}{2}\bar{\lambda}\varepsilon + 3\bar{\lambda}^3 - \frac{527}{96}\bar{\mu}_1\bar{\lambda}^2 - \frac{223}{48}\bar{\mu}_2\bar{\lambda}^2 + \frac{95}{32}\bar{\mu}_1^2\bar{\lambda} + \frac{5}{12}\bar{\mu}_2^2\bar{\lambda} + \frac{65}{16}\bar{\mu}_1\bar{\mu}_2\lambda, \quad (15a)$$

$$\partial_{\ell}\bar{\mu}_{1} = \frac{1}{2}\bar{\mu}_{1}\varepsilon + \frac{25}{32}\bar{\mu}_{1}^{3} - \frac{35}{96}\bar{\mu}_{1}^{2}\bar{\lambda} + \frac{45}{16}\bar{\mu}_{1}^{2}\bar{\mu}_{2} - \frac{71}{48}\bar{\mu}_{2}\bar{\mu}_{1}\bar{\lambda} + \frac{1}{2}\bar{\mu}_{2}^{2}\bar{\lambda} - 2\bar{\mu}_{2}\bar{\lambda}^{2}, \qquad (15b)$$

³Note that the latter identity is accidentally recovered at the fixed points of the dynamics when the nonlinear growth coupling is set to zero $(\lambda = 0)$ —even though the polarity-induced coupling is itself a nonequilibrium interaction and is not derivable from a free-energy functional [22].

$$\partial_{\ell}\bar{\mu}_{2} = \frac{1}{2}\bar{\mu}_{2}\varepsilon - \frac{49}{16}\bar{\mu}_{2}^{2}\bar{\lambda} + \frac{45}{16}\bar{\mu}_{1}\bar{\mu}_{2}^{2} - \bar{\lambda}^{2}\bar{\mu}_{2} + \frac{19}{32}\bar{\mu}_{1}\bar{\mu}_{2}\bar{\lambda} + \frac{25}{32}\bar{\mu}_{1}^{2}\bar{\mu}_{2} - \frac{1}{48}\bar{\mu}_{1}^{2}\bar{\lambda}.$$
(15c)

These one-loop RG equations are the main technical result of this paper. Consistently with the proximity to the Gaussian fixed point, we choose the values of χ , $\tilde{\chi}$ and z such that D, \mathcal{D}_0 and τ do not flow under RG, *i.e.*, we impose $\partial_{\ell}D = \partial_{\ell}\mathcal{D}_0 = \partial_{\ell}\tau = 0$. This choice is such that the scaling of the correlation length ξ , which is controlled by the ratio D/σ , is determined solely by the scaling of σ . Likewise, the density fluctuations in the renormalized system, which are controlled by the ratio $\mathcal{D}_0/(D\tau)$, remain unchanged at the critical point and their scaling can therefore be determined directly from χ , $\tilde{\chi}$ and z. Adopting this choice, we find

$$z = 2 + \frac{25}{48}\bar{\mu}_1^2 + \frac{15}{8}\bar{\mu}_1\bar{\mu}_2 - \frac{37}{48}\bar{\mu}_1\bar{\lambda} - \frac{53}{24}\bar{\mu}_2\bar{\lambda} + \frac{1}{3}\bar{\lambda}^2, \quad (16a)$$

$$\tilde{\chi} = -\frac{1}{2}(z+d+\bar{\lambda}^2), \qquad (16b)$$

$$\chi = -d - \tilde{\chi} - \bar{\lambda}^2 + \frac{5}{6}\bar{\mu}_1\bar{\lambda}.$$
(16c)

Lastly, the critical state of the system can be reached by fine-tuning σ to its critical value σ_c . This is a fluctuationinduced and non-universal quantity, and we report its value and RG flow in the SM.

