

Morphological parameters capture emergent properties of dynamic disordered cytoskeletal networks

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The actin cytoskeleton is an inherently disordered active system. The actomyosin cortex and reconstituted actomyosin systems are globally disordered, yet undergo transitions between distinct disordered states as parameters like motor and crosslinker concentration and filament length and rigidity change. In cells, these changes are related to genetic mutations or differences in cell state and dictate fundamental biological processes. However, we do not have well-established methods to detect and classify differences in disordered polymer networks. Image-based morphology techniques provide a noninvasive, high-throughput method of extracting information about a system. In this work, we simulate biopolymer networks under varying conditions and develop and use morphological descriptors to construct trajectories in morphospace. Using statistical analysis, we find that morphological descriptors are able to distinguish between different trajectories of the system, including differences not apparent to the eye. However, no single descriptor alone is able to capture all the differences in the simulated trajectories. Nematic order parameters typically perform the worst for our simulations, while curvature and texture descriptors can collectively distinguish between dynamic trajectories. This work helps develop quantification of cytoskeleton dynamics for classification and data-driven modeling.

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I. INTRODUCTION

The cellular cytoskeleton comprises interconnected networks of actin filaments, microtubules, and intermediate filaments that play a central role in cellular processes through continuous spatiotemporal remodeling. Dynamic remodeling of actin, microtubules, and intermediate filaments regulates intracellular organization, organelle positioning, and cytoskeletal crosstalk across the cell interior [1–4]. Cytoskeletal remodeling also regulates cellular mechanical state, force transmission, and mechanosensitivity through coupled interactions between filament systems, adhesion complexes and linker of the nucleoskeleton to the cytoskeleton (LINC) complexes [5–8]. Cytoskeletal architecture is tightly integrated with signaling pathways governing differentiation, stress adaptation, apoptosis, immune activation, and tissue morphogenesis through mechanochemical feedback [9–13]. Due to its central role in so many cellular processes and its dynamic nature, cytoskeletal

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organization should reflect the continuously evolving cell state. This motivates the question: Can image-based morphological metrics function as an information-rich coordinate system that represents the temporal evolution of cytoskeletal organization? In this paper, we address this question using dynamic simulations of cytoskeletal networks. We show that trajectories of image-based morphological metrics are sensitive to differences in polymer network dynamics arising from perturbations of underlying parameters. Our results motivate the use of morphology for dynamic modeling, such as for predicting cellular mechanics or functional behavior.

Our main focus is the actin cytoskeleton, which is one of the fundamental determinants of cell function, serving as both a structural scaffold and a dynamic engine for mechanical processes. It is being increasingly recognized that the specific architecture of cellular actin determines how a cell grows, moves, generates force, and responds to its environment [14–24]. Around 400 proteins are believed to control actin architecture, from polymerization to higher-order networks [25], underlining its importance in cell function. In the generation of force, for example, cells transition between different actin architectures to modulate their contractile output [21–23,26]. In platelets, radial versus circumferential actin filament orientation determines the magnitude and localization of traction forces, critical for stable adhesion during the clotting process [20].

While there are a few important phenomena in which the cytoskeleton is ordered, such as the actin contractile ring in mitosis [27], the microtubule spindle during interphase, or actomyosin sarcomeres in muscle cells, in most cases the cytoskeleton presents itself as a disordered dynamic network. Nevertheless, identifiable attractor states in response to external perturbation [17] or genetic mutations [15] have been observed, suggesting that there are yet to be discovered higher-order principles that govern cytoskeletal architecture. The significance of cytoskeletal architecture raises the question of how it can be described quantitatively. Since much of the information about network organization derives from light microscopy, a natural framework for describing cytoskeletal organization is through image-derived morphological metrics.

Cytoskeletal polymers are semiflexible; i.e., they have bending rigidity characterized by a persistence length that ranges from around 20 μm for actin to millimeters for microtubules when measured *in vitro* [28]. Despite their high bending rigidity, microtubules are frequently curved in cells due to the compressive loads they bear from the contractile actomyosin cytoskeleton [29]. The intermediate filament vimentin is also highly curved and even wavy in cell images [30] and forms rings around the nucleus during cell spreading [31]. Actin typically assembles into shorter linear filaments that form higher-order structures that resemble actin rings [32]; however, force-induced curvature of short actin filaments has also been observed [33]. Specialized proteins can also curve actin filaments, like septins or IQGAP (IQ-motif containing GTP-ase proteins) [34].

Since curvature encodes substantial information about force generation and transmission within the cell and its surroundings, these observations motivated us to construct curvature-based measures, described in detail in Sec. II.

Of the components that make up the actin cytoskeleton, the actin cortex and the lamellipodia are highly crosslinked networks of predominantly branched linear filaments that are inherently disordered and spatially heterogeneous. To the eye, differences in network organization resemble differences in texture, motivating the application of textural measures to characterize the network structure.

Haralick features are particularly well suited for capturing emergent structural patterns in disordered and spatially heterogeneous images. Haralick features are one of the most widely used texture descriptors, computed from the gray-level co-occurrence matrix, which summarizes how often intensity value pairs occur for a given distance and direction. These matrix data are then converted into interpretable measures, such as contrast, correlation, energy, and homogeneity [35]. Haralick feature analysis has been used on a wide variety of cytoskeletal systems. They have been shown to be informative in classifying cell types [36], quantify changes in actin architecture during wound repair [37], and measure changes in microtubule organization [38,39] and vimentin networks [40].

We reasoned that using both curvature and texture measures would allow us to capture complementary information about system state. Curvature encodes the effect of forces and constraints at the filament level, while the texture features encode network organization at the scale of the entire image. In addition, we also applied two other types of morphological metrics: measures of nematic ordering of polymer filaments [14] and a recently published set of morphological measures for soft matter dynamics that represent texture as an array of blobs and voids and compute temporal statistics of these structures [41].

We then asked whether these morphological metrics can distinguish between differences in dynamic trajectories of cytoskeletal networks that arise due to differences in basic parameter values.

We address this question using simulations, where individual parameters governing assembly like filament length, rigidity, motor, and crosslinker concentrations can be systematically varied. This allows us to directly assess the sensitivity of morphological metrics to specific model parameters.

II. MATERIALS AND METHODS

A. System

1. Simulation system

We simulate a polymer network using Cytosim [42], containing filaments, motors, and crosslinkers. We adapted and developed a previously published simulation [43,44] on the actin cytoskeleton.

The crosslinkers are represented by a connector with identical binders that can bind anywhere along the filament, similar to alpha-actinin or filamin, while the motors are represented by a connector with two motor subunits that can bind anywhere along the filament, like motors of the family of kinesin 5 or myosin IV [43]. For simplicity, we do not model periodic boundary conditions or the expansion or shrinkage of the filaments. We also assume that connectors do not interfere with each other, and that the subunits of connectors are noninteracting in the bound state. There is no limitation on the number of connectors that may bind to a filament. The motion of motors along a filament is unobstructed. Their velocity depends on force, but their detachment rate does not.

The networks evolve from an initially unorganized state via binding-unbinding of crosslinkers and motor movement. For every replicate, we generate a random initial state and vary the parameters as discussed below. In case of different filament lengths, we generate smaller filaments by cutting the longer filaments into two, while maintaining their initial randomized positions, to ensure that the morphology of the initial condition is the same.

In contrast to earlier work, we intentionally sample a broader and more diverse parameter space, generating a wide set of systems with distinct combinations of biophysical parameters that can be explored using our morphological measures. All simulations are carried out in two dimensions for simplicity and computational speed. Each simulation runs for 200 000 frames with a time step of 0.001 s each, from which 600 evenly spaced frames were recorded. All measures were calculated from every fifth frame, balancing computational efficiency with sufficient temporal resolution.

