

Topological Flowscape Reveals State Transitions in Nonreciprocal Living Matter

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Nonreciprocal interactions—where forces between entities are asymmetric—govern a wide range of nonequilibrium phenomena, yet their role in structural transitions in living and active systems remains elusive. Here, we demonstrate a transition between nonreciprocal states using starfish embryos at different stages of development, where interactions are inherently asymmetric and tunable. Experiments, interaction inference, and topological analysis yield a nonreciprocal state diagram spanning crystalline, flock-like, and fragmented states, revealing that weak nonreciprocity promotes structural order while stronger asymmetry disrupts it. To capture these transitions, we introduce topological landscapes, mapping the distribution of structural motifs across state space. We further develop topological flowscapes, a dynamic framework that quantifies transitions between collective states and detects an informational rate shift and an emergent proofreading from the experimental state transition. Together, these results establish a general approach for decoding nonequilibrium transitions and uncover how asymmetric interactions sculpt the dynamical and structural architecture of active and living matter.

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Nature produces diverse structures and behaviors whose complexity greatly surpasses equilibrium constraints [1,2]. From flocks of birds [3,4] and colonies of microbes [5–9] to cellular tissues [10,11] and synthetic active materials [12,13], remarkable forms and functionalities emerge spontaneously from local interactions among constituents, without external coordination. This self-organized emergence, driven by the agency of individual components, not only underpins biological complexity but also inspires new classes of active and adaptive materials, where nonequilibrium dynamics are harnessed for novel functionalities [14–19].

At the core of these complex phenomena lie nonreciprocal interactions, where action and reaction between components are inherently asymmetric [19–23]. Such asymmetry profoundly influences nonequilibrium behavior, driving rich dynamical phenomena including traveling waves [21,22,24,25], spontaneous oscillations [23,26,27],

and chiral flows [28]. Yet, despite growing recognition of their significance, how nonreciprocity shapes structural transitions and the emergence of stable configurations remains largely unexplored [29–34]. Furthermore, the extent to which nonreciprocity governs information transfer and state evolution in living systems is unclear [35,36].

Here, we address this gap by investigating how nonreciprocity orchestrates collective self-organization and structural transitions in a biologically tunable system: starfish embryos at distinct developmental stages, which interact through inherently asymmetric fluid-mediated forces. Building upon our previous discovery of living chiral crystals composed of homogeneous embryo ensembles [37], we systematically examine binary mixtures of embryos at different developmental ages. Through experiments integrated with interaction inference (Sec. I) and novel topological analyses (Sec. II), we identify distinct emergent states, including crystalline, self-propelled crystalline, flock-like, and fragmented configurations. We introduce topological landscapes (Sec. III), revealing symmetry-breaking transitions between these nonreciprocal states, and topological flowscapes (Sec. IV), quantifying the informational trajectory of the transitions. These conceptual tools provide a versatile framework to uncover structural and dynamic transitions across biological and synthetic active matter.

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I. A NONRECIPROCAL MIXTURE OF STARFISH EMBRYOS TRANSITIONS FROM A TRAVELING STATE TO A FLUCTUATING STATE

To experimentally uncover how nonreciprocity shapes collective dynamics, we developed a living nonreciprocal system composed of embryos from the starfish *Patiria miniata*. Unlike homogeneous embryo populations, which display emergent nonreciprocity through broken chiral symmetries [37,38], our heterogeneous system exhibits tunable interactions between two types of embryos (E1 and E2), controlled by their developmental ages [Fig. 1(a)]. Embryos act as building blocks in this reconfigurable system, and can interact in both a symmetric (with same-type neighbors) and asymmetric (with different-type neighbors) manner. Quantitative video microscopy reveals

a striking run-and-chase dynamic: younger E1 embryos actively pursue older E2 embryos, whereas E2 embryos move preferentially away from E1 [Fig. 1(b), Supplemental Material Video 1, and Secs. I.A and I.B [39]]. As in previous studies of chiral swimmers [5,38], the dynamics of anterior-posterior (AP) axes offer mechanistic insights. Further, experiments demonstrate that this broken symmetry arises from asymmetric precession of the embryos' AP axes, establishing a clear physical mechanism underlying nonreciprocity (Supplemental Material Sec. I.B.3 and Video 2 [39]). In addition to this bound pair dynamics [5], when embryos are apart, they approach each other with asymmetric speeds, demonstrating nonreciprocity in their hydrodynamic attractions (Supplemental Material Video 1 and Secs. I.B.4 and I.C [39]).

