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To cite this article: M Dedenon *et al* 2026 *New J. Phys.* **28** 024401

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**PAPER****OPEN ACCESS****RECEIVED**
25 August 2025**REVISED**
6 January 2026**ACCEPTED FOR PUBLICATION**
26 January 2026**PUBLISHED**
11 February 2026Original Content from
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The importance of being discrete: fluctuations, defects, and density-orientation coupling in agent-based active nematics

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E-mail: karsten.kruse@unige.ch and j.elgeti@fz-juelich.de**Keywords:** active matter, agent-based model, active nematics, spontaneous flowSupplementary material for this article is available [online](#)**Abstract**

We propose an agent-based model of active flexible rods. Inspired by cytoskeletal flows, we introduce activity by an internal flow that contributes to the dissipative forces. The active force between our agents is central and reciprocal, ensuring linear and angular momentum conservation. For nematic activity, we find spontaneous, thresholdless flows and stochastic flow-reorientation, which is accompanied by the formation of topological defects. Defects appear and vanish with activity-dependent rates, and $+1/2$ -defects self-propel. These hallmarks of active turbulence are present even on the scale of individual agents. The particle-based interactions lead to an emergent coupling between density and orientation that generates density dipoles around $+1/2$ -defects. Finally, we highlight the versatility of our agent-based model by presenting spontaneous flows in three dimensions and tissue growth. Our framework opens the way for an integrated description of living materials, including several forms of activity in the same system.

1. Introduction

Living systems are maintained out of thermodynamic equilibrium: their constituents continuously convert chemical energy from the environment into other forms, notably mechanical work. For example, suspensions of purified cytoskeletal proteins can exhibit contractile or extensile mechanical stress generated by molecular motor activity [3, 6, 42]. The constituents of living matter like the cytoskeleton or cell cultures are typically elongated. When they align, these systems can exhibit orientational order on scales larger than the size of the constituents [14, 26, 42]. Often, though, there is no preferred front or back, in which case one refers to nematic order. As a consequence of orientational order, active stress is generally anisotropic [40]. Anisotropic active stress plays a central role, for instance, in chromosome segregation [8], establishment of the anterior–posterior axis in the worm *Caenorhabditis elegans* [33], or convergence–extension during wing development in *Drosophila melanogaster* [16]. Orientational order fields often present singularities, which are called topological defects. Such defects play an important role in numerous biological processes such as stress organization, shape formation or density accumulation [22, 25, 32, 43].

Hydrodynamic theories of living matter describe the dynamics of a small number of coarse-grained physical variables averaging out the discrete nature of constituents [40]. On the one hand, hydrodynamic equations have a firm basis in symmetries and conservation laws like momentum or density. In this phenomenological approach, the link between the coarse-grained material parameters and the microscopic parameters is unknown. Furthermore, it is unclear on which length scales these continuum descriptions are valid. Hallmarks of active nematic fluids such as spontaneous shear flows [7, 13, 28, 50] or spontaneous defect unbinding [37, 42] were first reported using this type of approach.

On the other hand, ‘the importance of being discrete’ [23] can only be uncovered by agent-based models. In this framework, activity is typically introduced in the form of agent self-propulsion [4, 9, 24, 48], agent turnover [5, 10, 23], or explicitly modeled with molecular motors [35, 49, 53]. Agent-based models have unveiled long-range orientational order in two-dimensional active systems [48] and illustrate concepts like homeostatic pressure [5]. By bridging the gap to smaller length scales, such models allow to test the validity of hydrodynamic descriptions. Most importantly, they allow one to readily avoid assumptions commonly made in continuum theories, like constant density or homogeneity of activity, and retain the ultimately granular nature of active systems. This has led to discoveries like motility-induced phase separation or negative homeostatic pressure [39, 46]. Yet, few agent-based models conserve momentum, limiting their applicability to specific active systems. An intermediate framework between continuous and discrete approaches conserving momentum is multi-particle collision dynamics [30, 45], which was recently applied to active nematic fluids [27].

In this work we develop a versatile agent-based model for active nematic fluids to uncover the role of granularity, fluctuations, and limits of the hydrodynamic approach. It features tunable, extensile or contractile active stress, conserves linear and angular momentum, has a proper thermal (i.e. non active) limit, and is compatible with other forms of activity like growth and self propulsion. Specifically, inspired by cytoskeletal flows, we introduce activity by an internal flow inside the filamentous agents (figure 1). Through friction with the neighbors, this generates an extensile or contractile force dipole, depending on the sign of the flow. Basing our model on earlier agent-based models of tissue growth [5, 41], it accounts for active mechanical stress and can readily be extended to include other, independent forms of activity, such as growth or division. Our framework describes one-component materials or suspensions at high density where fluid-mediated interactions can be absorbed into effective parameters.

We use this model to study the spontaneous emergence of orientational order and flows in active nematic fluids. Remarkably, our simulations show that phenomena uncovered by hydrodynamic analysis can be found down to agent scales. For example, we observe the emergence of spontaneous flows and self-propulsion of $+1/2$ -defects. Furthermore, we explore effects due to the granularity of our system that are not captured by hydrodynamics. Specifically, in channel geometries, we found novel correlations between the nematic orientational field and the flows of agents. The fluctuations naturally present in our simulations lead to dynamic flow fields with bursts of activity and spontaneous creation of topological defects. Also, we report on density variations around defect cores. Finally, we show how this framework can be extended to three dimensions and how to include other active processes present in living systems like growth or self-propulsion.

2. Method: a multi-particle agent-based model of an active nematic fluid

We consider N agents consisting each of P particles connected by harmonic bonds into a chain with additional bending rigidity (figure 1(A)). Between agents, short range repulsion accounts for steric effects, while intermediate attraction with cut-off distance r_c mimics, for example, the effects of cross-linking proteins on cytoskeletal filaments or of cell–cell adhesion molecules like cadherins. In addition, all particles interact via pairwise dissipative and random forces by a dissipative particle dynamics-like thermostat [21]. In this framework, linear and angular momentum are conserved (figure 1(B)) and the system relaxes to thermal equilibrium in the absence of any other force. Newton’s equation of motion are integrated by an adapted Velocity-Verlet algorithm [36]. Up to this point, the model is similar to dissipative particle dynamics for solutions of semi-flexible polymers.