By varying motor concentrations and filament length, we observe four distinct phenotypes:

- (1) *Low motor/short filament* (LM-SF): weakly organized networks with slight contractility.
- (2) *High motor/short filament* (HM-SF): strong condensation into compact aggregates or asters.
- (3) *Low motor/long filament* (LM-LF): largely unorganized networks with minimal contractility.
- (4) *High motor/long filament* (HM-LF): condensation into aggregates or asters that are less compact than in the short-filament case.

Motor densities are set to 6.25 and 100 motors per μm^2 for the low-motor (LM) and high-motor (HM) regimes, respectively, while the crosslinker density is initially fixed at 250 per μm^2 . The total filament length across all filaments is held constant across all simulations. In long-filament (LF) systems, the average filament length is approximately $1.54 \mu\text{m}$. Short-filament (SF) systems are generated by splitting each long filament into two equal segments.

Although all four states are globally disordered, their local morphology encodes distinct biophysical parameters of the system. LM systems exhibit a stalled network, whereas HM systems undergo

condensation that is readily discernible by eye. While systems with different filament lengths behave similarly at the same motor concentrations, subtle differences arise in these cases that are not readily apparent by visual inspection.

We also sample the previous cases over two rigidities: $0.075 \text{ pN } \mu\text{m}^{-1}$ which is the same as actin filaments (AR), which should be easier to bundle, and $0.01 \text{ pN } \mu\text{m}^{-1}$, which reflects a filament of much lower rigidity (LR), which should be more pliable to the motors. This interplay should result in systems that show similar general trends but are still distinctly different.

Because crosslinker-mediated stabilization and bundling play a crucial role in determining the final system state at late trajectory times [43], in addition to the initial “high” regime [high crosslinker concentration (HCL), density = 250] used previously, where bundling should predominate at late trajectory times, we also sample a “low” regime [low crosslinker concentration (LCL), density = 15.625], where this crosslinker-mediated stabilization is significantly weaker.

Simulations take place in a box of side $4 \mu\text{m}$. Since in real life, filaments will likely stay in confined systems, we examine the role of external space constraints. We perform an additional set of simulations in which the cytoskeletal network is confined within a fixed circular boundary representing a simplified cell-like circular geometry of diameter $4 \mu\text{m}$. This constraint introduces geometric and mechanical restrictions that should alter filament organization, allowing us to directly assess how confinement modifies the curvature and texture metrics relative to the unconfined systems.

Across this parameter space, we aim to use different morphological descriptors to distinguish between and gain insights about systems that may appear qualitatively similar, but arise from distinct underlying biophysical regimes.

2. External validation on published cytoskeletal images

To validate our proposed morphological parameters, we also apply a subset of them to cell images published by Hauke *et al.* [45]. All experimental procedures, including staining of cytoskeletal filaments (actin, vimentin, and microtubules), substrate preparation across five stiffness conditions, and image acquisition, were carried out in the original study. Briefly, human mesenchymal stem cells were cultured on elastic polyacrylamide gels with different Young’s moduli and glass, all coated with collagen I. Cells were fixed after 24 h and then stained. Here, we use only the published images as an external validation dataset (see Ref. [45] for details).

B. Morphological parameters

We look at three scales of parameters for our study.

- (1) *Global textural parameters*: Haralick features.
- (2) *Filament-level features*: nematic order parameters, mean alignment order of filaments.
- (3) *Local features*: mean curvature of filament segments.

We explore the behavior of these features across an ensemble of 20 simulations each, for all the cases mentioned above.

1. Haralick features

Haralick texture features are statistical descriptors derived from the gray-level co-occurrence matrix, originally introduced by Haralick *et al.* [35] to quantify spatial relationships between pixel intensities in images. These features capture key aspects of image texture such as contrast, homogeneity, entropy, correlation, and energy, providing a compact numerical representation of structural organization beyond simple intensity-based metrics. For example, local variation can be measured by multiple Haralick features: “Contrast” is a measure of the amount of local variation in an image, with a higher value indicating larger amount of such variations, while “angular second moment (ASM)” is a measure of homogeneity of the image, where images with a large number of small transitions have a smaller ASM, while images with large transitions have a larger ASM. Each

of these metrics represents a different aspect and holds different interpretations that can be found in Haralick’s original paper.

In our work, we use Haralick features to serve as quantitative texture descriptors to characterize spatial organization within cytoskeletal networks, enabling systematic comparison across experimental conditions without worrying about segmentation or filament tracking. To ensure that the features are rotationally invariant, we average the features calculated over angles 0° , 45° , 90° , and 135° .

Haralick features are sensitive to free space. For experimental images that are not as sharply resolved as our simulation images, segmenting the cell allows the calculation of the Haralick features as normal, ignoring the transitions to and from zero intensities in the gray-level co-occurrence matrix. This makes it consider only the object system and not the empty space around it. Since our simulation results have a very high resolution and our nonfilament background is zero, ignoring the zero transitions would lead to calculation of texture only along the filaments. If we do not ignore the zero transitions, it would lead to classification of systems that do and do not condense, based mainly on the free space, instead of internal texture due to the filament system. So, we try to find a reasonable area that contains a representative snapshot of the system, without too much free space. We do this by asymmetrically cropping these systems around the centroid of the system, such that the cropped region contains 70% of the bright pixels, before calculating Haralick features on the resulting simulation images.

2. Nematic order parameters

The nematic order parameters are a measure of how aligned a collection of elongated objects is. They are commonly used to quantify alignment in actin bundles, stress fibers, and contractile structures, and are especially powerful for studying order-disorder transitions. We test four of the morphological parameters laid out by Akenywa *et al.* [14], namely, mean angle [46], angular variation, parallelness [47], and order parameter. Mean angle is a measure of orientation, while the other three are a measure of ordering. However, for our active disordered systems, they do not perform well (see Fig. S1 of the Supplemental Material [48]), probably because our simulation systems do not show any global nematic ordering.

3. Mean curvature of filament segments

Mean curvature is a measure of the average degree of filament bending within the network. Filament coordinates obtained from Cytosim are discretized into segments of length $0.5\ \mu\text{m}$. For each filament, curvature is computed at each segment using the standard planar curvature expression

$$\kappa = \frac{|x'(t)y''(t) - y'(t)x''(t)|}{(x'(t)^2 + y'(t)^2)^{3/2}}, \quad (1)$$

where $x(t)$ and $y(t)$ denote the Cartesian coordinates of a filament and the primes indicate derivatives taken along the filament. The numerator measures how rapidly the filament changes direction, while the denominator normalizes this change to yield a geometric measure of curvature.

The absolute value of κ is retained so that curvature reflects bending magnitude independent of direction. Curvature values are computed for all filament segments and the overall mean for the system is retained.

A higher mean curvature implies more bending of the filaments. However, since this is a small-scale feature, care should be taken while selecting the segmentation length at which the curvature is measured. For very small segmentation distances, even for curved filaments, local sections may appear straight.

4. Mean alignment order of filaments

The mean alignment order of filaments is a measure of the average curvedness of filaments of a system, compared to a system with only straight filaments. For each filament, we create a “director,”

which is a straight line joining the ends of a given filament. We then take each filament section of size $0.5\ \mu\text{m}$ as discussed earlier, and calculate the angle each section makes with its respective filament director using dot product. Let $\mathbf{v}_i = (\Delta x_i, \Delta y_i)$ denote the local segment direction, and let $\mathbf{v}_{\text{dir}} = (\Delta x_{\text{dir}}, \Delta y_{\text{dir}})$ denote the filament director. The angle θ_i between the segment and the director is then given by

$$\theta_i = \cos^{-1} \left(\frac{\mathbf{v}_i \cdot \mathbf{v}_{\text{dir}}}{\|\mathbf{v}_i\| \|\mathbf{v}_{\text{dir}}\|} \right), \quad (2)$$

where $\mathbf{v}_i \cdot \mathbf{v}_{\text{dir}}$ is the dot product and $\|\cdot\|$ denotes the Euclidean norm. Angles are computed for all filament segments and the overall mean for the system is retained.

