

Entropic, active, and frictional forces in cytoskeletal crosslinking

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(Received 3 April 2026; accepted 7 July 2026; published 29 July 2026)

The forces that mixtures of motorized and passive crosslinking proteins collectively generate between cytoskeletal filaments within our cells are the key drivers of active cellular mechanics. Despite their importance, a unified theory connecting measurable crosslinker properties to force generation between filament pairs has so far been missing. In this paper, we derive a theory that predicts the forces generated collectively by crosslinking proteins linking two biopolymer filaments from experimentally accessible filament and crosslinker properties, using out-of-equilibrium thermodynamics. Our framework allows us to decompose the forces generated by crosslinkers into three separate components: entropic, active, and frictional. In doing so, it offers a clear physical interpretation of the fundamental mechanisms by which crosslinking proteins self-organize and collectively generate forces. We demonstrate the robustness and utility of this framework by applying it to four different experiments that probe the combined roles of passive and motorized crosslinkers. For each experiment, our theoretical approach allows us to disentangle the relative contributions of entropic, active, and frictional forces, clarifying how different physical processes underpin collective force production. In turn, this makes it possible to quantitatively compare and predict how various crosslinker combinations influence force generation between filaments, pattern formation along filaments, and the dynamics of filament pairs.

DOI: [10.1103/6vjh-ym11](https://doi.org/10.1103/6vjh-ym11)

I. INTRODUCTION

The forces that crosslinking proteins generate between cytoskeletal filaments determine how cells divide, migrate, and mechanically deform [1–4]. At the single-molecule level, the kinetic and mechanical properties of many crosslinkers are well characterized [5–10]. At the collective level, force-velocity relationships between crosslinked filaments have been measured for various motor and crosslinker combinations [11–16]. Yet a theory connecting these scales—predicting collective forces from measurable filament and crosslink properties—has been missing.

The complex phenomenology seen in experiment has inspired numerical simulations using agent-based models [17–30]. These simulations provide intriguing insight into biologically important questions. Examples are the generation of stable overlap regions in spindle midzones [26], collective behaviors of crosslink mixtures between filaments [29], and density-dependent transport and clustering phenomena in motor-filament systems [21,22,31]. However, generalizing their results has remained difficult. The novelty of the present work is to derive force generation, crosslinker transport, and interfilament friction within a common nonequilibrium thermodynamic framework. This yields force and flux laws

expressed in terms of measurable molecular parameters and provides a unified language for quantitatively comparing different crosslinker systems and crosslinker behaviors. For instance, entropic force generation and motor crowding are two manifestations of the competition of crosslinkers for available space on filaments and can be described with the same crosslinker free energy. Our work here establishes a thermodynamically grounded framework that allows this unified description of different crosslinking scenarios.

Previous continuum theories for filament bundles [32–35] and networks [36–40] postulate phenomenological force or flux laws. Our framework derives these laws, showing how they emerge from crosslinker thermodynamics and identifying when each applies. Several studies have shown how collective self-organization in motor-filament systems can emerge from local filament interactions, including density-driven clustering, active turbulence, and large-scale pattern formation [22,40–42]. Likewise, network-scale mechanical responses can arise from the propagation of forces generated between filament pairs [29,43]. In this context, the force and flux laws derived here should be viewed as elementary interaction rules between crosslinked filaments that can serve as building blocks for future coarse-grained descriptions of larger cytoskeletal assemblies and active materials.

We show that three classes of forces between crosslinked rigid filament pairs—entropic, active, and frictional—emerge within our common formalism whose parameters can be linked to experimentally measurable molecular properties. This connection enables quantitative comparison across different crosslinker systems and clarifies the physical assumptions underlying existing continuum descriptions. By comparing to experiments, we demonstrate that for

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cytoskeletal systems, forces generated by crosslinkers between filament pairs dominate over friction against an external medium by one or two orders of magnitude. Finally, our work highlights the role of entropic forces between filaments, which can endow filament pairs with an effective elasticity, even in the regime of rapid crosslinker unbinding.

In the first part of this paper, we present the main results of our framework. By using ideas from nonequilibrium thermodynamics [44–47] and the hydrodynamics of active gels [35,48,49], we show that the forces on filaments can be written in terms of four contributions: (1) entropic forces, (2) active forces, (3) crosslinker-mediated interfilament friction, and (4) fluid-mediated friction on the filaments, of which the first three contributions [(1)–(3)] are directly set by crosslinkers. Further, we describe the collective dynamics of the crosslinkers bound to the filaments within the same framework. Most importantly, we give expressions for each of these contributions in terms of measurable properties of crosslinkers and filaments.

In the second part of the paper, we demonstrate the power and utility of this framework by applying it to different experiments involving passive, motorized, and mixtures of motorized and passive crosslinkers, all described within the same unifying language. We show that for all of the experiments considered here, the dynamics of the system can be recovered with our theory using predominantly experimentally determined parameters. For each of the experiments, we discuss the relative importance of interfilament friction, external friction, active forces, and entropic forces. We find that for all the experiments considered here, friction against the external medium is negligible compared to other forces.

In total, our thermodynamically consistent theory for force generation and pattern formation between crosslinked cytoskeletal filaments provides a unified description of crosslinked filament pairs. By expressing the resulting force and flux laws in terms of theoretically measurable parameters, it establishes a foundation for future coarse-grained theories of cytoskeletal assemblies, active bundles, and engineered polymer networks.

II. SETUP

We study a system consisting of two rigid filaments, denoted by A and B , which are connected by crosslinkers distributed continuously along their lengths (see Fig. 1). In our description, both filaments and crosslinkers are represented by continuous one-dimensional number densities $n^{(i)}$, where the superscript i labels the various crosslink and filament species. Specifically, $n^{(A)}$ and $n^{(B)}$ denote the number densities of the particles that constitute filaments A and B , respectively. The space available for crosslinker attachment is taken to be proportional to $n^{(A)}$ and $n^{(B)}$, and for simplicity we set the proportionality constant to unity. We consider motorized and passive crosslinkers that can be in one of four binding states: unbound, bound to filament A , bound to filament B , or simultaneously bound to both filaments. We denote the corresponding number densities by $n^{(u)}$, $n^{(a)}$, $n^{(b)}$, and $n^{(ab)}$, and in cases of several crosslinker types coexisting we add an additional subscript for the particle type. For instance, $n_{\text{Ase1}}^{(ab)}$ will represent the density of doubly bound crosslinkers of the type

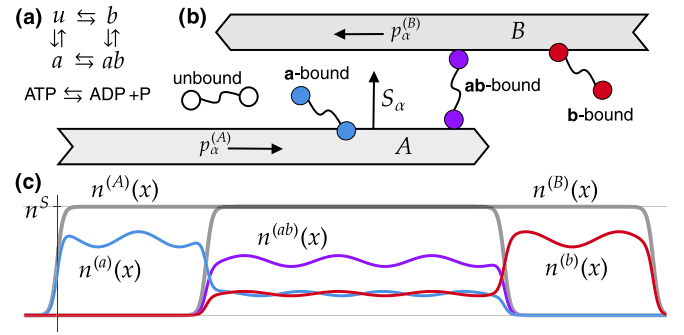


FIG. 1. Sketch and continuous description of crosslinkers and filament pair. (a) Chemical reaction network: We consider binding reactions between a , b , ab , and u states and hydrolysis of ATP to ADP+P. (b) Sketch of the system. The filaments A and B are decorated with a -bound, b -bound, or ab -bound crosslinkers. Each filament has a polarity vector $p_\alpha^{(A)}$ or $p_\alpha^{(B)}$. The vector perpendicular to the filaments direction pointing from A to B is S_α . (c) Sketch of the continuous description in one dimension. The filaments (A , B) and crosslinkers (a , b , ab) are described by continuous fields, $n^{(A)}$, $n^{(B)}$, $n^{(a)}$, $n^{(b)}$, and $n^{(ab)}$, respectively. The maximum number density of crosslinkers on filament is n^S .

Ase1. Finally, the polarity vectors $p_\alpha^{(i)}$ reflect the orientation of the filament(s) to which a crosslinker is attached. Specifically, $p_\alpha^{(a)} = p_\alpha^{(A)}$ for crosslinkers bound to filament A , $p_\alpha^{(b)} = p_\alpha^{(B)}$ for those bound to filament B , and $p_\alpha^{(ab)} = (p_\alpha^{(A)} + p_\alpha^{(B)})/2$ for doubly bound crosslinkers. This is particularly important for active transport terms (i.e., molecular motors), where chemical energy input drives motion along filament polarity.

III. FORCES ON CROSSLINKED FILAMENTS

The central result of this paper is that the force density on filaments A and B can be written as

$$f_\alpha^{(A,B)} = \partial_\alpha \Pi^{(A,B)} + \mathcal{A}_\alpha^{(A,B)} + \mathcal{F}_\alpha^{(A,B)} - \gamma (V_\alpha^{(A,B)} - v_\alpha), \quad (1)$$

which we derive in Sec. VII [see Eqs. (10)–(16)]. The four terms of Eq. (1) have distinct physical meanings: entropic forces, active forces, interfilament friction, and friction against the external environment. Throughout this work, $f_\alpha^{(A,B)}$ denotes a force density (force per unit of filament length), while the total force acting on a filament is obtained by integrating the force density along its length. All force contributions discussed below should therefore be understood as force densities unless stated otherwise.

The entropic force $\partial_\alpha \Pi$ arises since crosslinkers compete for a finite number of binding sites [12,15,50]. The entropic force in the filaments is $\Pi^{(A,B)} = -n^{(A,B)} \mu_{\text{TS}}^{(A,B)}$, where $\mu_{\text{TS}}^{(i)} = -T \partial s / \partial n^{(i)}$ is the entropic contribution to the chemical potential $\mu^{(i)} = \mu_H^{(i)} + \mu_{\text{TS}}^{(i)}$ of species i . Here, s is the entropy density and T the temperature, and $\mu_H^{(i)}$ is the enthalpic chemical potential that stems from particle interactions. The entropy density s depends on the densities of available attachment space, i.e., to $n^{(A,B)}$, and the densities of bound crosslinkers $n^{(a,b,ab)}$. Because s increases when more space becomes accessible, the entropic contribution drives the system toward maximizing the overlap between filaments A and B .

Importantly, the value of s , and thus the entropic force Π can be derived by counting the number of possible crosslinkers binding configurations (see Appendix A).

The active force $\mathcal{A}_\alpha$ arises when molecular-scale motors convert chemical energy into mechanical work [13,18,51]. We show that we can set $\mathcal{A}_\alpha^{(A,B)} = n_m^{(ab)} p_\alpha^{(A,B)} \zeta \Delta\mu^{\text{ATP}}$ (see Sec. VII). Importantly $\mathcal{A}_\alpha$ is proportional to both the number $n_m^{(ab)}$ of motorized crosslinkers within the overlap region and the chemical potential difference $\Delta\mu^{\text{ATP}}$ between the fuel [adenosine triphosphate (ATP)] and its reaction products [adenosine diphosphate (ADP) + inorganic Phosphate (P)]. Note that more complex motor models than the ones discussed in this paper can be built by allowing for several distinct bound states. By symmetry, the transitions between motor states can couple to all thermodynamic fluxes, which in turn allows to describe complex motor force-velocity curves, force-dependent unbinding kinetics, or cooperative behavior. Here, we stick to the single state motor model for simplicity, because the data analyzed here do not require this additional structure. The phenomenological coefficient ζ characterizes motor force generation. Dimensionally, $\zeta \Delta\mu^{\text{ATP}}$ is a force per motor and is linked to the motor stall force. In principle, $\zeta \Delta\mu^{\text{ATP}}$ can be measured by setting up an experiment in which motor forces balance against an externally applied force. At the level considered here, ζ should be interpreted as an effective coarse-grained parameter.

Interfilament friction is generated when crosslinked filaments are sliding relative to each other [52]. This interfilament friction is captured by the term $\mathcal{F}^{(A,B)} = S_\beta \Sigma_{\alpha\beta}$. Here, S_β is the vector that points from filament A to filament B (see Fig. 1) and $\Sigma_{\alpha\beta}$ is the stress in the bound crosslinkers. On viscous timescales, we show that $\mathcal{F}^{(A,B)} = \pm \gamma^\times n^{(ab)} (V_\alpha^{(B)} - V_\alpha^{(A)})$, where $V_\alpha^{(A)}$, $V_\alpha^{(B)}$ are the velocities of filaments A and B, respectively. Here, $\gamma^\times$ is the effective friction coefficient associated with a single doubly bound crosslinker. The product $\gamma^\times n^{(ab)}$ therefore corresponds to a friction coefficient per unit filament length, such that $\mathcal{F}^{(A,B)}$ has the dimensions of a force density. The positive sign applies to filament A and the negative sign to filament B, such that the friction forces acting on the two filaments are equal in magnitude and opposite in direction, consistent with action-reaction symmetry. The coefficient $\gamma^\times$ can be measured by pulling on filaments [52]. Note that for cases with several crosslinker types, each type of crosslinker (motorized or passive) contributes to interfilament friction. For motorized crosslinkers, $\zeta \Delta\mu^{\text{ATP}} / \gamma^\times$ corresponds to the speed at which otherwise force-free (i.e., free of external or entropic forces) filaments would slide past each other.

