Spatial distribution of thermal energy in equilibrium

Yohai Bar-Sinai and Eran Bouchbinder

Department of Chemical Physics, Weizmann Institute of Science, Rehovot 7610001, Israel

The equipartition theorem states that in equilibrium, thermal energy is equally distributed among uncoupled degrees of freedom that appear quadratically in the system's Hamiltonian. However, for spatially coupled degrees of freedom, such as interacting particles, one may speculate that the spatial distribution of thermal energy may differ from the value predicted by equipartition, possibly quite substantially in strongly inhomogeneous or disordered systems. Here we show that for systems undergoing simple Gaussian fluctuations around an equilibrium state, the spatial distribution is universally bounded from above by $\frac{1}{2}k_B T$. We further show that in one-dimensional systems with short-range interactions, the thermal energy is equally partitioned even for coupled degrees of freedom in the thermodynamic limit and that in higher dimensions nontrivial spatial distributions emerge. Some implications are discussed.

Equilibrium thermal fluctuations play a key role in physics, chemistry, and biology and the framework that captures their properties, statistical thermodynamics, is a central branch of physics. One of the renowned results obtained in this field is the equipartition theorem [1], which in its simplest form states that the total thermal energy of the system is equally distributed among its uncoupled degrees of freedom (DOFs). In addition, each uncoupled DOF appearing quadratically in the Hamiltonian has on average an energy of $\frac{1}{2}k_B T$, where k_B is the Boltzmann constant and T is the absolute temperature [1].

The equipartition theorem holds only for uncoupled DOFs and strictly speaking does not state anything about the energy of coupled DOFs. Quadratic Hamiltonians can always be decomposed into a set of uncoupled DOFs (mutually orthogonal normal modes) and the theorem applies to them. It is intriguing, though, to ask in all generality whether the average potential energy of coupled DOFs can significantly deviate from the value predicted by equipartition. Put simply, we ask what can be said in general about the spatial distribution of thermal energy.

One may speculate that a localized enhancement or inhibition of thermal energy may have some effect on various local processes. For instance, if local thermal fluctuations activate chemical reactions, these might be facilitated or hindered in the presence of enhanced or reduced fluctuations. Other processes that might be affected are structural changes, such as severing of biopolymers [2,3]. Related effects may also be observed in elastic-network models of protein folding, where local (nearest-neighbor) fluctuations are assumed to dictate bond rupture [4]. We note that while much attention has been devoted to the effect of disorder on nonequilibrium transport properties (see, e.g., [5–7]), here we explore the spatial distribution of thermal energy strictly in equilibrium.

As a prelude, we begin by solving a very simple problem, depicted in Fig. 1. Consider a system of two particles interacting via linear springs with each other and with bounding walls. Its potential energy is

$$U = \sum_{\alpha=1}^{3} \epsilon_\alpha = \frac{1}{2}k_1 x_1^2 + \frac{1}{2}k_2 (x_2 - x_1)^2 + \frac{1}{2}k_3 x_2^2, \quad (1)$$

where ϵ_α is the energy of the αth spring and the x_i denote the deviation of the ith particle from its equilibrium position (when
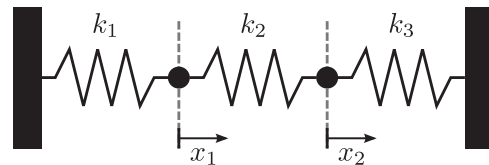

FIG. 1. Model system of two masses and three linear springs, connected in series between fixed walls. Here x_i measures the deviation of the ith particle from its equilibrium position.

possible, we adopt the convention that latin indices denote DOFs, while greek indices denote interactions). In Eq. (1) we assume that the rest length of the entire chain is identical to the distance between the bounding walls. As is typical in such systems, the kinetic energy $\sum_i \frac{1}{2}m_i \dot{x}_i^2$ is a sum of quadratic uncoupled terms. Thus, diagonalizing the kinetic contribution is trivial and hence in what follows we disregard the kinetic energy of the system.

