

Universal center-of-mass scaling shapes segment fluctuations and chromatin dynamics

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We show that cancellation of internal forces together with spatially uncorrelated noise generically enforces a universal $1/s$ scaling of the center-of-mass (COM) diffusivity for polymer segments of contour length s , independent of model details. Within an active generalized Rouse-Langevin (A-GRLE) framework for fractal polymers in a viscoelastic bath with weak activity, we derive closed-form links between segment COM motion and the short-time behavior of two-point fluctuations. The same COM law predicts transient s^{-3} tangent-tangent correlations along the contour following a temperature quench. Reanalyzing recent two-locus chromatin tracking, we extract a dynamic COM exponent $\xi = 0.77 \pm 0.16$, suggesting topological constraints. These results identify model-independent signatures of collective polymer dynamics and clarify that the observed Rouse-like scaling of chromatin loci reflects transient, unentangled dynamics with an inevitable crossover to an entangled regime at longer times.

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I. INTRODUCTION

Polymer dynamics in complex environments has been a central theme in soft matter physics since de Gennes' pioneering work on reptation in obstacle arrays [1] and the subsequent development of the tube model by Doi and Edwards [2]. Classical Rouse and Zimm models describe ideal chain dynamics; however, real polymeric systems exhibit more complex behavior due to topological constraints and memory effects [3–7], leading to nonideal chain statistics, as seen in melts of unknotted nonconcatenated polymer rings [8,9].

The emergence of high-resolution experimental data on polymer systems—such as chromatin [10–12]—has motivated renewed examination of classical results in polymer dynamics [13]. Theoretical models of chromatin often build on the Rouse framework, incorporating additional physical ingredients such as viscoelasticity [14–16], fractal folding of the chromatin fiber [14,17–19], and active processes [20–25]. While the resulting dynamical exponents can often be related through scaling arguments à la de Gennes [12,14,17], derivations from underlying physical mechanisms are frequently lacking. A deeper understanding that identifies universal dynamical features emerging from collective polymer motion, without relying on detailed model assumptions, is therefore desirable.

While earlier studies focused on characterizing dynamic exponents, here we identify *universal* features emerging from collective polymer dynamics in complex and active media. Assuming only reciprocal internal forces between beads (see, however, Ref. [26]), and spatially uncorrelated stochastic noise, we find that the center-of-mass (COM) diffusivity of a polymer segment exhibits a universal $1/s$ scaling with segment length s , independent of structural or environmental details. This COM scaling imprints characteristic dynamic corrections onto two-point fluctuations, which can be observed via recent two-locus chromatin tracking experiments [11,12], enabling access to collective chromatin dynamics based on two-locus tracking data [Fig. 1(a)].

Additionally, we show that following a quench in temperature, center-of-mass dynamics generates transient long-range tangential correlations along the chain, decaying as $\sim 1/s^3$ [Fig. 1(b)]. This provides a clear signature of nonequilibrium behavior, absent in equilibrium ideal chains. The effect is distinct from the $\sim 1/s^{3/2}$ bond-bond correlations that arise in dense polymer melts due to excluded volume and the correlation hole effect [27,28].

Our results provide a resolution to the long-standing discrepancy between structural and dynamical measurements of chromatin. Hi-C experiments reveal genome-wide contact probabilities $P(s) \sim s^{-1}$ for loci separated by genomic distances $s \approx 0.1\text{--}5\text{--}10\text{ Mb}$ [29,30], most clearly in cohesin-depleted cells [31]. Via a mean-field relation [29], this scaling implies root-mean-square distances $R(s) \sim s^{1/d_f}$ with fractal dimension $d_f = 3$ [32–34], indicating that chromatin adopts crumpled rather than ideal random-walk conformations. Theoretically, such fractal packing should slow dynamics compared to an ideal chain ($d_f = 2$): The generalized Rouse model predicts single-locus mean-squared displacements (MSDs) $M_1(t) \sim t^z$ with $z = 2/(d_f + 2) = 2/5$, while

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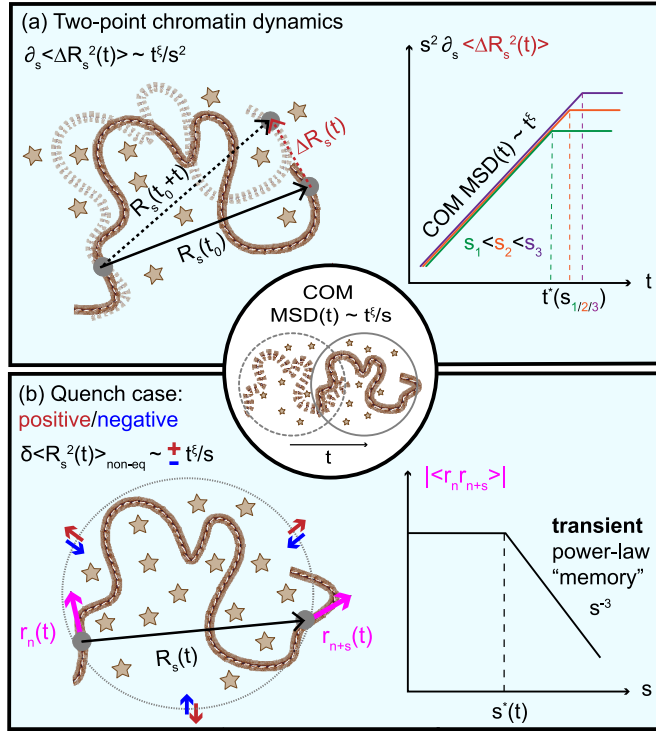