The drag force between the filament and the surrounding medium is $-\gamma(V_\alpha - v_\alpha)$, where v_α is the local center-of-mass velocity of the system. The drag coefficient γ can be calculated from the filament geometry and the properties of the surrounding medium [53–55].

Together, these four contributions fully characterize the physical forces acting along pairs of crosslinked filaments. Most importantly, all parameters that enter these forces are experimentally accessible, in principle, either through direct measurements or predicted using structural and dynamical data from filaments and crosslinkers. Since these forces emerge from crosslinker dynamics, we now turn to

examining the collective behavior of crosslinkers along a filament pair.

IV. CROSSLINKER DYNAMICS

Each crosslinker density obeys a continuity equation in the form

$$\partial_t n^{(i)} = -\partial_\alpha (j_\alpha^{(i)} + n^{(i)} v_\alpha) + r^{(i)}, \quad (2)$$

where $j_\alpha^{(i)}$ are the spatial fluxes relative to the center of mass and the chemical fluxes $r^{(i)}$ represent source terms due to chemical reactions.

Chemical fluxes $r^{(i)}$ describe chemical and binding reactions [see Fig. 1(a)]. These include attachment and detachment from individual filaments, as well as transitions between singly bound and doubly bound states. We will use the capital index I to denote the different reactions allowed in the system. The source terms obey

$$r^{(i)} = -\sum_I a^{(iI)} \bar{\Lambda}^{(I)} \Delta\mu^{(I)} \simeq \sum_I k^{(i,I)} (n_\star^{(i,I)} - n^{(i)}), \quad (3)$$

where $\Delta\mu^{(I)}$ are the chemical potential differences between the species at the nodes linked by chemical reaction I , $a^{(iI)}$ are the stoichiometric coefficients, and $\bar{\Lambda}^{(I)}$ are the scalar Onsager coefficients. Note that we ignored cross terms between chemical reactions and other forces in the system, for simplicity (see Appendix B for the general expression). By linearizing around the steady-state concentrations $n_\star^{(i,I)}$ at which $\Delta\mu^{(I)} = 0$, we approximated $r^{(i)}$ in terms of the rate constants $k^{(i,I)}$, which can be measured using standard techniques such as fluorescence recovery after photobleaching (FRAP) [3,56].

Spatial fluxes $j_\alpha^{(i)} = -\Lambda^{(i)} \partial_\alpha \mu^{(i)} + \lambda^{(i)} \Delta\mu^{\text{ATP}} p_\alpha^{(i)}$ describe the motion of crosslinkers relative to the center of mass of the system. Importantly, $\Lambda^{(i)} = D^{(i)} \chi^{(ii)} / (k_B T)$ denotes the mobilities. They are linked to the diffusion coefficients of species i via the fluctuation dissipation theorem, which ensures agreement with Fick's law of diffusion [45,47,57,58]. The susceptibilities $\chi^{(ik)}$ are defined as $\chi^{(ik)} = k_B T (\partial \mu_{\text{TS}}^{(i)} / \partial n^{(k)})^{-1}$, with k_B the Boltzmann constant. The susceptibilities $\chi^{(ik)}$ are also called isothermal (cross) compressibility [59].

The second term, containing $\Delta\mu^{\text{ATP}}$, describes directed motion driven by ATP hydrolysis, with $\lambda^{(i)}$ characterizing how the chemical energy input is transformed into motion along the polarity vector $p_\alpha^{(i)}$. See Ref. [49] and Sec. VII for a detailed derivation. In full analogy to the relation between mobility and diffusion, we relate the active transport coefficient $\lambda^{(i)}$ to the force-free velocity $v_0^{(i)}$ of motorized crosslinkers via $v_0^{(i)} = (\lambda^{(i)} / \chi^{(ii)}) \Delta\mu^{\text{ATP}}$.

In dilute systems, the susceptibility $\chi^{(ii)}$ goes to $n^{(i)}$. Thus, $\lambda^{(i)} \Delta\mu^{\text{ATP}} \simeq v_0^{(i)} n^{(i)}$ and $\Lambda^{(i)} k_B T \simeq n^{(i)} D^{(i)}$. In denser regions, $\chi^{(ii)}$ accounts for the crowding effect, including traffic-jam-like behavior. Traffic-jam formation and density-dependent transport are well-known features of molecular-motor systems and have previously been studied using lattice-gas and continuum descriptions [21,22,31,41]. Within the present framework, these effects emerge naturally through the density dependence of the thermodynamic susceptibility.

Together, these expressions lead us to write the spatial flux of particles as

$$j_\alpha^{(i)} = - \sum_k D^{(ik)} \partial_\alpha n^{(k)} + \chi^{(ii)} \left(\frac{D^{(ii)}}{k_B T} \partial_\alpha \mu_H^{(i)} + v_0^{(i)} p_\alpha^{(i)} \right). \quad (4)$$

Here, $D^{(ik)} = D^{(i)} \chi^{(ii)} / \chi^{(ik)}$ is the (cross-)diffusion matrix. Most importantly, the diffusion coefficients $D^{(ii)}$ and the force-free velocities $v_0^{(i)}$ can be measured [6,15] and the susceptibilities $\chi^{(ik)}$ can be known from structural information on crosslinkers and the filaments that they bind to Appendix A. The first term of Eq. (4) encodes the physics of diffusion ($\propto \partial_\alpha n^{(i)}$) and cross diffusion ($\propto \partial_\alpha n^{(k)}$). The behavior of bound crosslinkers near filament ends is set by the same term via the contributions proportional to $\partial_\alpha n^{(A,B)}$. The second term, proportional to $\partial_\alpha \mu_H^{(i)}$, describes transport in a potential. In the rest of this paper, we will treat cases where $\partial_\alpha \mu_H^{(i)} = 0$ for all crosslinkers and motors. This refers to crosslinkers that do not directly interact with one another and whose binding energies to filaments are not dependent on the position along the filament. The last term, proportional to $v_0^{(i)}$ encodes active transport. In Appendix C, we recover Hill's formalism [51] for motors under a load from Eq. (4) in the low-density limit.

Altogether, Eqs. (1)–(4) describe crosslinker dynamics and the forces acting on the filaments in terms of measurable, in principle, crosslink and filament properties. All model parameters and their units are summarized in Table III, in Appendix F.

V. APPLICATIONS

We next illustrate how our framework provides a unified description of crosslinker-mediated interactions between filaments by applying it to several prototypical experimental situations. Depending on their crosslinker composition, such systems exhibit distinct mechanical behaviors. Filaments connected solely by passive crosslinkers display entropic overlap expansion and interfilament friction [12,52], whereas motorized crosslinkers alone can generate collective patterns such as traffic jams and exert forces that compete with entropic effects [24,60]. When passive and motorized crosslinkers act together, their interplay can lead to stable sliding dynamics and a pronounced slowing down of microtubules (MTs) [61].

Across the following applications, we distinguish two settings. In force-balance simulations, filament velocities are obtained dynamically by solving Eq. (1) under the condition of vanishing total force, thereby yielding the emergent motion of the system. In movement-constrained simulations, filament trajectories are imposed from experimental measurements, and the theory is used to compute the corresponding forces. This second approach enables direct comparison with force readouts in controlled pulling experiments, while the first provides a fully predictive description of filament dynamics.

We begin with the simplest case of an externally driven passive system, where entropic forces dominate the dynamics.

A. Passive crosslinkers induce entropic contractility in crosslinked bundles

In the experiment of Ref. [12] the passive crosslinker anillin has been shown to lead to contractions of filament

bundles and rings. By pulling filament bundles apart in steps of 100 nm using an optical trap, the authors showed that the pulling forces increase as the overlap length decreases. In this experiment, the relative filament motion is externally imposed by the optical trap, and the force required to maintain this prescribed motion is measured. Accordingly, in our simulations, we impose the experimentally measured filament velocity and solve Eq. (1) to compute the resulting force. We show how these data can be quantitatively explained using our force decomposition, which allows us to distinguish between two models.

In Model 1, we only consider doubly bound (ab) crosslinkers, while in Model 2 we consider (a, b) bound and doubly bound (ab) crosslinkers [see Figs. 2(a) and 2(d)]. In both cases, we will take the system as passive and neglect fluid drag and interfilament friction, i.e., $v_0 = \gamma = \gamma^\times = 0$. This approximation is justified because the experimental force is measured only during the plateau phases, where the filament positions are held fixed ($v = 0$); consequently, velocity-dependent frictional contributions vanish and do not affect the measured force traces, and we can choose the friction coefficients to be zero without affecting the measured force curves, for simplicity. The diffusion coefficient of singly bound crosslinkers has been measured and is $D^{\text{meas}} = 0.0088 \mu\text{m}^2 \text{s}^{-1}$ (see Ref. [12]). We estimate that the diffusion coefficient of doubly bound crosslinkers should be approximately half that value. The maximum number of crosslinkers on filaments is estimated from the length and width of the crosslinkers [62]. We estimate this number to be approximately 4000 crosslinkers per unit length (i.e., per unit length along the one-dimensional bundle axis). This should be interpreted as a coarse estimate, given that the precise size and geometry of the crosslinkers remain uncertain, and that the number of filaments in a bundle is itself only approximately known (estimated to be around five [12]).

The chemical binding and unbinding rates between unbound and singly bound states have been measured in Ref. [12]. The difference between subsequent plateaus in the force measurement allows to infer the initial overlap length under the assumption that unbinding of singly bound crosslinkers is slow (see Appendix E 1). The free parameters of the model are the equilibrium concentration of doubly bound crosslinkers, and for Model 2 the concentration of singly bound crosslinkers and the transition rate between doubly and singly bound states. The equilibrium concentration is inferred from the initial force measured (see Appendix E 1). The equilibrium concentration of singly bound crosslinkers is set to be small compared to doubly bound concentration; we choose $n^{(ab)} / n^{(a)} = 20$, which corresponds to a binding energy difference of $4k_B T$. We take the transition rate between singly and doubly bound to be fast compared to the transition from unbound to singly bound. We choose $k^{(a,b \rightleftharpoons ab)} = 1000 k^{(u \rightleftharpoons a,b)}$, which allows doubly bound crosslinkers to transiently unbind during pulling event.

The full equations of motion and all parameter values used are given in Appendix E and have been solved in a custom code [63], built around the DEDALUS framework [64]. In our numerical setup, we impose the same relative movement of filaments as in experiment and measure the force required to do so using Eq. (1). The goal is therefore to compare predicted

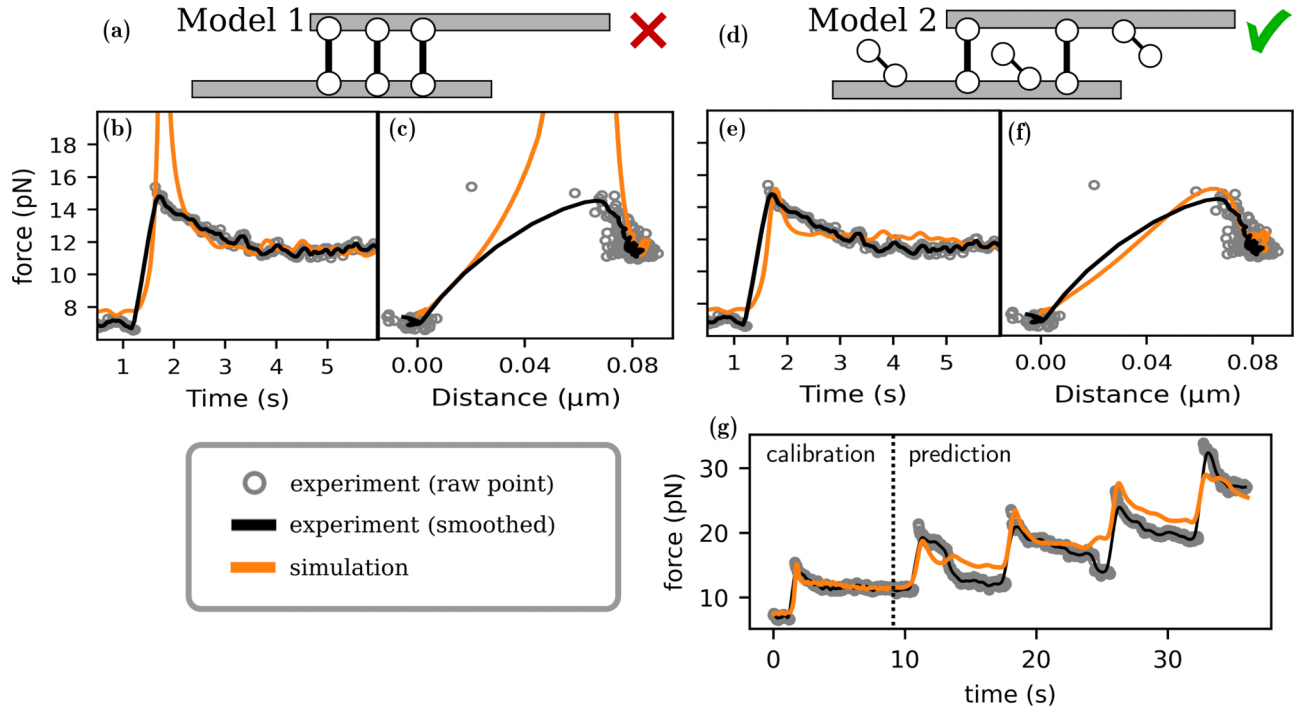


FIG. 2. Passive crosslinkers induce entropic contractility in crosslinked bundles. (a) Sketch of Model 1 of doubly bound crosslinkers between two filaments. (b) Force-time curves of Model 1 (legend in the gray frame). (c) Force-overlap curves of Model 1. (d) Sketch of Model 2 with singly and doubly bound crosslinkers. (e) Force-time curves of Model 2. (f) Force-overlap curves for Model 2. (g) Force-time curves used in panel (e) and for the next four pulling events, done with an independent simulation with the same parameters as in panel (e).

forces with measured force traces. Our results are shown in Fig. 2 and Movie S1 in the Supplemental Material [65].