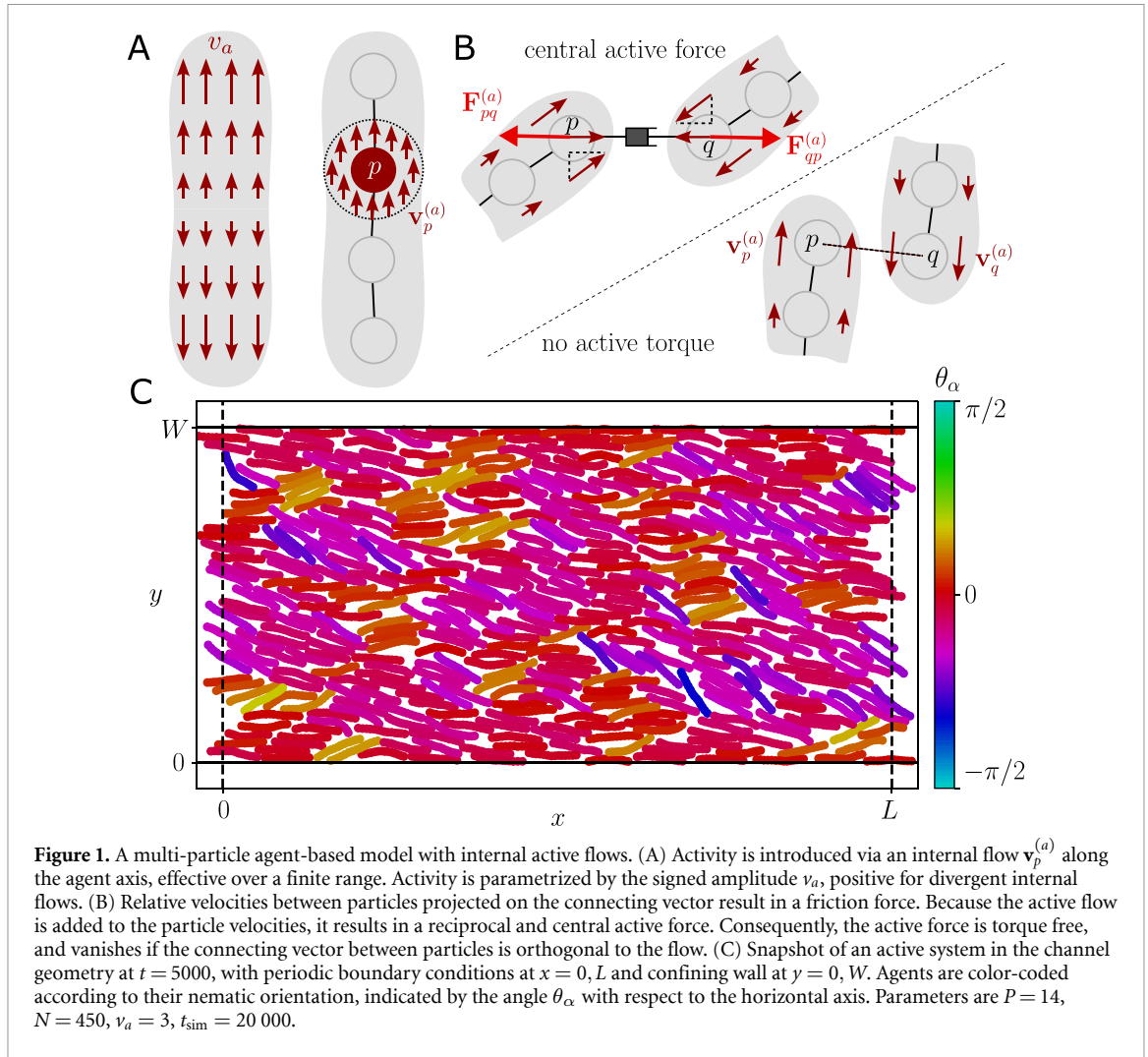
We introduce an active force that is inspired by the retrograde actin flow in migrating cells, and ensures nematic symmetry (figure 1(A)). Each particle p of an agent α generates an internal active flow with a prescribed velocity $\mathbf{v}_{a,p}$ oriented along the agent axis $\hat{\mathbf{u}}_\alpha = (\mathbf{r}_p - \mathbf{r}_1)/|\mathbf{r}_p - \mathbf{r}_1|$ with

$$\mathbf{v}_{a,p} \cdot \hat{\mathbf{u}}_\alpha = v_a \left(2 \frac{p-1}{P-1} - 1 \right) \quad (1)$$

for $p = 1, 2, \dots, P$. For an activity parameter $v_a > 0$, the internal active flow is divergent, whereas it is convergent for $v_a < 0$. This flow is added to the particle’s velocity when calculating dissipative forces, resulting in an active force dipole. The active force applied by particle q on particle p then reads

$$\mathbf{F}_{pq}^{(a)} = -\xi \omega(|\mathbf{r}_p - \mathbf{r}_q|)^2 \left[\frac{\mathbf{r}_p - \mathbf{r}_q}{|\mathbf{r}_p - \mathbf{r}_q|} \cdot (\mathbf{v}_{a,p} - \mathbf{v}_{a,q}) \right] \frac{\mathbf{r}_p - \mathbf{r}_q}{|\mathbf{r}_p - \mathbf{r}_q|}, \quad (2)$$

where ξ is the inter-agent dissipation coefficient and $\omega(r)$ is a dimensionless weight factor to ensure short-ranged interactions. As we show below, divergent (convergent) flow generates an active extensile



(contractile) stress. Note also that the active forces are central and have an opposite reaction force such that linear and angular momentum are still conserved (figure 1(B)), a key property not retained for example in Vicsek-like models [48]. Further details can be found in supplementary text with parameters in table S1.