What is the average energy stored in the αth spring? In particular, can it significantly deviate from the value predicted by equipartition? For such a simple system the answer is readily calculable through the correlations between the x_i. For example, $\langle \epsilon_2 \rangle$ is given by

$$\langle \epsilon_2 \rangle = \left\langle \frac{k_2}{2}(x_2 - x_1)^2 \right\rangle = \frac{k_2}{2}\left(\langle x_1^2 \rangle + \langle x_2^2 \rangle - 2\langle x_1 x_2 \rangle \right),$$

where $\langle \cdot \rangle$ denotes thermal averaging. Since the energy is quadratic, the correlation matrix $\boldsymbol{C}$ is given in terms of the Hamiltonian $\boldsymbol{H}$ by [1]

$$C_{ij} = \langle x_i x_j \rangle = k_B T (\boldsymbol{H}^{-1})_{ij}, \quad (2)$$

where the Hamiltonian (or the Hessian) is defined as $H_{ij} \equiv \frac{\partial^2 U}{\partial x_i \partial x_j}$. With these formulas, an explicit calculation yields[1]

$$\langle \epsilon_\alpha \rangle = \frac{1}{2}k_B T \left[1 - \frac{k_\alpha^{-1}}{k_1^{-1} + k_2^{-1} + k_3^{-1}} \right]. \quad (3)$$

———

[1]Whenever $\boldsymbol{H}$ is noninvertible, i.e., in the presence of Goldstone modes, the notation $\boldsymbol{H}^{-1}$ should be interpreted as the Moore-Penrose pseudoinverse [8,9]. See Ref. [10] for details.

A few insights can be gained from this very simple example. First, a clear-cut answer is given to the question presented above: For a general choice of the k_α, the thermally averaged energy of a given spring may differ from the value predicted by equal partition. Second, since the system consists of two DOFs (i.e., the Hamiltonian has two normal modes), each contributes $\frac{1}{2}k_B T$ to the total energy and thus $\sum_\alpha \langle \epsilon_\alpha \rangle = k_B T$, as expected. That is, the spatial average of the energy agrees, by construction, with the equipartition theorem and reads $(N+1)^{-1} \sum_\alpha \langle \epsilon_\alpha \rangle = \frac{1}{3}k_B T$ (with $N = 2$). Third, we note that $\langle \epsilon_\alpha \rangle$ is bounded between 0 and $\frac{1}{2}k_B T$, which means that inhomogeneity in the k_α might either increase or decrease it relative to the spatially average value of $\frac{1}{3}k_B T$, depending on the inhomogeneity. Finally, we note that for a homogeneous system, i.e., $k_\alpha = k$, the energy is equally partitioned among the springs and equals $\frac{1}{3}k_B T$.

These results might appear somewhat restricted as they involve a system with a small number of DOFs $N = 2$ and involve specific boundary conditions that may play a nontrivial role, especially in a small system. Consequently, we next aim at understanding how the spatial distribution of thermal energy depends on the number of DOFs and on the boundary conditions.

We first consider a system of N DOFs $x = (x_1, \ldots, x_N)^T$ and $N+1$ springs. The potential energy is

$$U = \sum_{\alpha=1}^{N+1} \epsilon_\alpha, \quad \epsilon_\alpha = \frac{1}{2}k_\alpha(x_\alpha - x_{\alpha-1})^2, \qquad (4)$$

where $1 \leqslant \alpha \leqslant N+1$, ϵ_α is the potential energy of the αth spring, and the k_α are non-negative constants. Formally, Eq. (4) makes reference to x_0 or x_{N+1}. These are not real DOFs but rather boundary conditions imposed by the fixed walls and should be taken as $x_0 = x_{N+1} = 0$. The general question that we pose is what can be stated about the distribution of $\langle \epsilon_\alpha \rangle$, for general k_α.

The conventional procedure for addressing such a question is to diagonalize the Hamiltonian H and work in the basis of its normal modes. Then $\langle \epsilon_\alpha \rangle$ can be reconstructed, at least conceptually, by summing over the contributions of the individual modes [e.g., Eq. (9) in [11]]. While this generic recipe is very useful in most cases, in this case working with the normal modes obfuscates the structure of the problem, since there is no simple way to describe them for a general distribution of the k_α.