We first sought to reproduce the force/time and force/distance curves of a single pulling event. We find that Model 1 is inconsistent with the experimental results. Specifically, the forces massively overshoot in the pulling process [see Figs. 2(b) and 2(c)]. In contrast, Model 2 describes the data of the pull [see Figs. 2(e) and 2(f)]. We conclude that the dynamic of entropic forces in the system is set by both singly and doubly bound crosslinkers.

To assess the consistency of the model beyond the initial calibration, we asked whether the parameters extracted from a single pulling event would also accurately predict the forces in subsequent pulls. To this end, we performed an independent simulation using the parameters obtained from the first pulling event, and imposed the filament movements as measured in the next four experimental pulls. Remarkably, the simulation reproduces the subsequent pulls [see Fig. 2(g)]. This demonstrates that our theory correctly describes entropic forces.

B. Passive crosslinkers generate interfilament friction

Crosslinkers can also generate friction between sliding filaments. To demonstrate how our theory relates to the experimental findings, we will compare to experiment on friction generated by crosslinkers [52]. In this experiment, two microtubules coupled by the passive crosslinker PRC1 were pulled against each other and the resulting resisting force was measured. Forces were measured at different velocities and crosslinker numbers. The key finding of Ref. [52] was a resisting force that was independent of overlap length.

We model this system by again allowing for singly and doubly bound crosslinkers [see Fig. 3(a)]. The interfilament friction coefficient was measured in experiment and is $\gamma^\times = 2 \text{ pN}/(\mu\text{m s}^{-1})$ per crosslinker. Using parameters from experiments and imposing the filament sliding velocity (see Table II), we recover the main observation of Ref. [52] which is that the interfilament friction force generated by the crosslinkers is approximately independent of the filaments overlap. Over a numerical pulling experiment, the total force (black line) barely varies [see Fig. 3(b) and Movie S2 in the Supplemental Material [65]]. The force consists of a frictional contribution proportional to $\gamma^\times$, and an entropic one. Only near disconnection, the entropic contribution to the force (red) increase, for the reasons discussed in the previous section. Moreover, the friction (blue) slightly decreases from the loss of crosslinkers during pulling. Both of these effects have opposite signs and the total change is negligible in the regime in which the experiments of Ref. [52] were conducted.

We next sought to better understand in which regime the observation of constant friction would hold. We perform the same simulation varying the pulling velocity V and the initial number N of crosslinkers in the overlap [see Figs. 3(c)–3(e)]. We measure $\Delta F = F(t=0) - F(t=t_d)$, where t_0 is the initial time, t_d is the time at which the filaments disconnect, and F is the force required to pull at the set velocity V . Thus, large ΔF corresponds to a large change in resistive force when pulling the filaments. In Fig. 3(e), we show the result of this parameter exploration and find regimes where entropic and/or friction forces become important. We find that the experimental regime of Ref. [52] requires a sufficiently large pulling velocity. At low crosslinker number and lower

velocity, entropic effects start to dominate, since frictional forces are small both from low velocity and low crosslinker number. Conversely, at high crosslinker numbers, the loss of crosslinkers via unbinding becomes increasingly important if the pulling is too slow. To avoid this, the timescale of pulling needs to be faster than the characteristic timescale of crosslinker unbinding.

We next investigated the same experiment with different crosslinker binding/unbinding dynamics. We change the Damköhler number $\mathcal{D}_a = k^{(a,b \rightarrow ab)} L^2 / D^{(ab)}$ (where $L = 20$ nm is the typical length of the crosslinker) and the initial crosslinker number N . The Damköhler number characterizes the balance between reaction and diffusion timescales. Low values correspond to crosslinkers that unbind slowly, and thus typically diffuse over several crosslinker sizes throughout their life, while large numbers describe crosslinkers that unbind before diffusing over any important length. In Figs. 3(f) and 3(g), we show force-overlap curves for different values of $\mathcal{D}_a$ and number of crosslinkers. The results of this numerical investigation are summarized in Fig. 3(h). From this, we expect deviations from the constant resistive force at large $\mathcal{D}_a$ or very low densities. Again, the experimental regime of Ref. [52] corresponds to parameters where friction is important enough to dominate over entropic forces and crosslinker unbinding is rare.

These numerical experiments demonstrate that our theory captures frictional forces correctly and allows us to place experimental results in a larger space of parameter values. Note also that in this experimental setup, crosslink-mediated friction is the dominant contribution, being approximately 200

times larger than fluid-mediated friction. Thus, these experiments are in the highly crosslinked regime [66].

C. The interplay of motor activity and available space determines patterning of motors on single filaments

We next discuss the behavior of motorized crosslinkers on a single filament. It has been shown experimentally in Ref. [24] that traffic jams of motorized crosslinkers can occur on filaments. To reproduce this, we model a single species (a) of motorized crosslinkers walking on a single filament (A) [see Fig. 4(a) and Movie S3 in the Supplemental Material [65]]. Importantly, all model parameters were measured in Ref. [24] (see Table II). With this, Eq. (4) fully determines the dynamics of the system. At high enough density, the competition for space on filament balances motor-driven fluxes, which are the origin of the observed traffic jams. In our model, the susceptibility is $\chi^{(a)} = n^{(a)}(n^{(A)} - n^{(a)})/n^{(A)}$, we thus retrieve the same density-dependent transport law used in the exclusion-process description of Refs. [21,24] as a consequence of the thermodynamic susceptibility that describes competition for finite attachment space on the filament.

The density profiles that emerge from solving this system are shown in Fig. 4(c). As in the experiment, motorized crosslinkers accumulate at the filament end. In Fig. 4(b), we show that the numerically determined growth of the traffic jam region is in quantitative agreement with the measured behavior (dashed white line). This shows that our framework naturally captures concentration-dependent motor

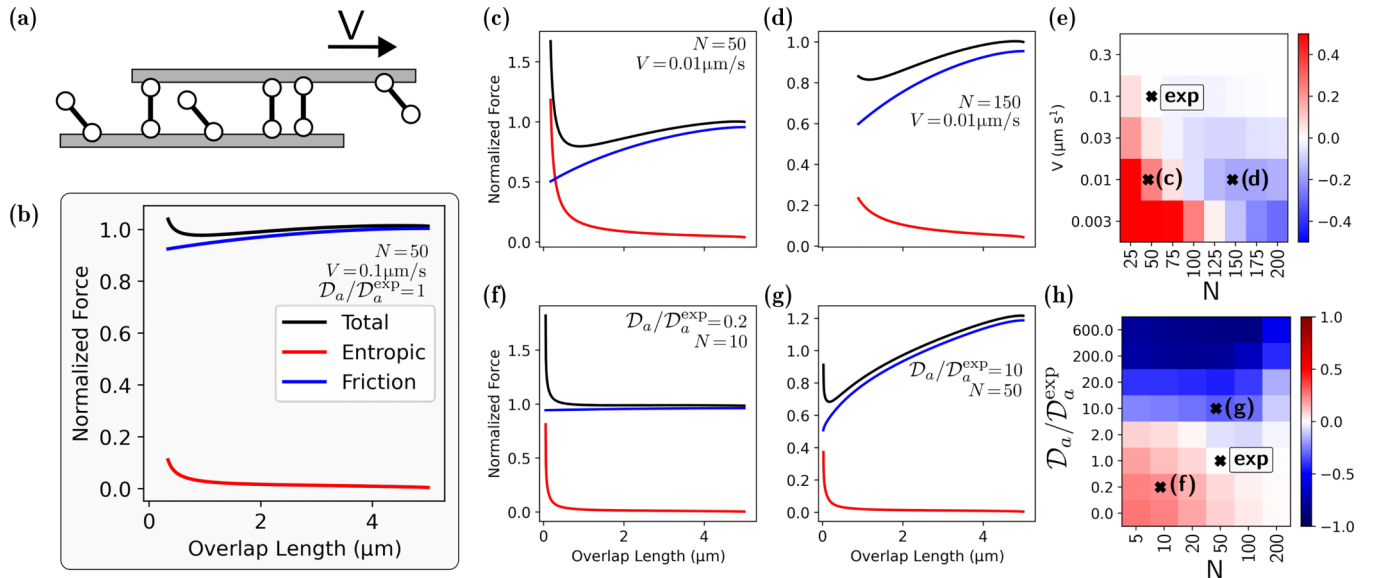


FIG. 3. Passive crosslinkers generate interfilament friction. (a) Sketch of the model used in the simulation. (b) Normalized force-overlap curve obtained in simulation with experimental parameters and $V = 0.1 \mu\text{m s}^{-1}$, for $N = 50$ crosslinkers in the overlap. The total force is in black, the entropic and friction contributions are in red and blue, respectively. (c) Normalized force-overlap curve with $V = 0.01 \mu\text{m s}^{-1}$ and $N = 50$. (d) Normalized force-overlap curve with $V = 0.01 \mu\text{m s}^{-1}$ and $N = 150$. (e) Heat map of the normalized total force difference varying the V and N . Crosses indicate the locations of the simulations shown. At fixed velocity ($V = 0.1 \mu\text{m s}^{-1}$), we change the parameter $\mathcal{D}_a/\mathcal{D}_a^{\text{exp}}$ and the density. (f) Force-overlap curve $\mathcal{D}_a/\mathcal{D}_a^{\text{exp}} = 0.2$. (g) Force-overlap curve $\mathcal{D}_a/\mathcal{D}_a^{\text{exp}} = 10$. (h) Heat map of the normalized total force difference varying the Damköhler number $\mathcal{D}_a$ and the density.

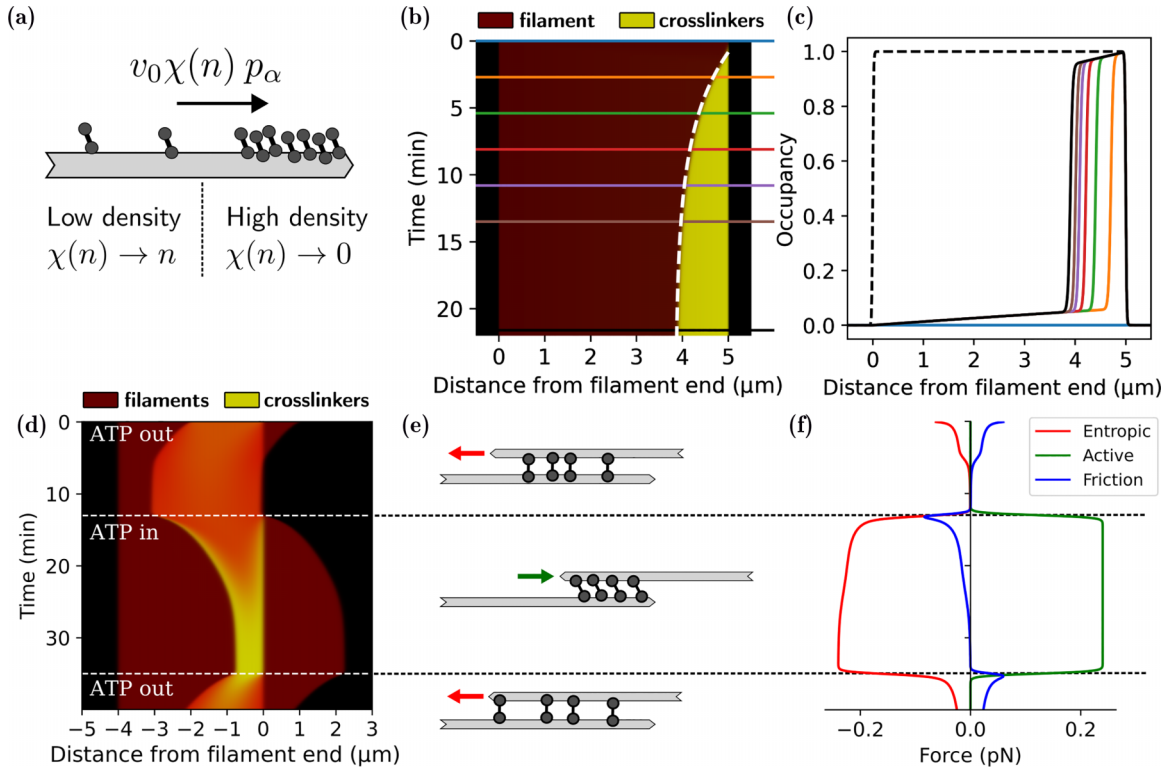


FIG. 4. Motorized crosslinkers patterning on a single filament and the active force generated between two filaments. (a) Sketch of a group of motors walking along a single filament with two different density showing two limits of the susceptibility value. (b) Kymograph of the density profile. Color lines correspond to the times at which density profiles are plotted. The filament is shown in red and the motorized crosslinkers in yellow, with color intensity indicating the local density in arbitrary units. White dotted curve is the model for the size of traffic jam $(L - a)(1 - \exp(-bt))$, with $a = 3.85 \mu\text{m}$ and $b = 0.003 \text{ s}^{-1}$ as measured in Ref. [24]. (c) Density profiles at different times. Color lines are the density of motor, black dashed line is the density of filament A, which is the available attachment space for motors. (d) Kymograph of the simulation with motorized crosslinkers between two filaments. The filaments are in red and the motorized crosslinkers in yellow. White dotted lines represent the change of external ATP load. (e) Sketch of the filaments and crosslinkers states during the three phases of the simulation. (f) Entropic (red), friction (blue), and active (green) forces during the simulation.