FIG. 1. Schematic of the main results. (a) Two-point dynamics: Short-time collapse of $s^2 \partial_s M_2(s, t)$ reflects the COM-induced correction $M_2(s, t) - 2M_1(t) \sim -t^\xi/s$. (b) Postquench correlations: The nonequilibrium contribution to the segment MSD, $\delta \langle R_s^2(t) \rangle_{\text{noneq}} \sim \pm t^\xi/s$, generates tangential correlations $\langle r_n r_{n+s} \rangle \sim s^{-3}$ for separations $s > s^*(t)$. In both panels (a) and (b), the behavior is due to the universal COM diffusivity (center).

scaling arguments including topological constraints predict even smaller exponents, $z = 2/7$ for the fractal loopy globule [35] and $z \approx 0.26$ for annealed lattice animals [36]. In contrast, recent live-cell imaging instead reports Rouse-like dynamics with $z = 1/2$ over times $t \sim 1\text{--}100$ s [10–12].

We argue that this apparent contradiction reflects a temporal crossover set by the minimal scale at which polymer entanglements emerge—the entanglement length N_e . At short times ($t < \tau_e = \tau_0 N_e^2$, with τ_0 the microscopic Rouse time), monomer motion is not yet constrained by entanglements. For chromatin, estimates $N_e \sim 10^2$ kb and $\tau_0 \sim 10^{-2}$ s [30] imply Rouse-like ($z = 1/2$) dynamics up to $t \sim 100$ s. At longer times ($t > \tau_e \sim 200\text{--}500$ s), entanglements are expected to slow dynamics toward $z \approx 0.3\text{--}0.4$, consistent with theoretical predictions [14,35,36]. Hints of such slowing are visible in recent data [10,12], but the limited experimental time window prevents a clear resolution.

Crucially, two-locus dynamics indirectly probe the collective COM motion of chromatin segments, which encodes information on topological constraints at times currently accessible to experiments ($t \approx 1\text{--}100$ s). We show that the COM motion manifests as a universal short-time correction to the two-loci fluctuations. Reanalyzing recent two-locus data, we extract a COM MSD exponent $\xi = 0.77 \pm 0.16$, significantly below the Rouse prediction $\xi = 1$, and in quantitative agreement with theoretical models of topologically

constrained dynamics [35,36]. This supports the view of chromatin as a crumpled polymer with a crossover governed by entanglements, thereby reconciling structural signatures from Hi-C with dynamical behavior observed in live imaging.

II. MODEL

We consider a general framework for out-of-equilibrium chromatin dynamics at intermediate times $t > \tau_0 \approx 10^{-2}$ s, corresponding to the microscopic Rouse time of a chromatin locus with the spatial size $a \approx 0.1$ μm on order of the Kuhn length [11,12]. Our model incorporates three key ingredients: chromatin fractality, viscoelasticity of the nucleoplasm, and weak spatially inhomogeneous activity along the chromatin fiber.

We represent chromatin as a polymer of N beads connected by Hookean springs of rigidity $\kappa = 3T/a^2$, and subject to reciprocal non-nearest-neighbor interactions f_{nk}^{vol} . The overdamped dynamics of bead coordinates $\{x_i(t)\}_{i=1}^N$ is described by

$$\begin{aligned} \Gamma(3-\alpha) {}_c D^\alpha x_n(t) = & \kappa \gamma_\alpha^{-1} (x_{n+1} - 2x_n + x_{n-1}) \\ & + \gamma_\alpha^{-1} \sum_{k \neq n \pm 1} f_{nk}^{\text{vol}}(\{x_i, \dot{x}_i\}_{i=1}^N, t) \\ & + \xi_n(t) + \eta_n(t), \end{aligned} \quad (1)$$

where ${}_c D^\alpha$ denotes the Caputo fractional derivative of order $\alpha \leq 1$ [14,16,20,37] and γ_α is the corresponding friction coefficient. This derivative captures the non-Newtonian, viscoelastic response of the nucleoplasm, consistent with experimentally observed subdiffusion of tracer particles in both eukaryotes and prokaryotes [38,39]. Such subdiffusion persists over 10–100 s with MSD exponent $\alpha \approx 0.7$, although we allow arbitrary α in the model.

The noise $\xi_n(t)$ represents passive Gaussian fluctuations associated with the viscoelastic friction. In accordance with the fluctuation-dissipation theorem, its covariance reads

$$\langle \xi_n(t) \xi_m(t') \rangle = 6T \gamma_\alpha^{-1} K_\alpha(|t - t'|) \delta_{nm}, \quad (2)$$

with the kernel $K_\alpha(t) = (2 - \alpha)(1 - \alpha)t^{-\alpha}$. Equation (2) reduces to the white-noise limit of a Newtonian fluid at $\alpha = 1$.