What is then a useful basis to work with? To answer this question we first note that for any linear change of variables $\tilde{x} \equiv Ax$, where A is an invertible $N \times N$ matrix, the modified Hamiltonian takes the form $\tilde{H} = A^{-T}HA^{-1}$, where A^{-T} stands for $(A^{-1})^T$ (note that this is not a similarity transformation, as A is not orthogonal). Straightforward matrix manipulations show that even for the nonorthogonal variables $\tilde{x}$ the correlation matrix is given by the inverse of the relevant Hamiltonian, i.e., $\tilde{C} \equiv \langle \tilde{x}\tilde{x}^T \rangle = k_B T \tilde{H}^{-1}$. The main insight gained from this brief discussion is that one should not be constrained to using an orthogonal basis in transforming the Hamiltonian into a desired form. This turns out to be important for solving the problem at hand.

Following this insight, we look for new variables $\tilde{x} \equiv Ax$ such that $\tilde{H}$ will be, loosely speaking, almost diagonal. A clue for finding a useful basis is obtained by inspecting Eq. (4), which is already written in an almost diagonal form, if we identify the new variables simply as $\tilde{x}_i \equiv x_i - x_{i-1}$. That is, we take the combinations that make up the interactions as the new variables. This defines the transformation matrix $A_{ij} \equiv \delta_{ij} - \delta_{i,j+1}$.

Under this choice of nonorthogonal variables, almost all of the spring energies in Eq. (4) become $\epsilon_\alpha = \frac{1}{2}k_\alpha \tilde{x}_\alpha^2$. The last relation, however, is valid only for $1 \leqslant \alpha \leqslant N$. Clearly, a one-to-one correspondence between the DOFs and the interactions (springs) is impossible since the number of springs exceeds N. Indeed, an explicit calculation shows that in terms of the new variables the energy is not strictly decoupled, but only almost,

$$U = \sum_{\alpha=1}^{N} \frac{1}{2}k_\alpha \tilde{x}_\alpha^2 + \frac{1}{2}k_{N+1}(\tilde{x}_1 + \cdots + \tilde{x}_N)^2,$$

$$\tilde{H}_{ij} = k_i \delta_{ij} + k_{N+1} \text{ or } \tilde{H} = K + k_{N+1}\tilde{b}\tilde{b}^T, \qquad (5)$$

where $K \equiv \text{diag}(k_1, \ldots, k_N)$ and $\tilde{b}$ is a vector of 1's.

Equation (5) is very useful since the inverse $\tilde{H}^{-1}$ is readily calculated using the Sherman-Morrison formula [12], which can be expressed in the form

$$(H + kvv^T)^{-1} = H^{-1} - \frac{H^{-1}vv^T H^{-1}}{k^{-1} + v^T H^{-1}v} \qquad (6)$$

and is valid whenever both H and $H + kvv^T$ are invertible (here v is a vector and k is a scalar). Applying this formula to Eq. (5), we obtain the generalization of Eq. (3) to any N

$$\langle \epsilon_\alpha \rangle = \frac{1}{2}k_B T \left[1 - (N+1)^{-1} \frac{k_\alpha^{-1}}{\langle\!\langle k^{-1} \rangle\!\rangle} \right], \qquad (7)$$

where $\langle\!\langle k^{-1} \rangle\!\rangle \equiv (N+1)^{-1} \sum_\alpha k_\alpha^{-1}$ is the quenched average.

Two features of this result will prove important. First, it can be seen that $\langle \epsilon_\alpha \rangle < \frac{1}{2}k_B T$ regardless of the choice of k_α (moreover, the order in which the k_α are distributed in space makes no difference and $\langle \epsilon_\alpha \rangle$ depends only on k_α^{-1} and the average $\langle\!\langle k^{-1} \rangle\!\rangle$). Second, it is evident that $\langle \epsilon_\alpha \rangle$ tends towards $\frac{1}{2}k_B T$ in the thermodynamic limit $N \to \infty$, as long as $k_\alpha^{-1}/\langle\!\langle k^{-1} \rangle\!\rangle$ does not increase with N.