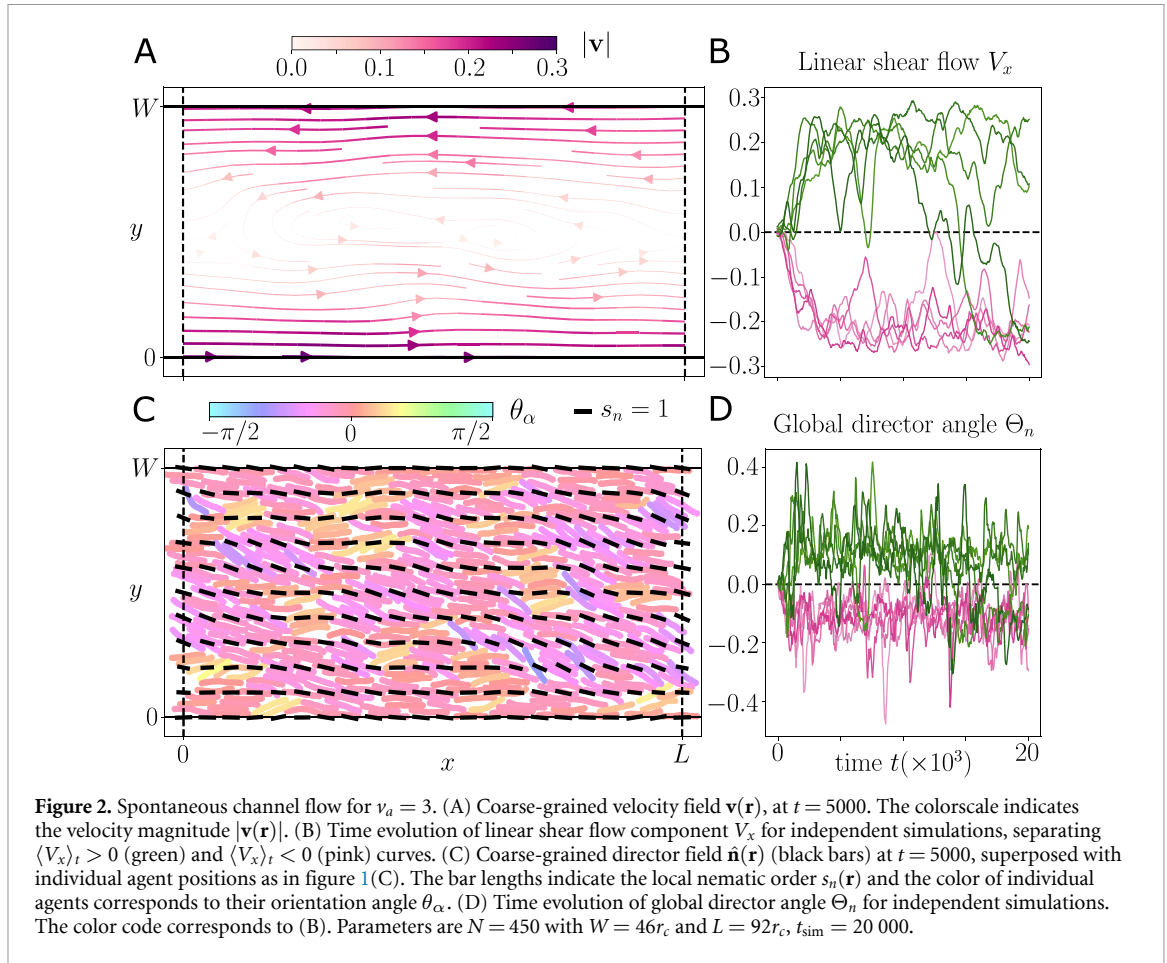
3. Results

3.1. Spontaneous channel flow

A hallmark of active nematics is spontaneous flow in a channel [31, 50]. We demonstrate the power of our model by showing the emergent flow and characterize fluctuations and correlations.

We simulate active agents confined in an infinite channel of width W , with perfect slip walls and periodicity L (figure 1(C)). Without activity $v_a = 0$, we confirm that the system behaves as a nematic fluid (supplementary text, figure S2). We chose simulation times $t_{\text{sim}} \sim 10^4$ to assure relaxation to equilibrium or out-of-equilibrium steady-state. The system is characterized by velocity and nematic tensor fields, $\mathbf{v}(\mathbf{r})$ and $\mathbf{q}(\mathbf{r})$, which are computed by locally averaging over a small area containing ~ 10 agents the velocities and orientations of individual agents, respectively (supplementary text). The largest eigenvalue of the nematic tensor field $\mathbf{q}(\mathbf{r})$ is the local nematic order $s_n(\mathbf{r})$, which is zero in the disordered phase and unity in the perfectly ordered phase. The corresponding eigenvector is the director field $\hat{\mathbf{n}}(\mathbf{r})$ representing the average orientation of agents in the vicinity of \mathbf{r} . Equivalently, averaging over all agents defines a global nematic order S_n and a global director $\hat{\mathbf{N}} = (\cos \Theta_n, \sin \Theta_n)$ with orientation angle Θ_n , where the nematic symmetry is reflected by limiting $-\pi/2 \leq \Theta_n \leq \pi/2$ (supplementary text).

For extensile activity, $v_a > 0$, a shear flow emerges spontaneously (figure 2(A), movie 1). The instantaneous flow fields frequently exhibit transient vortices (figure 2(A) and figure S3C) and are clearly more complex than simple shear. For analysis, we average out these complexities and quantify the linear shear flow by projecting on the first Legendre polynomial with resulting coefficient V_x (supplementary text).

