Supplementary Material: Stochastic Voronoi Tessellations as Models for the Cellular Neighborhoods in Simple Multicellular Organisms

Anand Srinivasan,^{1,*} Steph Höhn,^{1,†} and Raymond E. Goldstein^{1,‡}

¹Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences, University of Cambridge, Wilberforce Road, Cambridge CB3 0WA, United Kingdom

(Dated: March 11, 2024)

This file contains additional theoretical and computational details pertaining to the models discussed in the main body.

I. BACKGROUND ON RANDOM VARIABLES

Many of the following are standard facts, recalled for a self-contained reference.

A. Transforms of random variables and convergence in distribution

Definition I.1 (Pushforward measure). Let $g : \mathbb{R}^n \to \mathbb{R}^n$ be a diffeomorphism and Y = g(X). The pushforward probability measure μ_Y is, for all measurable $U \subset \mathbb{R}^n$,

$$\mu_Y(U) = \mu_X(g^{-1}(U)). \tag{S1}$$

a. Transforms of random variables. When μ_X has a Radon-Nikodym derivative f_X with respect to the Lebesgue measure —i.e. is expressible by the probability density $\mu_X(U) = \int_U f_X(x) dx$ —then by the rule for integration under a diffeomorphic change of coordinates y = g(x),

$$\mu_X(U)(g^{-1}(U)) = \int_{g^{-1}(U)} f_X(x) dx = \int_U f_X(g^{-1}(y)) \left| \det \frac{\partial g^{-1}}{\partial y}(y) \right| dy.$$
(S2)

with $\partial g^{-1}/\partial y$ denoting the Jacobian of the inverse. As this is true for all U we conclude

$$f_Y(y) = f_X(g^{-1}(y)) \left| \det \frac{\partial g^{-1}}{\partial y}(y) \right|.$$
(S3)

When preferable to work with g rather than g^{-1} , we may apply the chain rule to $g^{-1} \circ g = 1$ to convert (S3) to

$$f_Y(g(x)) = f_X(x) \left| \det\left(\frac{\partial g}{\partial x}(x)\right)^{-1} \right| =: f_X(x)J^{-1}(x).$$
(S4)

Due to this fact, we will abbreviate the scaling factor as J^{-1} , denoting the inverse Jacobian determinant. For affine transforms Y = cX + b, (S3) becomes

$$f_Y(y) = \frac{1}{c} f_X\left(\frac{y-b}{c}\right). \tag{S5}$$

b. Sums of random variables. Let X, Y be independent random variables taking values in $U_X, U_Y \subseteq \mathbb{R}$. Then their sum is distributed as the convolution

$$X + Y = Z \sim f_Z(z) = \int_{x \in U_x, \ x \le z} f_X(x) f_Y(z - x) dx = f_X * f_Y.$$
(S6)

This can alternatively be deduced by applying the transform rule (S3) to the map $(X, Y) \mapsto (X, X + Y)$.

^{*} as3273@cam.ac.uk

[†] sh753@cam.ac.uk

[‡] R.E.Goldstein@damtp.cam.ac.uk

Definition I.2 (Convergence in distribution). A sequence of random variables $\{X_n\}$ taking values in an interval $U \subseteq \mathbb{R}$ is said to *converge in distribution* if, for all x at which the cumulative distribution function F_X is continuous, the c.d.f.s. F_{X_n} converge pointwise, i.e.

$$\lim_{n \to \infty} F_{X_n}(x) = F_X(x). \tag{S7}$$

B. Several properties of the exponential and gamma random variables

Let us recall with proof some properties of the gamma random variable (and the exponential, which is a special case).