To incorporate active processes that drive chromatin out of equilibrium, we add an independent Gaussian noise $\eta_n(t)$ with covariance

$$\langle \eta_n(t) \eta_m(t') \rangle = A_n \gamma_\alpha^{-1} \mathcal{C}(t - t') \delta_{nm}, \quad (3)$$

where A_n is the local activity with the average level $A_0 = \overline{A_n}$ and $\mathcal{C}(t)$ the normalized correlation of excitations. This term models local, sequence-dependent activity arising from transcriptional processes along chromatin [21]. Proteins such as RNA polymerase II convert chemical energy into mechanical work, thereby breaking detailed balance; consequently, the noise term $\eta_n(t)$ does not satisfy the fluctuation-dissipation relation, in contrast to the passive noise ξ_n coupled with the viscoelastic friction (2). For simplicity, we deal with sufficiently weak active forces in our model that do not violate the equilibrium fluctuation-dissipation relation between viscoelasticity and thermal noise.

A particularly tractable limit of Eq. (1) arises for quadratic interactions, which generate linear Hookean forces $f_{nk}^{\text{vol}} = \mathcal{L}_{nk}(x_n - x_k)$. If the spring constants scale with separation as $\mathcal{L}_{nk} \sim -|n - k|^{-\delta}$ [18], the resulting polymer configurations are fractals of dimension $d_f = 2/(\delta - 2)$. Under these conditions, Eq. (1) reduces to the active generalized Rouse-Langevin equation (A-GRLE), which extends the equilibrium GRLE framework of polymer dynamics [14]. A similar model was studied previously by Grimm and Dolgushev in Ref. [37] for the dynamics of regular fractal trees in viscoelastic bath and correlated activity with $\mathcal{C}(t) \sim \exp(-t/t_A)$, where t_A is the characteristic decorrelation time.

Here we adopt the white-noise approximation $\mathcal{C}(t) = \delta(t)$ valid at times larger than the excitation decorrelation time $t \gg t_A$ and define the dimensionless activity:

$$\chi_n = \frac{A_n \tau_0^{\alpha-1}}{3T}, \quad \chi = \overline{\chi}_n = \frac{A_0 \gamma_\alpha^{-1}}{\Theta_1 \tau_0^{1-\alpha}}, \quad \Theta_1 = 3T \gamma_\alpha^{-1}, \quad (4)$$

where χ is averaged over the sequence and Θ_1 is the thermal diffusivity of a single bead. The parameter $\chi \lesssim 1$ quantifies the relative strength of weak active over passive forces. While our results hold more generally, the A-GRLE with delta-correlated excitations provides an analytically tractable framework that we focus on in the main text.

III. DYNAMICS OF THE CENTER-OF-MASS

Despite modeling a quite general situation, Eq. (1) generates a universal scaling for the diffusivity of COM of the chain. Indeed, reciprocity of internal forces ($f_{nk}^{\text{vol}} = -f_{kn}^{\text{vol}}$) results in the straightforward out-of-equilibrium dynamics for the vector $x_{\text{COM}} = N^{-1} \sum_{i=1}^N x_i$, governed by

$$\Gamma(3 - \alpha)_c D^\alpha x_{\text{COM}}(t) = \tilde{\xi}_{\text{COM}}. \quad (5)$$

Here, $\tilde{\xi}$ is the total noise combining passive and active terms. The covariance of the total COM noise acquires a universal $1/N$ factor due to the assumed independence of bead-level fluctuations:

$$\langle \tilde{\xi}_{\text{COM}}(t) \tilde{\xi}_{\text{COM}}(t') \rangle = 2\Theta_1 N^{-1} \mathcal{D}(t - t'), \quad (6)$$

where $\mathcal{D}(t) = K_\alpha(t) + \frac{1}{2} \chi \tau_0^{1-\alpha} \delta(t - t')$ is the normalized correlation of the total noise. Equation (5) describes the dynamics of a single particle in a bath subject to the above noise correlations. Consequently, the polymer COM fluctuations with the diffusion coefficient

$$\Theta_N = N^{-1} \Theta_1, \quad (7)$$

reduced by a factor of N in comparison with the single-bead diffusivity Θ_1 . This scaling is well known for the Rouse model of polymer dynamics [3,4,40], but also holds for a much wider class of stationary out-of-equilibrium dynamics (in particular, nonlinear), satisfying bead-level independence of random forces and reciprocity of internal pairwise interactions.

The diffusivity of segments of the contour length s depends on their particular position in the genome due to the sequence-modulated magnitude of excitations, A_n . For concreteness, let us consider a sinusoidal modulation of activities, $A_n = A_0(1 + \varepsilon \cos(\pi n/\lambda))$, mimicking the alternation into active and inactive chromatin regions with a typical length λ

