

ELECTRONIC SUPPLEMENTARY INFORMATION

Four-cell system

As a simpler system to understand the observed behaviour of transition point l^* in ordered systems, we study a mean-field model for a T1 process composed of a 4-cell hexagonal system. We study the non-linear response to a T1 transition, by minimizing Eq. 1 in the main text for every value of T1-edgelenh l between the edge's rest length and zero across different values of s_0 as shown in Fig. SI 1. To perform such minimizations, we must constrain the geometry using symmetry considerations. Specifically, a 4-cell system comprised of hexagons is expected to have a total of 16 vertices and hence 32 degrees of freedom (DOFs). If we assume symmetry about the x- and y-axes, this reduces the system to eight orthogonal DOFs. For each energy minimization step the T1 length is fixed, resulting in seven DOFs. Since there are 8 constraints (2 on each cell) imposed by the energy functional, we can solve the resulting system of equations uniquely.

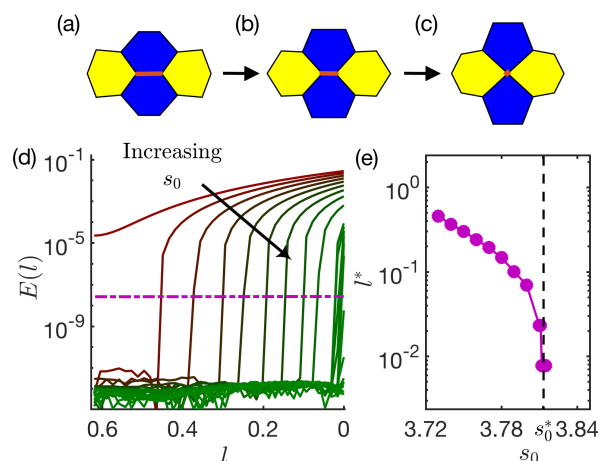


FIG. SI 1. **Four-cell energy profile:** (a-c) In an ordered initial configuration of 4 cells with, the T1 edge, shrinks to zero length (left to right as directed by the arrows). (d) In this process, the total energy of the 4-cell unit, E , is plotted against the shrinking T1 edgelenh l for increasing values of s_0 (3.72 to 3.81 in steps of 0.01 and 3.810 to 3.825 in steps of 0.001) varying from red to green. The cut-off for the energy is shown by the magenta dash-dot line. (e) The critical edgelenh l^* associated to the cut-off shown in (d) is plotted for each s_0 value in the magenta circles. The dashed line indicates critical s_0^* found for disordered tissues.

A typical T1 edge is shown in Fig. SI 1(a-c) along with energy profiles for different s_0 values shown in Fig. SI 1(d). Similar to the many-cell system, infinitesimal perturbations cost energy for $s_0 < 3.722$. For $s_0 > 3.722$, perturbing the system a small amount costs zero energy,

but as the T1 proceeds further into non-linear regime, the energy becomes non-zero after a threshold value of l^* . This l^* goes to zero as s_0 approaches ~ 3.813 as shown in Fig. SI 1(e). We observe that the energy profile is qualitatively similar to that of a many-cell system (Fig. 2) which confirms that a simple 4-cell unit is a suitable mean-field model for T1 processes in ordered tissues.

Vibrational mode structure of bulk ordered systems

In vertex and other network models, an index theorem [1, 2] relates the number of constraints, degrees of freedom, zero modes, and the number of states of self-stress. Normally, in jammed systems, the states of self-stress only arise when the system is overconstrained. However, recent work on disordered vertex models (and also underconstrained fiber network models) has shown an inherent geometric incompatibility that generates states of self-stress at a critical point in the shape parameter. These states of self-stress are not associated with additional constraints and they rigidify the system (i.e. remove all the non-trivial zero modes) [3, 4].

To study this in our ordered system, we compute vibrational modes using standard techniques [3, 4], by evaluating the dynamical matrix of second derivatives of the vertex model energy with respect to vertex positions, and diagonalizing it to identify eigenvalues and eigenvectors. The total number of zero modes in the system is computed by counting all the modes with eigenvalues below a very small threshold, which we chose to be 10^{-8} .

In the ordered case, we find something similar to disordered systems. Apparently, the geometric incompatibility introduces self-stresses in response to linear perturbations starting at $s_0 = 3.722$. Even though naive constraint counting suggests the system is floppy for any value of s_0 , we find that the system is rigid for $s_0 < 3.722$, where all the non-trivial eigenmodes have positive eigenvalues, consistent with phonons in a finite system. For $s_0 > 3.722$ the system is floppy with an extensive number of zero modes (Fig. SI 2(b)). Although the number of zero modes decreases between 3.722 and 3.81, there is no obvious signature in the linear spectra, suggesting that self-stresses only occur in response to nonlinear perturbations between those values of the control parameter.