velocity relations and the emergence of motorized crosslinker traffic jams. Similar motor exclusion effects have been incorporated in kinetic models of motor-driven MT self-organization using a granular-pressure closure [22], where they serve as an ingredient for computing effective MT-MT alignment interactions; here, we derive this behavior from free-energy considerations.

D. Motorized crosslinkers between filaments generate stable overlaps by an interplay of active and entropic forces

We now discuss the behavior of motorized crosslinkers between two filaments, similar to the experimental setup in Ref. [60], from which we also take our simulation parameters (Table II). We consider the motorized crosslinkers between two overlapping antiparallel filaments [see Figs. 4(d)–4(f) and Movie S4 in the Supplemental Material [65]]. Unlike the previous pulling experiments, the filament motion is not imposed here. Instead, filament velocities are obtained dynamically from the force balance, making this a fully dynamical simulation of overlap evolution. Motorized crosslinkers can produce an active force on filaments as discussed with Eq. (1). We simulate a case where the motors are first ATP starved

($\Delta\mu^{\text{ATP}} = 0$ and thus $v_0 = 0$), constraining them to behave like passive crosslinkers and producing an entropic force which increases the overlap length [see Fig. 4(e)]. With the addition of ATP ($\Delta\mu^{\text{ATP}} \neq 0$), the crosslinkers become motorized and act against the entropic force, reducing the overlap length to a stable value. Taking away ATP takes the crosslinkers back to their passive state. This demonstrates that our theory captures the competition between motor activity and entropic expansion, which can lead to reversible control of filament overlap. The forces in this scenario are displayed in Fig. 4(f) and highlight the importance of entropic forces for stabilizing nonequilibrium steady states in cytoskeletal structures. To demonstrate this further, we next turn to a system in which active and passive crosslinkers coexist.

E. Motorized and passive crosslinkers compete to define the overall force balance and sliding movement

We next investigate a system composed of a mixture of motorized and passive crosslinkers on overlapping filaments, inspired by the experiment of Ref. [61]. In this experiment, the molecular motor Ncd slides a moving MT past a fixed

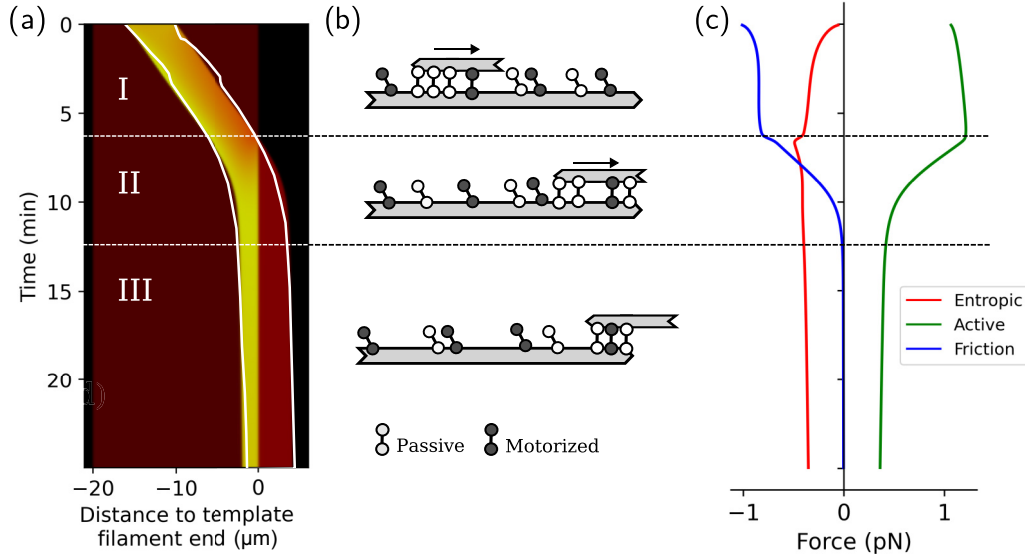


FIG. 5. Motorized and passive crosslinkers compete to define the overall force balance and sliding movement. (a) Kymograph of the simulation. Template filament is in dark red, sliding filament in red, and passive crosslinkers in green. Motorized crosslinkers are not shown. White plain curve is the outline of the experimental observation of Ref. [61]. White Dashed lines separate the phases I, II, and III. (b) Sketches of the system for each phase. (c) Plot of the entropic, active, and friction forces.

template microtubule. Furthermore, the passive crosslinking protein Ase1 is also present. The experimentalists identified three distinct phases of the dynamics. In phase I, the sliding microtubule moves along the template MT at about 30 nm/s. As the sliding MT reaches the end of the template MT, the dynamics changes (phase II), and finally comes to a halt (phase III). This behavior is attributed to the changes of motor and passive crosslinker numbers caused by the change in overlap geometry (see Fig. 5 and Movie S5 in the Supplemental Material [65]). We will employ our theory to disentangle the role of entropic, frictional, and active forces at play.

To model this system, we use our framework with six species: (a, b, ab) -bound passive crosslinkers and (a, b, ab) -bound motorized crosslinkers [see Fig. 5(b)]. We set the velocity of the filament A (template filament) to zero, but the filament B (sliding filament) is free to move, and the total force acting on it is null. The motion of filament B therefore emerges from the force balance and is not prescribed externally. Most parameters of the model were measured [see Table II].

The only unknown parameters of the model are $\zeta \Delta\mu^{\text{ATP}}$ and $\gamma^{\times}$. For simplicity, we will choose the same friction coefficient for Ase1 and Ncd. Further, we estimate that $\zeta \Delta\mu^{\text{ATP}}/\gamma^{\times} = 2v_0$, which corresponds to assuming that at low density Ncd slides filaments at twice its walking speed, which is $v_0 = 100 \text{ nm s}^{-1}$ [67]. Thus, effectively $\gamma^{\times}$ becomes our only fit parameter, which we adjust to reproduce the experimental dynamics measured in Ref. [61].

As observed in the experiment [white outline in Fig. 5(a)], the filament B slides (phase I) and slows down to near halting when the crosslinkers accumulate in the overlap (phases II and III). Our framework allows us to explain this behavior in terms of the changing relation between active,

entropic, and frictional forces. In phase I, active forces work against crosslinker friction and entropic forces, generated by the asymmetric accumulation of passive crosslinkers in the trailing edge of the sliding filament. This predicts that in a hypothetical experiment where all the motors were switched off suddenly in phase I, the sliding filament would snap back. The entropic force is predicted to create an effective elastic response.

The change of the entropic force in phase II is due to the rearrangement of crosslinkers in the changing overlap geometry. In this phase, the entropic forces increase slightly and are still dominated by crosslinkers near the trailing edge of the sliding filament. Simultaneously, the number of motors in the overlap, and thus the motor forces, decreases until active and entropic forces reach a near balance. As the filament motion slows to a halt, frictional forces drop and become negligible as phase III is reached [see Fig 5(c)]. The minimal residual motion in phase III is a consequence of slow unbinding of passive crosslinkers. Note also that throughout the simulation with realistic parameters, the effect of fluid-mediated friction remains small compared to that of crosslinker-mediated friction. Specifically, in phase I, the ratio of the interfilament force over the drag force is approximately 75, and near the end of phase III is 35. This implies that the system is highly crosslinked [66] throughout the experiment.

VI. DISCUSSION

We have presented a thermodynamically grounded framework that derives, from first principles, the forces generated collectively by mixtures of passive and motorized crosslinkers between two biopolymer filaments. The central result [Eq. (1)] decomposes these forces into four contributions: entropic,

active, interfilament frictional, and fluid mediated. Each force is expressed in terms of independently accessible crosslinker and filament properties. This resolves a long-standing gap between experimental characterization and collective force-velocity measurements: Rather than fitting phenomenological interaction rules [32,36,38], the theory derives them and identifies the microscopic origin of each contribution. All parameters have a clear physical interpretation and are, in principle, accessible from independent measurements or structural information.

Using this unifying language, we show that a single formalism describes crosslinker patterning and the force produced between filaments in many experimental scenarios. We quantitatively describe the forces generated by transient passive crosslinkers between two actin filaments [12] and show them to be entropic in nature (see Fig. 2). We also consider the effect of passive crosslinkers between microtubules [52]. In this experiment, where filaments are more sparsely decorated, interfilament friction dominates the dynamics. By studying the dependence of this effect on parameters, we show that the interplay between entropic effects and interfilament friction can be tuned by modulating the binding properties of crosslinkers (see Fig. 3).

Turning to motors, we show that motor traffic jams [24], motor-induced filament sliding [60], and the competition between motorized and passive crosslinkers [61] can all be described within the same framework. A key finding is that entropic and active forces are not independent: At high crosslinker density, the entropic tension resists motor-driven sliding, while motor activity can stabilize finite overlaps by counteracting entropic retraction. Our framework makes the conditions for each regime explicit in terms of measurable parameters. In particular, the force balance between active and entropic contributions implies a critical interplay between motorized and passive crosslinkers: the entropic restoring force built up by the accumulating passive crosslinkers. A testable prediction of this is that any motor-crosslinker system in which passive crosslinkers have accumulated asymmetrically across the overlap will exhibit elastic snap back if motors are suddenly inhibited by ATP depletion, photoinactivation, or pharmacological stall. The passive crosslinker distribution retains an entropic tension that drives the filaments back toward maximum overlap independently of active force generation. This is a general consequence of the theory and distinguishes transiently crosslinked systems from permanently bonded ones, which cannot store and release elastic energy through crosslinker redistribution. Note that the present description of motor activity is coarse grained, with active forces encoded in effective coefficients that summarize collective motor behavior. More detailed mechanochemical effects, such as force-velocity relations, load-dependent detachment, and processivity, could be incorporated through refined constitutive relations for the active force and multiple-state motor models. Within this coarse-grained description, different motor architectures, such as single-ended motor crosslinkers and bipolar motor crosslinkers, are not distinguished explicitly and instead enter through different values of the effective active-force and walking velocity parameters. The different microscopic stepping mechanisms are then absorbed into the effective parameters ζ and v_0 . Note

that this is not a fundamental limitation of the framework, but a deliberate simplification: The data analyzed here do not require this additional structure. By introducing a more complex network of motor states and the transitions between them, as allowed by the couplings introduced in Table I, one can encode complex behaviors and force-velocity curves, which will be the subject of future work.

The physical mechanisms identified here (entropic forces from crosslinker exclusion, friction from crosslinker-mediated momentum transfer, and active pumping by molecular motors) are general to any system of transiently crosslinked polymers, not just the cytoskeleton. Recent work on dynamic covalent polymer networks has highlighted the same physics in the context of vitrimers [68] and recyclable polymer materials [69,70]. Since we can now delineate the link between crosslink mixture properties and the forces that they generate, our work is relevant for engineering applications beyond living matter and can guide the design of crosslink mixtures with desirable mechanical properties, including through crosslinker geometry: The maximum site density n^S is determined by the physical footprint of the crosslinker on the filament, so bulkier or longer crosslinkers reduce n^S and thereby reduce the magnitude of the entropic tension at any given fractional occupancy. Crosslinker arm length thus provides an independent handle on the entropic contribution, separable from binding kinetics or crosslinker number, and testable via crosslinker mutants or synthetic crosslinker variants of varying size.