Our next task is to generalize Eq. (7). It will be shown that these two features are general for a wide class of physical systems, namely, systems with local interactions undergoing Gaussian fluctuations around a stress-free equilibrium. As we will show, for these systems $\frac{1}{2}k_B T$ is a strict upper bound for $\langle \epsilon_\alpha \rangle$. This result is entirely general, independent of dimensionality or interaction range. Second, the fact that $\langle \epsilon_\alpha \rangle = \frac{1}{2}k_B T$ plus a negative correction of order N^{-1}, which depends on the inhomogeneity, is the general rule for one-dimensional systems with short-range interactions. In particular, in such systems the distribution of thermal energy becomes spatially constant in the thermodynamic limit. These are two main results of this work.

Consider a system with N DOFs and total energy $U = \sum_{\alpha=1}^{n} \epsilon_\alpha$, where n is the number of interactions. The most

general expansion of ϵ_α in the DOFs reads

$$\epsilon_\alpha = \epsilon_0^{(\alpha)} + \sum_i F_i^{(\alpha)} x_i + \frac{1}{2} \sum_{i,j} x_i C_{ij}^{(\alpha)} x_j + O(\boldsymbol{x}^3). \quad (8)$$

The linear term vanishes under thermal averaging as long as anharmonic contributions to the energy are neglected and hence is omitted hereafter (note that $\sum_\alpha F_i^{(\alpha)} = \partial U / \partial x_i$ vanishes due to global equilibrium). The only assumption we adopt is that $\sum_{i,j} x_i C_{ij}^{(\alpha)} x_j$ can be written as $(\sum_i B_{\alpha i} x_i)^2$, where $\boldsymbol{B}$ is an $n \times N$ matrix that describes the interactions in the system [for example, $\boldsymbol{B}$ can be easily read off Eq. (4)]. In this case, the Hamiltonian is given by $H = \boldsymbol{B}^T \boldsymbol{B}$.

This is a generic form of local interaction energies for a broad class of physical systems. (i) In discrete field theories, or discrete approximations to continuum field theories, the energy density takes the form $[\mathcal{L}(f)]^2$, with some spatial linear differential operator $\mathcal{L}$ and field f. Relevant examples include, among many others, the Euler-Bernoulli theory of elastic beams [13], the Föppl–von Kármán theory of thin sheets [13], and the Helfrich theory of membrane elasticity [14]. (ii) In systems of discrete particles interacting via a radially symmetric pairwise potential, at equilibrium all particle pairs are at a stress-free configuration. Relevant examples include glassy systems near jamming [15] and elastic networks [4].

Using Eq. (2), $\langle \epsilon_\alpha \rangle$ can be readily expressed in terms of the interaction matrix $\boldsymbol{B}$, as

$$\langle \epsilon_\alpha \rangle = \tfrac{1}{2} k_B T P_{\alpha\alpha}, \quad \boldsymbol{P} \equiv \boldsymbol{B}(\boldsymbol{B}^T \boldsymbol{B})^{-1} \boldsymbol{B}^T. \quad (9)$$

The matrix $\boldsymbol{P}$ is an orthogonal projection operator [9], since $\boldsymbol{P}^2 = \boldsymbol{P}$ (this holds even when $\boldsymbol{B}^T \boldsymbol{B}$ is not invertible [10]). Note that $P_{\alpha\alpha}$ refers to the $\alpha\alpha$ diagonal element of $\boldsymbol{P}$, and no summation is implied. A general property of such operators is that all their elements are smaller than unity in absolute value. We thus prove a central result of this work, i.e., that

$$\langle \epsilon_\alpha \rangle = \tfrac{1}{2} k_B T P_{\alpha\alpha} \leqslant \tfrac{1}{2} k_B T. \quad (10)$$