We also plot an example of a zero mode for a system that is linearly unstable with $s_0 = 3.75$ (Fig. SI 2(a)). Since there are an extensive number of such degenerate modes, we do not expect that an individual mode such as this one demonstrates any useful features of the energy landscape.

We also study the eigenspectrum for a single system during the course of a T1 perturbation (i.e. as we manually shrink the T1 edge). We find that the number of zero modes decreases as the T1 edgelenh shrinks below

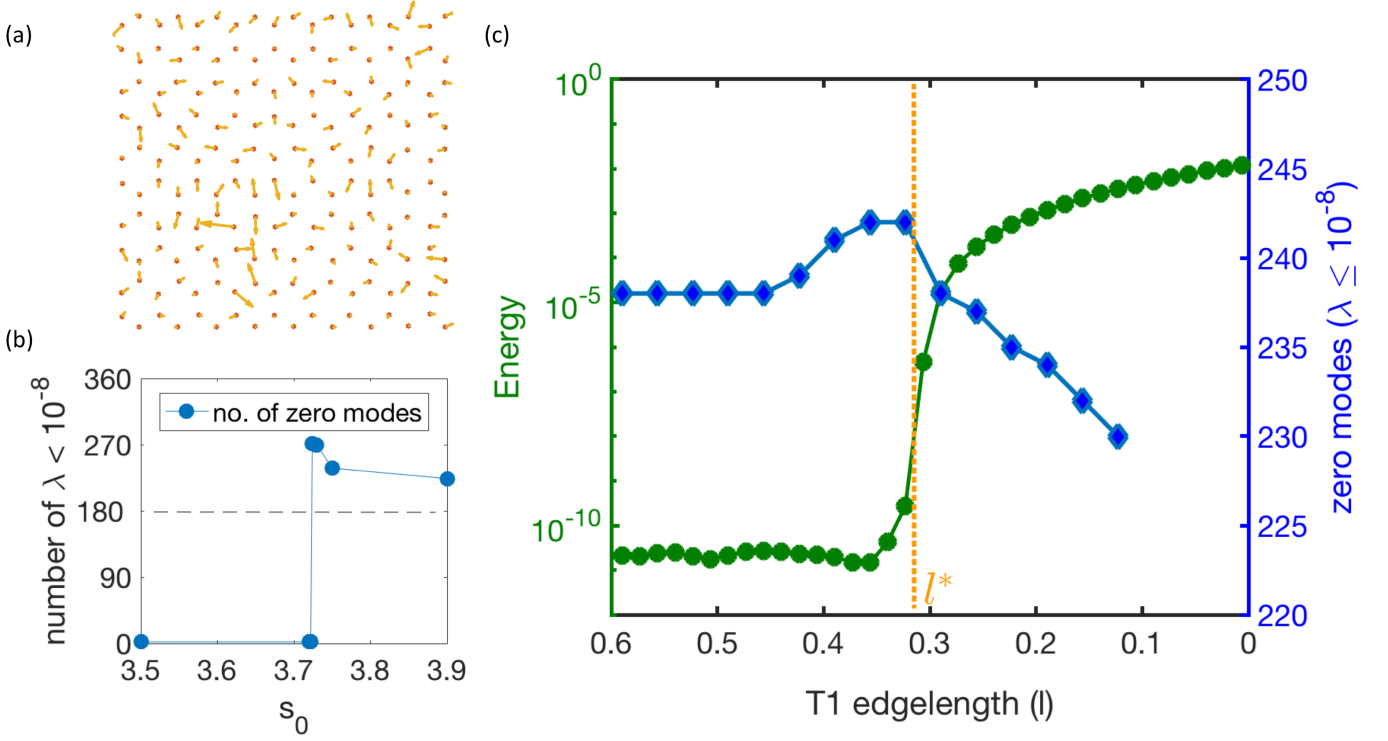


FIG. SI 2. **Vibrational mode analysis:** (a) A sample zero mode for bulk ordered tessellation with $s_0 = 3.75$. (b) The number of zero modes sharply increases after $s_0 = 3.722$. (c) The number of zero-valued eigenvalues of an ordered tessellation at a fixed value of the shape index, $s_0 = 3.75$, is studied along a T1 reaction coordinate. At the cusp in the potential energy landscape, l^* , where the energy changes by several orders of magnitude, the number of zero modes begins to systematically decrease.

the transition value (Fig. SI 2(c)). This suggests that there might be a local rigidification affecting the cells neighboring the T1 edge.