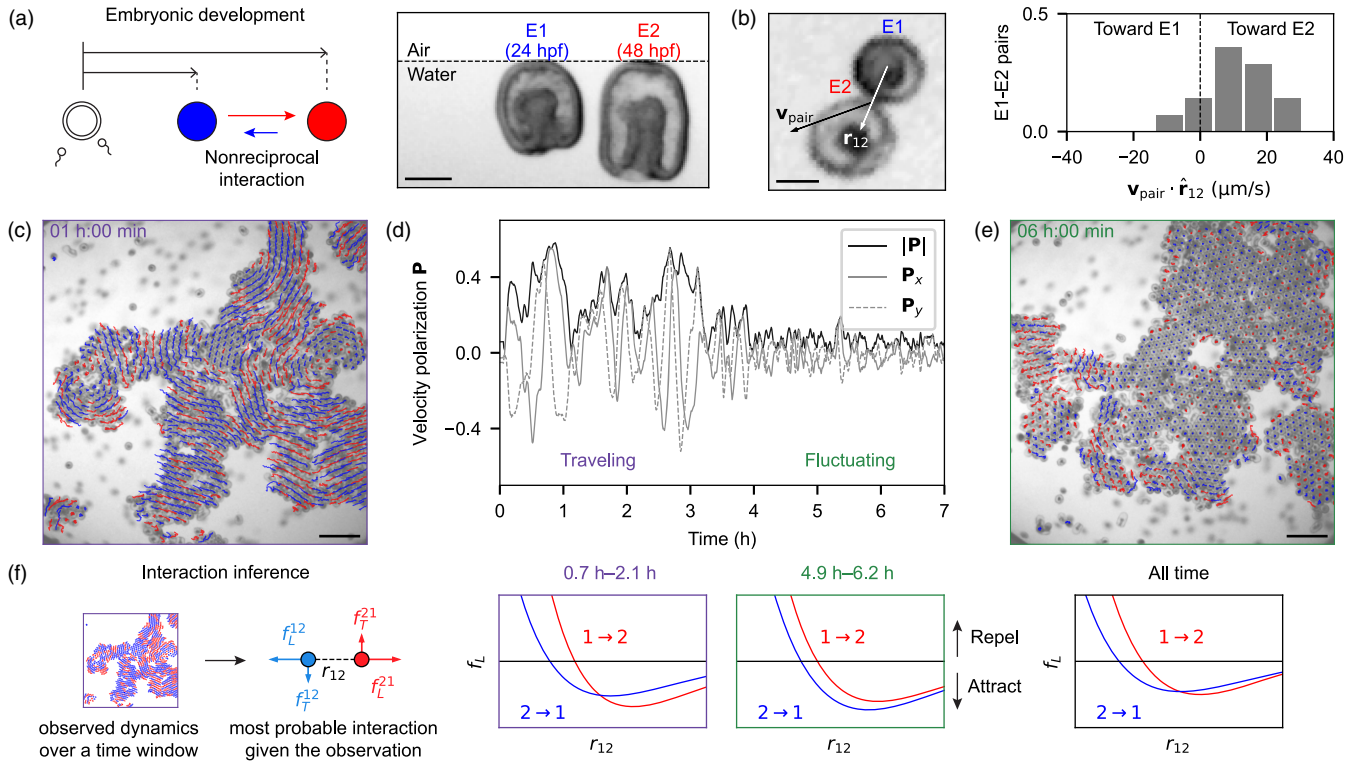


FIG. 1. A nonreciprocal mixture of starfish embryos transitions from a traveling state to a fluctuating state. (a) Nonreciprocity arises from a developmental gap between embryos. An E1 embryo (24 h post-fertilization) and an E2 embryo (48 h post-fertilization) form a bound pair [5] at the air-water interface. Scale bar: 100 μm . (b) The velocity of the embryo pair, $\mathbf{v}_{\text{pair}}$, tends to align with the displacement vector $\mathbf{r}_{12}$ from E1 to E2. The average drift speed toward E2, $\mathbf{v}_{\text{pair}} \cdot \hat{\mathbf{r}}_{12}$, is 12 ± 3 $\mu\text{m/s}$ (SEM, $n = 14$). Scale bar: 100 μm . (c) Snapshot of an E1–E2 mixture at 1 h, overlaid with 2-min trajectories (blue: E1, red: E2). Scale bar: 1 mm. (d) Time series of velocity polarization, $\mathbf{P}(t) \equiv \{1/[N(t)]\} \sum_{i=1}^{N(t)} [\mathbf{v}_i(t)/|\mathbf{v}_i(t)|]$, reveals a transition from a traveling state to a fluctuating state. Oscillations and a phase shift between $\mathbf{P}_x$ and $\mathbf{P}_y$ highlight the chirality of the velocity polarization, which rotates clockwise during the traveling state. (e) Snapshot of the same mixture at 6 hours, overlaid with 2-min trajectories (blue: E1, red: E2). Scale bar: 1 mm. (f) Interaction inference quantifies the nonreciprocal interaction and its time evolution. Left: we implement Bayesian inference to quantify pairwise inter-embryo interactions $f_{L/T}^{ij}(r)$, which depend on embryo types i, j and pairwise distance r , from embryo trajectories (see Supplemental Material Sec. II [39]). Center: f_L^{21} (red) and f_L^{12} (blue), the longitudinal interactions by E1 on E2 and by E2 on E1, respectively, are inferred using data from early and late times. As embryonic development continues over the experiment, interactions become less nonreciprocal. Right: f_L^{21} (red) and f_L^{12} (blue) are inferred using data from all time. We use this all-time inference as a basis for our inference-based model (Fig. 2).

When thousands of E1 and E2 embryos are mixed, the system spontaneously exhibits collective translation, a hallmark of nonreciprocal interactions [22]. Initially, the embryos flock together, forming a dynamically ordered *traveling* state characterized by strong polar alignment, quantified by the velocity polarization order parameter $\mathbf{P}(t) \equiv [1/N(t)] \sum_{i=1}^{N(t)} [\mathbf{v}_i(t)/|\mathbf{v}_i(t)|]$, where $N(t)$ is the number of embryos at time t and $\mathbf{v}_i(t)/|\mathbf{v}_i(t)|$ is the direction of i th particle's instantaneous velocity [Figs. 1(c) and 1(d), Supplemental Material Videos 3–4, and Sec. I.D [39]]. Remarkably, this polar order emerges exclusively in mixed-age embryo populations, whereas it is absent in homogeneous populations. This experimentally verifies the theoretical prediction that nonreciprocity is an ingredient that can lead to emergent polar order [21,22]. The velocity polarization $\mathbf{P}$ is time dependent, rotating clockwise with a fluctuating magnitude [Fig. 1(d) and Supplemental Material Sec. I.D.3 [39]]. This rotation arises from broken chiral symmetry of individual embryos rather than from emergent chirality via nonreciprocal alignment [23]. Furthermore, we find that E2 embryos consistently lead E1 in collective translation, suggesting that nonreciprocity drives the flocking of embryos (Supplemental Material Sec. I.D.4 [39]).

After hours of collective translation, the embryo mixture transitions into a distinct self-organized state (Supplemental Material Videos 3–4 [39]). In this *fluctuating* state, embryos arrange into an ordered lattice, while small fluctuations arise from their persistent velocity moduli that lack alignment [Fig. 1(e), Supplemental Material Sec. I.D.5 [39]]. As a result, the velocity polarization $\mathbf{P}$ exhibits near-zero fluctuations, demarcating the departure from the traveling state [Fig. 1(d)].