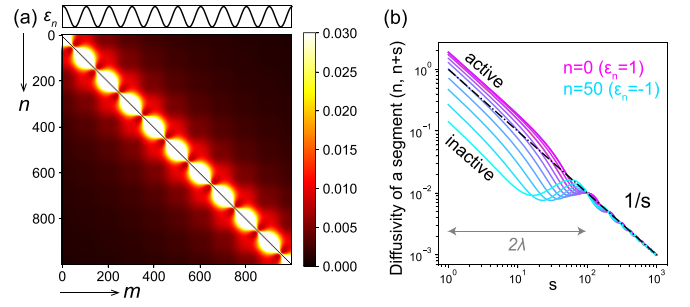


FIG. 2. (a) Heatmap of the active contribution $\Theta_{n,m}^{(A)}$ to the COM diffusivity [Eq. (8)] for various segments in a chain of length $N = 1000$. Bright regions correspond to higher diffusivity values. (b) Segment-length dependence of $\Theta_{n,m}^{(A)}$ for different starting positions n (from $n = 0$ to $n = \lambda$), showing how activity modulates the diffusivity. The dashed line shows the $1/s$ scaling valid for an average segment. Parameters: $A_0/\gamma_\alpha = 1$, $\varepsilon = 0.9$, and correlation length $\lambda = 50$.

and with ε being the amplitude of activity oscillations. An ensemble of polymer conformations generated by such an activity pattern reproduces the checkerboard structure of the contact probability maps from Hi-C experiments [21]. In the dynamics context, this modulation of activities results in a similar checker-board structure of the activity-induced diffusivities $\Theta_{n,m}^{(A)}$ of segments of various lengths $s = |n - m|$ [see Fig. 2(a)]:

$$\Theta_{n,m}^{(A)} = \frac{A_0}{s\gamma_\alpha} \left(1 + \frac{2\varepsilon\lambda}{\pi s} \sin \frac{\pi(n+m)}{2\lambda} \sin \frac{\pi s}{2\lambda} \right). \quad (8)$$

This result is rather suggestive: It connects structural and dynamical patterns through the same mechanism. Generally, the behavior of the COM diffusivity with s dramatically depends on the position n in the genome and can even increase with s for n residing in inactive domains [see Fig. 2(b)]; however, for long segments $s = |n - m| \gg 1$, $\Theta_{n,m}^{(A)} \sim s^{-1}$ reveals the universal Rouse-like scaling.

Since the detailed sequence dependence is unknown and we are mainly interested in scaling behavior, we focus on sequence-averaged quantities in what follows. The average diffusivity $\overline{\Theta_{n,n+s}^{(A)}}$ describing the sequence-averaged MSD of the typical segment of length s in the chain restores the universal $1/s$ behavior at all s [dashed line in Fig. 2(b)]:

$$\overline{\Theta_{n,n+s}^{(A)}} = (N - s)^{-1} \sum_{n=1}^{N-s} \Theta_{n,n+s}^{(A)} = \frac{A_0}{s\gamma_\alpha}. \quad (9)$$

Thus, the average collective diffusivity of segments of size s follows the corresponding relation (7) for the entire chain. This result admits a natural interpretation in terms of a scaling picture based on independently relaxing blobs: A polymer segment of contour length s and fractal dimension d_f relaxes over a characteristic time $\tau(s) \sim s^w$. At short times $t \ll \tau(s)$, the segment comprises s/s^* independently diffusing blobs of size $(s^*)^{1/d_f}$ yielding

$$\langle x_{\text{COM}}^2(s, t) \rangle \sim (s/s^*)^{-1} (s^*(t))^{2/d_f} \sim s^{-1} t^\xi, \quad (10)$$

where $\xi = (2 + d_f)(wd_f)^{-1}$ is the short-time MSD exponent of COM. In the A-GRLE framework, we show

that for not very strong viscoelasticity ($1/2 < \alpha < 1$) the COM MSD consists of two different power-law terms: $\sim s^{-1}(t/\tau_0)^\alpha$ produced by the passive noise and a subdominant $\sim \chi s^{-1}(t/\tau_0)^{2\alpha-1}$ term from the active excitations. Thus, despite the active noise, the COM MSD crossovers to the equilibrium power-law behavior governed by the GRLE exponent $\xi = \alpha$ at times $1 \ll t/\tau_0 \ll s^w$, where $w = (d_f + 2)/(\alpha d_f)$ is the relaxation time exponent.

IV. TWO-POINT DYNAMICS

The universality of COM dynamics also underlies two-point fluctuation measurements, providing indirect access to the coupling between chromatin structure and dynamics. We quantify this via the MSD of the vector $R(s, t) = x_n(t) - x_{n+s}(t)$ connecting beads n and $n + s$ at the same time t :

$$M_2(s, t) = \overline{\langle (R(s, t) - R(s, 0))^2 \rangle}, \quad (11)$$

where the overline denotes averaging over sequence-dependent heterogeneity, which removes oscillatory contributions from transcriptional activity.

By construction, $\overline{M_2(s, t)}$ evolves from zero at $t = 0$ to its saturation value $2\langle R_s^2 \rangle \sim 2a^2 s^{2/d_f}$ for $t \gg \tau(s) \sim s^w$. At shorter times $t \ll \tau(s)$, the two beads have not yet sensed their connectivity and fluctuate independently. In this regime, the relative motion is simply the sum of two single-bead contributions,

$$M_2(s, t) \approx 2M_1(t) \simeq 2\Theta_1 \left(\frac{t}{\tau_0} \right)^\xi, \quad (12)$$

where $M_1(t) = \overline{\langle (x_n(t) - x_n(0))^2 \rangle}$ is the single-bead MSD and ξ is its dynamic exponent.