In summary, our framework unifies passive and active crosslinking phenomena into a thermodynamically consistent description. It explains a wide range of observations and provides a practical toolkit to discriminate microscopic mechanisms and guide future experiments on cytoskeletal force generation. Two results stand out. First, entropic forces (arising from the competition of crosslinkers for available binding sites) endow crosslinked filament pairs with an effective elasticity even when crosslinkers turn over rapidly. Second, across all experimental systems examined, forces generated between the filaments by crosslinkers exceed friction with the surrounding fluid by one to two orders of magnitude, demonstrating that the interfilament interaction rules, rather than external dissipation, set the dynamics of cytoskeletal structures. All parameters of the theory are, in principle, experimentally accessible, and the framework provides a principled basis for engineering polymer materials with tailored mechanical properties.

VII. METHODS

A. Numerical simulation

The governing equations are integrated numerically in Python using the DEDALUS package [64]. The scripts used are available in Ref. [63] and the equations solved are shown in Appendixes D and E.

B. Conservation laws

Each particle type (including crosslinkers and filaments) obeys the continuity equation Eq. (2). Note that mass conservation leads to $\sum m^{(i)} j_\alpha^{(i)} = -m^{(0)} j_\alpha^{(0)}$, where $m^{(i)}$ are the

masses of a particle i and the index 0 denotes the solvent in which the particles are embedded.

Further, we consider momentum conservation in the complete system composed of filament particles, crosslinkers, and solvent. While momentum is conserved in the complete system, momentum can be exchanged between filament particles and solvent, for instance. The force balance reads $\partial_\beta \sigma_{\alpha\beta}^{\text{tot}} = 0$, where $\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta}^{\text{E}} + \sigma_{\alpha\beta}$ is the total stress tensor, and $\sigma_{\alpha\beta}^{\text{E}}$, $\sigma_{\alpha\beta}$ denote the Ericksen stress and the deviatoric stress, respectively. Einstein's summation convention is implied. This fully defines the conservation laws at play.

C. Thermodynamic forces and fluxes

To get the system dynamics, we follow Refs. [35,48,49] and postulate a free-energy density $f(g_\alpha, n^{(i)})$ for the system where g_α is the momentum density. With this, we define the chemical potentials $\mu^{(i)} = \partial f / \partial n^{(i)}$. Translation invariance implies that the hydrostatic Ericksen stress obeys $\sigma_{\alpha\beta}^{\text{E}} = (f - \mu^{(i)} n^{(i)}) \delta_{\alpha\beta}$ and the Gibbs-Duhem relation $\partial_\beta \sigma_{\alpha\beta}^{\text{E}} = -n^{(i)} \partial_\alpha \mu^{(i)}$ (see Refs. [48,49,71]). The entropy production rate $\dot{\Theta}$ of the system is, at constant temperature,

$$T \dot{\Theta} = \int d^3x (\sigma_{\alpha\beta} v_{\alpha\beta} - j_\alpha^{(i)} \partial_\alpha \bar{\mu}^{(i)} + r^{(I)} \Delta \mu^{(I)}), \quad (5)$$

where $\bar{\mu}^{(i)} = \mu^{(i)} - \frac{m^{(i)}}{m^{(0)}} \mu^{(0)}$ is the reduced chemical potentials, $v_{\alpha\beta} = (\partial_\alpha v_\beta + \partial_\beta v_\alpha)/2$ is the strain rate tensor, and $\Delta \mu^{(I)} = \sum_i a^{iI} \mu^{(i)}$ is the difference of chemical potential associated with reaction I . Note that in what follows, we will take $\mu^{(0)}$ to be constant, which implies $\partial_\alpha \bar{\mu}^{(i)} = \partial_\alpha \mu^{(i)}$, for simplicity.

From the entropy production Eq. (5), we identify the thermodynamic fluxes $\{\sigma_{\alpha\beta}, j_\alpha^{(i)}, r^{(I)}\}$ and their conjugate thermodynamic forces $\{v_{\alpha\beta}, -\partial_\alpha \bar{\mu}^{(i)}, \Delta \mu^{(I)}\}$. We assume the near-equilibrium regime where the fluxes follow a linear expansion in the conjugate forces [44–47,71,72]. Symmetry considerations then determine which couplings between forces and fluxes are allowed. The polarity of the filaments $p_\alpha^{(A,B)}$ and the surface-to-surface vector S_α break spatial symmetry. The full set of symmetry allowed terms is given in the Appendix B. We only consider a subset of these coefficients to be nonzero, for simplicity.

D. Chemical fluxes and reaction rates

The rates of crosslinker binding/unbinding reactions ($i = a, b, ab, u$) obey $r^{(i)} = -\sum_I \bar{\Lambda}^{(I)} a^{iI} \Delta \mu^{(I)}$. We expressed the rates $r^{(i)}$ with the contribution from different reactions I , i.e., $r^{(i)} = -\sum_I a^{iI} r^{(I)}$, and kept the complexity at its minimum by not including any cross couplings or active terms. The phenomenological coefficients $\bar{\Lambda}^{(I)}$ are linked to the binding/unbinding rates. To establish this link, we linearize around the steady-state concentration $n_\star^{(i,I)}$ such that the flux through the edge I of the reaction network vanishes [45], i.e., $r^{(I)} = 0$

when $n^{(i)} = n_\star^{(i,I)}$. With this, the fluxes $r^{(i)}$ are

$$\begin{aligned} r^{(i)} &\approx -\sum_I \bar{\Lambda}^{(I)} a^{iI} \frac{\partial \Delta \mu^{(I)}}{\partial n^{(i)}} \bigg|_{n_\star^{(i,I)}} (n^{(i)} - n_\star^{(i,I)}) \\ &\approx \sum_I (k^{(i,I)} (n_\star^{(i,I)} - n^{(i)})), \end{aligned} \quad (6)$$

which defines the rates constant $k^{(i,I)}$

$$k^{(i,I)} = \bar{\Lambda}^{(I)} a^{iI} \frac{\partial \Delta \mu^{(I)}}{\partial n^{(i)}} \bigg|_{n_\star^{(i,I)}}. \quad (7)$$

In this paper, we assume that ATP and ADP densities, and thus the chemical potential difference $\Delta \mu^{\text{ATP}}$, are kept constant by a chemostat, which is typical in cells. In general, if one wishes to describe closed systems, the hydrolysis reaction that converts ATP to ADP + P can be treated analogously to other chemical reactions. Finally, we assume that $r^{(A)} = r^{(B)} = 0$, corresponding to chemically inert filaments.

E. Diffusive fluxes and active transport

The fluxes of crosslinkers ($i = a, b, ab$) obey $j_\alpha^{(i)} = -\Lambda^{(i)} \partial_\alpha \mu^{(i)} + \lambda^{(i)} p_\alpha^{(i)} \Delta \mu^{\text{ATP}}$. Here, we did not allow for coupling between the flux of particles $j_\alpha^{(i)}$ and shear strain $v_{\alpha\beta}$.

The transport coefficients $\Lambda^{(i)}$ and $\lambda^{(i)}$ are linked to the diffusion coefficient $D^{(i)}$ and force-free velocity $v_0^{(i)}$ by the relations

$$D^{(i)} = \frac{\Lambda^{(i)}}{\chi^{(ii)}} k_B T \quad \text{and} \quad v_0^{(i)} = \frac{\lambda^{(i)}}{\chi^{(ii)}} \Delta \mu^{\text{ATP}}. \quad (8)$$

The fluxes of filaments ($i = A, B$) obey

$$j_\alpha^{(A,B)} = -\Lambda \partial_\alpha \mu^{(A,B)} + \lambda p_\alpha^{(A,B)} \Delta \mu^{(\text{ATP})} \mp \nu S_\beta v_{\alpha\beta}. \quad (9)$$

Here, we include the coupling between filaments fluxes and the strain rate with the coefficient ν . The vector S_β points from the filament to its binding partner [see Fig. 1(b)]. Note that filament A couples with S_β and filament B with $-S_\beta$. We consider that both filaments are identical and set $\Lambda^{(A)} = \Lambda^{(B)} = \Lambda$, $\nu^{(A)} = \nu^{(B)} = \nu$, and $\lambda^{(A)} = \lambda^{(B)} = \lambda$. The parameters Λ , λ , and ν scale in the same way as the crosslinker coefficients; this implies that they are proportional to the number of filament particles $n^{(A,B)}$. Importantly, the coefficient λ describes the active flux of the filament generated by energy-consuming processes. Then, $\lambda \Delta \mu / \Lambda$ is the force that motors exert locally on the filament. Thus, the magnitude of λ will also depend on local motor densities. Moreover, the coefficient ν describes the flux of filaments generated by the strain rate $v_{\alpha\beta}$, so $\nu v_{\alpha\beta} / \Lambda$ is the force that crosslinkers generate from internal shear stress, thus its magnitude will depend on doubly bound crosslinkers density.

F. Filament tension

The chemical potentials of filaments are

$$\mu^{(A,B)} = \mu_H^{(A,B)} + \mu_{\text{TS}}^{(A,B)}. \quad (10)$$

The enthalpic parts $\mu_H^{(A,B)}$ contain elastic energies stored within stretched filaments and are the Lagrange multipliers

that enforce the filament inextensibility constraints. These constraints read

$$j_{\alpha}^{(A,B)} + n^{(A,B)} v_{\alpha} = n^{(A,B)} V_{\alpha}^{(A,B)} \quad (11)$$

and ensure that filament particles are convect at filament speeds $V_{\alpha}^{(A,B)}$. Note that in general $V_{\alpha}^{(A,B)}$ can be a function of the position along the filament, for instance, when filaments rotate. Importantly, Eq. (10) and the constraints Eq. (11) in Eq. (9) yield two differential equations for $\mu_H^{(A,B)}$, which read

$$\begin{aligned} \partial_{\alpha} \mu_H^{(A,B)} = & -\partial_{\alpha} \mu_{TS}^{(A,B)} + \frac{\lambda}{\Lambda} p_{\alpha}^{(A,B)} \Delta \mu^{\text{ATP}} \\ & \mp \frac{\nu}{\Lambda} S_{\beta} v_{\alpha\beta} - \frac{n^{(A,B)}}{\Lambda} (V_{\alpha}^{(A,B)} - v_{\alpha}). \end{aligned} \quad (12)$$

Note that $\partial_{\alpha} \mu_H^{(A,B)}$ are forces per particle and thus $n^{(A,B)} \mu_H^{(A,B)}$ are the elastic stresses in filaments A and B , respectively.

Forces on transiently crosslinked biopolymers. In order to get the force density acting on each filament, we multiply the force per particles $\partial_{\alpha} \mu_H^{(A,B)}$ by the density of filament particles $n^{(A,B)}$. The force density on each filament is then $f_{\alpha}^{(A,B)} = n^{(A,B)} \partial_{\alpha} \mu_H^{(A,B)}$. With this, using Eq. (12) leads to Eq. (1), which is the sum of the entropic force $\partial_{\alpha} \Pi$, the active force $\mathcal{A}_{\alpha}$, the interfilament friction force $\mathcal{F}_{\alpha}$, and the drag force between filament and surrounding fluid.

The entropic tension is given by

$$\Pi^{(A,B)} = -n^{(A,B)} \mu_{TS}^{(A,B)}. \quad (13)$$

The active force, which is generated by motorized crosslinkers, is

$$\mathcal{A}_{\alpha}^{(A,B)} = \zeta \Delta \mu^{\text{ATP}} n_m^{(ab)} p_{\alpha}^{(A,B)}, \quad (14)$$

where we set $(\lambda/\Lambda)n^{(A,B)} = \zeta n_m^{(ab)}$. Here, we identified the active part of Eq. (12) with the standard expression for the force produced by active crosslinkers. This identification allows us to relate the filaments Onsager coefficients λ and Λ to the experimentally measurable force-generation parameter $\zeta \Delta \mu^{\text{ATP}}$ of motorized crosslinkers.

The shear stress in the crosslinkers that connect the two filaments generates a friction force between the filaments, which is given by

$$\mathcal{F}_{\alpha}^{(A,B)} = \pm \gamma^{\times} n^{(ab)} (V_{\alpha}^{(B)} - V_{\alpha}^{(A)}), \quad (15)$$

where we used the approximation $v_{\alpha\beta} \approx (V_{\alpha}^{(B)} - V_{\alpha}^{(A)})/d$, with d the interfilaments distance, and set $\gamma^{\times} = \nu n^{(A,B)}/(\Lambda d)$. This approximation assumes that the separation between filaments remains constant and small compared to their lengths, so that the velocity field can be expressed as a difference of the filament velocities. We identified the shear force in Eq. (12) with the usual shear force expression. This leads to link the filaments Onsager coefficient ν and Λ to the effective interfilament friction coefficient $\gamma^{\times}$ generated by crosslinkers.