The rank of $\boldsymbol{P}$, which equals that of H and $\boldsymbol{B}$, carries important information. For example, since $\boldsymbol{P}$ is a projection operator that works in a space of dimension n, in the case that $\text{rank}(P) = n$ we can immediately conclude that $\boldsymbol{P}$ is the identity and thus $\langle \epsilon_\alpha \rangle = \tfrac{1}{2} k_B T$ identically. This happens whenever the rows of the interaction matrix $\boldsymbol{B}$ are linearly independent (and in particular $n \leqslant N$). The case $n = N$, for nearest-neighbor interactions, corresponds to isostatic systems, i.e., systems where the number of constraints (interactions) equals the number of DOFs [15].

Equation (10) puts strict bounds on the possible values of $\langle \epsilon_\alpha \rangle$, but much more can be said about the behavior within these bounds. Specifically, we can derive the analog of Eq. (7) in the general case of one-dimensional systems with short-range interactions. The detailed derivation can be found in [10] and it follows verbatim the structure of the derivation of Eq. (7), as outlined here: For one-dimensional systems, where each DOF interacts with its m nearest neighbors, the number of interactions generally exceeds the number of DOFs by m. A nonorthogonal transformation is used to put the Hamiltonian into the form $\tilde{H} = \boldsymbol{K} + \sum_\alpha k_\alpha \tilde{\boldsymbol{b}}_\alpha \tilde{\boldsymbol{b}}_\alpha^T$, where $\boldsymbol{K}$ is diagonal and the second term is a sum over the m excess interactions. Then the Sherman-Morrison formula is iteratively applied m times

to calculate the inverse. Because of the short-range nature of the interactions, the magnitude of the nondiagonal correction to $\tilde{\boldsymbol{H}}^{-1}$ is of order m/N and vanishes in the thermodynamic limit. Thus, $\langle \epsilon_\alpha \rangle = \tfrac{1}{2} k_B T + O(N^{-1})$.

This is another central result of this work: In one-dimensional systems with short-range interactions, the spatial distribution of thermal energy becomes essentially flat in the thermodynamic limit. The crux of the argument lies in the fact that the number of interactions does not greatly exceed the number of DOFs and that the ratio between them approaches unity in the thermodynamic limit.

Returning to the problem of the spring-mass chain and having solved the problem of the N dependence for fixed boundary conditions, we now turn to explore the effect of boundary conditions for a fixed N. For instance, semi-fixed boundary conditions can be obtained by removing the constraint of one of the walls, by setting, say, $k_1 = 0$. In doing so we obtain $n = N$ independent interactions and thus $\langle \epsilon_\alpha \rangle = \tfrac{1}{2} k_B T$ is identically constant for any N. Fully free boundary conditions are obtained by setting both k_1 and k_{N+1} to zero and give rise to a single Goldstone mode (uniform translation). In this case we have $n = N - 1$ independent interactions and again $\langle \epsilon_\alpha \rangle$ is identically constant [clearly, both these results can also be obtained by properly taking limits of Eq. (7)]. This also shows that in one-dimensional systems the effect of boundary conditions in nonlocal, i.e., every spring in the system is affected by the bounding walls.

The general approach discussed above can be applied to different types of interactions. For example, bending fluctuations are described by local interactions of the form $\epsilon_\alpha = \tfrac{1}{2} \kappa_\alpha (x_{\alpha-1} - 2x_\alpha + x_{\alpha+1})^2$, where the κ_α are the local bending rigidities. Identical arguments show that in a chain with free boundary conditions, the spatial distribution of bending fluctuational energy is exactly constant, regardless of the choice of the κ_α.

This result offers the first application of the theoretical development described in this paper, as it seems to refute a recently conjectured mechanism for severing of actin filaments, one of the most important and ubiquitous biopolymers in eukaryotic cells [16]. In [17–19] it was hypothesized that thermal energy may be concentrated at the boundaries between relatively softer and stiffer regions of the biopolymer (softening is induced by a different molecule, cofilin, which partially binds actin [17,20]) and that the excess thermal energy is responsible for the experimentally observed preferential severing near these boundaries. Our result shows, at least within the framework of a discrete description of quadratic bending fluctuations, that no such energy concentration takes place.