Within the A-GRLE framework [41], the single-bead MSD $M_1(t)$ at intermediate times $\tau_0 \ll t \ll \tau(N)$ is governed predominantly by the passive noise. In this regime, the dynamics follows the equilibrium GRLE scaling with dynamic exponent $z = 2\alpha/(d_f + 2)$ [14]. The effect of activity is subdominant, contributing an additional term $\sim \chi a^2 (t/\tau_0)^{\alpha[1-w^{-1}(2\alpha-1)^{-1}]}$, which becomes relevant only at the microscopic timescale $t \sim \tau_0$.

While the short-time behavior of two-loci fluctuations $M_2(s, t)$ ($t \ll \tau(s)$) has often been attributed solely to the single-bead dynamics $M_1(t)$ [Eq. (12)], recent experiments reveal a surprising s dependence of $M_2(s, t)$, suggesting an apparent segment-length-dependent diffusivity $\Theta_2(s) \equiv M_2(s, t)t^{-\xi}$ at short times [12]. To rationalize this observation, we explicitly evaluate Eq. (11) within the A-GRLE framework. We find that the universal s^{-1} scaling of the COM diffusivity (10) manifests as a characteristic short-time correction to

$$M_2(s, t) = 2C_2(s, 0) - 2C_2(s, t), \quad (13)$$

where $C_2(s, t)$ is the autocorrelation function of the vector $R(s, t)$. Decomposition into normal modes $u_p(t)$ (see the Supplemental Material [41]) expresses $C_2(s, t)$ as a weighted sum over the autocorrelation functions (ACFs) of the normal

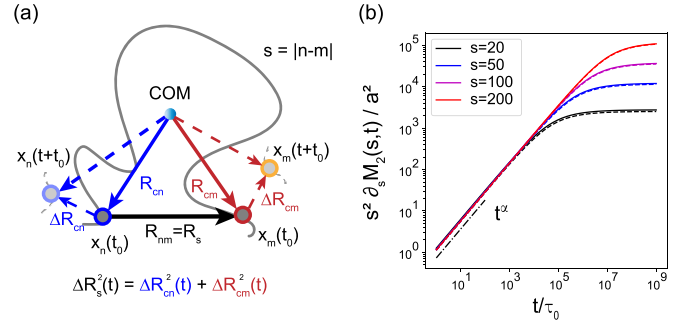


FIG. 3. (a) Schematic illustration of the derivation of the two-point fluctuations $M_2(s, t)$ and the correction arising from COM dynamics. (b) Scaled s derivative, $\partial_s M_2(s, t) s^2$ from the A-GRLE theory, shown in units of $a^2 \approx 4 \times 10^{-4} \mu\text{m}^2$ as a function of rescaled time t/τ_0 ($\tau_0 \approx 0.1$ s is the microscopic Rouse time). For each separation s , two cases are shown: strong activity ($\chi = 2$, solid) and passive dynamics ($\chi = 0$, dashed). Other parameters are $\alpha = 0.7$ and $\beta = w\alpha = 5/3$ (corresponding to fractal dimension $d_f = 3$).

modes $G_p(t) = \langle u_p(t)u_p(0) \rangle$ as follows:

$$C_2(s, t) = \frac{2}{N} \sum_{p=1}^{N-1} G_p(t) \left(1 - \cos \frac{2\pi ps}{N} \right), \quad (14)$$

where $G_p(t) = G_p(0) E_\alpha(-c_\alpha (\frac{t}{\tau_p})^\alpha)$ is given by the one-parameter Mittag-Leffler function E_α and c_α is a numerical constant. The ACFs $G_p(t)$ describe the relaxation of modes of wavelength N/p and are unaffected by activity, as is the spectrum of mode relaxation times $\tau_p = \tau_0(N/p)^w$. Plugging Eq. (14) into Eq. (13) and passing to the continuum limit, one finds that in the short-time regime $t \ll \tau(s)$ the two-loci fluctuations acquire a universal correction to the naive $2M_1(t)$ scaling. Specifically, we find

$$M_2(s, t) - 2M_1(t) \simeq -a^2 s^{-1} \left(\frac{t}{\tau_0} \right)^\xi, \quad \xi = \alpha, \quad (15)$$

with the exponent ξ inherited from the COM motion. This result is general and holds both in equilibrium and in out-of-equilibrium settings for $s \gg 1$.¹ Thus, we obtain an apparent enhancement of two-loci diffusivity at large genomic separations,

$$\Theta_2(s, t) \simeq 2\Theta_1 - 2s^{-1} B t^{\xi-z}, \quad (16)$$

which, at fixed time t , saturates to a constant $2\Theta_1$ as s increases. This saturation reflects a robust polymeric effect that is independent of the microscopic details of the polymer dynamics. Notably, the correction in Eq. (16) is always *negative*.

The above result can be understood more simply by expressing the segment fluctuations in the COM frame. At short times, the end points fluctuate independently around the COM: $M_2(s, t) = \langle [\Delta R_{cn}(t) - \Delta R_{cm}(t)]^2 \rangle = 2\langle \Delta R_{cn}^2(t) \rangle$ [see Fig. 3(a)]. In this time interval, fluctuations of the

¹Activity introduces subdominant corrections $\sim s^{-(1+w(1-\alpha))}$ that vanish at large s , but crucially leave the temporal scaling $\sim t^\alpha$ unchanged.