Finally, the last contribution of the force is the drag force. We identify the part proportional to the velocity in Eq. (12) with the low Reynolds drag force, which sets $(n^{(A,B)})^2/\Lambda = \gamma$.

In the overdamped limit, the total force on either filament obeys

$$F_{\alpha}^{+(A,B)} + F_{\alpha}^{-(A,B)} + c \int_{L^{(A,B)}} f_{\alpha}^{(A,B)} dl = 0, \quad (16)$$

where $F_{\alpha}^{+(A,B)}$ and $F_{\alpha}^{-(A,B)}$ are the forces that external processes apply to the filament tips on their $\pm$ ends, respectively, and $L^{(A,B)}$ are the lengths of the filaments A , B , and c is the cross section of the whole system, which we consider constant. Because we set c constant along the system and assume that it is small compared to the filament lengths, the description is effectively one dimensional. However, the theoretical framework itself is not restricted to this limit and can be readily extended to three-dimensional geometries. In this paper, we discussed situations where filaments are free of external forces and slide just under the effect of motorized crosslinkers ($F_{\alpha}^{\pm} = 0$) and situations where filaments are actuated on either end via experimental devices, in which case a force acts on the corresponding filament end.

ACKNOWLEDGMENTS

This project has been funded by the Vienna Science and Technology Fund (WWTF) [10.47379/VRG20002]. Calculations were performed using supercomputer resources provided by the Austrian Scientific Computing Infrastructure (ASC). This research was supported in part by Grant No. NSF PHY-2309135 to the Kavli Institute for Theoretical Physics (KITP). We thank Daniel Needleman, Peter Foster, and Alexandra Zampetaki for insightful comments on the manuscript.

DATA AVAILABILITY

The data that support the findings of this article are openly available, and all codes are made available via a git repository [63].

APPENDIX A: BOLTZMANN ENTROPY OF BINDING CONFIGURATIONS

We calculate a Boltzmann entropy for filament binding. The spirit of the calculation that follows is essentially the same as in the classic Flory-Huggins [73] calculation for mixing entropy in bulk. We consider two overlapping filaments A and B with $N^{(A)}$ and $N^{(B)}$ total binding sites, respectively. The filament overlap region constitute available site for doubly bound particles. We denote these sites with $N^{(AB)} = \min(N^{(A)}, N^{(B)})$. To determine the Boltzmann entropy $S = k_B \ln \Omega$ of the system, we count the number of possible binding configurations Ω in which in singly bound ($N^{(a)}$ and $N^{(b)}$) and doubly bound ($N^{(ab)}$) fulfill their respective sites $N^{(A)}$, $N^{(B)}$, and $N^{(AB)}$. Note that when a doubly bound crosslink occupy its site, it takes away possible binding site for singly bound particles.

In detail, we count the number of configuration for $N^{(ab)}$ particles in $N^{(AB)}$ available sites, then $N^{(a)}$ particles in $N^{(A)} - N^{(ab)}$ available sites on filament A , and also $N^{(b)}$ particles in $N^{(B)} - N^{(ab)}$ available sites on filament B . With this, the

number of possible configurations Ω is

$$\Omega = \frac{N^{(AB)}!}{N^{(ab)}!(N^{(AB)} - N^{(ab)})!} \frac{(N^{(A)} - N^{(ab)})!}{N^{(a)}!(N^{(A)} - N^{(ab)} - N^{(a)})!} \frac{(N^{(B)} - N^{(ab)})!}{N^{(b)}!(N^{(B)} - N^{(ab)} - N^{(b)})!}. \quad (\text{A1})$$

Moreover, the energy of the system U contains binding energies from crosslinkers and elastic energies stored within stretched filaments. We suppose that both kinds of energy are proportional to the number of particles and set $U = \sum_i \mu_H^{(i)} n^{(i)}$, where $\mu_H^{(i)} = \varepsilon^{(i)}$ are the binding energy of crosslinkers ($i = a, b, ab$) or the Lagrangian multiplier of filaments inextensibility ($i = A, B$).

Considering a local volume element $\mathcal{V}$, we assess the entropy density $s = S/\mathcal{V}$

$$\begin{aligned} s = & k_B (n^{(AB)} \ln(n^{(AB)}) - n^{(ab)} \ln(n^{(ab)}) - (n^{(AB)} - n^{(ab)}) \ln(n^{(AB)} - n^{(ab)}) \\ & + (n^{(A)} - n^{(ab)}) \ln(n^{(A)} - n^{(ab)}) - n^{(a)} \ln(n^{(a)}) - (n^{(A)} - n^{(ab)} - n^{(a)}) \ln(n^{(A)} - n^{(ab)} - n^{(a)}) \\ & + (n^{(B)} - n^{(ab)}) \ln(n^{(B)} - n^{(ab)}) - n^{(b)} \ln(n^{(b)}) - (n^{(B)} - n^{(ab)} - n^{(b)}) \ln(n^{(B)} - n^{(ab)} - n^{(b)})). \end{aligned} \quad (\text{A2})$$

The free-energy density is directly $f = \sum_i \mu_H^{(i)} - Ts$. We can now assess the chemical potentials $\mu^{(i)}$ and the susceptibilities $\chi^{(ik)}$. Note that the number density of available site for doubly bound $n^{(AB)}$ depends on $n^{(A)}$ and $n^{(B)}$. We introduce the dimensionless filaments functions $\varphi^{(A,B)}$ defined with $n^{(A,B)} = n^S \varphi^{(A,B)}$ with $0 \leq \varphi^{(A,B)} \leq 1$ and n^S the typical maximal number of crosslinker on filament. Note that n^S is a constant while $\varphi^{(A,B)}$ are continuous functions. With this, we assume that the density of site for the doubly bound crosslinkers is $n^{(AB)} = n^S \varphi^{(A)} \varphi^{(B)}$. The chemical potentials are defined as $\mu^{(i)} = \partial f / \partial n^{(i)}$. The chemical potentials of the crosslinkers are

$$\mu^{(a)} = \varepsilon^{(a)} + k_B T \ln \left(\frac{n^{(a)}}{n^{(A)} - n^{(ab)} - n^{(a)}} \right), \quad (\text{A3})$$

$$\mu^{(b)} = \varepsilon^{(b)} + k_B T \ln \left(\frac{n^{(b)}}{n^{(B)} - n^{(ab)} - n^{(b)}} \right), \quad (\text{A4})$$

$$\mu^{(ab)} = \varepsilon^{(ab)} + k_B T \left(\ln \left(\frac{n^{(ab)}}{n^{(AB)} - n^{(ab)}} \right) + \ln \left(\frac{n^{(A)} - n^{(ab)}}{n^{(A)} - n^{(ab)} - n^{(a)}} \right) + \ln \left(\frac{n^{(B)} - n^{(ab)}}{n^{(B)} - n^{(ab)} - n^{(b)}} \right) \right), \quad (\text{A5})$$

and the chemical potentials of the filaments are

$$\mu^{(A)} = \mu_H^{(A)} - k_B T \left(\varphi^{(B)} \ln \left(\frac{n^{(AB)}}{n^{(AB)} - n^{(ab)}} \right) + \ln \left(\frac{n^{(A)} - n^{(ab)}}{n^{(A)} - n^{(ab)} - n^{(a)}} \right) \right), \quad (\text{A6})$$

$$\mu^{(B)} = \mu_H^{(B)} - k_B T \left(\varphi^{(A)} \ln \left(\frac{n^{(AB)}}{n^{(AB)} - n^{(ab)}} \right) + \ln \left(\frac{n^{(B)} - n^{(ab)}}{n^{(B)} - n^{(ab)} - n^{(b)}} \right) \right). \quad (\text{A7})$$

The susceptibility is defined as $\chi^{(ik)} = k_B T (\partial \mu_{TS}^{(i)} / \partial n^{(k)})^{-1}$. We write the most important for what follows: the susceptibilities $\chi^{(ii)}$ of the singly bound crosslinkers ($i = a, b$) and the cross susceptibilities $\chi^{(ik)}$ between the doubly bound crosslinkers ($i = ab$) and the filaments ($k = A, B$):

$$\chi^{(aa)} = \frac{n^{(a)}(n^{(A)} - n^{(ab)} - n^{(a)})}{n^{(A)} - n^{(ab)}}, \quad (\text{A8})$$

$$\chi^{(bb)} = \frac{n^{(b)}(n^{(B)} - n^{(ab)} - n^{(b)})}{n^{(B)} - n^{(ab)}}, \quad (\text{A9})$$

$$\begin{aligned} \chi^{(abA)} = & - \left(\frac{\varphi^{(B)}}{n^{(AB)} - n^{(ab)}} \right. \\ & \left. + \frac{n^{(a)}}{(n^{(A)} - n^{(ab)})(n^{(A)} - n^{(ab)} - n^{(a)})} \right)^{-1}, \end{aligned} \quad (\text{A10})$$

$$\begin{aligned} \chi^{(abB)} = & - \left(\frac{\varphi^{(A)}}{n^{(AB)} - n^{(ab)}} \right. \\ & \left. + \frac{n^{(b)}}{(n^{(B)} - n^{(ab)})(n^{(B)} - n^{(ab)} - n^{(b)})} \right)^{-1}. \end{aligned} \quad (\text{A11})$$

We highlight here that the information of the free energy f fully determines the chemical potentials $\mu^{(i)}$ and the

susceptibilities $\chi^{(ik)}$, and one could, in principle, derive this quantities even for more complex systems.

APPENDIX B: ONSAGER COEFFICIENTS AND CONSTITUTIVE EQUATIONS

We expand the thermodynamic fluxes $(-\partial_\alpha \bar{\mu}^{(i)}, \Delta \mu^{(I)}, v_{\alpha\beta})$ in terms of thermodynamic forces $(j^{(i)}, r^{(I)}, \sigma_{\alpha\beta})$ to obtain constitutive equations of the system. In Table I, we list all the possible coupling coefficients given the broken

TABLE I. Table of the Onsager coefficients linking the thermodynamic fluxes to the generalized forces.

	$-\partial_\alpha \bar{\mu}^{(j)}$	$\Delta \mu^{(J)}$	$v_{\alpha\beta}$
$j_\alpha^{(i)}$	$\Lambda^{(ij)}$	$p_\alpha^{(i)} \lambda^{(Ij)}$	$-S_\beta^{(i)} v^{(i)}$
$r^{(I)}$	$p_\alpha^{(j)} \lambda^{(Ij)}$	$\bar{\Lambda}^{(IJ)}$	$-\xi_{\alpha\beta}^{(I)}$
$\sigma_{\alpha\beta}$	$S_\beta^{(j)} v^{(j)}$	$\xi_{\alpha\beta}^{(J)}$	η

symmetries of the system $(p_\alpha^{(i)}, S_\alpha)$. With these coefficients, the fluxes are, in their most general forms,

$$j_\alpha^{(i)} = -\Lambda^{(ij)} \partial_\alpha \bar{\mu}^{(j)} + p_\alpha^{(i)} \lambda^{(ij)} - S_\beta v^{(i)} v_{\alpha\beta}, \quad (\text{B1})$$

$$r^{(I)} = -p_\alpha^{(j)} \lambda^{(Ij)} + \bar{\Lambda}^{(IJ)} \Delta \mu^{(J)} - \xi_{\alpha\beta}^{(I)} v_{\alpha\beta}, \quad (\text{B2})$$

$$\sigma_{\alpha\beta} = -S_\beta v^{(j)} \partial_\alpha \bar{\mu}^{(j)} + \xi_{\alpha\beta}^{(J)} \Delta \mu^{(J)} + \eta v_{\alpha\beta}, \quad (\text{B3})$$

where Einstein's summation convention is implied. The matrix $\xi_{\alpha\beta}^{(I)}$ can, in principle, be constructed from the different broken symmetries $p_\alpha^{(i)}$ and S_α .

APPENDIX C: RECOVERING HILL THEORY

In his seminal 1974 work [51] Hill proposed a phenomenological theory for molecular motors. Classic Hill theory can be recovered from our formalism in the limit of low motor density. In Hill's work, a single motor operates against an external force f_α^{ext} [see Fig. 4(a)]. In our framework, such an external force can be introduced by considering a motor that operates in a potential, such that we can rewrite $\partial_\alpha \bar{\mu} = \partial_\alpha \bar{\mu}_{\text{TS}} - f_\alpha^{\text{ext}}$. In our formalism, this leads to

$$j_\alpha = -D \partial_\alpha n + \frac{D\chi}{k_B T} f_\alpha^{\text{ext}} + v_0 \chi p_\alpha. \quad (\text{C1})$$

If we now consider the case of low motor density, such that $\partial_\alpha n \rightarrow 0$ and $\chi \rightarrow n$, we can cast this into the form given in Hill's paper [51] and find

$$v_\alpha^{\text{motor}} = \lambda_{11} f_\alpha^{\text{ext}} + \lambda_{12} \Delta \mu, \quad (\text{C2})$$

where $v_\alpha^{\text{motor}} = j_\alpha/n$, $\lambda_{11} = D/(k_B T) = \Lambda/n$, and $\lambda_{12} = \lambda/n$. Hill's second equation gives the rate of fuel consumption and is easily recovered from our formalism and reads

$$r^{(\text{ATP} \rightleftharpoons \text{ADP} + \text{P})}/n = \lambda_{22} \Delta \mu^{\text{ATP}} + \lambda_{12} p_\alpha f_\alpha^{\text{ext}}. \quad (\text{C3})$$

Note that Hill's theory naturally emerges when considering a single state motor molecule. More complex motor models can be formulated by introducing more complex networks of chemical reactions, and multistate motor models such as the two-state models discussed in Ref. [18] can be formulated by making the appropriate choices for the potentials in which motors exist. Multistate motor models can deviate substantially from simple Hill behavior, as has been demonstrated in Ref. [74].