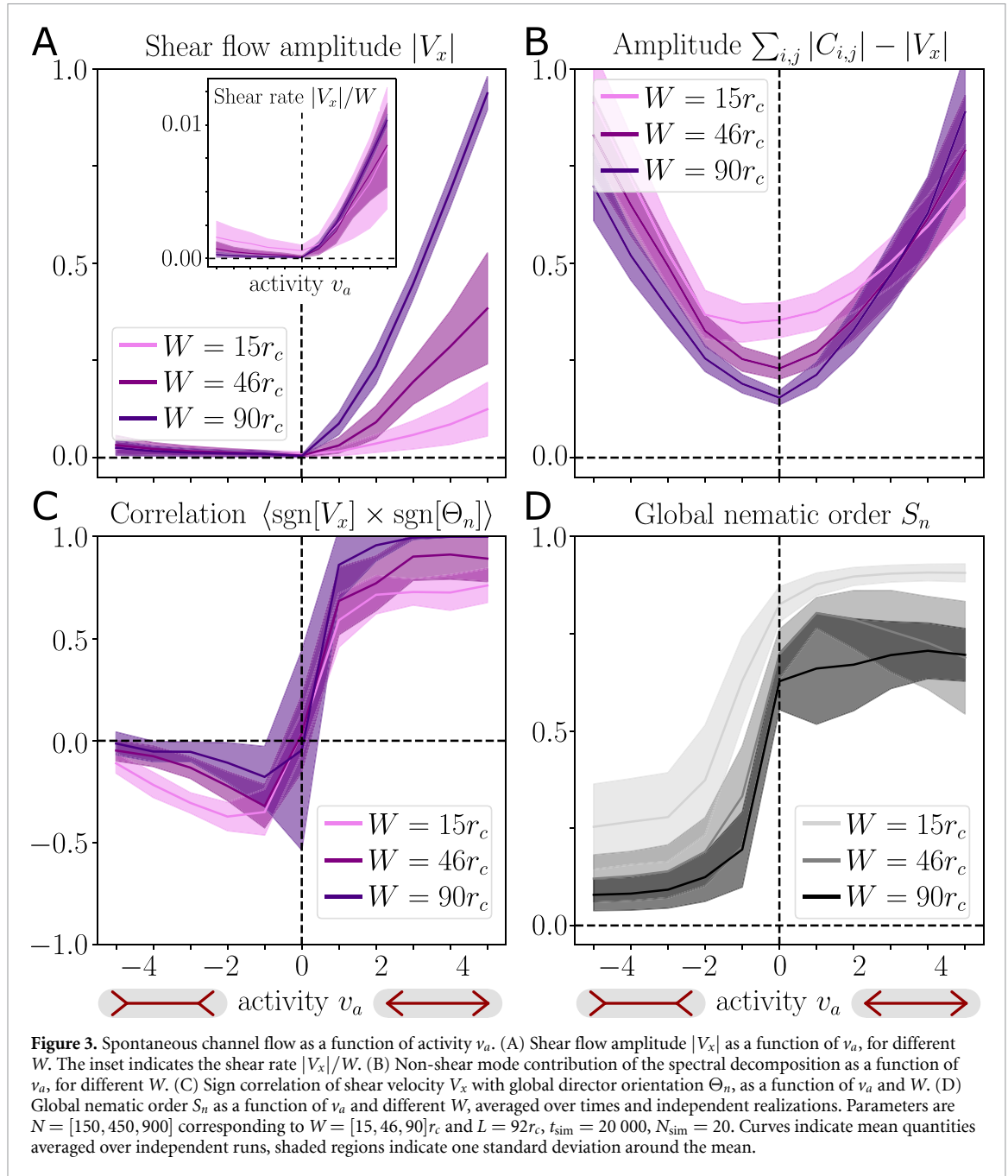


The shear flow fluctuates strongly in time (figure 2(B)) and can even occasionally reverse sign. The stronger the activity and the wider the channel, the more persistent the flow seems to be. For narrow channels and low activity, we observe many flow reversals, which become increasingly rare as the channel widens and activity increases (figure S4). For the orientation, we find that the local nematic order s_n is largely uniform throughout the channel, and the director field $\hat{\mathbf{n}}$ aligns with the boundaries but fluctuates in space and time (figure 2(C)). Yet, the global director orientation Θ_n is non-zero and correlates with shear flow direction (figures 2(B) and (D)).

Averaging the shear flow amplitude reveals a transition from a nearly vanishing flow for contractile activity to spontaneous shear flow for extensile activity (figure 3(A)). The shear flow amplitude grows roughly linearly with activity and with channel width—the latter implies a shear rate that is independent of the channel width. Notably, shear flows exist even for channel widths for which the system granularity is apparent ($W = 15r_c$ corresponding to ~ 2 agent lengths) (figure 3(A) and figure S3A). While the shear flow dominates, other modes defined by projection on higher order Legendre polynomials in x and Fourier modes in y contribute strongly. Summing up all other modes shows that activity adds higher order fluctuations to the flow (figure 3(B) and figure S5). For these additional fluctuations, contractile and extensile activity seem to have similar effects.

For extensile activity, our simulations behave as we expect from hydrodynamic theory [13, 50]. The agents are well-aligned throughout the system, and tilt of the nematic orientation strongly correlates with the shear flow (figures 3(C) and (D) and figure S6). On the other hand, contractile activity leads to a break down of global nematic order, and consequentially we observe little average shear flow. This break down of global order for contractile activity is caused by the nucleation of defects—see further discussion below and figure S10A. However, occasionally, we see order and flow appearing in the system. In these cases, the flow and orientation are in opposite directions, leading to a negative correlation of the two (figures S5D,E). This is consistent with hydrodynamics where an instantaneous tilt of the director field generates flows, where the direction depends on the sign of the activity. However in the contractile case, the flows tend to relax the tilt and no persistent flow is obtained.

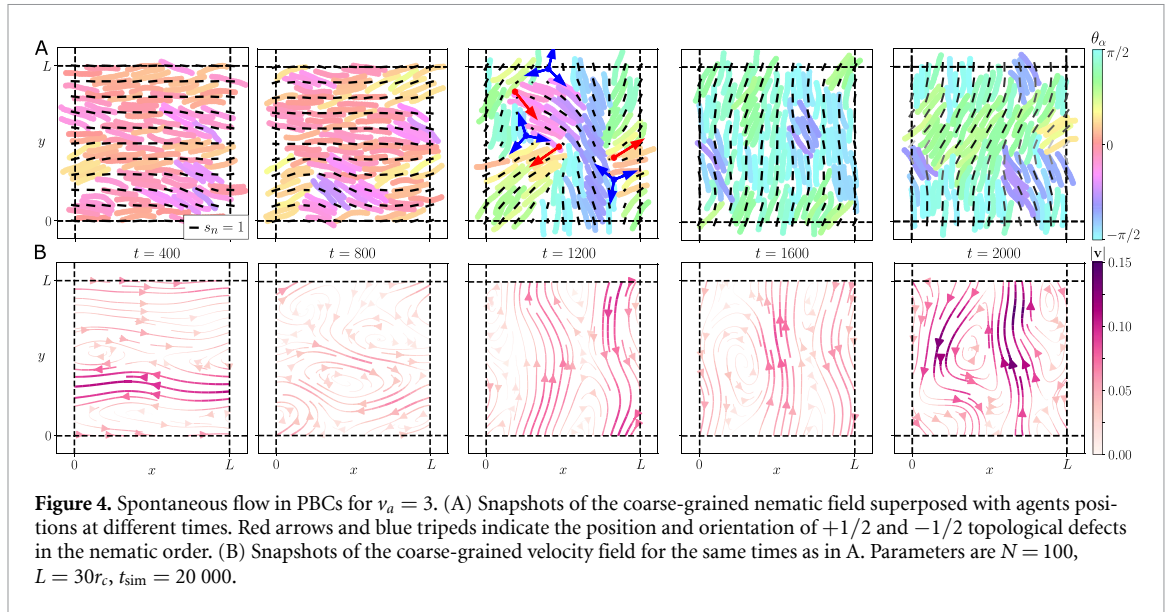
Overall, the results highlight that our model produces spontaneous flows as described by hydrodynamics. Yet contrary to the hydrodynamic theory, we do not observe any measurable threshold in



activity for the onset of spontaneous flows. An equivalent threshold in terms of channel width is found using hydrodynamic theory. Here, the channel width only controls the flow persistence without any measurable threshold, suggesting that we are in a regime, where the threshold width is of the order of agent size. Beyond hydrodynamics, we find transient flows correlated with orientation for contractile activity. Furthermore, noise leads to flow reversal at a rate that decreases with the flow amplitude.