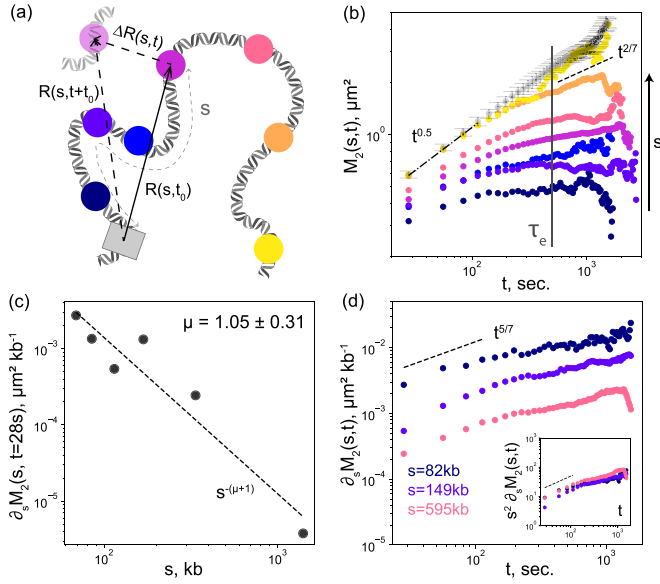


FIG. 4. Analysis of imaging data from Ref. [45]. (a) Experimental design: Reporter loci (colored) were placed at genomic distances $s=58, 82, 88, 149, 190, 595$, and 3300 kb from a central locus (gray rectangle). (b) MSD of two-point separation $R(s, t)$ for various s [color corresponds to panel (a)]. The doubled single-locus MSD $2M_1(t)$ is overlaid using gray points, with error bars representing standard deviation across both loci and cells. (c) Derivative $\partial_s M_2(s, t)$ versus s at initial time point $t = 28$ s, with best-fit slope $\mu + 1$, where $\mu \approx 1.05 \pm 0.31$. (d) Time evolution of $\partial_s M_2(s, t)$ for three most stable genomic distances s . The inset shows the curves collapsed by s^2 with the exponent of COM MSD for fractal loop globule.

monomers are also decoupled from the COM, leading to $M_1(t) = \langle x_{\text{COM}}^2(s, t) \rangle + \langle \Delta R_{\text{cn}}^2(t) \rangle$. Using $M_1(t) = \Theta_1 t^z$ and $\langle x_{\text{COM}}^2(s, t) \rangle = B t^\xi s^{-1}$, Eq. (15) follows. This makes it possible to deduce COM dynamics from two-point measurements. In particular, removing the leading term by differentiating with respect to s gives

$$s^2 \partial_s M_2(s, t) \sim a^2 (t/\tau_0)^\xi, \quad t \ll \tau(s). \quad (17)$$

Equation (17) provides a method to determine the center-of-mass dynamic exponent ξ from two-point chromatin tracking experiments. As shown in Fig. 3(b), the s^2 -scaled derivatives (17) obtained within the A-GRLE framework collapse onto a single curve at short times and display universal growth $\sim t^\xi$ with $\xi = \alpha$, where α is the viscoelasticity parameter of the A-GRLE. This behavior is independent of the presence or absence of activity.

V. ANALYSIS OF IMAGING DATA

Recent advances in two-locus chromatin tracking now allow direct measurement of the two-point MSD $M_2(s, t)$ in live nuclei [11, 12] [Fig. 4(a)]. Reanalysis of data from Ref. [12] confirms that short-time fluctuations increase systematically with genomic separation s [Fig. 4(b)]. While earlier interpretations attributed this to scale-dependent two-loci diffusivity $\Theta_2(s)$ [12], we find that this apparent s dependence instead can arise naturally from the COM correction term in Eq. (16).

A first indication comes from the furthest separations $s = 595$ kb and 3.3 Mb, where $M_2(s, t)$ converges to twice the single-locus MSD, as predicted from Eq. (15) for $s \rightarrow \infty$. The reduced fluctuations at finite s , reflecting collective dynamics, can be quantified by analysis of $\partial_s M_2(s, t)$: At early times (e.g., $t_0 = 28$ s), Fig. 4(c) reveals power-law scaling $\sim s^{-(\mu+1)}$ with $\mu = 1.05 \pm 0.31$, in agreement with the expected s^{-1} correction from Eq. (17). The analysis involving larger time points exhibits similar exponents (see Figs. S2(a)–S2(c) in the Supplemental Material [41]). These results provide experimental support for this universal COM-induced scaling in chromatin dynamics.