Fixed points. The system of equations (15) admits the Gaussian fixed point $\bar{\mu}_1^{\star} = \bar{\mu}_2^{\star} = \bar{\lambda}^{\star} = 0$ as a solution, which is unstable below the upper critical dimension $d < d_c = 6$ and stable above it. In the parameter space, we then focus on the plane $(\bar{\mu}_1, \bar{\mu}_2, \bar{\lambda}^{\star} = 0)$, for which eqs. (15) reduce to a closed system in the variables $(\bar{\mu}_1, \bar{\mu}_2)$. The RG flow on this plane is governed by the stable lines of fixed points defined by the conics

$$\bar{\mu}_{2}^{\star} = -\frac{8\varepsilon}{45\bar{\mu}_{1}^{\star}} - \frac{5\bar{\mu}_{1}^{\star}}{18} \quad \text{and} \quad \bar{\lambda}^{\star} = 0.$$
 (17)

The asymptotic lines corresponding to these hyperbolas separate regions of the reduced couplings plane where the RG flow runs away to infinity, shown by the blue arrows in the top panel of fig. 1, from the basin of attraction of the fixed points that are shaded in red in the same figure. (See ref. [22] for a detailed analysis of the flow equations of the chemotactic model without the nonlinear growth term.)

As discussed in ref. [22], the runaway behavior of the one-loop RG flows in the $\lambda = 0$ plane could hint to several different scenarios, and thus it calls for further investigations. In particular, it may be an artifact of the one-loop approximation used here. On the other hand, the runaway solution could signal a first-order phase transition, or, alternatively, it may suggest that the critical behavior of the dynamics is ruled by a strong-coupling fixed point that is not within the reach of the perturbative RG calculations. The latter possibility is supported by a connection



Fig. 1: Top: one-loop RG flows in the parameter space. The red hyperbolas in the $\lambda = 0$ plane correspond to the fixed-point solutions in eq. (17). The blue arrows show four instances of RG flow lines with $\lambda \neq 0$, all appearing to exhibit runaway behavior. Bottom: projected RG flow on the plane $\mu_2 = -2\mu_1$ (gray plane in the top panel). Note the crossover behavior of the trajectories starting from $\lambda \neq 0$, which first approach the line of fixed points at $\lambda = 0$ before diverging.

between the chemotactic Langevin dynamics (6) and the KPZ equation [37], which describes the fluctuations of a growing interface and is known to exhibit a nonperturbative behavior [38,39]. We further discuss this connection below.

For chemotactic dynamics with logistic growth, our oneloop analysis shows that no stable real-valued RG fixed point exists in the space $(\bar{\mu}_1, \bar{\mu}_2, \bar{\lambda} \neq 0)$ and in the vicinity of the upper critical dimension (see the SM for a discussion of possible fixed points at lower dimensions). A linear stability analysis which considers a perturbation around the fixed-point solutions (18) gives the eigenvalues $\theta_{1,2,3}$ of the associated stability matrix as

$$\theta_1 = -\varepsilon, \quad \theta_2 = 0, \quad \theta_3 = \frac{16 - 220\bar{\mu}_1^2 + 2275\bar{\mu}_1^4}{1215\bar{\mu}_1^2}\varepsilon.$$
 (18)

The eigenvalue θ_1 is negative for $\varepsilon > 0$ and indicates that the line of fixed points is attractive in the plane $\lambda = 0$, as already discussed above. The eigenvalue $\theta_2 = 0$ is the marginal direction along the line of fixed points. The eigenvalue θ_3 is always positive for $\varepsilon > 0$ and with $\bar{\mu}_1 \in \mathbb{R}$, and it indicates that the perturbations in a direction orthogonal to the plane $\lambda = 0$ are unstable.

The analysis presented above therefore shows the absence of stable perturbative fixed point for the chemotactic system with growth. This contrasts with the findings of ref. [13] where a stable fixed point was reported for the dynamics of dividing chemotactic cells without the polarityinduced coupling. Importantly, even if not present at the microscopic level, the polarity-induced chemotactic term proportional to μ_2 is immediately generated by the presence of the growth term $\propto \lambda$ (see eqs. (15)). This observation highlights the fundamental role played by the polarity-induced mechanism in describing the macroscopic properties of dividing chemotactic colonies.