What happens in higher dimensions? As the crux of the argument lies in the relative number of DOFs and interactions, dimensionality appears to be crucial. In fact, in dimensions higher than one the argument seems to fail qualitatively as generally there are significantly more interactions than DOFs. In this case, we also expect local topological variations, bond strength disorder, defects, holes, free boundaries, and the like to play a role.

To see this, consider a hexagonal portion of a two-dimensional triangular lattice of $\tfrac{1}{2} N$ particles (which amounts
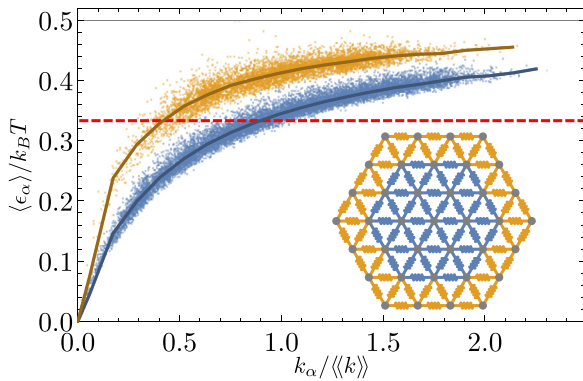
FIG. 2. (Color online) Average thermal energy $\langle \epsilon_\alpha \rangle$ (in units of $k_B T$) as a function of $k_\alpha / \langle\langle k \rangle\rangle$ for a hexagonal portion of a two-dimensional triangular lattice. The data are partitioned into bulk (blue) and boundary springs (yellow) (cf. the inset). Spring constants are distributed normally with mean 1 and variance 0.3. Each side of the hexagon consists of 20 springs, which means $N = 2522$ (a smaller system, with 3 springs on each side and $N = 74$, is shown in the inset for illustration). No quantitative change was observed with increasing N. The points show data from 30 realizations and the solid lines are guides to the eye. The dashed line shows the asymptotic value $\frac{1}{3}$, corresponding to $\langle \epsilon_\alpha \rangle$ in the bulk of a homogeneous triangular lattice in the thermodynamic limit.

to N DOFs), interacting via linear springs, as shown in the inset of Fig. 2. Clearly, in the limit of large systems the number of springs n approaches $\frac{3}{2} N$. When all of the springs are identical, i.e., with no bond strength disorder, we expect the average energy of a spring far from the free boundary to approach $\langle \epsilon_\alpha \rangle \approx \frac{1}{2} k_B T \times \frac{N}{n} \rightarrow \frac{1}{3} k_B T$ (this was verified by an explicit calculation). There is no reason, however, to expect the thermal energy to be spatially uniform in the presence of inhomogeneities, either in the lattice topology or in the bond strength.

To test this, we considered the lattice in the inset of Fig. 2 with bond strength disorder, where the k_α are normally distributed.[2] Here $\langle \epsilon_\alpha \rangle$ is plotted vs k_α in the main panel, where the average energy of bulk springs in a homogeneous system $\frac{1}{3} k_B T$ is shown as well. Bulk and boundary springs are distinguished. Several key observations can be made. (i)

Unlike in one-dimensional systems, thermal energy spans the whole interval between 0 and $\frac{1}{2} k_B T$, both below and above the homogeneous system bulk value $\frac{1}{3} k_B T$. (ii) The average thermal energy $\langle \epsilon_\alpha \rangle$ appears to vary systematically with the local spring strength k_α. (iii) Boundary springs have higher energy than bulk springs. This is a purely topological effect in which boundary springs have fewer neighbors than bulk springs, an effect that persists near free boundaries in fully ordered systems. In general, disordered systems (e.g., glassy ones [15]) feature also bulk topological disorder.