APPENDIX D: NUMERICAL METHODS

In this Appendix, we discuss the equations of motion solved for the application section. We first discuss how simulations are performed, next how we treat the stiff filaments common to all experiments, and then give details on the individual setups. The parameter values for all simulations are summarized in Table II. Note that while many parameters used throughout this work have been independently measured in previous experiments, some quantities remain difficult to access directly and are therefore inferred from fitting procedures. This limitation reflects the current experimental state of the field rather than a restriction of the theoretical framework.

1. Numerical framework

All numerical simulations were performed using the DEDALUS spectral framework [64], an open-source Python package designed for solving partial differential equations. It allows us to solve initial-value problems involving all equations used. In all our simulations, we use periodic boundary conditions applied to the computational domain (i.e., the simulation box, not individual filaments).

2. Treatment of stiff filaments

Filaments and crosslinkers are described by continuous fields. To obtain a smooth filament field $n^{(A,B)}$, we use a solution to the Cahn-Hilliard equation

$$0 = -D \partial_x^2 (-2n^{(A,B)} + 4(n^{(A,B)})^3 - 6(n^{(A,B)})^2 + G \partial_x^2 (n^{(A,B)})), \quad (\text{D1})$$

where $\int n^{(A,B)} dx = L$ sets the filament length and the smoothing length scale is set by $\sqrt{G}$. Throughout this paper, we use $\sqrt{G} \approx 0.1 \mu\text{m}$, which is sufficient to smear the interface out over approximately 10 grid points in our numerical simulations. This value is approximate and may be adjusted between simulations.

In all problems, the filaments are treated as stiff filaments moving at velocity $V^{(A,B)}$, and their equations of motion are then $\partial_t n^{(A,B)} = -\partial_x (n^{(A,B)} V^{(A,B)})$. For simulation stability, we instead use

$$\partial_t n^{(A,B)} = -D \partial_x^2 (-2n^{(A,B)} + 4(n^{(A,B)})^3 - 6(n^{(A,B)})^2 + G \partial_x^2 (n^{(A,B)})) - \partial_x (n^{(A,B)} V^{(A,B)}). \quad (\text{D2})$$

The additional Cahn-Hilliard term in these equations drives numerical errors back toward the desired filament shape, and stays small throughout the simulation.

APPENDIX E: SIMULATIONS: EQUATIONS OF MOTION AND PARAMETER VALUES AND ADDITIONAL INFORMATION

1. Entropic forces increase filament overlap

Model 1. We consider only doubly bound (*ab*) passive crosslinkers, which can bind within the filament overlap. The number of accessible microstates is set by Eq. (A1) taking $n^{(a)} = n^{(b)} = 0$. With this, we can derive the chemical potentials and susceptibilities of the doubly bound crosslinkers and filaments. The system is then fully defined with Eqs. (1)–(4). Note that in this simple model, the “cross-diffusion” coefficients between the crosslinkers ($i = ab$) and the filament ($k = A, B$) take the simple form

$$D^{(ik)} = -D^{(ii)} \frac{n^{(i)}}{n^{(k)}}. \quad (\text{E1})$$

Note the negative sign in the previous equation, which makes it clear that the filament ends act as a barrier against crosslinkers diffusion.

Model 2. We now have (*a*)-, (*b*)-, and (*ab*)-bound crosslinkers. This model is then the same as presented in Appendix A, and the results are then directly used to solve Eqs. (1)–(4).

TABLE II. Parameters used in the simulations.

Description		Value	Notes
Entropic forces increase filament overlap			
$D^{(a,b)}$	Singly bound anillin diffusion coefficient	$0.0088 \mu\text{m}^2 \text{s}^{-1}$	[12]
$D^{(ab)}$	Doubly bound anillin diffusion coefficient	$0.0044 \mu\text{m}^2 \text{s}^{-1}$	Estimated to be $D^{(a,b)}/2$
$k^{u \rightleftharpoons a,b}$	Single bound unbinding rate	0.06s^{-1}	[12]
$k^{a,b \rightleftharpoons ab}$	Doubly bound unbinding rate	60s^{-1}	1000 times single-bound unbinding rate, from experiment fitting
$\Delta\epsilon$	Difference of energy between (a, b) and (ab)	$4 k_B T$	Leads to a ratio of ≈ 20 between doubly bound and singly bound crosslinkers
n^S	Maximal concentration of crosslinkers	$4000 \mu\text{m}^{-1}$	Estimation from bundle of 5 filaments, for elongated proteins of a size of 124 kDa [62]
Friction between filaments			
$D^{(a,b)}$	Singly bound PRC1 diffusion coefficient	$0.13 \mu\text{m}^2 \text{s}^{-1}$	[52,75]
$D^{(ab)}$	Doubly bound PRC1 diffusion coefficient	$0.04 \mu\text{m}^2 \text{s}^{-1}$	[52,75]
$k^{(u \rightleftharpoons a,b)}$	Single bound unbinding rate	0.002s^{-1}	Value used in simulation in Ref. [52]
$k^{(a,b \rightleftharpoons ab)}$	Doubly bound unbinding rate	0.002s^{-1}	Value used in simulation in Ref. [52]
$\Delta\epsilon$	Difference of energy between (a, b) and (ab)	$2 k_B T$	Leads to a ratio of ≈ 5 between doubly bound and singly bound crosslinkers
γcL	Drag coefficient between filament and solvent	$0.4 \text{pN}/(\mu\text{m} \text{s}^{-1})$	Estimated for a MT sized cylinder in solvent 100 more viscous than water
$\gamma^\times$	Effective drag coefficient per crosslinkers	$2 \text{pN}/(\mu\text{m} \text{s}^{-1})$	$\sim 0.2 \text{pN}/\text{crosslinkers}$ at $V = 0.1 \mu\text{m} \text{s}^{-1}$ [52]. The friction created by one crosslinkers is five times the friction between filament and surrounding fluid ($\gamma^\times = 5\gamma cL$).
n^S	Maximal concentration of crosslinkers	$200 \mu\text{m}^{-1}$	Minimal spacing of 5 nm between crosslinkers
The interplay of motor forces and entropy on single filament			
D	Diffusion coefficient	$0.001 \mu\text{m}^2 \text{s}^{-1}$	[10]
v_0	Preferred velocity of motors	$0.05 \mu\text{m} \text{s}^{-1}$	[24]
$k^{(u \rightleftharpoons a)}$	Pnbinding rate	0.027s^{-1}	[24]
n^S	Maximal concentration of crosslinkers	$200 \mu\text{m}^{-1}$	Minimal spacing of 5 nm between crosslinkers
Motorized crosslinkers between filaments can generate stable overlaps by an interplay of motor and entropic forces			
$D^{(ab)}$	Diffusion coefficient	$0.05 \mu\text{m}^2 \text{s}^{-1}$	$\simeq$ value from Ref. [60]
$\zeta \Delta\mu^{\text{ATP}}$	Force per crosslinkers	$8 \cdot 10^{-3} \text{pN}$	
$\gamma^\times$	Effective drag coefficient from crosslinkers	$0.8 \text{pN}/(\mu\text{m} \text{s}^{-1})$	
γcL	Drag coefficient between filament and solvent	$0.4 \text{pN}/(\mu\text{m} \text{s}^{-1})$	Estimated for an MT sized cylinder in solvent 100 more viscous than water
n^S	Maximal concentration of crosslinkers	$200 \mu\text{m}^{-1}$	Minimal spacing of 5 nm between crosslinkers
Competition between motorized and passive crosslinkers			
$D_{\text{Ase1}}^{(a,b)}$	Singly bound Ase1 diffusion coefficient	$0.09 \mu\text{m}^2 \text{s}^{-1}$	[15]
$D_{\text{Ase1}}^{(ab)}$	Doubly bound Ase1 diffusion coefficient	$0.011 \mu\text{m}^2 \text{s}^{-1}$	[15]
$D_{\text{Ncd}}^{(a,b)}$	Singly bound Ncd motor diffusion coefficient	$0.05 \mu\text{m}^2 \text{s}^{-1}$	[76]
$D_{\text{Ncd}}^{(ab)}$	Doubly bound Ncd motor diffusion coefficient	$0.025 \mu\text{m}^2 \text{s}^{-1}$	$D_{\text{Ncd}}^{(a,b)}/2$
$k^{(u \rightleftharpoons a,b)}$	Singly bound Ase1 unbinding rate	0.0017s^{-1}	[61]
$k^{(a,b \rightleftharpoons ab)}$	Doubly bound Ase1 unbinding rate	1.7s^{-1}	Same ratio as in sim 1
$\Delta\epsilon_{\text{Ase1}}$	Difference of energy between (a, b) and (ab)	$3 k_B T$	Leads to a ratio of ≈ 10 between doubly bound and singly bound crosslinkers
$k^{(u \rightleftharpoons a,b)}$	Singly bound Ncd unbinding rate	0.01s^{-1}	Chosen that in does not accumulate in the overlap based on the observation of Ref. [61]
$k^{(a,b \rightleftharpoons ab)}$	Doubly bound Ncd unbinding rate	30s^{-1}	Chosen that in does not accumulate in the overlap based on the observation of Ref. [61]

TABLE II. (Continued.)

Description		Value	Notes
$\Delta\epsilon_{\text{Ncd}}$	Difference of energy between (a, b) and (ab)	$1.5k_B T$	Leads to a ratio of ≈ 2 between doubly bound and singly bound crosslinkers
v_0	Preferred velocity of motors	$0.1 \mu\text{m s}^{-1}$	
γcL	Drag coefficient between filament and solvent	$0.4 \text{ pN}/(\mu\text{m s}^{-1})$	Estimated for a MT sized cylinder in solvent 100 more viscous than water
$\gamma^\times$	Effective drag coefficient from crosslinkers	$0.1 \text{ pN}/(\mu\text{m s}^{-1})$	Fitting parameter
$\zeta \Delta\mu^{(\text{ATP})}$	Force per crosslinkers	$2 \times 10^{-2} \text{ pN}$	
n^S	Maximal concentration of crosslinkers	$200 \mu\text{m}^{-1}$	Minimal spacing of 5 nm between crosslinkers

In both models, the initial crosslinker number density $n_i^{(ab)}$ and the initial overlap length L_i^o are chosen by measuring the force while varying the doubly bound crosslinker number density. The crosslinker number density is varied manually, and the force measured is compared to the experimental force. The initial and final concentrations of crosslinkers are then measured when the simulation force is equal to the initial or final state experimental force [see Fig. (6)]. The initial overlap length is then calculated by the relation $n_i^{(ab)} L_i^o = n_f^{(ab)} L_f^o$, using the assumption that there is no loss of crosslinker during one pulling event. We have then $L_f^o = L_i^o + \Delta L$, where ΔL is the length of the pulling step and is known from the experimental data. The force-matching procedure is used to determine the initial overlap and initial concentration in both the single-pulling and multiple-pulling simulations. All other model parameters are calibrated from the first, single-pulling event and then kept fixed for the subsequent pulls, so that the resulting forces are predictions of the calibrated model rather than independent per-pull fits. In the case of Model

2, the concentration of singly bound crosslinkers is chosen to be small compared to the concentration of doubly bound crosslinkers, i.e., $n^{(ab)}/n^{(a,b)} \approx 20$, which corresponds to a binding energy difference of few $k_B T$ between binding states. We take typically $n^{(ab)} \approx 0.5n^{(AB)}$ and $n^{(a)} \approx 0.02n^{(A)}$ (same for $n^{(b)}$).

2. Friction between filaments

In this simulation, the counting state is the same as in the Model 2 in Appendix E 1. Moreover, we include the frictional and drag friction forces. The forces on the filaments are then

$$F_x^{(A)} = c \int_{L^{(A)}} (\partial_x \Pi_x^{(A)} - \gamma V_x^{(A)} + \gamma^\times n^{(ab)} (V_x^{(B)} - V_x^{(A)})) dl, \quad (\text{E2})$$

$$F_x^{(B)} = c \int_{L^{(B)}} (\partial_x \Pi_x^{(B)} - \gamma V_x^{(B)} - \gamma^\times n^{(ab)} (V_x^{(B)} - V_x^{(A)})) dl. \quad (\text{E3})$$

The total number of crosslinkers $N^{(ab)}$ is measured in experiment. We choose the concentration $n^{(ab)}$ accordingly. For the simulation where we change the number of doubly bound crosslinkers, we explore a values between $N^{(ab)} = 5$ and $N^{(ab)} = 200$, which translate into $n^{(ab)} = 0.005n^{(AB)}$ and $n^{(ab)} = 0.2n^{(AB)}$. Finally, the imposed filament velocities $V^{(A)}$ and $V^{(B)}$ are constant during each simulation until the filament disconnect, i.e., when the simulation crashes because $n^{(ab)} > n^{(AB)}$.