Alignment order of 0 implies that the filament is completely aligned with the director, while higher values imply more curves in the filament body.

5. Biomaterial activity readouts to categorize, optimize, design, and engineer

Biomaterial Activity Readouts to Categorize, Optimize, Design, and Engineer (BARCODE) is a recently published open-access software that calculates a set of morphological metrics on optical microscopy videos and outputs summary statistics representing the entire trajectory [41].

We utilized the code provided in the above cited paper and ran all three independent analysis branches: image binarization, intensity distribution, and optical flow on our videos, which were converted to grayscale one-channel tiff files. To maintain a balance between resolution and computation speed, statistics were calculated on every five frames, using the settings detailed in the paper above. This resulted in 17 BARCODE features. We used all of these features except the feature ‘‘Connectivity,’’ which we dropped, since due to the presence of the bounding circular cell, it was not applicable to some of our videos.

C. Principal component analysis

Principal component analysis (PCA) provides a low-dimensional representation of the data that preserves the most variance along orthogonal directions. It is used to reduce the dimensionality of the feature space and to summarize dominant linear patterns in the data.

PCA was applied to the data containing 120 time points for distributions of standardized filament-level features and rotation-invariant Haralick texture features over 8–16 cases at a time, each with 20 replicates. With 36 bins equally distributed over the two filament features or the 14 Haralick features, some of which are highly correlated, a highly complicated feature space emerges, which can be simplified using the PCAs. The PCA was computed using a singular-value-decomposition-based algorithm, calculating the top 10 principal components for each observation and retained along with metadata identifying experimental condition, time frame, and replicate.

The resulting principal component scores were used for visualization and exploratory analysis. The first two components explained a lot of the variance, so they were plotted for visualization, along with time-resolved visualizations to track the evolution of observations in principal component space. PCA loadings and explained variance ratios were examined to assess the contribution of individual features to each component and to guide interpretation of dominant linear patterns in the data.

D. Uniform manifold approximation and projection

To complement PCA and possibly decode nonlinear structure in the data, uniform manifold approximation and projection (UMAP) was employed as a nonlinear dimensionality reduction technique for visualization. UMAP was applied to the principal components calculated in the PCA analysis. UMAP was computed by first creating a weighted nearest-neighbor graph in the original high-dimensional PCA feature space, from which a low-dimensional embedding is created that optimally tries to preserve local neighborhood relationships while maintaining aspects of the global

structure. UMAP embeddings were calculated using a Euclidean distance metric on standardized features, with the number of neighbors = 30 and the minimum distance parameter = 0.05. We sampled different values for the number of neighbors (15, 30, and 50) that have been used in the literature and provided the others in Figs. S2–S9 of the Supplemental Material [48]. We decided to use 30 as it seems to decode local feature clustering well enough, without losing global trends. The UMAP embedding was fit once on the relevant PCA results, and the resulting low-dimensional coordinates were retained for visualization and temporal analysis. Observations were visualized in two-dimensional UMAP space, colored by experimental condition, and time-resolved visualizations were constructed by slicing the global embedding by frame to track the evolution of system dynamics over time. To help interpret the embeddings, Pearson correlations between original standardized features and UMAP coordinates were also computed.

III. RESULTS

A. Simulation data reveal differences in dynamic trajectories in different parameter regimes

Our simulations show dramatic differences in system dynamics. Despite differences in filament length, rigidity, and motor and crosslinker concentration, every simulation starts from exactly the same initial cytoskeletal architecture (see Sec. II) but soon diverges into a stalled network, multiple asterlike clusters, or a single central condensed cluster that coarsens into a giant aster. Below, we describe these visual differences associated with different simulation conditions in detail.

Representative snapshots of simulations are shown in Fig. 1 for a box geometry of size $4\text{ }\mu\text{m}$. Panel (I) shows the effect of low-motor concentrations [rows (a) and (c)] versus high-motor concentrations [rows (b) and (d)] for filaments with rigidity comparable to actin and a high cross-linker concentration. We can see the high-motor simulations condensing to a central dense structure at early times, while in the low-motor case, the filaments bundle, and the network coarsens and stalls. For the high-motor cases, short-filaments in row (b) show only partial condensation compared with the long-filaments of row (d). Careful visual analysis also reveals differences in bundling dynamics between short and long filaments for low-motor concentrations.

Panels (I)–(IV) are organized similarly. In panel (II), we see that decreasing the rigidity of the polymer (LR) at HCL increases the ability of motors to condense filaments. More enhanced bundling can be seen in row (a) (SF-LM), and asterlike structures form in all the other cases, including the LM-LF case [row (c)]. Panels (III) and (IV) show what happens when we reduce crosslinker concentrations (LCL) with either actin rigidities [panel (III)] or low rigidities [panel (IV)]. While row (a) (LM-SF) in both cases looks generally unaffected, a higher motor concentration [row (b)] leads to multiple asters forming [row (b)]. Interestingly, the lower crosslinker concentration is insufficient to form condensed structures when the motor concentration is low for the longer filaments [row (c)]. This difference is very apparent when comparing the two low-rigidity cases [panels (II) and (IV)]. Row (d) looks similar across all panels.

In Fig. S10 of the Supplemental Material [48], we show representative snapshots from simulations in a circular box of diameter $4\text{ }\mu\text{m}$, which acts as a geometric constraint compared with the box. The effect of this constraint is to enhance condensation, which we can see by comparing the global organization of condensation in Fig. S10, panels (I) and (II), of the Supplemental Material [48], with its counterpart for the square cell. Similarly, constraining the filaments to a circular cell [Fig. S10, panels (III) and (IV), of the Supplemental Material [48]] in the low-crosslinker regime helps to achieve global condensation again for the HM-SF case [row (b)] compared to the local condensations shown by the corresponding case for the square cell.

1. Filament-level features show separation based on mechanical properties of the polymers

Filament-level descriptors are based on polymer bending, represented either as the angular difference from the end-to-end vector or as local curvature (see Sec. II). Since polymer bending depends upon rigidity as well as segment length, the temporal evolution of these measures should reveal how motor concentration, filament length, rigidity, crosslinker density, and confinement shape