In passing, we mention that along the line $(\bar{\mu}_1^* = 0, \bar{\mu}_2^* = 0, \bar{\lambda})$, we find two imaginary RG fixed points with coordinates $\bar{\lambda}^* = \pm i \sqrt{\varepsilon/6}$. These correctly describe the dynamics of the Yang-Lee edge singularity [40,41] for which, at one-loop order, we recover the known critical exponents $z = 2 - \varepsilon/18$ and $\chi = -2 + 5\varepsilon/9$ [42,43].

As a final remark, we discuss the relation between eq. (6) and the KPZ dynamics [37]. Consider the roughening of an interface with height profile $h(\mathbf{r}, t)$ and subject to a long-ranged correlated noise $\tilde{\eta}$. The corresponding dynamics reads [25]

$$\partial_t h = D\nabla^2 h + g(\nabla h)^2 + \tilde{\eta}, \tag{19}$$

where the noise $\tilde{\eta}$ has correlations $\langle \tilde{\eta}(\mathbf{k}, \omega) \tilde{\eta}(\mathbf{k}_1, \omega_1) \rangle = 2\mathcal{D}_{\text{LR}}k^{-2\theta}\delta^d(\mathbf{k} + \mathbf{k}_1)\delta(\omega + \omega_1)$, with θ characterizing the long-range nature of its spatial correlations (the original short-ranged KPZ equation is recovered for $\theta = 0$). By taking the Laplacian of eq. (19), one then arrives at

$$\partial_t \nabla^2 h = D \nabla^2 (\nabla^2 h) + g \nabla^2 (\nabla h)^2 + \eta, \qquad (20)$$

the noise is now characterized bv where η $\langle \eta(\mathbf{k},\omega)\eta(\mathbf{k}_1,\omega_1)\rangle = 2\mathcal{D}_{\mathrm{LR}}k^{4-2\theta}\delta^d(\mathbf{k}+\mathbf{k}_1)\delta(\omega+\omega_1)$ In the absence of the nonlinearities μ_1 and λ , the Langevin equation (6), which now describes the dynamics of chemotactic particles with only the polarity-induced mechanism, can be mapped to the KPZ model (20) with long-range correlated noise, by setting $\theta = 2$ and identifying $\phi \leftrightarrow h$ and $\mu_2 \leftrightarrow g$. The pseudo-Galilean symmetry (8) of the original chemotactic model then corresponds to the Galilean symmetry of the KPZ equation. Note that in this case, eq. (16) yields the critical exponents z = 2, $\chi = -2 - \varepsilon/2$ and $\tilde{\chi} = -4 + \varepsilon/2$, which are consistent with the fact that these exponents should not acquire correction at any order of the perturbation theory with ε -expansion (rather than a "fixed-d" scheme) [38,44]. A scenario which resembles the one described for polarityinduced chemotaxis [22] was recently analyzed in the context of conserved surface growth [45]. The authors corrected the original conserved KPZ equation by the introduction of a novel interaction term, responsible for the emergence of a new growth phase, possibly ruled by a strong-coupling fixed point [46]. Even if the two models share formally identical nonlinear terms, in chemotaxis one is interested at the evolution of the density field $\rho = -\nabla^2 \phi$, namely $\partial_t \nabla^2 \phi$, rather than that of the field ϕ itself. This seemingly innocuous statement, however, is such that chemotaxis is characterized by the emergence of a pseudo-Galilean symmetry, resulting in exact dynamical scaling exponents. The emergence of this symmetry prevents the generation of other nonlinearities which could in principle be considered based on scaling arguments [22,46].