How to reconcile fractal folding of chromosomes with the observed Rouse-like single-locus dynamics with the dynamic exponent $z = 1/2$ [10–12]? As we have shown, introduction of the weak activity cannot affect this exponent at the times of interest $t \gg \tau_0 \approx 10^{-2}$ s. Instead, we suggest that it could well reflect transient scaling at times shorter than the entanglement time $\tau_e \sim 200$ – 500 s [Fig. 4(b)]. Such crossover suggests topological constraints emerging only on longer timescales. Using estimates $N_e \sim 10^2$ kb and $\tau_0 = (a^2/D_R)^2 \sim 10^{-2}$ s, based on Kuhn length $a \approx 0.1$ μm [42] and Rouse coefficient $D_R \approx 5 \times 10^{-2} \mu\text{m}^2 \text{s}^{-1/2}$ [12], we obtain consistent timescales. The associated entanglement length N_e and time $\tau_e = \tau_0 N_e^2$ can be enhanced in looped, comblike chromosomes [25, 31, 43, 44].

Although a slight slowing of single-locus MSDs appears for $t > 200$ s, the experimental window remains too narrow to fully resolve the crossover (see Fig. 4(b) and Fig. S2(d) in the Supplemental Material [41]). However, the COM motion extracted from two-loci dynamics [Eq. (17)] exhibits no crossover at τ_e , enabling direct extraction of the collective motion exponent ξ . While the original imaging data contain significant noise (particularly in derivatives, see Fig. S2(e) in the Supplemental Material [41]), our analysis of the most stable curves [Fig. 4(d), for $s = 82, 149$, and 595 kb] is close to the s^2 scaling as in Eq. (17). Remarkably, the resulting $\xi = 0.77 \pm 0.16$ from short-time behavior falls below the Rouse prediction ($\xi = 1$) and agrees with the predictions of the COM dynamic exponents for the crumpled polymer models: $\xi = 5/7$ for fractal loop globule [35] and $\xi \approx 0.65$ for annealed lattice animals [36] (see Ref. [41]). These results provide strongly support the relevance of topological constraints in chromatin dynamics.

VI. QUENCH

In living cells, the level of activity (stochastic force) driving chromatin motion can either change through natural processes such as cell cycle progression or can be induced experimentally through changes in temperature T (thermal noise) or activity level A_0 in the nucleoplasm (athermal noise). Motivated by this biological relevance, we use our framework to explore the dynamical signatures of such quenches in polymer systems, focusing in particular on their impact on tangential correlations [Fig. 1(b)].

The clearest manifestation of a quench is the emergence of transient, long-range *tangent-tangent correlations* along the chain. These can be expressed via the segment displacement

$R(s, t)$ as

$$\langle r_n r_m \rangle = \frac{1}{a^2} \left\langle \frac{\partial x_n}{\partial n} \frac{\partial x_m}{\partial m} \right\rangle = \frac{1}{2a^2} \frac{\partial^2}{\partial s^2} \langle R^2(s) \rangle, \quad (18)$$

At steady state, these correlations are determined solely by the chain's fractal dimension d_f ,

$$\begin{aligned} \langle r_n r_m \rangle|_{\text{eq}} &\sim \delta_{s,0} = \delta_{nm}, \quad d_f = 2, \\ \langle r_n r_m \rangle|_{\text{eq}} &\sim \frac{(2/d_f)(2/d_f - 1)}{s^{2(1-d_f^{-1})}}, \quad d_f \neq 2. \end{aligned} \quad (19)$$

We now consider a sudden change in the temperature $T_1 \rightarrow T_2$, focusing on the case without activity, $\chi = 0$ (GRLE). The quench is performed at $t = 0$, initiating a transition to another equilibrium state. The spatial size can be more ($T_1 < T_2$; positive quench) or less ($T_1 > T_2$; negative quench) extended, while retaining the original fractal dimension d_f and dynamic exponents. In the GRLE framework, this quench modifies the normal mode amplitudes, $\phi_p(t) = \langle u_p^2(t) \rangle$, which evolve from $\phi_{p,1}(t=0) = 3T_1\kappa^{-1}\lambda_p^{-1}$ to $\phi_{p,2}(t \gg \tau_p) = 3T_2\kappa^{-1}\lambda_p^{-1}$.

At $t \ll \tau(s)$, the resulting tangential correlations are given by (see Ref. [41] for full derivation)

$$\begin{aligned} \langle r_n r_m \rangle &= \langle r_n r_m \rangle|_{\text{eq}} + \langle r_n r_m \rangle|_{\text{non-eq}}, \\ \langle r_n r_m \rangle|_{\text{noneq}} &= \frac{1}{Na^2} \sum_{p=1}^{N/s} \tilde{\phi}_p(t) \left(\frac{2\pi p}{N} \right)^2 \cos \left(\frac{2\pi ps}{N} \right), \end{aligned} \quad (20)$$

where $\tilde{\phi}_p(t) \propto 6\Delta T \gamma_\alpha^{-1} t^\alpha$ captures the transient response to a quench $\Delta T = T_2 - T_1$. Substitution of $\tilde{\phi}_p(t)$ into Eq. (20) yields the key result:

$$\langle r_n r_m \rangle|_{\text{non-eq}} \sim \frac{\Delta T}{T} \left(\frac{t}{\tau_0} \right)^\xi \frac{1}{s^3}, \quad t \ll \tau(s), \quad (21)$$

where $\tau_0 = \gamma_\alpha \kappa^{-1}$ is the microscopic Rouse time. Equation (21) reveals universal s^{-3} scaling of correlations postquench. The overall sign reflects the direction of the quench, with $\Delta T > 0$ (positive quench) producing positive correlations, and vice versa.