Comparison of the analytic nonlinear ansatz to numerical data

In our analytic ansatz, we assume that cell shapes are isotropic with equal length edges except for the T1 edge that shrinks to zero. Here, we show numerical data from bulk simulations for the shapes of cells undergoing a T1. We focus on the observed edge average and standard deviation (error bars) of an edge length, which we have grouped into “T1-adjacent” edges (L_A) and “non-T1-adjacent” edges (L_B). For a fixed value of shape $s_0 = 3.75$, we find that along a T1 process, the distributions converge to different mean values near the transition point l^* , as shown in Fig. SI 3. Specifically, for this case, the ratio $\xi = L_A/L_B$, is 1.21. This is different from our initial assumption of equal edgelengths. Hence we check the robustness of the single-cell results with respect to ξ .

We next generalize the single-cell calculation to accommodate possible differences between L_A and L_B i.e $\xi \neq 1$.

To implement this, we start with a polygon very similar to the one displayed in Fig. 4, with the equal-edge criterion lifted. We instead have the three “non-T1-adjacent” edges of the same length (L_A) and the two “T1-adjacent” edges of length L_B , such that $L_A/L_B = \xi$. We then study the perimeter change of this polygon as it transforms from a hexagon to a pentagon, for a fixed ξ , in an area-preserving manner. An intermediate polygon for each of the extreme ratios is displayed in Fig. SI 4.

We find that, for $s_0 > 3.722$, the preferred perimeter is attained for several combinations of ξ, l^* . But l^* corresponding to these newly found roots, is always higher than the one for $\xi = 1$. Hence, the simple ansatz we initially chose provides a robust lower bound for transition lengths (Fig. SI 4). In addition, the variation in l^* is quite small across a range of ratios ξ , indicating the simple geometric ansatz with only one length scale is quite a good predictor of the nonlinearity. Therefore, we focus on this simplest case in the main text.

Comparison to disordered packings

To compare our results on ordered systems to those in disordered systems, we investigate the onset of non-

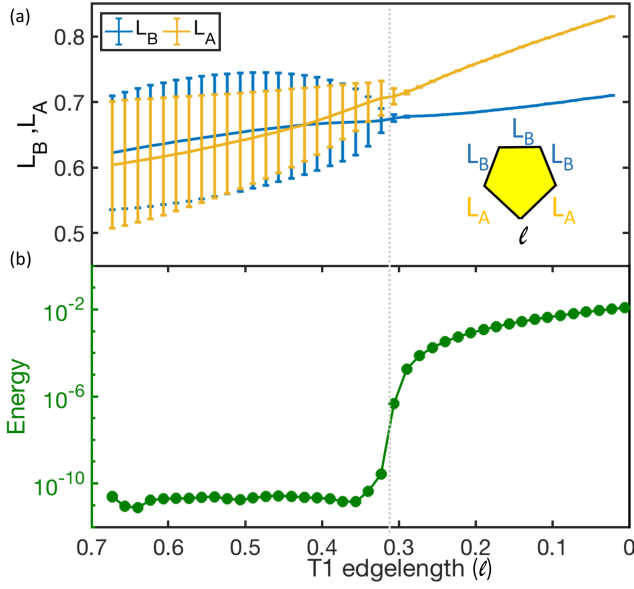


FIG. SI 3. **Computational results for the lengths of cell edges during a forced T1 transition in an ordered tessellation:** (a) In a bulk ordered system with $s_0 = 3.75$, we compute the lengths of edges on a cell undergoing a forced T1 transition, grouping the edges into “T1-adjacent” (L_A) and “non-T1-adjacent” (L_B) bins, which show different trends and become tightly constrained near the transition point, highlighted in (b) as the point at which the energy profile for $s_0 = 3.75$ has a cusp.

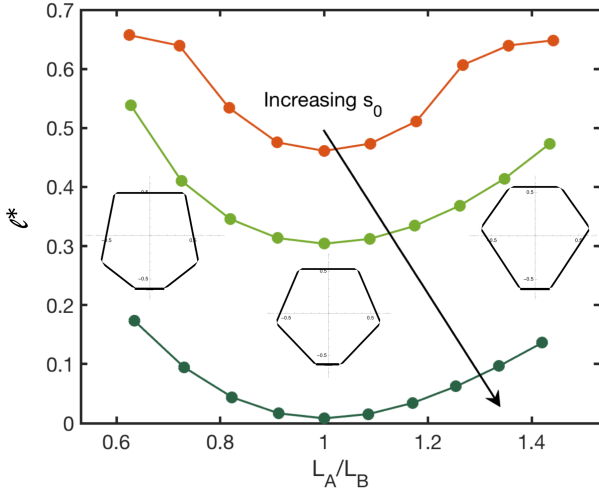


FIG. SI 4. **The transition length is minimum for a ratio of unity:** For a single-cell ansatz, we allow the ratio L_A/L_B to differ from unity. The transition points are plotted with respect to varying ratios for increasing s_0 values- 3.73 (red), 3.75 (green) and 3.81 (dark green).

linearities in maximally disordered systems. We then study the properties of systems with shrinking T1 edges from 50 different initializations. As in most previous work in this field, we assume homogeneous line tensions.