Conclusion. – Starting from a microscopic model of chemotactic particles undergoing birth and death processes, we have derived a coarse-grained, field-theoretical description for the dynamics of density fluctuations in a growing self-chemotactic colony (see eq. (6)). In this Langevin description, we identify a pseudo-Galilean symmetry, which is also present in the case of non-dividing chemotactic particles [22]; this symmetry is reminiscent of the Galilean symmetry of the Kardar-Parisi-Zhang equation [37]. We then use perturbative RG techniques to investigate the scaling behavior of the dynamics at its critical point. Crucially, due to the interplay between the Keller-Segel chemotactic interactions and the logistic growth nonlinearity, fluctuations generate the so-called polarity-induced chemotactic coupling ($\propto \mu_2$ in eq. (6)) at macroscopic scales. Although the microscopic origin of this unconventional coupling may be attributed to particle polarity effects in chemotactic dynamics [22], its generation along the RG flow in the presence of growth processes shows that it needs to be incorporated in models of dividing chemotactic particles, even if the cells have an isotropic gradient-sensing mechanism with no polarity effects at the microscopic level.

We show that including the polarity-induced coupling changes the critical picture of the system compared to the analysis of ref. [13]. In particular, the chemotactic lines of fixed points that exist in the absence of the growth coupling λ [22] are unstable in the direction of λ , and we report the absence of any stable fixed point of the one-loop perturbative RG flow near the upper critical dimension $d_c = 6$ (see the SM for the discussion of a stable fixed point in d = 2). Importantly, even in the absence of a stable fixed point, the behavior of large but finite systems can still be dictated by the presence of the line of fixed points in the plane $\lambda = 0$, as illustrated by the crossover behavior in fig. 1. Determining whether a stable perturbative fixed point would be found at higher order in the perturbative expansion, or whether the absence of a stable perturbative fixed point is the signature of a strong-coupling critical point that would govern the critical behavior, requires further investigation, e.g., using nonperturbative RG techniques [47-50].

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REFERENCES

- KELLER E. F. and SEGEL L. A., J. Theor. Biol., 26 (1970) 399.
- [2] GRIMA R., Phys. Rev. Lett., 95 (2005) 128103.
- [3] GOLESTANIAN R., *Phys. Rev. Lett.*, **102** (2009) 188305.
- [4] SENGUPTA A., VAN TEEFFELEN S. and LÖWEN H., Phys. Rev. E, 80 (2009) 031122.
- [5] TAKTIKOS J., ZABURDAEV V. and STARK H., Phys. Rev. E, 85 (2012) 051901.
- [6] BRENNER M. P., LEVITOV L. S. and BUDRENE E. O., *Biophys. J.*, **74** (1998) 1677.
- [7] CHAVANIS P.-H. and SIRE C., Phys. Rev. E, 69 (2004) 016116.
- [8] GOLESTANIAN R., Phys. Rev. Lett., 108 (2012) 038303.
- [9] THAKUR S. and KAPRAL R., Phys. Rev. E, 85 (2012) 026121.
- [10] COHEN J. A. and GOLESTANIAN R., Phys. Rev. Lett., 112 (2014) 068302.
- [11] AGUDO-CANALEJO J., ILLIEN P. and GOLESTANIAN R., Nano Lett., 18 (2018) 2711.
- [12] AGUDO-CANALEJO J. and GOLESTANIAN R., Phys. Rev. Lett., **123** (2019) 018101.
- [13] GELIMSON A. and GOLESTANIAN R., *Phys. Rev. Lett.*, 114 (2015) 028101.
- [14] KRUSE K., JOANNY J. F., JÜLICHER F., PROST J. and SEKIMOTO K., Eur. Phys. J. E, 16 (2005) 5.
- [15] TÄUBER U. C., Critical Dynamics: A Field Theory Approach to Equilibrium and Non-Equilibrium Scaling Behavior (Cambridge University Press, Cambridge, UK) 2014.
- [16] KARDAR M., Statistical Physics of Fields (Cambridge University Press, Cambridge, UK) 2007.
- [17] TONER J. and TU Y., Phys. Rev. Lett., **75** (1995) 4326.
- [18] RISLER T., PROST J. and JÜLICHER F., Phys. Rev. Lett., 93 (2004) 175702.
- [19] CABALLERO F., NARDINI C. and CATES M. E., J. Stat. Mech.: Theory Exp., 2018 (2018) 123208.
- [20] CAVAGNA A., DI CARLO L., GIARDINA I., GRANDINETTI L., GRIGERA T. S. and PISEGNA G., *Phys. Rev. Lett.*, 123 (2019) 268001.