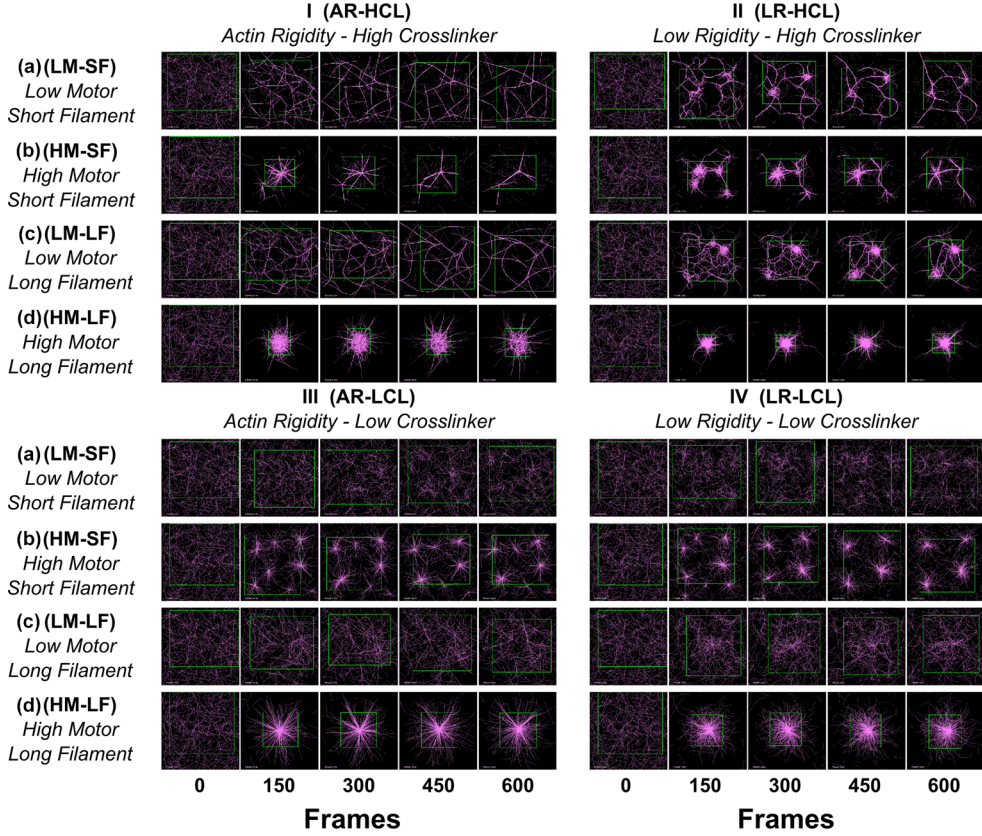


FIG. 1. System evolution of filament trajectories in a box of side = 4. Panel columns (I)–(IV) denote rigidity–crosslinker-density regimes: (I) AR-HCL, (II) LR-HCL, (III) AR-LCL, and (IV) LR-LCL. Panel rows (a)–(d) denote motor-filament regimes: (a) LM-SF, (b) HM-SF, (c) LM-LF, and (d) HM-LF. Rigidities: AR = $0.075 \text{ pN } \mu\text{m}^{-1}$ and LR = $0.01 \text{ pN } \mu\text{m}^{-1}$. Crosslinker densities: HCL = 250 and LCL = 15.625. Columns within each trajectory panel correspond to frames 0, 150, 300, 450, and 600.

overall network organization. For all parameter regimes, both filament-level features show the most temporal variation during an early-trajectory “condensation phase” (from frame 0 to around frame 75, changing for different cases), followed by gradual convergence as the system transitions into a “bundling phase” at later trajectories (Fig. 2 and Fig. S11 of the Supplemental Material [48]).

During condensation, motor-driven activity causes rearrangements that the network accommodates primarily through filament bending and reorientation. Curvature therefore increases sharply at early times for all systems, with different dynamics. The low-motor short filaments show an initial increase followed by stabilization at a low value, while the corresponding long-filament case shows a more significant increase with a slower decay. For the high-motor systems, however, there is a sharper increase in curvature followed by a fast decline, with long filaments dominating the short filaments in each case, as expected due to the differences in bending energy.

Alignment order similarly changes significantly during condensation as well. Here too, the most significant quantitative changes are in the high-motor systems. Interestingly, the high-motor long-filament systems show a slower decrease after the initial increase compared with the high-motor short-filament case, probably because shorter filaments are easier to move around with motors. The low-rigidity systems show a uniformly higher value for this metric compared with the respective high-rigidity cases due to bending energy differences.

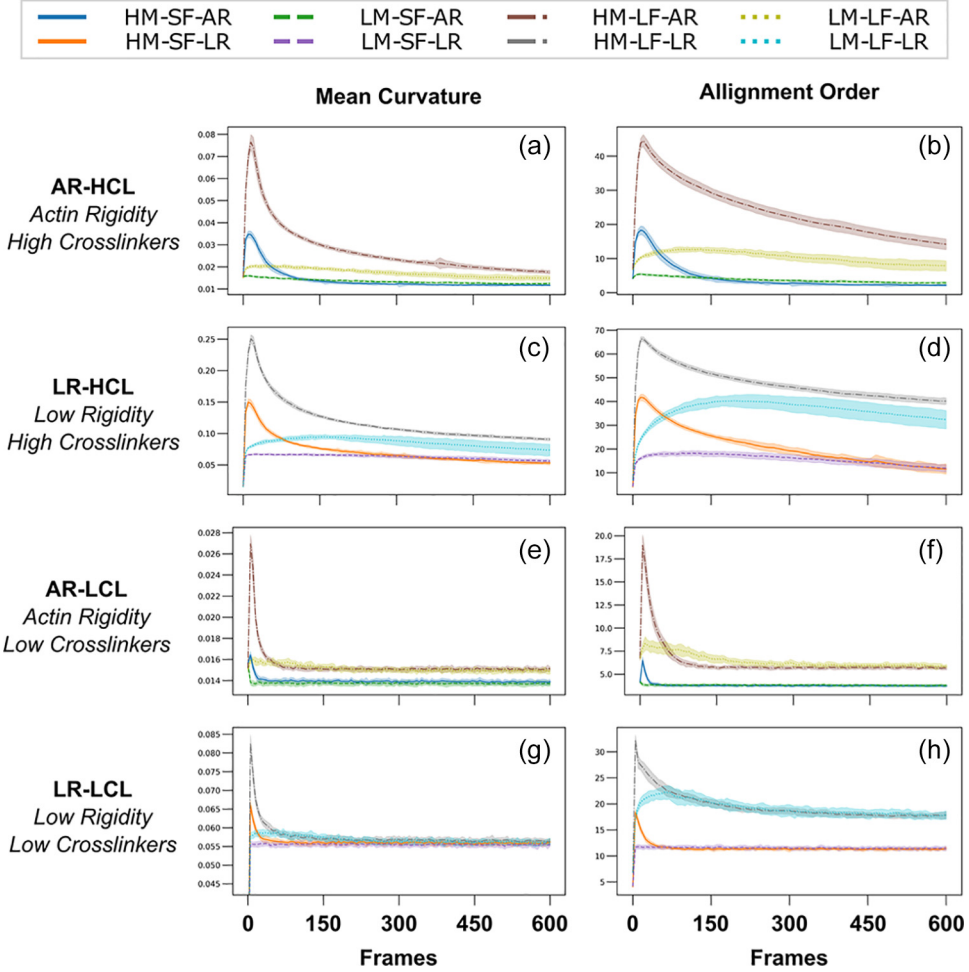


FIG. 2. Ensemble averages of the evolution of filament features for box of side = 4. Mean curvature [panels (a), (c), (e), and (g)] and alignment order [panels (b), (d), (f), and (h)] for rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ [panels (a), (b), (e), and (f)] and $0.01 \text{ pN } \mu\text{m}^{-1}$ [panels (c), (d), (g), and (h)], and crosslinker densities 250 [panels (a)–(d)] and 15.625 [panels (e)–(h)].

As the system evolves, filament-level features begin to converge as fibers bundle and become thicker. With more time for crosslinker binding, filament-filament contact points are stabilized, rearranging filaments into mechanically coupled bundles. These bundles behave as stiffer composite structures, making them harder to bend and reducing both curvature and alignment order. As can be seen from Fig. 2, while all trajectories separate out during early times, there is a drop in both alignment order and curvature, and a convergence to three groups at longer times for the cases with high-crosslinker density and one to two groups for those with low-crosslinker density.

Geometric confinement (see Fig. S11 of the Supplemental Material [48]) further increases early curvature changes by probably increasing interactions between the filament and the boundary, forcing mostly longer filaments to bend and reorganize due to the restricted volume. This leads to sharper drops for both mean curvature and alignment order for these cases.