3.2. Results: bulk properties—spontaneous flow and bend-instability induced reorientation

In bulk, the system exhibits a similar spontaneous flow transition as in the channel geometry: for sufficiently strong extensile activity, spontaneous flow emerges (figure S7). For $L = 30r_c$, we observe extended phases with shear flows that are either oriented in the horizontal or vertical directions (figure 4 and movie 2). Other directions are suppressed by the limited number of available wavevectors in periodic boundary conditions. These phases persist for a finite time and stochastically switch directions. This is reminiscent of active bursts of reorientation observed in the hydrodynamics of compressible nematics [20]. During the transition periods, the director field bends and topological defect pairs are created (figure 4(A)).



To quantify this behavior, we define a nematic flow tensor that characterizes the alignment of the flow analogously to the nematic orientation tensor (supplementary text). Here, the degree of nematic order of the flow is measured by S_v , while Θ_v measures the orientation tilt. The orientation and flow fields are strongly correlated (figures 5(A)–(C)). Without activity, asymmetric viscosity induces a correlation between agent orientation and velocity, as expected.

For extensile activity, the orientation-flow correlation initially decreases with increasing activity, then it increases reaching a maximum around $v_a \sim 3$, and again decreases for even larger activities (figure 5(C)). While the decrease at large activity could be expected from hydrodynamic theory due to active turbulence, the minimum and increase at moderate activity are unexpected. Closer visual inspection of time resolved orientations (figures S8(A)–(D)) indicates that at small activity, the additional activity increases fluctuations, reducing correlations. At larger activity, the emerging macroscopic flows are strongly correlated to particle orientation. For contractile activity, the correlation increases reaching a maximum at $v_a \sim -1$, and then decreases for larger activities (figure 5(C)).

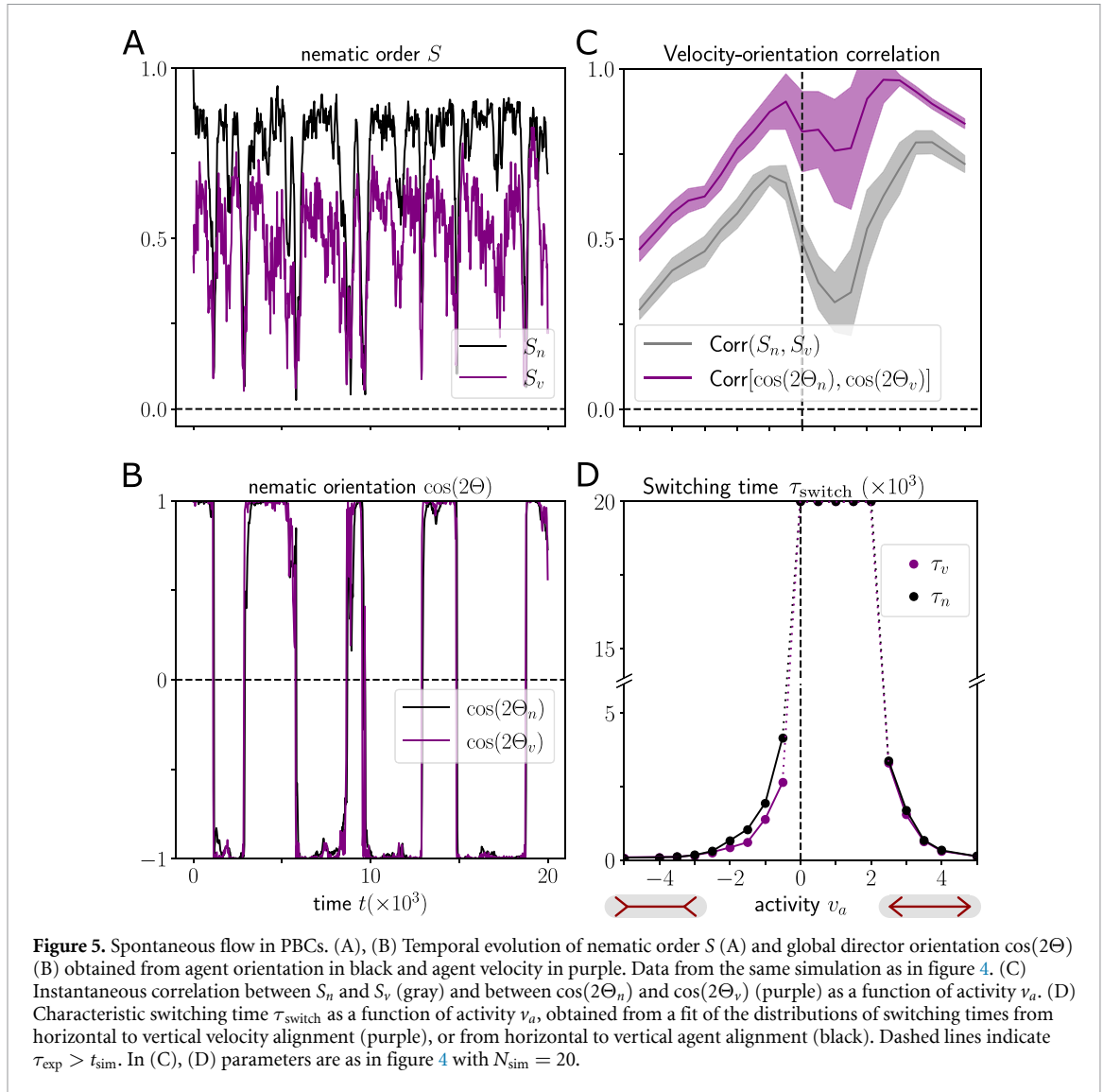
The nematic flow tensor further allows us to characterize the orientational switching of the flow (figures 5(B) and (D)). The flow exhibits a clear orientation, and then suddenly switches to a different orientation. The times between switching events follow an exponential distribution with a characteristic switching time τ_{switch} (figures S8E–H and supplementary text). For small activity ($0 < v_a < 2$) we observe no switching events during our simulations, indicating stable phases. For stronger extensile activity, we observe an increase in frequency of switching.

3.3. Results: defect dynamics and density-orientation coupling

Simulating larger system sizes $L = 302r_c$ allows us to study topological defects and flow patterns showing swirls and chaotic behavior characteristic of active turbulence [2, 17, 44] (figures 6(A) and (B), movies 3, 4 and figure S9(B)). We observe a continuous creation of $\pm 1/2$ -defect pairs driven by activity, balanced by annihilation events. While for extensile activity ($v_a > 0$) we observe the linear increase of density of defects with activity expected from hydrodynamic theory [17, 47], for contractile activity the density saturates (figure 6(C)). Note in particular the minimum of defects for zero activity, and the much larger slope for contractile than for extensile activity. This asymmetry between contractile and extensile activity was not reported in results obtained by hydrodynamic analysis [17, 47] or multiparticle collision dynamics [27].