To confirm the nonreciprocity, we extracted the underlying interactions from many-body experimental trajectories using a data-driven inference method that reconstructs the most likely longitudinal and transverse forces between embryo pairs as functions of their separation and types (E1 or E2) [67,68] (Supplemental Material Sec. II [39]). Applied to the full experimental dataset [Fig. 1(f)], this inference yields an E1–E2 longitudinal interaction that is nonreciprocal, in agreement with the isolated run-and-chase dynamics [Fig. 1(b)], and evolves to be less asymmetric over time (Supplemental Material Sec. II.B [39]).

The transition from ordered dynamics to ordered configurations reveals a rich state space of nonequilibrium behaviors that depend on nonreciprocity. By tuning nonreciprocity, the system exhibits a wide variety of emergent collective states, including chiral orbits and demixed regimes. This tunability highlights the versatility of the experimental platform (Supplemental Material Sec. I.E and Videos 5–6 [39]).

II. TOPOLOGICAL ORDER PARAMETER DISTINGUISHES EMERGENT STATES IN AN INFERENCE-BASED MODEL OF NONRECIPROCAL MIXTURES

Motivated by the diversity in self-organization and dynamics of the experimental platform, we systematically mapped the nonequilibrium states of nonreciprocal mixtures. We developed a pairwise interaction model that allows us to tune the nonreciprocity $\mathcal{N}$ *in-silico*. Here, nonreciprocity $\mathcal{N}$ encapsulates the asymmetry of the inter-type longitudinal interactions. Through the model, we identify different states as a function of $\mathcal{N}$ that we characterize with velocity polarization and a novel topological order parameter.

To construct a tunable model, we take the interaction inference as baseline, and define nonreciprocity parameter $\mathcal{N}$ such that

$$\begin{aligned} f_L^{12}(r; \mathcal{N}) &= f_L^S(r) + \mathcal{N} f_L^A(r), \\ f_L^{21}(r; \mathcal{N}) &= f_L^S(r) - \mathcal{N} f_L^A(r), \end{aligned} \quad (1)$$

where $f_L^S(r) \equiv [f_L^{12}(r) + f_L^{21}(r)]/2$ and $f_L^A(r) \equiv [f_L^{12}(r) - f_L^{21}(r)]/2$ are the symmetric and antisymmetric parts of the inferred longitudinal interactions [Figs. 1(f) and 2(a)].

This form ensures that the system is reciprocal when $\mathcal{N} = 0$, and matches the inferred interactions when $\mathcal{N} = 1$. We explore a range of values including weaker ($\mathcal{N} < 1$) and stronger ($\mathcal{N} > 1$) nonreciprocity to elucidate its effect on emergent behaviors [Fig. 2(a), Supplemental Material Sec. IV and Video 7 [39]].

At $\mathcal{N} = 0$ (reciprocal interactions), we find a *crystalline* state that rotates clockwise, recapitulating homogeneous embryos forming living chiral crystals [37]. For $0 < \mathcal{N} < 1$ (weak nonreciprocity), we observe a *self-propelled crystalline* state, where a crystal undergoes collective translation. At $\mathcal{N} = 1$ (nonreciprocity inferred from experiment), the system exhibits flock-like dynamics, maintaining collective motion but not a global crystalline arrangement. Instead, the crystals repeatedly merge and fragment, reflecting the early dynamics observed in embryo mixture experiments [Fig. 1(d) and Supplemental Material Sec. III.C [39]]. For $\mathcal{N} > 1$ (strong nonreciprocity), the system is further *fragmented*, with each fragment propelling itself in different directions.

Although existing theories of nonreciprocal interactions predict a jump in velocity polarization $|\mathbf{P}|$ as the system enters a traveling state [22,23] (Supplemental Material Sec. VII.F [39]), our model reveals a richer complexity [Fig. 2(b)]. The broken chiral symmetry in transverse interactions causes clusters to rotate rather than move in a straight line, competing with collective translation induced by nonreciprocity. This interplay leads $|\mathbf{P}|$ to rise