These trends show that curvature-based features encode rich, regime-dependent information during condensation, but may lose discriminative power as filaments bundle and become harder to bend.

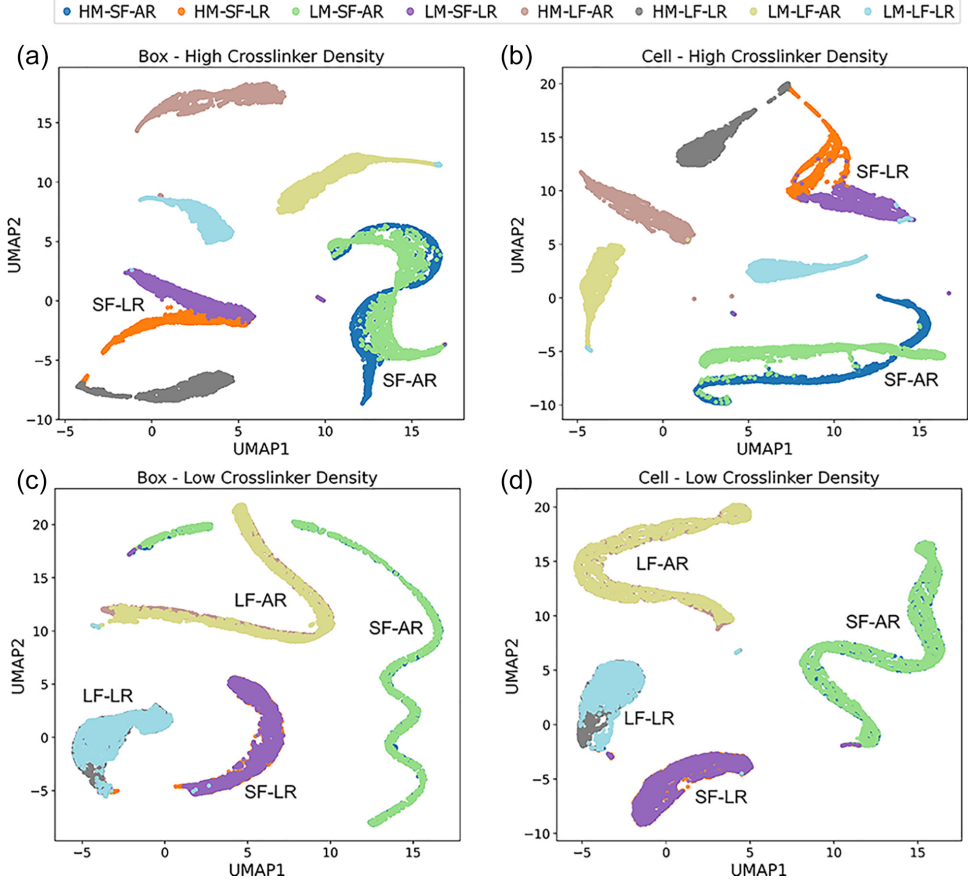


FIG. 3. UMAP plots for the bins of the filament features along with time for box of side = 4 [panels (a) and (c)] and constrained cell of diameter = 4 [panels (b) and (d)] including rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ (AR) and $0.01 \text{ pN } \mu\text{m}^{-1}$ (LR) for crosslinker densities 250 [panels (a) and (b)] and 15.625 [panels (c) and (d)].

2. Filament-level features cluster along the filament-length and filament-rigidity axes

We asked whether systems with different underlying parameters cluster distinctly in the space of morphological features. To examine this, we projected the high-dimensional feature space into lower dimensions using two common methods: PCA and UMAP.

Principal component analysis was carried out by treating the distribution of curvatures or alignment angles, respectively, as a vector of counts for each frame. The PCA was performed on standardized distributions of the two filament features across 120 time points, with each feature distribution represented by 18 equally spaced bins and 20 replicates per simulation case. Eight cases were included in each PCA, jointly capturing variations in motor density, filament length, and filament rigidity for a given combination of crosslinker density and confinement. Since the first two PCAs account for more than 70% of the explained variance for all the cases (see Fig. S12 of the Supplemental Material [48]), we project the data into a two-dimensional morphospace (see Fig. S13 of the Supplemental Material [48]). As Fig. S13 of the Supplemental Material [48] shows, the combined PCA over all time (which we refer to by the term “static PCA”) does not show separation between the different cases, despite the separation of the mean values in Fig. 2. Since dimensionality reduction methods like UMAP are better optimized at separating data clusters than PCA, we performed UMAP on the PCA values and obtained significantly better separation of the different simulation cases from each other, shown in Fig. 3. In particular, for

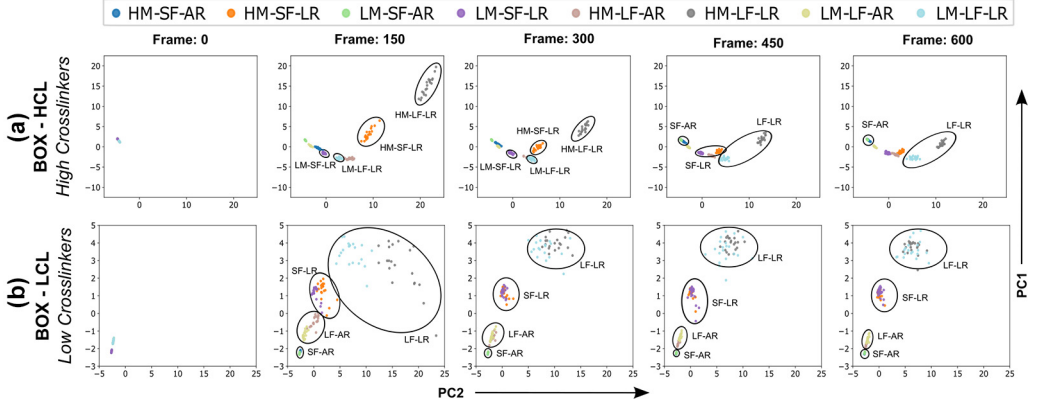


FIG. 4. Evolution of trajectories of PCA plots for the bins of the filament features for box of side = 4 [panels (a) and (b)] including rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ (AR) and $0.01 \text{ pN } \mu\text{m}^{-1}$ (LR) for crosslinker densities 250 [panel (a)] and 15.625 [panel (b)]. Columns: (left to right) frames = 0, 150, 300, 450, and 600.

high-crosslinker cases, all the long-filament simulations cluster separately, while the short-filament simulations cluster by rigidity, for both box and cell geometries. In contrast, for the low-crosslinker simulations, similar to the short-filament simulations, the long-filament cases also cluster together by rigidity.

We then asked whether the time-resolved PCA, calculated by explicitly tracking the system evolution, would offer greater insight. As Fig. 4 shows, after starting at the same location due to initial conditions, the systems typically diverge during condensation before converging back during bundling. Over time, the clusters mainly group themselves along the filament length-rigidity pairs, as indicated by the ellipses in Fig. 4. For example, in row (b) we get four distinct clusters corresponding to LF-LR, SF-LR, LF-AR, and SF-AR. At high-crosslinker density [panel (a)], at long times, due to bundling, there is a loss of discrimination power and the higher-rigidity groups slowly start to merge together. However, as we go to low-crosslinker densities [panel (b)], the long filaments form two different groups based on rigidity quite early. The results look similar for the circular constrained cell as well (see Fig. S14 of the Supplemental Material [48]).

As with the static PCA, the time-resolved UMAP trajectories (see Fig. S15 of the Supplemental Material [48]) separate out all eight conditions for a major part of the trajectory for the high-crosslinker cases. In the low-crosslinker regime, we find four distinct clusters through most of the trajectory, separating out the four cases where we vary filament length and rigidity.