As depicted in the inset of figure 6(D), $+1/2$ -defects have a polarity $\mathbf{p} = \nabla \cdot \mathbf{q} / |\nabla \cdot \mathbf{q}|$. Together with activity, this asymmetry leads to self-propulsion of $+1/2$ -defects [42]. In agreement with hydrodynamic theory [18, 19, 38], defects move opposite to their polarity \mathbf{p} for extensile activity, and along the polar direction for contractile activity (figure 6(D)). Note the asymmetry between extensile and contractile activity with faster self-propulsion in the extensile case for the same amplitude of v_a .

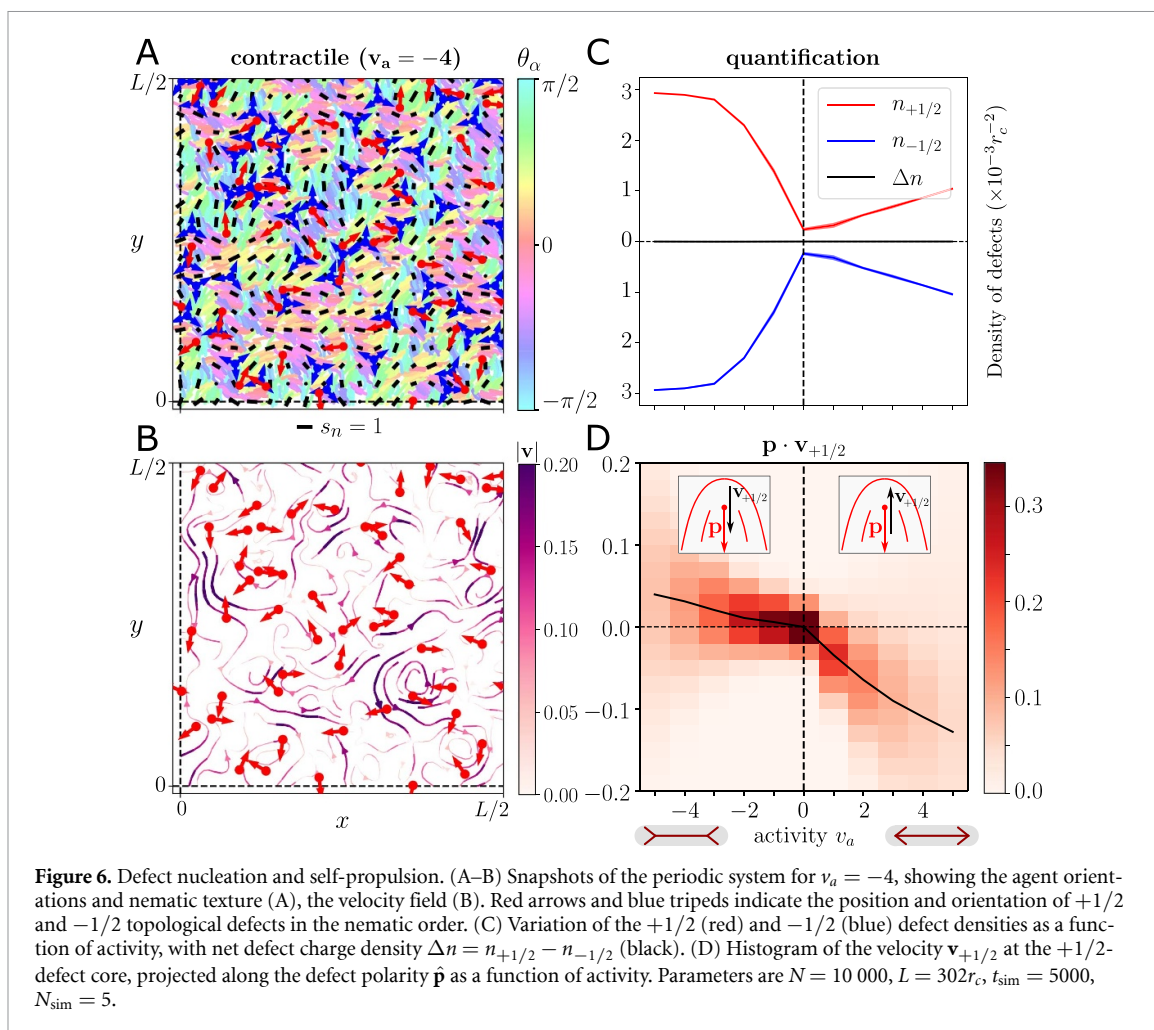
One advantage of our particle-based framework is an emerging coupling between density and other fields like the orientation, compared to hydrodynamic theories where one typically has to choose between a multitude of possible couplings [29, 52]. In figure 7(A), we show the relative variation $\Delta\hat{\rho} = [\rho(\mathbf{r}) - \bar{\rho}] / \bar{\rho}$ of the local density $\rho(\mathbf{r})$ with respect to the global density $\bar{\rho} = N / (L_x L_y)$. We observe strong



variations of density, and identify giant number fluctuations for sufficiently large activity (figure 7(B)). Again, an asymmetry between extensile and contractile activity emerges. Giant number fluctuations can also be observed for switching self-propelled agents in contact with a substrate with extensile-like active stress [24].

Close to a defect, we compute the dipole of density variations d at $+1/2$ -defect sites, defined in figure S9E. For contractile activity, the dipole is typically positive, meaning a region of dilation at the head and a region of compression at the tail of a $+1/2$ -defect (figures 7(A) and (C)). A histogram reveals that this positive dipole persists even for $v_a = 0$ (figure 7(C)), while sufficiently extensile activity ($v_a > 2$) promotes negative dipole with compression at the head. More generally, we find that the Hessian $\mathbf{H} = \nabla \nabla \hat{\rho}$ of the density is anisotropic (figure 7(D) and figure S9H). Its principal directions align with those of the nematic tensor \mathbf{q} , such that the scalar quantity $\mathbf{q} : \mathbf{H}$ is negative on average for $v_a = 0$ (supplementary text, figure S9(I)). In terms of a continuum theory of equilibrium compressible nematics, these findings suggest the existence of a coupling term $f_w = w \mathbf{Q} : \mathbf{H}$ in the free energy density, where the coupling coefficient $w > 0$. This term leads to density dipoles near $+1/2$ -defects with the same orientation as in figure 7(C) for $v_a = 0$ (supplementary text).

We conclude that hydrodynamics describes the propulsion of defects down to the scale of individual agents. Indeed, we observe very similar trends in defect density and defect–density interactions in much smaller systems and in the channel geometry (figure S10). However, we find that higher order terms in the free energy of nematic fluids are necessary to capture salient features of our simulations. From the simulations we can furthermore infer the relevant higher order terms.