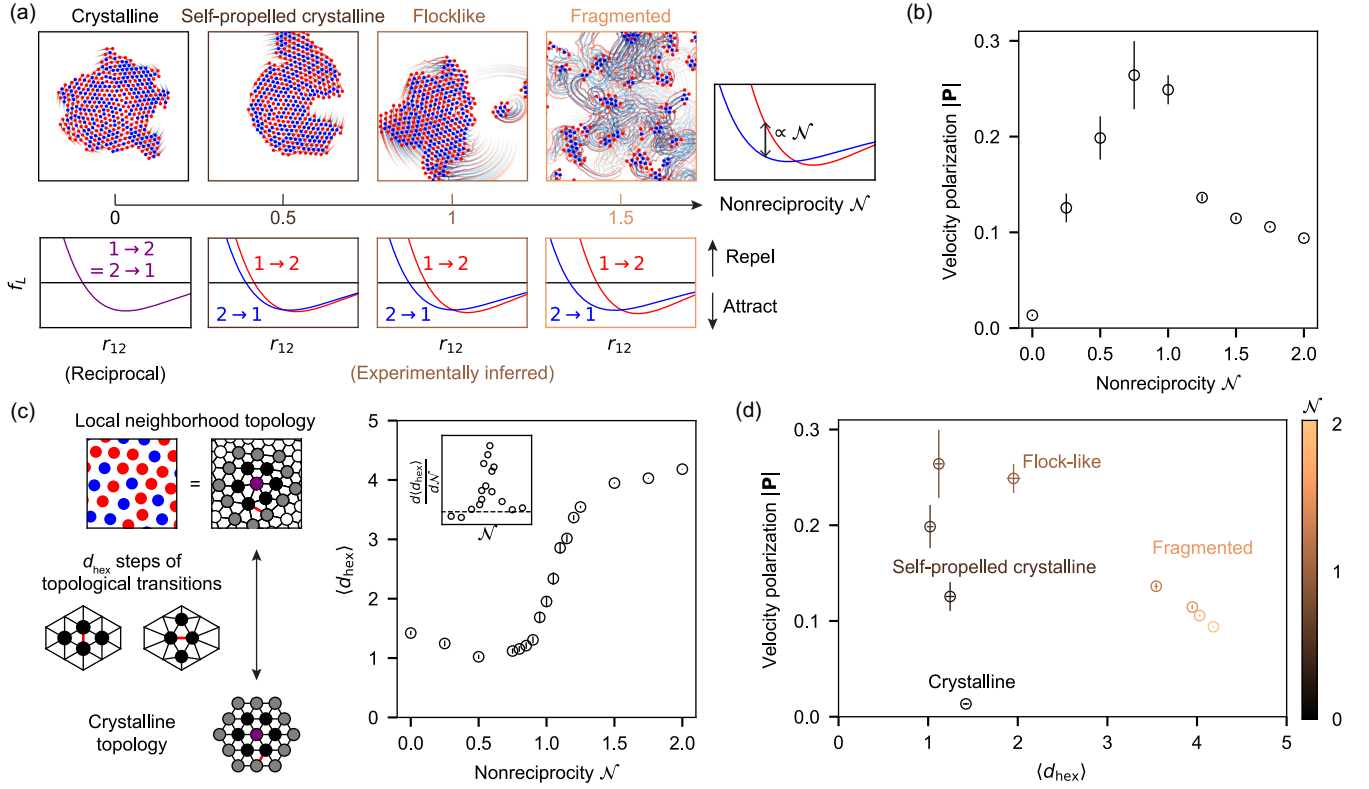


FIG. 2. Topological order parameter distinguishes emergent states in an inference-based model of nonreciprocal mixtures. (a) In the inference-based model, we use experimentally inferred pairwise interactions $f_{ij}^{L/T}$, except for longitudinal inter-type interactions whose nonreciprocity is scaled by $\mathcal{N}$. The model exhibits four distinct states as the nonreciprocity $\mathcal{N}$ increases: crystalline, self-propelled crystalline, flock-like, and fragmented states. (b) Velocity polarization magnitude $|\mathbf{P}|$ as a function of $\mathcal{N}$, averaged over 20 initial configurations (error bars: SEM). $|\mathbf{P}|$ decreases for $\mathcal{N} > 1$. (c) Left: the structural metric d_{hex} quantifies the number of local topological (T1) transitions relative to a perfect hexagonal crystal; red edges highlight topology-changing transitions. Right: the structural order parameter $\langle d_{\text{hex}} \rangle$ reaches a minimum at $\mathcal{N} = 0.5$ and rises at $\mathcal{N} = 1$ (error bars: SEM, $n = 20$). Inset: the slope $d\langle d_{\text{hex}} \rangle / d\mathcal{N}$ is negative for small $\mathcal{N}$ and peaks near $\mathcal{N} = 1$ (dotted line is at zero). (d) State diagram of nonreciprocal mixtures, summarizing emergent states across the pairwise nonreciprocity $\mathcal{N}$.

continuously, rather than abruptly, with increasing $\mathcal{N}$. Surprisingly, we find that $|\mathbf{P}|$ peaks near $\mathcal{N} = 1$ and then decreases for $\mathcal{N} > 1$, a behavior explained by fragmentation into independently moving clusters whose internal self-propulsion dominates interactions between clusters. Consequently, states with disparate collective dynamics, such as self-propelled crystals and fragmented clusters, exhibit similar velocity polarization magnitudes despite their distinct differences in structure.

To robustly distinguish these structurally diverse states beyond velocity polarization $|\mathbf{P}|$ alone, we need a structural order parameter. Notably, while nonreciprocity can drive structures far away from translational or orientational order, these complex arrangements can still be systematically compared through their topologies [4,69]. Hence, we define a topological metric d_{hex} based on a recently developed topological packing statistics framework [69,70]. This metric quantifies structural order by counting the number of local T1 topological rearrangements required to reach a perfect crystalline arrangement from a given local neighborhood also

known as “motif” [Fig. 2(c) and Supplemental Material Sec. V [39]]. Accordingly, the system-average $\langle d_{\text{hex}} \rangle$ serves as a measure of the topological distance between the system’s self-organized structure and a perfect crystal.

The structural order parameter $\langle d_{\text{hex}} \rangle$ quantifies the average topological distance from a crystal [Fig. 2(c)]. At small $\mathcal{N}$, $\langle d_{\text{hex}} \rangle$ indicates crystalline structures whose local neighborhoods are on average within one to two T1 transitions from a hexagonal motif. Interestingly, in this regime, we find that $\langle d_{\text{hex}} \rangle$ decreases with increasing $\mathcal{N}$. We call this counterintuitive trend nonreciprocal error correction [71–73]: topological motifs with defects, which are unstable under nonreciprocity-driven stress, are annealed into a crystalline motif which remains stable (Supplemental Material Sec. IV.D [39]). This behavior reflects a selective stabilization of low-defect configurations under nonequilibrium driving. The crystalline motif eventually becomes unstable under a sufficiently strong nonreciprocity, such as the experimentally inferred $\mathcal{N} = 1$. This destabilization is captured by the steep increase in $\langle d_{\text{hex}} \rangle$ as an annealed

crystal transitions into a dynamic, multi-cluster structure (Supplemental Material Video 8 [39]).

Combining the two order parameters, $|\mathbf{P}|$ for dynamics and $\langle d_{\text{hex}} \rangle$ for structure, we construct a state diagram that maps all emergent nonreciprocal states [Fig. 2(d)]. As nonreciprocity increases from $\mathcal{N} = 0$, $\langle d_{\text{hex}} \rangle$ decreases and $|\mathbf{P}|$ increases. Once nonreciprocity reaches the experimental $\mathcal{N} = 1$, $\langle d_{\text{hex}} \rangle$ jumps while $|\mathbf{P}|$ remains large. Finally, for $\mathcal{N} > 1$, $\langle d_{\text{hex}} \rangle$ is large while $|\mathbf{P}|$ is small. Overall, our state diagram captures nonreciprocity-driven transitions in both collective translation, which onsets at weak nonreciprocity and peaks at intermediate nonreciprocity, and self-organized crystalline structure, which is enhanced by weak nonreciprocity but destabilized by strong nonreciprocity.