3. The interplay of motor activity and available space determines patterning of motors on single filaments

In this model, there is only one type of crosslinker on a single filament. We then use the results of Appendix A with $n^{(B)} = n^{(b)} = n^{(ab)} = 0$. Given the free energy of the system, we derive the chemical potential of the motorized crosslinkers and of the filament,

$$\mu^{(a)} = \epsilon^{(a)} + k_B T \ln \left(\frac{n^{(a)}}{n^{(A)} - n^{(a)}} \right), \quad (\text{E4})$$

$$\mu^{(A)} = \mu_H^{(A)} - k_B T \ln \left(\frac{n^{(A)}}{n^{(A)} - n^{(a)}} \right). \quad (\text{E5})$$

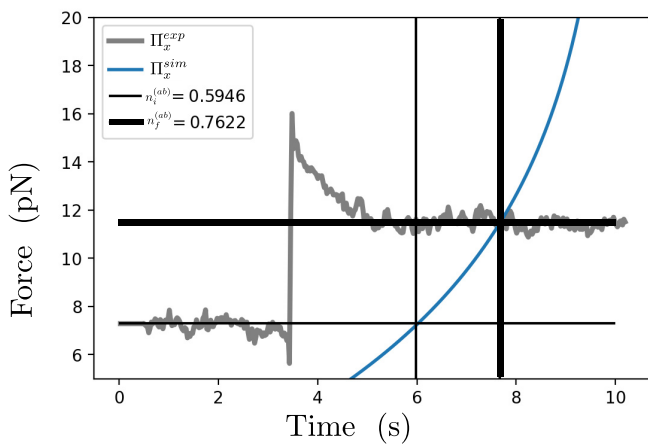


FIG. 6. Calibration of the initial crosslinker density and initial overlap length. Gray line is the force measured in experiment. Blue line is the force measured in simulation. Black lines are construction lines to measure when the experimental and simulation forces are equal. Thin black lines correspond to $n^{(ab)} = 0.59n^{(AB)}$ and thick black lines correspond to $n^{(ab)} = 0.76n^{(AB)}$. These two points correspond to initial and final crosslinker concentrations.

We are particularly interested in the susceptibility $\chi^{(aa)}$ that characterizes the active transport of crosslinkers, and the cross term $D^{(aA)}$ that characterizes boundary effect between the filament and the crosslinkers,

$$\chi^{(aa)} = \frac{n^{(a)}(n^{(A)} - n^{(a)})}{n^{(A)}}, \quad (\text{E6})$$

$$D^{(aA)} = -D^{(a)} \frac{n^{(a)}}{n^{(A)}}. \quad (\text{E7})$$

The spatial flux of the motorized crosslinkers is

$$j_\alpha^{(a)} = -D^{(a)} \partial_\alpha n^{(a)} - D^{(aA)} \partial_\alpha n^{(A)} + v_0^{(a)} \chi^{(aa)} p_\alpha^{(a)}, \quad (\text{E8})$$

with $\chi^{(aa)}$ and $D^{(aA)}$ as defined above.

The initial concentration of motorized crosslinkers is set to zero, like in the experiments and simulations [24].

4. Motorized crosslinkers between filaments can generate stable overlaps by an interplay of motor and entropic forces

In this situation, the motorized crosslinkers are now between two filaments, we then use the same equation of Model

1 in Appendix E 1, but now include the active and frictional forces. Because filaments are polar but antiparallel, the total polarity is $p_\alpha^{(A)} + p_\alpha^{(B)} = 0$ and the doubly bound motors do not walk in a particular direction. The total forces on filament A and B are

$$F_x^{(A)} = c \int_{L^{(A)}} (\partial_x \Pi^{(A)} - \gamma V_x^{(A)} + \gamma^\times n^{(ab)} (V_x^{(B)} - V_x^{(A)}) + \zeta \Delta \mu^{(\text{ATP})} n^{(ab)}) dl, \quad (\text{E9})$$

$$F_x^{(B)} = c \int_{L^{(B)}} (\partial_x \Pi^{(B)} - \gamma V_x^{(B)} - \gamma^\times n^{(ab)} (V_x^{(B)} - V_x^{(A)}) - \zeta \Delta \mu^{(\text{ATP})} n^{(ab)}) dl. \quad (\text{E10})$$

For this simulations, we choose arbitrarily the number density of motors to be $n^{(ab)} = 0.1 n^{(AB)}$; this allows us to have entropic, frictional, and active forces of similar amplitude.

5. Competition between motorized and passive crosslinkers

This model considers a more complex version than Appendix A with six different types of crosslinkers. The number of accessible configuration is

$$\Omega = \frac{N^{(AB)}!}{N_{\text{Ncd}}^{(ab)}! N_{\text{Ase1}}^{(ab)}! (N^{(AB)} - N_{\text{Ncd}}^{(ab)} - N_{\text{Ase1}}^{(ab)})!} \frac{(N^{(A)} - N_{\text{Ncd}}^{(ab)} - N_{\text{Ase1}}^{(ab)})!}{N_{\text{Ncd}}^{(a)}! N_{\text{Ase1}}^{(a)}! (N^{(A)} - N_{\text{Ncd}}^{(ab)} - N_{\text{Ase1}}^{(ab)} - N_{\text{Ncd}}^{(a)} - N_{\text{Ase1}}^{(a)})} \frac{(N^{(B)} - N_{\text{Ncd}}^{(ab)} - N_{\text{Ase1}}^{(ab)})!}{N_{\text{Ncd}}^{(b)}! N_{\text{Ase1}}^{(b)}! (N^{(B)} - N_{\text{Ncd}}^{(ab)} - N_{\text{Ase1}}^{(ab)} - N_{\text{Ncd}}^{(b)} - N_{\text{Ase1}}^{(b)})}. \quad (\text{E11})$$

We can then assess the entropy of the system

$$s = k_B (n^{(AB)} \ln(n^{(AB)}) - n_{\text{Ncd}}^{(ab)} \ln(n_{\text{Ncd}}^{(ab)}) - n_{\text{Ase1}}^{(ab)} \ln(n_{\text{Ase1}}^{(ab)}) - (n^{(AB)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)}) \ln(n^{(AB)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)})) \\ + (n^{(A)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)}) \ln(n^{(A)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)}) - n_{\text{Ncd}}^{(a)} \ln(n_{\text{Ncd}}^{(a)}) - n_{\text{Ase1}}^{(a)} \ln(n_{\text{Ase1}}^{(a)}) \\ - (n^{(A)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)} - n_{\text{Ncd}}^{(a)} - n_{\text{Ase1}}^{(a)}) \ln(n^{(A)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)} - n_{\text{Ncd}}^{(a)} - n_{\text{Ase1}}^{(a)}) \\ + (n^{(B)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)}) \ln(n^{(B)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)}) - n_{\text{Ncd}}^{(b)} \ln(n_{\text{Ncd}}^{(b)}) - n_{\text{Ase1}}^{(b)} \ln(n_{\text{Ase1}}^{(b)}) \\ - (n^{(B)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)} - n_{\text{Ncd}}^{(b)} - n_{\text{Ase1}}^{(b)}) \ln(n^{(B)} - n_{\text{Ncd}}^{(ab)} - n_{\text{Ase1}}^{(ab)} - n_{\text{Ncd}}^{(b)} - n_{\text{Ase1}}^{(b)})), \quad (\text{E12})$$

which is used to calculate each chemical potential. This fully defines the equation of motion of the six species. The filament A is fixed, meanwhile the filament B is free to move. The sliding velocity of the filament B is then calculated from $\int_{L^B} f_\alpha^{(B)} dl = 0$. This leads to

$$V_x^{(B)} = \frac{1}{\int_{L^{(B)}} (\gamma + \gamma^\times (n_{\text{Ase1}}^{(ab)} + n_{\text{Ncd}}^{(ab)})) dl} \left(\int_{L^{(B)}} (n^{(B)} \partial_x \bar{\mu}^B + \zeta \Delta \mu^{\text{ATP}} n_{\text{Ncd}}^{(ab)}) dl \right). \quad (\text{E13})$$

Based on the observation in Ref. [61], the motors Ncd do not accumulate in the overlap region of filaments, while the passive crosslinkers Ase1 accumulate. This means that Ncd do not gain much energy by binding to both filaments, while Ase1 does. We thus set $\Delta \varepsilon_{\text{Ncd}} \approx 1.5 k_B T$, which leads to a ratio of 2 between the doubly bound and singly bound motors. The difference of energy for Ase1 pas-

sive crosslinkers is $\Delta \varepsilon_{\text{Ase1}} \approx 3 k_B T$, which leads to a ratio of 10.

APPENDIX F: SUMMARY OF THE NOTATIONS USED

We summarize all the symbols in this paper and their units in Table III.

TABLE III. Parameters and notations used.

Symbol	Description	Units	Notes
$n^{(i)}$	Number density of species i	μm^{-1}	Includes filament particles and all crosslinker states
$f_{\alpha}^{(A,B)}$	Force density acting on filament A or B	$\text{pN } \mu\text{m}^{-1}$	
$F_{\alpha}^{\pm(A,B)}$	Boundary forces acting at the plus/minus ends of filament A or B	pN	Applied at filament boundaries
$\Pi^{(A,B)}$	Entropic force in filament A or B	pN	
$\mathcal{A}_{\alpha}^{(A,B)}$	Active force density acting on filament A or B	$\text{pN } \mu\text{m}^{-1}$	
$\mathcal{F}_{\alpha}^{(A,B)}$	Interfilament friction force density acting on filament A or B	$\text{pN } \mu\text{m}^{-1}$	
γ	Coefficient for friction between a filament-crosslinker system and the surrounding medium	$\text{pN s } \mu\text{m}^{-2}$	
$\gamma^{\times}$	Interfilament friction coefficient associated with a single doubly bound crosslinker	$\text{pN s } \mu\text{m}^{-1}$	Equivalent to $\text{pN s } \mu\text{m}^{-1}$ per crosslinker
$V_{\alpha}^{(A,B)}$	Velocity of filament A or B	$\mu\text{m s}^{-1}$	
$v_0^{(i)}$	Force-free active velocity of species i	$\mu\text{m s}^{-1}$	
$p_{\alpha}^{(i)}$	Polarity vector associated with species i	Dimensionless	Unit vector
S_{α}	Unit vector pointing from one filament A to filament B	Dimensionless	Unit vector
s	Entropy density of the crosslinker-filament system	$k_B \mu\text{m}^{-1}$	
T	Temperature	K	
$\mu^{(i)}$	Chemical potential of species i	$k_B T$	
$\varepsilon^{(i)}$	Binding or interaction energy associated with species i	$k_B T$	
$j_{\alpha}^{(i)}$	Spatial flux of species i relative to the center-of-mass velocity	s^{-1}	
$r^{(i)}$	Source term for species i due to chemical or binding reactions	$\mu\text{m}^{-1} \text{s}^{-1}$	
$r^{(I)}$	Chemical flux through reaction pathway I	$\mu\text{m}^{-1} \text{s}^{-1}$	
$a^{(il)}$	Stoichiometric coefficient of species i in reaction I	Dimensionless	Positive for products, negative for reactants
$\bar{\Lambda}^{(IJ)}$	Onsager coefficient coupling chemical reactions I and J	$(k_B T)^{-1} \mu\text{m}^{-1} \text{s}^{-1}$	
$\Lambda^{(ij)}$	Onsager mobility coefficient coupling the flux of species i to the chemical-potential gradient of species j	$(k_B T)^{-1} \mu\text{m s}^{-1}$	
$\lambda^{(i)}$	Active transport coefficient coupling ATP hydrolysis to the flux of species i	$(k_B T)^{-1} \text{s}^{-1}$	
η	Viscosity coefficient	$\text{pN s } \mu\text{m}^{-2}$	
ζ	Active-force coefficient converting chemical energy input into motor force per crosslinker	μm^{-1}	
$D^{(i)}$	Diffusion coefficient of species i	$\mu\text{m}^2 \text{s}^{-1}$	
$\chi^{(ik)}$	Thermodynamic susceptibility or cross-compressibility coupling species i and k	μm^{-1}	Reduces to $n^{(i)}$ in the dilute limit
$k^{(i \rightleftharpoons j)}$	Binding or transition rate between states i and j	s^{-1}	
$\mathcal{D}_a$	Damköhler number comparing reaction and diffusion timescales	Dimensionless	

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