These results show that both filament-feature PCA and UMAP can decode mechanical information encoded by our filament-level features, with temporal trajectories offering more insight. Specifically, we find that for high crosslinkers, filament features cluster separately for each of the eight cases, while for the low crosslinkers, the features can distinguish between SF-AR, SF-LR, LF-AR, and LF-LR but not between high-motor and low-motor cases.

3. Haralick features primarily separate trajectories along the high-motors–low-motors axes

Haralick texture descriptors quantify spatial correlations in image intensity and capture global properties of network organization such as condensation, interstitial pore topology, and aggregate compactness. Because the 14 Haralick features are highly correlated, dimensional reduction via PCA or UMAP is necessary. PCA was performed using the 14 Haralick features extracted from the simulation data across all 120 time points and 20 replicates per case. To examine the collective effects of changes in filament and motor properties, cases varying in motor density, filament length, and filament rigidity were analyzed together. This analysis was repeated separately for each combination of crosslinker density and confinement. Now, the first two PCAs account for more than

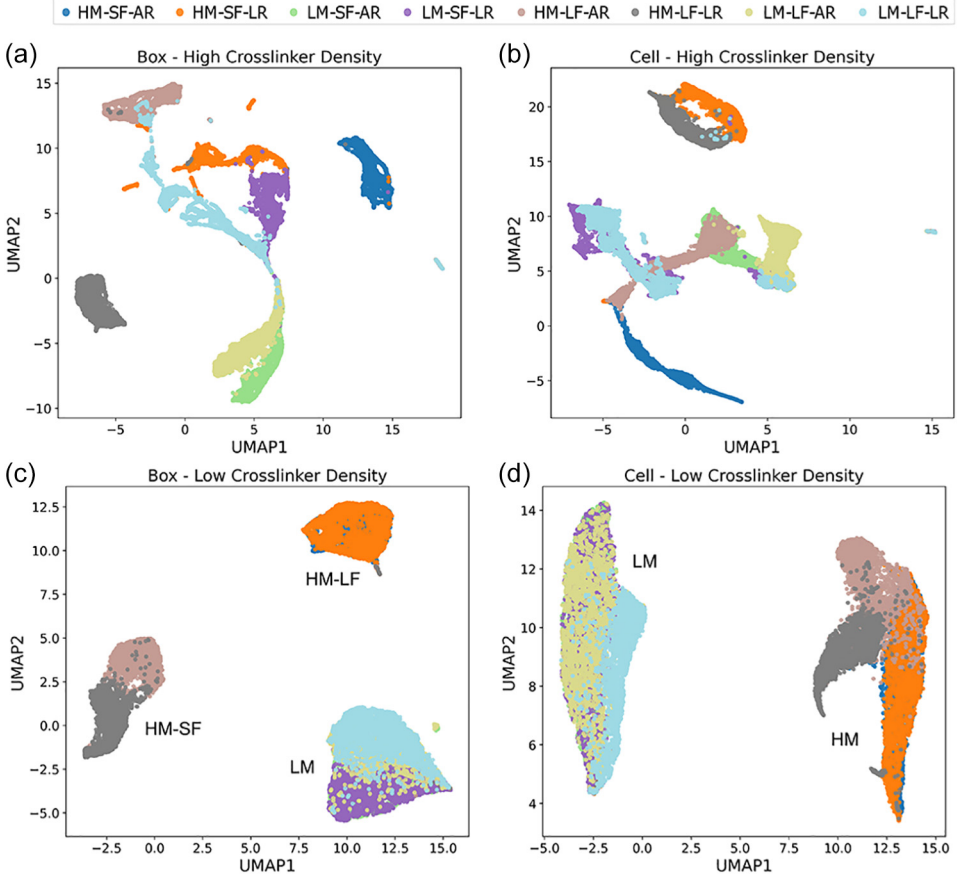


FIG. 5. UMAP plots for Haralick textural features along with time for box of side = 4 [panels (a) and (c)] and constrained cell of diameter = 4 [panels (b) and (d)] including rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ (AR) and $0.01 \text{ pN } \mu\text{m}^{-1}$ (LR) for crosslinker densities 250 [panels (a) and (b)] and 15.625 [panels (c) and (d)].

85% of the explained variance for all the cases (see Fig. S16 of the Supplemental Material [48]). We use UMAP on the PCA vectors to improve discrimination in two-dimensional space.

Unlike for the filament-level measures, static PCA of Haralick features robustly separates low-motor from high-motor systems for low-crosslinker density [see Fig. S17, panels (c) and (d), of the Supplemental Material [48]] but not for high-crosslinker density [panels (a) and (b)]. Low-motor systems cluster tightly due to weak reorganization of the texture, whereas the high-motor systems shift strongly in PCA space due to large-scale reorganization of textures. This contrast between high-crosslinker density and low-crosslinker density is probably due to the fact that in the absence of sufficient bundling in the latter, there is a greater textural difference between a stalled network and clustered network [see the Supplemental Material [48]; Fig. 1, panels (III) and (IV)]. Similar results are seen when UMAPs are computed for the same standardized feature sets (Fig. 5). At low-crosslinker density, high-motor systems further separate by filament length in static Haralick PCA [see Fig. S17, panel (c), of the Supplemental Material [48]], which is seemingly lost when looking at a circular constrained cell [panel (d)], where due to the spatial constraint, the filaments come closer, allowing for more bundling, which reduces the textural differences between the two cases [see Fig. S10, panels (III) and (IV), of the Supplemental Material [48]].

Time-resolved Haralick PCA trajectories recover these distinctions (Fig. 6). While the static UMAP for the high crosslinkers shows that the high-motor and low-motor cases overlap in

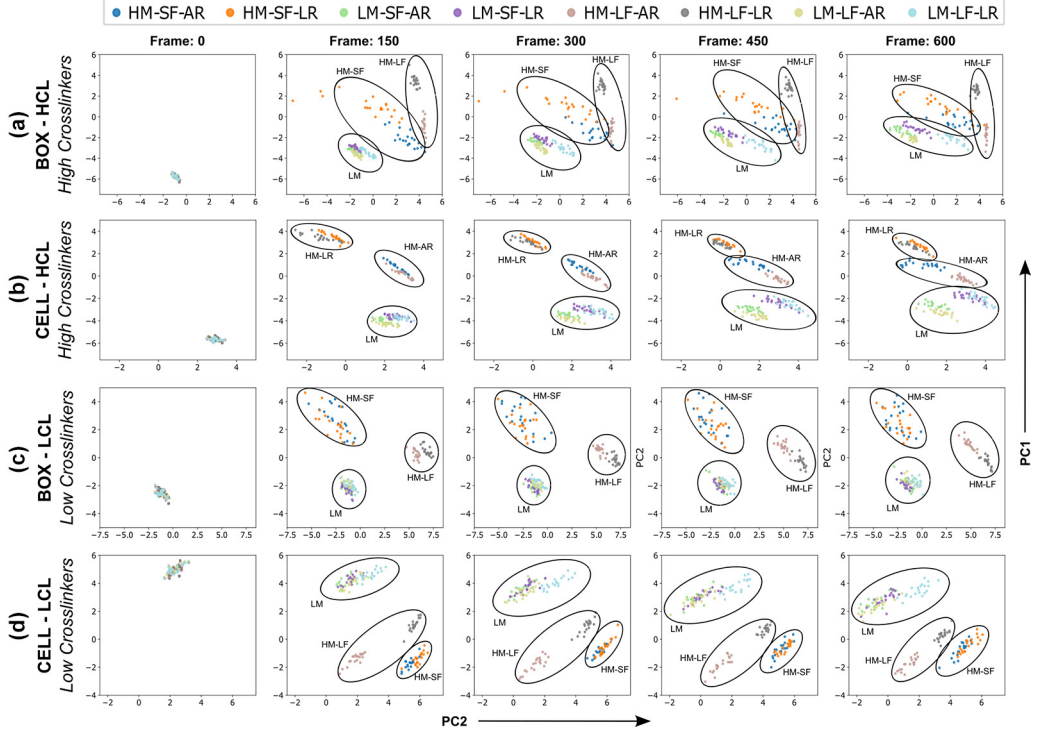


FIG. 6. Evolution of trajectories of PCA plots for Haralick features for box of side = 4 [panels (a) and (c)] and constrained cell of diameter = 4 [panels (b) and (d)] including rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ (AR) and $0.01 \text{ pN } \mu\text{m}^{-1}$ (LR) for crosslinker densities 250 [panels (a) and (b)] and 15.625 [panels (c) and (d)]. Columns: (left to right) frames = 0, 150, 300, 450, and 600.