III. TOPOLOGICAL LANDSCAPES REVEAL A SYMMETRY-BREAKING TRANSITION IN SELF-ORGANIZED STRUCTURES AS NONRECIPROcity INCREASES

Using the structural order parameter $\langle d_{\text{hex}} \rangle$, we observe that weak nonreciprocity stabilizes crystalline structures,

whereas strong nonreciprocity leads to structural destabilization. However, this average measure does not provide insight into the precise local structural changes driving these transitions. To address this limitation, we introduce a novel approach to systematically characterize the distribution of local topologies observed in our experiments and simulations, involving approximately 15 000 distinct motifs (Supplemental Material Sec. V [39]).

First, we recall that the topological motifs have a metric structure, determined by the number of T1 transitions between them, and thus that the motifs exist as points in a high-dimensional space [70]. Using these pairwise topological distances, we construct a two-dimensional manifold [Fig. 3(a)] which is a low-dimensional embedding of this metric space using classical multidimensional scaling (MDS) (Supplemental Material Sec. V.A [39]). This manifold positions motifs that differ by only a few T1 transitions close to each other, allowing an intuitive representation of structural proximity. We then construct *topological landscapes* by mapping motif frequencies onto this manifold as height values. The landscape $p(x, y)$ is found using kernel density estimation (Supplemental

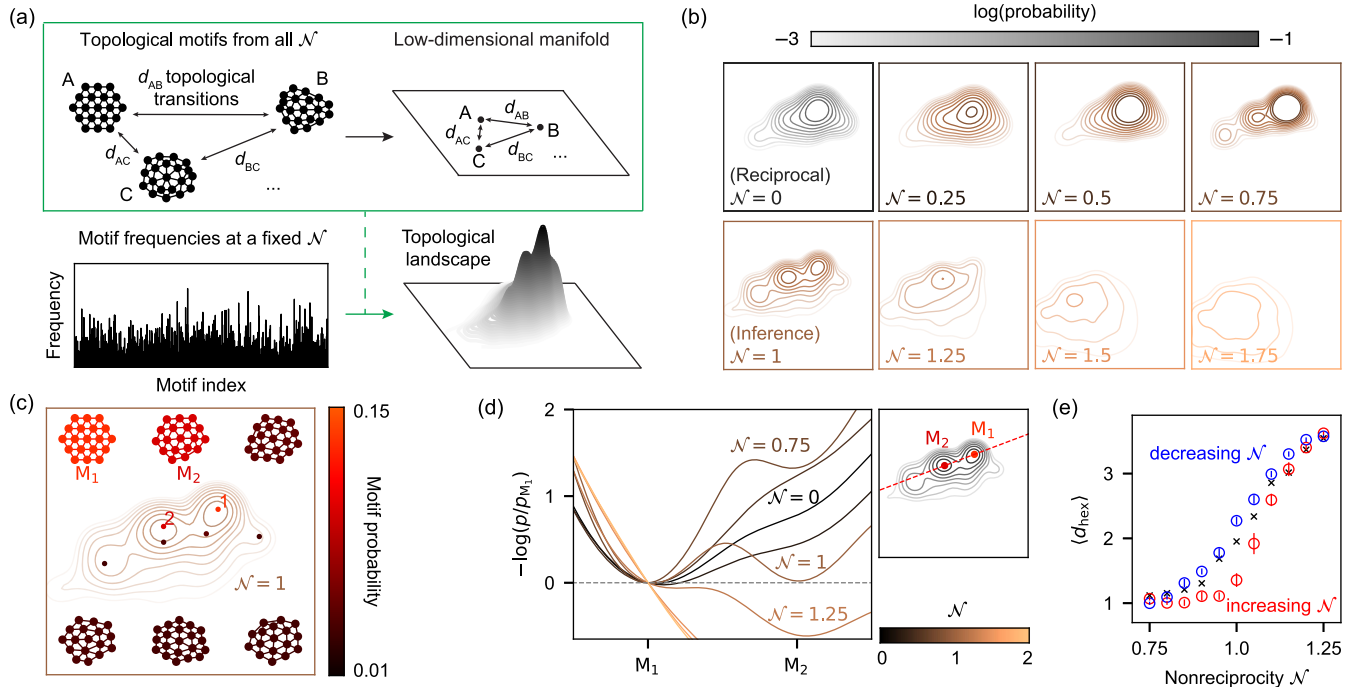


FIG. 3. Topological landscape reveals a symmetry-breaking transition in self-organized structures as nonreciprocity increases. (a) We construct a low-dimensional manifold of topological motifs based on their pairwise topological distances. The resulting *topological landscape* visualizes the probability distribution of local topologies (from each level of nonreciprocity $\mathcal{N}$) on this manifold. (b) Contour plots of topological landscapes display a transition from single-peaked to multi-peaked distributions as $\mathcal{N}$ increases. (c) At $\mathcal{N} = 1$ (experimentally inferred nonreciprocity), 14 topological motifs exhibit a frequency greater than 1%. In particular, the top two dominant motifs correspond to the two distinct peaks of the topological landscape. Top: motifs from M_1 to M_3 . M_1 is a perfect crystal, while M_2 contains a 5-defect. Bottom: motifs from M_4 to M_6 . See Supplemental Material Sec. V.C for an enlarged motif atlas with full annotations [39]. (d) Negative log-likelihood ratio relative to M_1 , measured along the M_1 - M_2 axis. At $\mathcal{N} = 0$, the system shows a single minimum at M_1 . Near $\mathcal{N} = 1$, the structures undergo a first-order-like transition from M_1 -dominated to M_2 -dominated states, with coexistence at $\mathcal{N} = 1$. (e) Nonreciprocal hysteresis emerges upon slowly decreasing or increasing $\mathcal{N}$ about $\mathcal{N} = 1$. Its existence is a testable hypothesis that stems from the analogy to a first-order phase transition and its metastability.