- [21] CAVAGNA A., DI CARLO L., GIARDINA I., GRIGERA T. S., MELILLO S., PARISI L., PISEGNA G. and SCAN-DOLO M., arXiv:2107.04432 (2021).
- [22] MAHDISOLTANI S., ZINATI R. B. A., DUCLUT C., GAM-BASSI A. and GOLESTANIAN R., *Phys. Rev. Res.*, 3 (2021) 013100.
- [23] Löffler R. C., BÄUERLE T., KARDAR M., ROHWER C. M. and BECHINGER C., *EPL*, **134** (2021) 64001.
- [24] RO S., KAFRI Y., KARDAR M. and TAILLEUR J., Phys. Rev. Lett., **126** (2021) 048003.
- [25] MEDINA E., HWA T., KARDAR M. and ZHANG Y.-C., *Phys. Rev. A*, **39** (1989) 3053.
- [26] NEWMAN T. J. and GRIMA R., Phys. Rev. E, 70 (2004) 051916.
- [27] DEAN D. S., J. Phys. A, **29** (1996) L613.
- $[28]\,$ Kawasaki K., Physica A, $\mathbf{208}$ (1994) 35.
- [29] CHAVANIS P.-H., Commun. Nonlinear Sci. Numer. Simul., 15 (2010) 60.
- [30] VAN KAMPEN N. G., Stochastic Processes in Physics and Chemistry (Elsevier Science, Amsterdam, The Netherlands) 1992.
- [31] GILLESPIE D. T., J. Chem. Phys., **113** (2000) 297.
- [32] BENITEZ F., DUCLUT C., CHATÉ H., DELAMOTTE B., DORNIC I. and MUÑOZ M. A., *Phys. Rev. Lett.*, **117** (2016) 100601.
- [33] DOERING C. R., MUELLER C. and SMEREKA P., *Physica* A, **325** (2003) 243.
- [34] CHAVANIS P.-H. and SIRE C., Physica A, 384 (2007) 199.
- [35] FORSTER D., NELSON D. R. and STEPHEN M. J., Phys. Rev. A, 16 (1977) 732.
- [36] ARON C., BIROLI G. and CUGLIANDOLO L. F., J. Stat. Mech.: Theory Exp., 2010 (2010) P11018.
- [37] KARDAR M., PARISI G. and ZHANG Y.-C., Phys. Rev. Lett., 56 (1986) 889.
- [38] WIESE K. J., J. Stat. Phys., 93 (1998) 143.
- [39] KLOSS T., CANET L., DELAMOTTE B. and WSCHEBOR N., Phys. Rev. E, 89 (2014) 022108.
- [40] YANG C. N. and LEE T. D., Phys. Rev., 87 (1952) 404.
- [41] LEE T. D. and YANG C. N., Phys. Rev., 87 (1952) 410.
- [42] FISHER M. E., Phys. Rev. Lett., 40 (1978) 1610.
- [43] BREUER N. and JANSSEN H. K., Z. Phys. B, 41 (1981) 55.
- [44] LÄSSIG M., Nucl. Phys. B, 448 (1995) 559.
- [45] CABALLERO F., NARDINI C., VAN WIJLAND F. and CATES M. E., *Phys. Rev. Lett.*, **121** (2018) 020601.
- [46] ŠKULTÉTY V. and HONKONEN J., Phys. Rev. E, 104 (2021) 024104.
- [47] CANET L., CHATÉ H., DELAMOTTE B. and WSCHEBOR N., Phys. Rev. E, 84 (2011) 061128.
- [48] DUCLUT C. and DELAMOTTE B., Phys. Rev. E, 95 (2017) 012107.
- [49] DUCLUT C. and DELAMOTTE B., Phys. Rev. E, 96 (2017) 012149.
- [50] DUPUIS N., CANET L., EICHHORN A., METZNER W., PAWLOWSKI J. M., TISSIER M. and WSCHEBOR N., Phys. Rep., 910 (2021) 1.