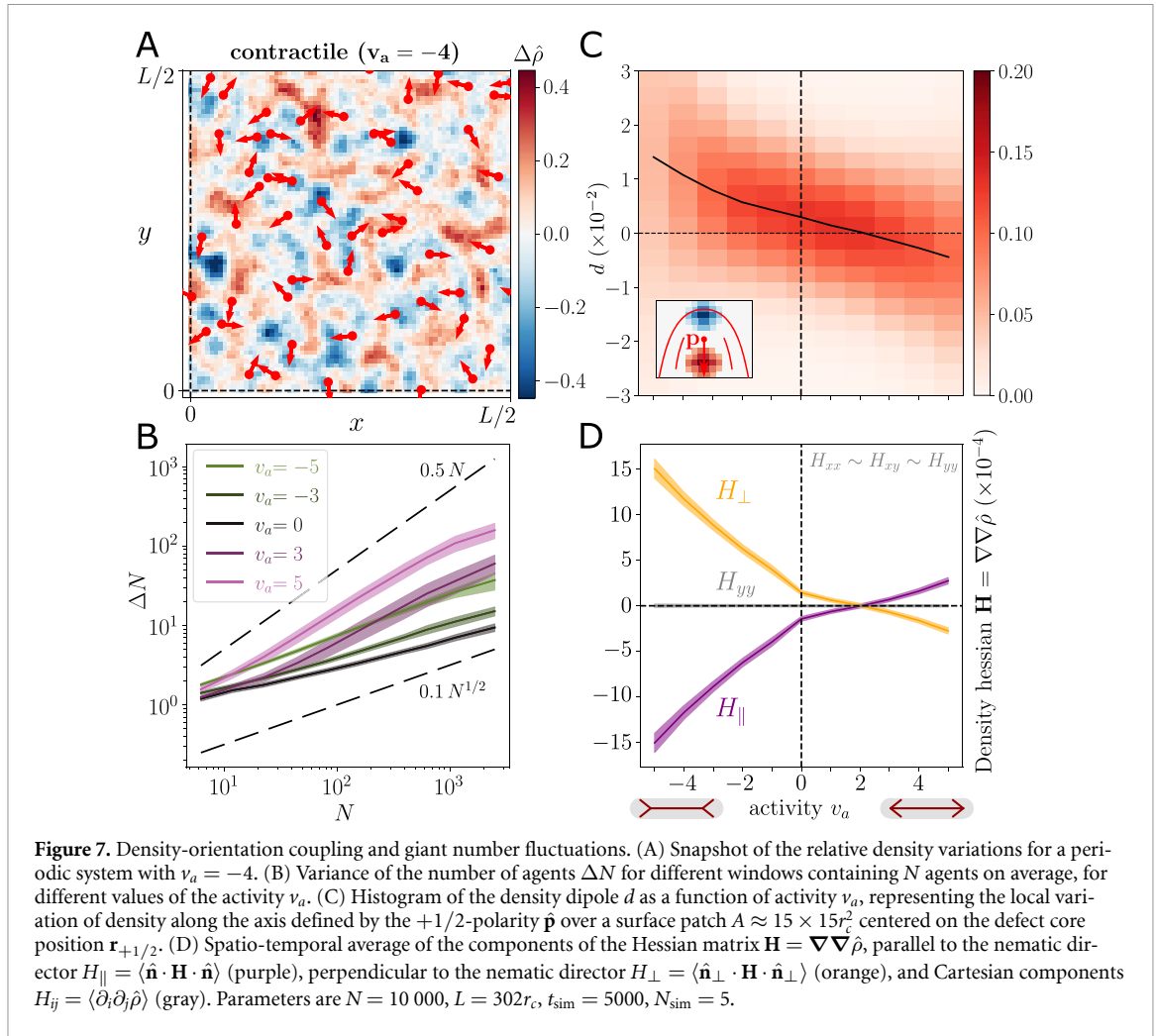


4. Scope & discussion

In this work, we present a new theoretical framework to describe active nematic fluids with an agent-based approach. We show that incorporation of internal active flows with nematic symmetry at the agent scale gives rise to spontaneous macroscopic flows and self-propulsion of $+1/2$ -defects, which are well-known hallmarks of active nematic fluids. Thus, our framework establishes a correspondence between the mesoscopic scale, where individual agents generate active force dipoles, and the hydrodynamic scale, where activity is captured by a component of the stress tensor. Indeed, it is a key advantage of our model compared to a hydrodynamic or more coarse-grained approach like multi-particle collision dynamics [27], that it is particularly suited to understand effects due to the discrete and individual nature of agents.

Activity is not limited to active stress. Indeed, cytoskeletal filaments and molecular motors constitute active nematics, while they also grow by assembly. Cells in eukaryotic tissues can crawl, generate nematic active stresses, and divide. Adding additional features like turnover, active stress, or self-propulsion to hydrodynamic descriptions of active matter is often achieved by introducing new dynamic fields. These new fields couple to the already existing fields, leading to additional parameters, which can be hard to interpret microscopically. An example is provided by various propositions for coupling density variations and orientational order [1, 12, 51]. Furthermore, symmetry typically allows for different possible expressions for the corresponding coupling terms. As a consequence choices have to be made, which are difficult to justify intrinsically. Similarly, some agent-based models serve a specific purpose and are sometimes not readily extended to account for additional features. In contrast, our framework readily allows for the introduction of active processes beyond active stress as we will show in the following.