Material Sec. V.B [39]). Specifically, p quantifies the probability density of motifs in the vicinity of (x, y) on the low-dimensional manifold. Thus, topological landscapes provide a comprehensive visualization of how local structural motifs distribute and evolve as nonreciprocity $\mathcal{N}$ varies. Similar to an autoencoder, these topological landscapes embed distributions in a lower-dimensional latent space.

As nonreciprocity increases near $\mathcal{N} = 1$, these landscapes exhibit a clear transition from single-peaked to multi-peaked distributions, indicating increased structural diversity [Fig. 3(b)]. Specifically, motif probabilities shift systematically towards a region of the manifold associated with less crystalline order. This trend aligns with the observed increase in the structural order parameter $\langle d_{\text{hex}} \rangle$, supporting the association between this manifold region and low-symmetry structures.

Further analysis identifies the atlas of frequent motifs at the experimentally inferred nonreciprocity level $\mathcal{N} = 1$ [Fig. 3(c)]. Among those are the two dominant motifs that contribute to the two peaks of the landscape: motif M_1 , corresponding to a perfect crystalline structure, and motif M_2 , representing an almost-crystalline structure with a single fivefold defect (Supplemental Material Sec. V.D and Video 9 [39]). Crucially, nonreciprocity not only breaks the sixfold symmetry inherent to the perfect crystal but also introduces directional anisotropy within the motif space, selecting a preferred structural transition pathway along the M_1 – M_2 axis. *A posteriori* analysis of this axis reveals its physical interpretation as an emergent order parameter, the number of fivefold defects contained within a motif (Supplemental Material Sec. V.A.III [39]). For example, moving away from M_1 , towards M_2 , and then to M_6 is associated with an increase in the number of fivefold defects.

To quantitatively capture this symmetry-breaking transition, we examine one-dimensional slices of the topological landscape along the M_1 – M_2 axis [Fig. 3(d)]. The negative log-likelihood ratio $-\log(p/p_{M_1})$, where p_{M_1} is the probability density at the location of motif M_1 , clearly reveals a global minimum at motif M_1 for low nonreciprocity levels. This minimum deepens as $\mathcal{N}$ increases, indicating enhanced stability of crystalline order through nonreciprocal error correction. A second minimum emerges at motif M_2 as $\mathcal{N}$ approaches 1, resulting in a coexistence at $\mathcal{N} = 1$ and a subsequent dominance of defect-containing motifs at higher nonreciprocity levels. This behavior is reminiscent of a first-order phase transition, where a state transition is mediated by the coexistence of distant configurations. Revealing such hidden analogies provides a concrete framework to analyze non-equilibrium state transitions that otherwise lack a standard thermodynamic description.

The analogy to a first-order phase transition points towards a set of testable hypotheses (Supplemental

Material Secs. V.E and V.F [39]). For example, we demonstrate the existence of nonreciprocal hysteresis in the structural order parameter $\langle d_{\text{hex}} \rangle$ as a function of $\mathcal{N}$ [Fig. 3(e) and Supplemental Material Video 12 [39]]. Such hysteresis may arise if the transition between M_1 and M_2 is separated by some kinetic barrier and must proceed via less likely motifs. In this case, near the crossover at $\mathcal{N} = 1$, an M_1 -dominated configuration does not immediately break, but instead requires an additional increase in $\mathcal{N}$ to destabilize M_1 . This metastability results in a nonreciprocal hysteresis in which $\langle d_{\text{hex}} \rangle$ forms a loop as a function of $\mathcal{N}$ [Fig. 2(c)], as $\mathcal{N}$ is slowly increased and decreased around the transition. We demonstrate this effect in our model [Fig. 3(e) and Supplemental Material Video 12, Sec. V.F [39]], supporting the coexistence of M_1 and M_2 motifs at the $\mathcal{N} = 1$ structural transition and highlighting the power of the analogy from topological landscapes.

Extending this analysis to experimental data, we construct time-resolved experimental topological landscapes by tracking motif frequencies within temporal windows [Fig. 4(a) and Supplemental Material Videos 10–11 [39]]. These experimental landscapes resemble the model predictions at $\mathcal{N} = 1$, displaying identical dual-peaked distributions around motifs M_1 and M_2 . Additionally, the experimental progression over time mirrors the model predictions under decreasing nonreciprocity [Fig. 4(b)], including passage through a coexistence regime at the onset of the transition from traveling to fluctuating states, as quantified by velocity polarization dynamics. This agreement implies that pairwise nonreciprocal interactions at the nearest neighbor level are the dominant driver of self-organized structures and dynamics in the experiment. It also reinforces our independent interaction inference that pairwise nonreciprocity between embryos decreases during the course of the experiment. All together, these results support a striking correspondence between time-driven transitions in the experiment and those induced by varying nonreciprocity in the theoretical model (Supplemental Material Sec. II.B [39]).