At early times, both equilibrium (19) and nonequilibrium (20) contributions are present. For nonideal chains ($d_f \neq 2$) the equilibrium contribution decays as $s^{-2(1-1/d_f)}$, eventually dominating the universal nonequilibrium term of s^{-3} . However, for ideal chains ($d_f = 2$) the equilibrium term vanishes, revealing the pure nonequilibrium signal:

$$\langle r_n r_m \rangle|_{d_f=2} \sim \frac{1}{s^*} \left(\frac{s^*}{s} \right)^3, \quad s > s^* = (t/\tau_0)^{\xi/2}, \quad (22)$$

which indicates the emergence of transient power-law effects in *ideal* polymer chains.

This prediction was confirmed by simulations of an ideal bead-spring polymer ($N = 10^5$) in a viscous fluid. We implemented a quench by instantaneously increasing the bead spacing a from 1 to 5, mimicking an effective temperature increase. As shown in Fig. 5(a), for $s > s^*$, the tangential correlations follow the predicted s^{-3} power law, while for $s < s^*$, segments have equilibrated. The correlation curves show clear shoulders at $s^*(t)$, confirming the s^{-1} scaling of Eq. (22). Rescaling $\langle r_n r_m \rangle \rightarrow \langle r_n r_m \rangle t^{1/2}$ and $s \rightarrow q = s/t^{1/2}$

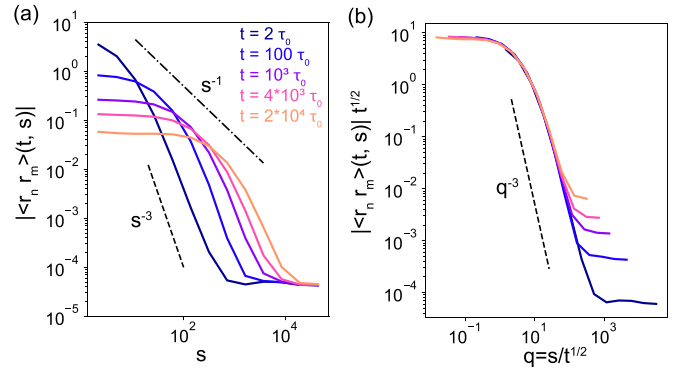


FIG. 5. Absolute value of tangent-tangent correlations $\langle r_n r_m \rangle$ in an ideal chain ($N = 10^5$ monomers) following a quench of the microscopic bead spacing from $a = 1$ to $a = 5$, obtained from molecular dynamics simulations. (a) Time evolution of correlations after the quench. For each t , correlations decay as $\sim s^{-3}$, for segment lengths $s > s^* = (t/\tau_0)^{1/2}$, and saturate the equilibrium level for $s < s^*$. (b) Data collapse of curves from panel (a) under rescaling $s \rightarrow s/t^{1/2}$, with normalization applied at $s = 2$. The rescaled curves exhibit constant behavior for $s < s^*$ and s^{-3} decay for $s > s^*$.

collapses the data [Fig. 5(b)], with constant behavior for $q < 1$ and q^{-3} decay for $q > 1$.

The physical origin of these transient power-law correlations lies again in the COM-driven term in the segment separation dynamics. The separation vector dynamics at $t \ll \tau(s)$ consists of two terms:

$$\langle (x_n(t) - x_{n+s}(t))^2 \rangle|_{\text{noneq}} = A t^\xi + B t^\xi s^{-1}, \quad (23)$$

where A and B are some constants. The monomer term $A t^\xi$ dominates the MSD, but does not contribute to the spatial derivative in Eq. (18). The s^{-1} COM term instead drives the observed long-range correlations. Thus, the universal s^{-3} scaling emerges as a direct consequence of postquench collective dynamics.

VII. CONCLUSION

We introduced an A-GRLE that unifies chain fractality, viscoelasticity, and active excitations, uncovering universal features independent of the model details. Assuming reciprocal interbead forces and spatially uncorrelated noise, we demonstrated a universal $1/s$ scaling of COM diffusivity for polymer segments of length s . This collective effect generates measurable corrections to two-point fluctuations, relevant across equilibrium, driven, and out-of-equilibrium regimes. Although nonreciprocal interactions have been suggested in enhancer-promoter communication [26], the observed $1/s$ scaling in imaging data is consistent with reciprocal dynamics and weakly correlated activity at the segment level.

By combining an analytically solvable A-GRLE model and scaling arguments, we derived a COM-induced correction to two-point MSDs. Reanalysis of two-locus tracking data [12] confirms this prediction and yields a dynamic exponent $\xi \approx 0.77$, consistent with crumpled globule models [35,36] and supporting the presence of topological constraints *in vivo*. Our results further suggest that the Rouse-like behavior reported in Refs. [10–12] corresponds to transient early-time dynamics

of a crumpled polymer, thus reconciling chromatin's fractal structure with Rouse-like motion.

Finally, we demonstrated that a sudden change in temperature induces transient s^{-3} tangent-tangent correlations—even in ideal chains—driven by universal COM dynamics. These nonequilibrium correlations act as a memory mechanism and extend the phenomenon of broken Flory ideality [27,28] to dynamically perturbed polymer systems.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [45].

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