The disorder is introduced to the initial conditions in a standard way, used in both jammed particle packings [5] and also in previous work on vertex models [6]. Specifically, we randomly uniformly distribute N points on a 2D plane. Next, we generate the unique Voronoi tessellation of those N points, which generates a random cellular network with 3-fold coordinated vertices. We then use standard minimization algorithms to find the local minimum for the vertex model energy functional that is closest to the initial condition in the potential energy landscape. During the initial equilibration process we use a higher $l_c = 0.15$ which allows the system to explore more states on the trajectory towards a local energy minimum. Once the system has arrived at a mechanically stable state, we start the same process of shrinking a random edge to a length as small as $l_c = 0.006$. Since this initial energy now is not necessarily zero for $s_0 > 3.722$, we look at the relative energy $\Delta E(l)$ from initial state at every edglength. We bin every T1 edglength into 40 bins. To look at the average trend of these profiles as a function of increasing shape, we average $\Delta E(l)$ for every bin. We have used the same color scheme as in previous plots, and so one can see that for the disordered case, the energy remains high at all values of l throughout the entire range explored previously (s_0 in 3.71-3.83). For $s_0 > 3.83$, the average energy drops precipitously at an l value smaller than the average. It is important to note that we have focused on average values in Fig. SI 5(a), but there are large fluctuations in edglength due to the disorder, and the system will be unstable if any edge in the system can move at zero cost. Therefore, to find the l^* for a given configuration, we should focus on the lowest l^* , not the average, as shown in Fig. SI 5(b).

For this energy profile, we use the same energy cut-off and identify the critical edglength l^* for an edge in every ensemble. We find that in general this ensemble exhibits a wide distribution of l^* s because disordered systems have a variety of edglengths. Therefore, we represent this data using a box and whisker plot as shown in Fig. SI 5(b).

As previous work suggests that linear curvature does not vanish until approximately 3.81 for disordered systems, for $s_0 < 3.81$ one should expect the energy to grow as soon as the edge starts shrinking, so that $l^* = l_0$. As for $s_0 > 3.81$ the system is fluid so it should be possible for some edges to shrink to zero length at no energy cost, so that $l^* = 0$.

As shown in Fig SI 5, our data is in line with these expectations. For $s_0 < 3.81$, l^* is large and approximately equal to l_0 , while for $s_0 > 3.81$, there are some edges for which l^* approaches zero, resulting in a near discontinuity in the plot.

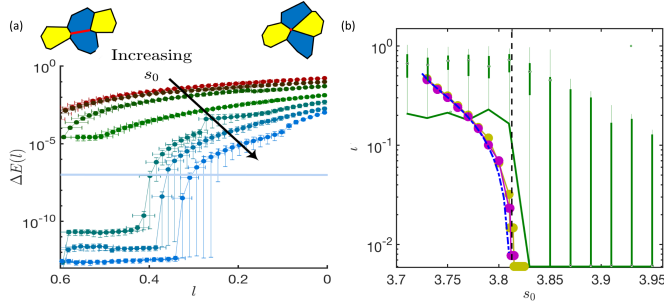


FIG. SI 5. **Many-cell disordered energy profile:** (a) In a disordered system of 90 cells, a randomly chosen edge undergoes a T1 transition for 50 different initializations. In this process, the relative energy of the tissue, $\Delta E(l)$, is plotted against the shrinking T1 edgelenlth l for increasing values of s_0 (3.71 to 3.95 in steps of 0.04) varying from red (3.71) to green (3.83) to blue (3.95). The cut-off for the energy is shown by a horizontal pale blue line for reference. (b) Critical edgelenlth l^* plotted against s_0 is superimposed for both-many-cell (yellow circles) and 4-cell systems (magenta circles). The analytical prediction from the geometric mechanism explained in the text is shown in blue dashed line. The dark green box and whisker plot in blue shows the l^* distribution in disordered systems.

-
- [1] J. C. Maxwell, The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science **27**, 294 (1864).
 - [2] C. Calladine, International journal of solids and structures **14**, 161 (1978).
 - [3] M. Merkel, K. Baumgarten, B. P. Tighe, and M. L. Manning, Proc. Natl. Acad. Sci. (2019), 10.1073/pnas.1815436116.
 - [4] D. M. Sussman and M. Merkel, Soft Matter **14**, 3397 (2018).
 - [5] C. S. O'Hern, L. E. Silbert, A. J. Liu, and S. R. Nagel, Phys. Rev. E **68**, 011306 (2003).
 - [6] D. Bi, J. H. Lopez, J. M. Schwarz, and M. Lisa Manning, Soft Matter (2014), 10.1039/c3sm52893f.