IV. TOPOLOGICAL FLOWSCAPES REVEAL INFORMATION FLOW AND DISSIPATION-DRIVEN BIAS IN COLLECTIVE STATE TRANSITIONS IN THE EXPERIMENT

Topological landscapes describe steady states without explicitly capturing the dynamic pathways connecting these states. While landscapes capture the key structural changes between snapshots, we also asked whether the latent representation adequately captures the nonequilibrium dynamic flows. To address this, we introduce the *topological flowscape*, a quantitative framework that assigns coordinates to entire landscapes, analogous to how individual topological motifs are embedded [Fig. 4(c)]. The coordinates for the flowscape are defined by Kullback-Leibler (KL) divergences from two informed choices of reference

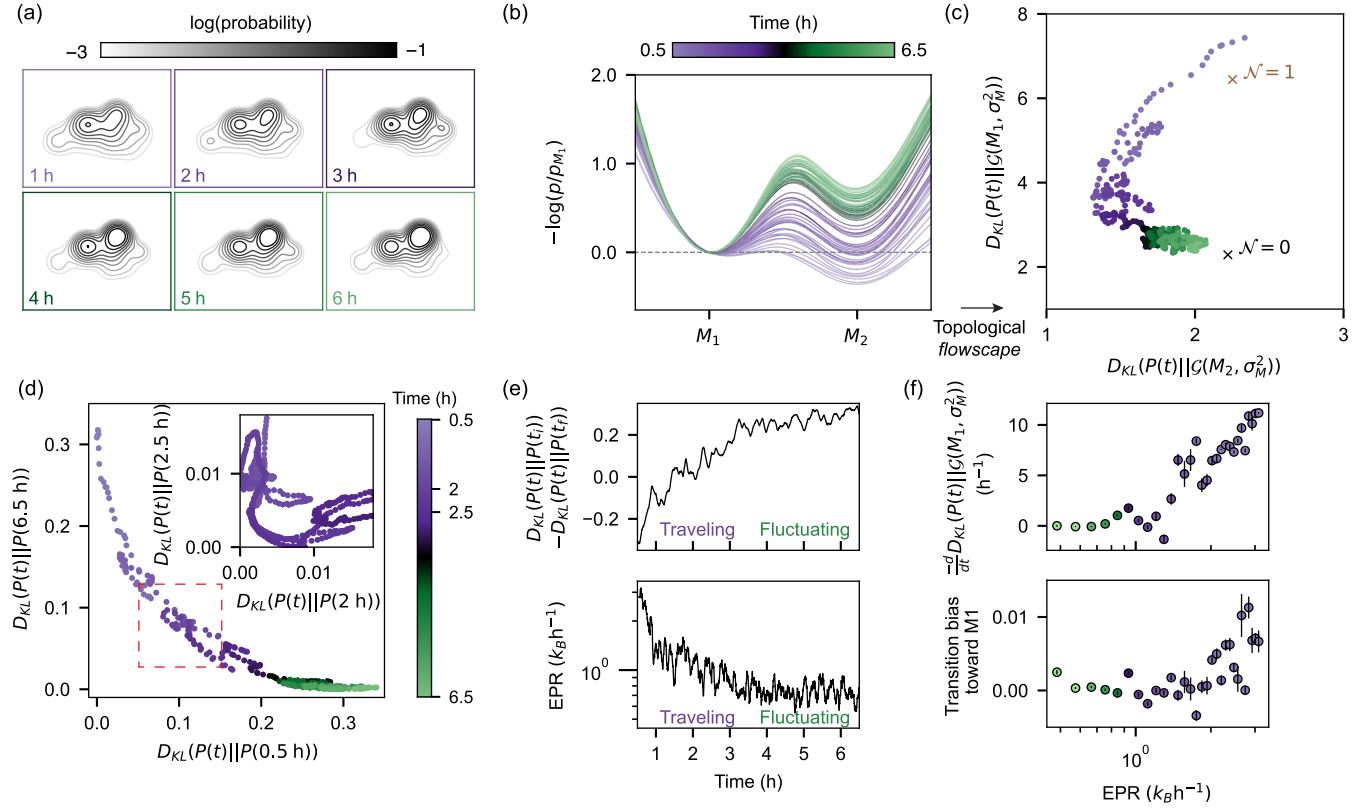


FIG. 4. Topological flowscapes reveal information flow and dissipation-driven bias in collective state transitions in the experiment. (a) Contour plots of experimental topological landscapes reveal a shifting balance between two dominant peaks over time. These peaks correspond to motifs M_1 and M_2 , previously identified in the model at the experimentally inferred nonreciprocity $\mathcal{N} = 1$. (b) Negative log-likelihood relative to M_1 , measured along the M_1 - M_2 axis. The self-organized structures transition from an M_2 -dominated to an M_1 -dominated state as the embryo mixture shifts from a traveling to a fluctuating state [Fig. 1(d)]. (c) Topological flowscape of the experiment. Each landscape is mapped to a point using KL divergence from two synthetic reference distributions centered at M_1 and M_2 , with widths σ_M matched to the kernel of experimental landscape (Supplemental Material Sec. VI.B [39]). The trajectory flows from a region near $\mathcal{N} = 1$ toward one resembling $\mathcal{N} = 0$. (d) Flowscape constructed using experimental states at different times as dynamic references. Using 0.5 h and 6.5 h as references captures a long-timescale transition. Inset: using 2 h and 2.5 h as references reveals short-timescale cycle transitions associated with clusters merging and breaking (Supplemental Material Sec. VI.E [39]). (e) Informational rate shift between experimental states. Top: diagonal displacement in the flowscape quantifies the log-likelihood “progress bar” of the current-time distribution from the initial state to the final state. The progress is rapid during the traveling state and slows significantly in the fluctuating state. Bottom: entropy production rate, estimated from changes in topological motif frequencies using thermodynamic speed limits, correlates with the rate transition found in the flowscape. (f) Emergent proofreading in topological motif transitions. Top: rate at which the system approaches the M_1 -dominated state, $-[d/(dt)]D_{KL}(P(t)||\mathcal{G}(M_1, \sigma_M^2))$, binned over the EPR estimates [colors indicate the average time of each bin with the same color bar as (b)]. The self-organized structure approaches M_1 faster under a higher dissipation. Bottom: transition bias toward M_1 , $(\sum_{i \neq 1} M_i \rightarrow M_1) - (\sum_{i \neq 1} M_1 \rightarrow M_i) / \sum_{i \neq j} M_i \rightarrow M_j$, binned over the EPR estimates (Supplemental Material Sec. VII.C [39]). The transition bias is enhanced with an increasing EPR estimate.

distributions, representing M_1 and M_2 , respectively (Supplemental Material Sec. VI [39]). These divergences quantify the distinguishability between observed system states and reference states based on local motif frequencies, providing an information-theoretic interpretation: each axis measures the informational “cost” of describing the entire system state in terms of either M_1 or M_2 . Thus, the flowscape, a low-dimensional projection of the landscapes, visually captures their temporal evolution as a continuous trajectory or “flow.”