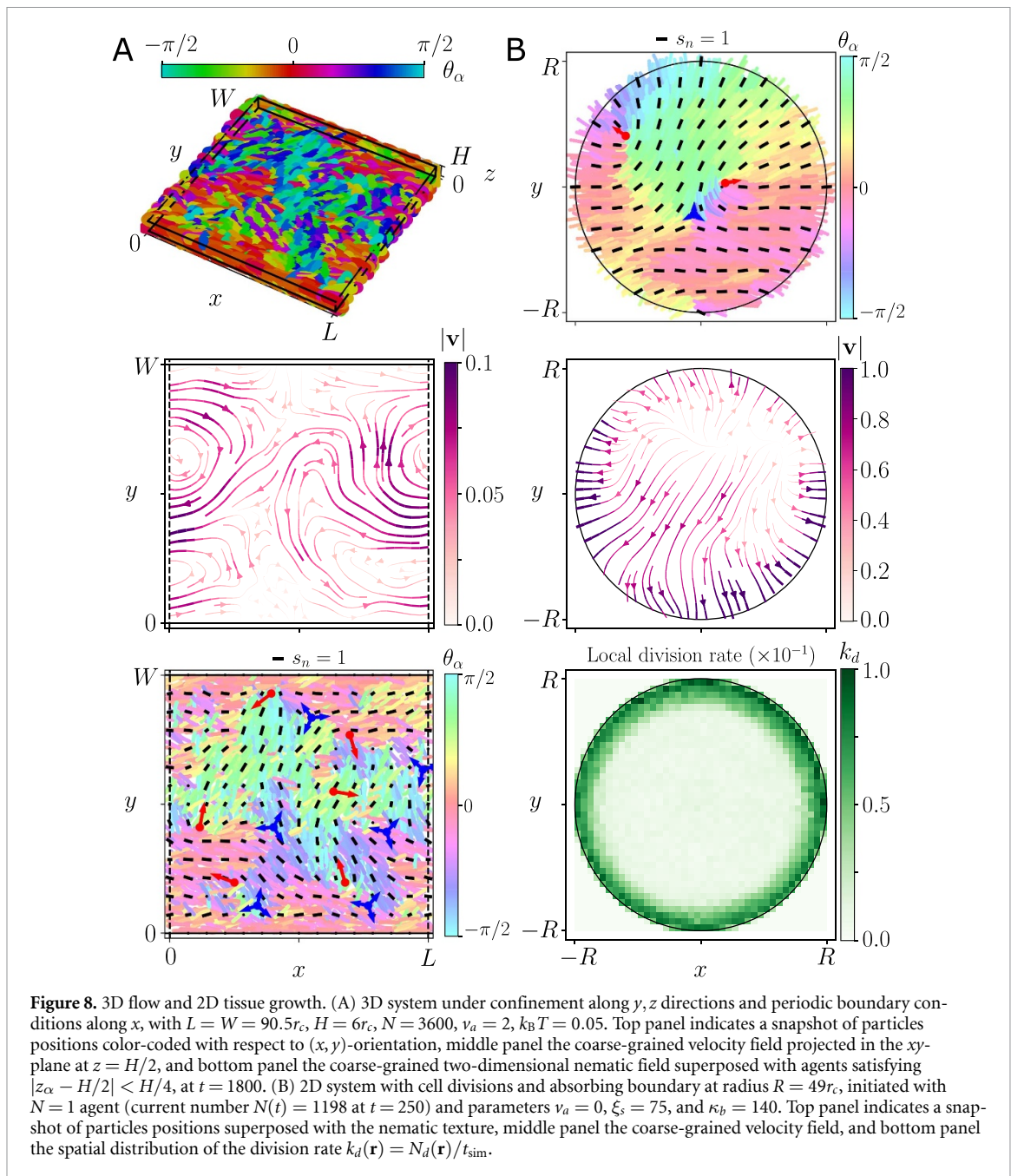
Up to this point, we have explored assemblies in two dimensions. However, an extension to three dimensions is straightforward. For example, thin layers of active filaments like the actin-cortex of cells



are usually treated in two dimensions. However, in two dimensions steric interactions are more constraining than in three dimensions. To assess the importance of this effect, we simulate the channel geometry presented above with a small but finite thickness $H = 6r_c$ (figure 8(A) and movie 5). We observe a shear flow pattern similar to figure 2(A), but the flows are less localized to the walls. The escape of agents towards the third dimension appears to limit the nematic order and the coherency of the active flows. This result highlights that even if small compared to lateral dimensions, the third dimension can play an important role.

Furthermore, our model is based on the two-particle growth model [5], which allows us to implement similarly agent growth, splitting and deletion mechanisms with mechanical feedback (supplementary text). Inspired by the free growth of cell colonies, we simulate a group of agents growing on a circular patch (figure 8(B) and movie 6). Further highlighting the versatility of our framework by readily implementing various boundary conditions, we consider an absorbing boundary such that agents escaping the patch are removed from the simulation. We observe large domains of uniform nematic order, transiently destabilized through bend deformations and nucleation of $\pm 1/2$ -defects (figure 8(B)). The outward flow is destabilized such that $+1/2$ -defects tend to self-propel as in extensile active nematics (figure 8(B)). Divisions are primarily located at the periphery, as observed for tumor spheroids and in the two-particle growth model [34, 39]. These results demonstrate that our model can readily be extended to include further forms of activity. Similarly, self-propulsion of filaments [15] can be included through tangential driving forces.

Given its versatility, our framework allows us to address a number of open challenges in the field. (1) The difficulty to design well-controlled experimental systems of active matter makes *in silico* experiments provided by agent-based simulations useful to test analytic theories. (2) Hydrodynamics is valid on length and time scales large compared to individual agents. Our framework can be used to check if the results from the hydrodynamic theory are preserved on scales relevant to experimental systems. (3)



Similarly, our simulations allow us to gain a microscopic understanding of the macroscopic parameters of continuum theory. (4) We highlighted here that a coupling between density and nematic order is relevant. Such couplings between fields can be inferred and quantified using our method. (5) Discreteness of constituents (cells, filaments, ...) can result in additional effects, even on the macroscopic scale. In particular, agent turnover is intrinsically a discrete micro-scale process, which is important to account for [23]. (6) Biological systems are inherently noisy. As we have shown above, our framework is capable of capturing noise effects. (7) Biological experiments often display a staggering complexity, ranging from dynamic boundaries, composite systems to multiple sources of activity. Our framework can handle this complexity, and study the role of different active contributions like agent turnover or self-propulsion.

Data availability statement

All data and code needed to evaluate the conclusions in the paper and reproduce the simulations are available at [11].

Spontaneous channel flow available at <https://doi.org/10.1088/1367-2630/ae3d5c/data1>.

Nematic director switching available at <https://doi.org/10.1088/1367-2630/ae3d5c/data2>.

Extensile active nematics available at <https://doi.org/10.1088/1367-2630/ae3d5c/data3>.

Contractile active nematics available at <https://doi.org/10.1088/1367-2630/ae3d5c/data4>.

Quasi-3D spontaneous flows available at <https://doi.org/10.1088/1367-2630/ae3d5c/data5>.

division-extensile nematics available at <https://doi.org/10.1088/1367-2630/ae3d5c/data6>.

Supporting Information available at <https://doi.org/10.1088/1367-2630/ae3d5c/data7>.

Acknowledgments

The computations were performed at University of Geneva on Baobab HPC cluster. We thank Thorsten Auth, Andrew Callan-Jones, Gerhard Gompper, Jean-François Joanny and Daniel Pearce for comments on the manuscript. M D thanks the Forschungszentrum Jülich for their hospitality during part of this work.

Author contributions

All authors designed research; M D performed simulations and analyzed the data; all authors wrote the paper.

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