low-dimensional morphospace, they are well separated in the temporal trajectories, which can also differentiate between filament length [panels (a), (c), and (d)] and rigidity [panel (b)]. The UMAP trajectories (see Fig. S18 of the Supplemental Material [48]) show similar trends but with generally better separation of the different cases.

These results show that both PCA and UMAP of Haralick features can resolve morphological features between high-motor and low-motor cases, and, in some cases, also between different filament lengths and different rigidities, especially when the time-resolved features are taken into account.

4. Complementary roles of filament and Haralick features

Together, these results demonstrate that filament and Haralick features capture complementary aspects of active network organization. Filament features resolve polymer-scale mechanics, rigidity effects, and filament-length-dependent bundling, while Haralick features robustly detect bundling and large-scale texture reorganization, especially emerging from differences in motor activity as well as intrinsic rigidity.

To confirm these findings, we calculated the PCA using both feature families together and performed subsequent PCA and UMAP visualizations. We also expanded the feature set used to calculate the PCA, to incorporate crosslinker density in addition to motor density, filament length, and filament rigidity, providing a further robustness test of whether the patterns identified in our simulations would be preserved. For the PCA scales to be visualized meaningfully though, PCA for all low-crosslinker and high-crosslinker cases is plotted separately. While there is a drop in the

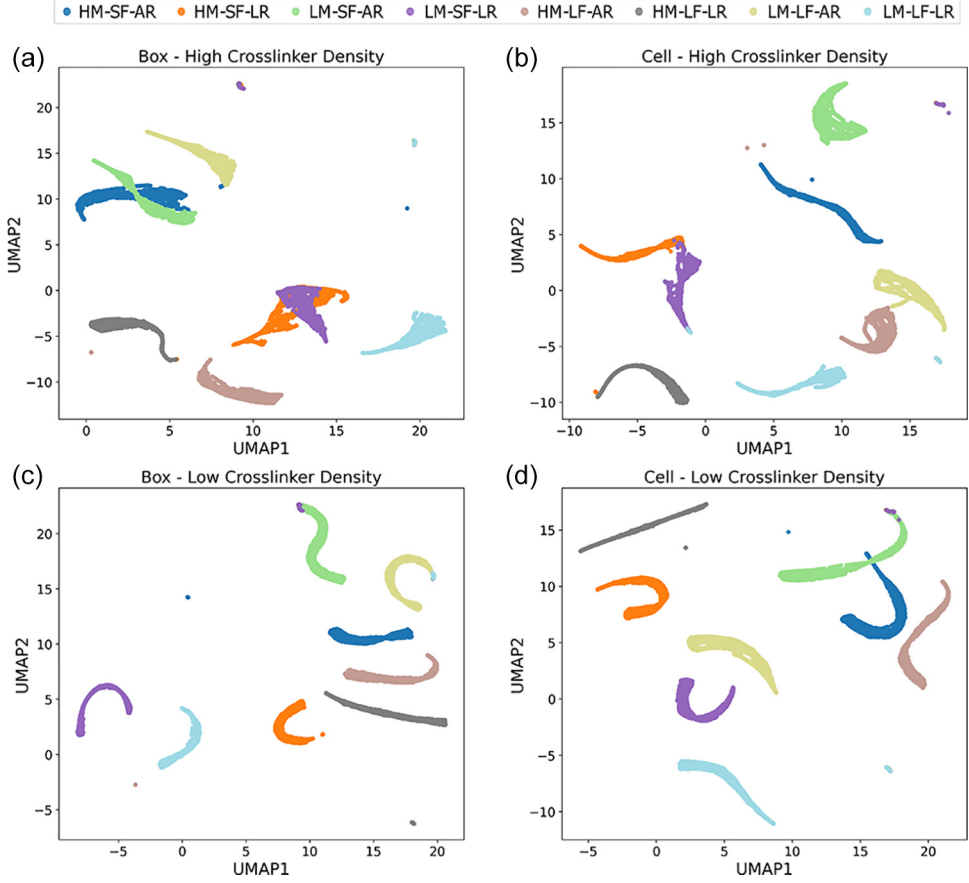


FIG. 7. UMAP plots for combined filament and textural features along with time for box of side = 4 [panels (a) and (c)] and constrained cell of diameter = 4 [panels (b) and (d)] including rigidities $0.075 \text{ pN } \mu\text{m}^{-1}$ (AR) and $0.01 \text{ pN } \mu\text{m}^{-1}$ (LR) for crosslinker densities 250 [panels (a) and (b)] and 15.625 [panels (c) and (d)].

explained variances for the first two components, they still account for more than 65% variation for both the cases (see Fig. S19 of the Supplemental Material [48]). The PCA plots of the first two components still show groupings by class (see Fig. S20 of the Supplemental Material [48]), but the difference is most clearly observed in the UMAP plots, where we can see a very clear distinction between the groups for all the cases (see the Supplemental Material [48]; Fig. 7). The low-crosslinker cases [panels (c) and (d)] that have weak stabilization show almost no overlap, whereas the high-crosslinker cases [panels (a) and (b)] show some overlap. All overlap disappears when looking at the temporal trajectories for both PCA and UMAP (see Figs. S21 and S22 of the Supplemental Material [48]).

These results support that dimensionality reduction is informative in regimes with weak stabilization, whereas time-resolved trajectories are essential in regimes dominated by larger changes over the cases over time. Combining both feature families with trajectory-based analysis is therefore necessary to provide a comprehensive framework for distinguishing active disordered systems across physical regimes.

5. BARCODE features cluster similar to time-resolved texture features

A new set of morphological features, named BARCODE, was recently published [41]. BARCODE represents each trajectory by a single 17-dimensional data point, and was designed to classify

videos of dynamical behavior of soft and active materials. Since these sets of measures are very different from the others we have used in this paper, we were curious to see whether they would be able to classify the different cases in our simulations. PCA was then performed on the 16 retained BARCODE features. As in the filament-level and Haralick analyses, cases varying in motor density, filament length, and filament rigidity were analyzed together, with the analysis repeated separately for each combination of crosslinker density and confinement. The explained variance of the first two PCAs accounts for about 70% of the explained variance for all the cases (see Fig. S23 of the Supplemental Material [48]) supporting a two-dimensional projection.

PCA of the 16 BARCODE features shows distinct clustering of low-motor and high-motor cases separately (see Fig. S24 of the Supplemental Material [48]). High-motor cases separate out based on filament length, whereas for the low-motor cases, we see more mixing between groups. When investigated separately, of the three analysis branches, the Intensity Distribution branch (see Figs. S25 and S26 of the Supplemental Material [48]) works best for our data and gives results comparable to the time-resolved Haralick PCA trajectories, albeit at a lower resolution. This is perhaps due to the fact that Haralick features are in essence statistical features of intensity distribution, so they probably encode similar information. The Binarization branch (see Figs. S27 and S28 of the Supplemental Material [48]) performs slightly worse, and the Optical Flow branch performs the worst (see Figs. S29 and S30 of the Supplemental Material [48]), since it is not really designed to capture the type of movements present in our simulations.