The topological flowscape quantitatively shows that the observed transition from an M_2 -dominated (disordered)

state toward an M_1 -dominated (ordered) state is not gradual [Fig. 4(c)]. Instead, around 3 h, the system undergoes a sharp directional change, initially moving rapidly toward both motifs to subsequently drifting slowly toward M_1 while moving away from M_2 . Moreover, while the model predicts that the intermediate states are more crystalline than the final state, the experimental path deviates from this behavior (Supplemental Material Secs. VI.C and VI.D [39]). This discrepancy indicates potential higher-order mechanisms in addition to the development-driven decrease in nonreciprocity (Supplemental Material Sec. II.B [39]),

highlighting the flowscape’s potential as a tool for dissecting complex experimental dynamics.

The flexibility of reference distributions in the flowscape framework further allows us to probe structural dynamics and its corresponding information flow across multiple temporal scales [Fig. 4(d)]. Large temporal gaps between references elucidate global structural transitions, while shorter intervals reveal rapid cyclic dynamics such as repeated cluster merging and fragmentations (Supplemental Material Sec. VI.E [39]). These cyclic dynamics indicate broken detailed balance between microscopic topological configurations in the experiment which persist at the level of information flow of the macroscopic structural state.

Beyond the directional shift towards or away from M_2 , the flowscape trajectory also exhibits a rate shift in the flow of structural information between the traveling and fluctuating states. In particular, the flowscape built with temporal references [Fig. 4(d)] provides a log-likelihood-based “progress bar” [Fig. 4(e)], defined by $D_{KL}(P(t)||P(t_i)) - D_{KL}(P(t)||P(t_f))$, whose rate tracks how quickly the system transitions from initial to final states. This displacement shows a clear decrease in the rate of information transfer that coincides with the independently measured shift in velocity polarization $|\mathbf{P}|$ from the traveling to fluctuating state [Fig. 1(d)], underlining a possible connection between macroscopic state transitions and microscopic structural changes. To validate this rate transition, we estimate a lower bound for the entropy production rate (EPR) using motif transition statistics and thermodynamic speed-limit principles [Fig. 4(e) and Supplemental Material Sec. VII.A [39]]. The EPR estimate exhibits a transition from high dissipation during the traveling state to lower dissipation in the fluctuating state, in concordance with the rate transition captured by the flowscape. Moreover, the information rate derived from information geometry also reveals a rate shift at the state transition (Supplemental Material Sec. VII.B [39]).

In addition, we analyze the rate at which the system approaches the M_1 -dominated reference state on the flowscape, $-[d/(dt)]D_{KL}(P(t)||\mathcal{G}(M_1, \sigma_M^2))$, and its relation with the EPR estimate [Fig. 4(f)]. The two rates are positively correlated suggesting that enhanced dissipation, which occurs primarily in the traveling state, speeds up information flow towards the M_1 -dominated state. In a generic nonequilibrium state transition, such a speed-up might simply arise from an overall upscaling of all transition fluxes. However, by normalizing the net influx toward M_1 by the total transition rate, we show that an increasing EPR estimate disproportionately enhances the directional bias toward the M_1 motif [Fig. 4(f), bottom]. Overall, we find that in the traveling state, higher dissipation biases motif-motif transitions in favor of low-defect configurations, including the M_2 motif (Supplemental Material Sec. VII.C [39]). In the fluctuating state when dissipation is lower, this information flow and

transition bias towards M_1 are likewise reduced. Because this directional bias suppresses structural defects, we interpret these results as an emergent proofreading, in which higher dissipation selectively favors information flow and transitions towards target states. Together, these results demonstrate that flowscapes uncover the experimental signatures of nonequilibrium dynamics underlying state transitions.

V. DISCUSSION

We have investigated the self-organization and state transitions driven by nonreciprocal interactions in active living matter. Through experiments on heterogeneous populations of starfish embryos, whose developmental ages control their nonreciprocal interactions, we identify two distinct nonequilibrium states: a traveling state characterized by dynamic flocking clusters, and a fluctuating state defined by a crystal-like structure and reduced collective motion. By developing a predictive model, we map out a broader spectrum of behaviors, revealing that collective motion peaks at intermediate levels of nonreciprocity, while weaker nonreciprocity enhances structural order and higher nonreciprocity induces structural instability and fragmentation.

To characterize these emergent states and their transitions, we introduced two complementary frameworks: *topological landscapes* and *topological flowscapes*. Topological landscapes provide a quantitative description of local structural distributions and symmetry-breaking phenomena, but do not encode how systems move between states. Topological flowscapes address this limitation by representing the evolution of landscapes as trajectories of information flow in a reduced space, capturing both the directions and rates of transitions. This dynamical representation reveals that nonequilibrium state transitions can be governed by directed probability flows, with measurable rates of progression and dissipation.

Our conceptual framework suggests a broader perspective on nonequilibrium organization. Topological landscapes elucidate the order of a system, while flowscapes reveal how this order evolves and, further, how irreversibility affects the dynamics of its evolution. Together, they comprise a physics-informed, low-dimensional representation of structure and information flow in nonequilibrium systems.

This perspective is broadly applicable to nonequilibrium systems whose behavior is also governed by transition dynamics between states, rather than by steady-state structure alone. Our framework connects structure, dynamics, information flow and thermodynamics to provide a general method for analyzing nonequilibrium transitions, unpacking how microscopic interactions give rise to macroscopic organization. More broadly, these results highlight the nonequilibrium principle that self-organization depends

not only on the states it occupies, but also on the directed flows between these states.

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DATA AVAILABILITY

The code and data for the main figures are available from Ref. [74].

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