In summary, in this work we posed a basic question in statistical physics: What is the spatial distribution of thermal energy in equilibrium? We showed that under the stated conditions it is strictly bounded between 0 and $\frac{1}{2} k_B T$ and that for one-dimensional systems with short-range interactions the spatial distribution of thermal energy becomes essentially flat in thermodynamic limit, even for highly disordered systems. The crux of the derivation lies in the fact that in one-dimensional systems the number of interactions is the same as the number of DOFs, up to an additive constant that is negligible in the thermodynamic limit. In higher dimensions this does not hold, as was explicitly demonstrated in a specific example. Systematically unraveling the relations between the spatial energy distribution and dimensionality, the system's geometry, and the form of disorder is a theoretical challenge for future work.

The most outstanding question that emerges from this work is what the influence of the spatial distribution of thermal energy on various physical processes and quantities might be. If local energy fluctuations can affect local process, as was suggested, for example, in the context of bond rupture in elastic-network models of protein folding [4], then one can imagine the possibility of tailoring high-dimensional systems in order to enhance or reduce thermal fluctuations in defined locations, to control local processes of interest. Another important future direction would be to explore the roles played by stresses (both internal and external).

---

[2]To keep the springs constants positive, we used $k_\alpha = \max(\kappa_i, \kappa_m)$, where κ_i are normally distributed and $\kappa_m > 0$ is a small cutoff that has little influence on the results.

---

[1] K. Huang, *Statistical Mechanics* (Wiley, New York, 1963).

[2] W. A. Elam, H. Kang, and E. M. De La Cruz, FEBS Lett. **587**, 1215 (2013).

[3] K. X. Ngo, N. Kodera, E. Katayama, T. Ando, and T. Q. Uyeda, eLife **4**, e04806 (2015).

[4] A. Srivastava and R. Granek, Phys. Rev. Lett. **110**, 138101 (2013).

[5] A. Casher and J. L. Lebowitz, J. Math. Phys. **12**, 1701 (1971).

[6] M. Rich and W. Visscher, Phys. Rev. B **11**, 2164 (1975).

[7] D. Livanov, M. Reizer, and A. Sergeev, Physica B **169**, 483 (1991).

[8] R. Penrose, Math. Proc. Cambridge Philos. Soc. **51**, 406 (1955).

[9] C. D. Meyer, *Matrix Analysis and Applied Linear Algebra* (SIAM, Philadelphia, 2000), p. 423.

[10] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevE.91.060103 for additional technical details.

[11] A. R. Atilgan, S. R. Durell, R. L. Jernigan, M. C. Demirel, O. Keskin, and I. Bahar, Biophys. J. **80**, 505 (2001).

[12] J. Sherman and W. J. Morrison, Ann. Math. Stat. **21**, 124 (1950).

[13] L. D. Landau and E. M. Lifshitz, *Theory of Elasticity*, 2nd ed. (Pergamon, Oxford, 1970), Vol. 7.

[14] S. A. Safran, *Statistical Thermodynamics of Surfaces, Interfaces, and Membranes* (Addison-Wesley, Reading, 1994).

[15] M. van Hecke, J. Phys.: Condens. Matter **22**, 033101 (2010).

[16] J. J. Bravo-Cordero, M. A. O. Magalhaes, R. J. Eddy, L. Hodgson, and J. Condeelis, Nat. Rev. Mol. Cell Biol. **14**, 405 (2013).

[17] B. R. McCullough, L. Blanchoin, J.-L. Martiel, and E. M. De La Cruz, J. Mol. Biol. **381**, 550 (2008).

[18] E. M. De La Cruz, Biophys. Rev. **1**, 51 (2009).

[19] B. R. McCullough, E. E. Grintsevich, C. K. Chen, H. Kang, A. L. Hutchison, A. Henn, W. Cao, C. Suarez, J.-L. Martiel, L. Blanchoin, E. Reisler, and E. M. De La Cruz, Biophys. J. **101**, 151 (2011).

[20] E. Prochniewicz, N. Janson, D. D. Thomas, and E. M. De la Cruz, J. Mol. Biol. **353**, 990 (2005).