B. Haralick features distinguish between actin and other filaments in experimental images

While Haralick features have been used extensively for cell morphology studies, they have not yet to our knowledge been used to distinguish between different constituents of the cytoskeleton. Our analysis shows that Haralick features should be able to distinguish polymer networks of different rigidities from each other. To test this, we used a publicly available database of static images of fluorescently labeled actin, microtubules, and vimentin in cells cultured on substrates of increasing stiffness (see Sec. II). We calculated Haralick features at various Haralick distances for these images (see Fig. S31 of the Supplemental Material [48]), and then performed a PCA, plotting the first two components and coloring them by filament classes (Fig. 8).

Across all substrate stiffnesses and Haralick distances, actin consistently clusters separately from vimentin and microtubules. Vimentin and microtubules, in contrast, lie closer to each other in PCA space, showing more mixing for the cases where stiffness of the substrate is above 1 kPa [panels (II)–(V)]. Significance tests (Bonferroni-corrected Dunn’s test) of the mean values support this, with actin significantly different from the other two polymers for all substrate rigidities, while vimentin and microtubules are statistically not different on three of the five substrates.

Thus, texture-based morphospace analysis can discriminate between cytoskeletal systems with distinct mechanical properties in real biological contexts. Together with the simulation results, this demonstrates that Haralick features capture physically meaningful differences in filament organization.

IV. CONCLUSION

In this paper, we carried out simulations of a disordered polymer network in two dimensions, whose dynamics are driven by motor proteins. For simplicity, we did not consider polymerization processes, but assumed that filament length remains fixed. However, we altered filament rigidity and used two geometries for our simulations, a square box of size 4 μm and a circle with the same diameter, which increased the confinement of the polymers a little. We altered motor concentration and crosslinker concentration and studied the resulting 16 different cases using morphological analysis of the simulation videos.

We concentrated on measures of filament bending (curvature and alignment order, referred to as filament features) and texture (Haralick features) since in our system the polymers did not show

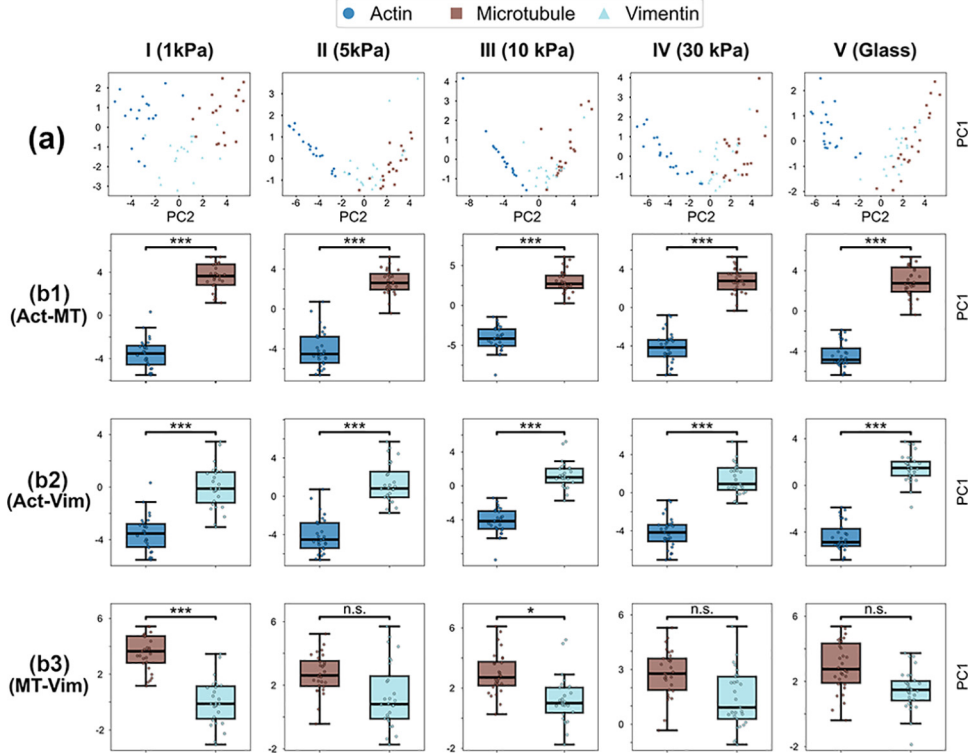


FIG. 8. PCA of the Haralick features for actin (Act), vimentin (Vim), and microtubules (MT) in experimental cells over substrate with stiffness 1 kPa [panel (I)], 5 kPa [panel (II)], 10 kPa [panel (III)], 30 kPa [panel (IV)], and glass [panel (V)], calculated for Haralick distance of 1 [row (a)]. Box plots showing differences of means for actin-microtubule [row (b1)] [$p(1 \text{ kPa}) = 2.82 \times 10^{-15}$, $p(5 \text{ kPa}) = 1.04 \times 10^{-12}$, $p(10 \text{ kPa}) = 1.04 \times 10^{-14}$, $p(30 \text{ kPa}) = 6.43 \times 10^{-14}$, $p(\text{glass}) = 1.09 \times 10^{-14}$], actin-vimentin [row (b2)] [$p(1 \text{ kPa}) = 2.28 \times 10^{-04}$, $p(5 \text{ kPa}) = 5.50 \times 10^{-07}$, $p(10 \text{ kPa}) = 1.75 \times 10^{-06}$, $p(30 \text{ kPa}) = 2.04 \times 10^{-07}$, $p(\text{glass}) = 1.31 \times 10^{-07}$], and microtubule-vimentin [row (b3)] [$p(1 \text{ kPa}) = 1.36 \times 10^{-04}$, $p(5 \text{ kPa}) = 1.18 \times 10^{-01}$, $p(10 \text{ kPa}) = 1.21 \times 10^{-02}$, $p(30 \text{ kPa}) = 7.42 \times 10^{-02}$, $p(\text{glass}) = 5.03 \times 10^{-02}$]. Respective significances are Bonferroni-corrected Dunn's significances and marked in the figure as follows: *** 0.001, ** 0.01, * 0.05, n.s.: not significant.

any global nematic ordering and hence order parameters that were measuring this aspect of network organization were not very informative (see Fig. S1 of the Supplemental Material [48]). We found that filament features did capture network dynamics involving bending and were successful in demarcating shorter and longer filaments due to this reason. To a lesser extent, they could also distinguish between low-motor and high-motor cases especially during the more dynamic phase of network evolution. While no Haralick feature could singly distinguish between different trajectories at all times, collectively they demarcated clusters corresponding to differences in motor concentration as well as filament rigidities. Thus, filament-based features and textural features provide complementary information, and together were able to completely characterize the 16 separate cases for the two geometries that we studied here. For partial validation of the usefulness of morphological features, we showed that they could distinguish actin from vimentin and microtubules in a set of publicly available cell images.

The goal of this paper is to understand the information content of time-resolved morphological features of disordered cytoskeletal networks, with a view to future development of data-driven modeling. By studying whether trajectories from the different simulation classes cluster separately

or together, we were asking whether the differences in dynamics are encoded in the morphological measures we calculated. We conclude that morphology provides a good representation of cytoskeletal dynamics and while no single feature was able to capture all the differences, collectively they were successful in distinguishing all the different cases.

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DATA AVAILABILITY

Simulation scripts and data are available in Ref. [49]. A permanent copy has also been archived on Zenodo and is available at [50].

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