Definition I.3 (Gamma random variable.). The gamma random variable $Y_{k,\lambda}$ with shape parameter k > 0 and rate $\lambda > 0$ is the continuous random variable with probability density function

$$f_Y(y) = \frac{\lambda^k y^{k-1} \exp(-\lambda y)}{\Gamma(k)}.$$
(S8)

Its namesake is the normalizing constant, the gamma function

$$\Gamma(k) = \int_0^\infty y^{k-1} e^{-y} dy.$$
(S9)

Lemma I.1 (Gamma random variables are closed under addition). The sum of two independent gamma random variables Y_1, Y_2 with $k_1, k_2 \in \mathbb{R}_{\geq 0}$ of common rate $\lambda > 0$ is $(k_1 + k_2)$ -gamma distributed.

Proof. Since $Y_1, Y_2 \in [0, \infty)$, by the convolution rule (S6),

$$Y_1 + Y_2 \stackrel{\text{pdf}}{\sim} f_{Y_1} * f_{Y_2} = \frac{\lambda^{k_1 + k_2}}{\Gamma(k_1)\Gamma(k_2)} \int_0^{y_2} y_1^{k_1 - 1} e^{-\lambda y_1} (y_2 - y_1)^{k_2 - 1} e^{-\lambda(y_2 - y_1)} dy_1.$$
(S10)

Taking the Beta function

$$B(k_1, k_2) = \int_0^1 t^{k_1 - 1} (1 - t)^{k_2 - 1} dt = \frac{\Gamma(k_1) \Gamma(k_2)}{\Gamma(k_1 + k_2)}$$
(S11)

with the change of variable $t = y_1/y_2$ yields

$$= \frac{1}{y_2^{k_1+k_2-1}} \int_0^{y_2} y_1^{k_1-1} (y_2 - y_1)^{k_2-1} dy_1.$$
(S12)

Substituting into (S10) and letting $x = y_2$, we obtain

$$(S10) = \frac{\lambda^{k_1 + k_2} x^{k_1 + k_2 - 1} e^{-\lambda x}}{\Gamma(k_1 + k_2)} \stackrel{\text{pdf}}{\sim} Y_{;k_1 + k_2,\lambda}.$$
(S13)

Corollary. The sum of k iid exponential random variables of rate λ are gamma-distributed with shape parameter k and rate λ .

Corollary. The gamma random variable is infinitely divisible.

Corollary. By the central limit theorem, $(\lambda Y_{k,\lambda} - 1)/\sqrt{k} \xrightarrow{d} W_{0,1}$ as $k \to \infty$.

Lemma I.2 (Beta-gamma convergence). Let $Z_{2,m}$ be a beta random variable. Then $\frac{m}{\alpha}Z_{2,m}$ converges in distribution as $m \to \infty$ to the gamma random variable $Y_{2,\alpha}$ of rate α .

Proof. By direct calculation,

$$\frac{m}{\alpha} Z_{2,m} \stackrel{\text{cdf}}{\sim} P\left[Z_{2,m} \le \frac{z\alpha}{m}\right] = \frac{1}{B(2,m)} \int_0^{\frac{z\alpha}{m}} t(1-t)^{m-1} dt \qquad z \in \left[0, \frac{m}{\alpha}\right],\tag{S14}$$

with the change of variables s = 1 - t,

$$=\frac{1}{\mathcal{B}(2,m)}\int_{1-\frac{\alpha z}{m}}^{1}(1-s)s^{m-1}ds$$
(S15)

$$= m(m+1) \left[\frac{1}{m} s^m - \frac{1}{m+1} s^{m+1} \right]_{1-\frac{z\alpha}{m}}^1$$
(S16)

$$=1-\left(\left(m+1\right)\left(1-\frac{z\alpha}{m}\right)^{m}-m\left(1-\frac{z\alpha}{m}\right)^{m+1}\right)$$
(S17)

$$=1-\left(1-\frac{z\alpha}{m}\right)^{m}\left(1+z\alpha\right)$$
(S18)

$$\xrightarrow{m \to \infty} 1 - e^{-z\alpha} (1 + z\alpha) \qquad z \in [0, \infty).$$
(S19)

Recalling the cumulative density function for $Y_{2,\alpha}$ (S8),

$$Y_{2,\alpha} \stackrel{\text{cdf}}{\sim} \int_0^z \alpha^2 y e^{-\alpha y} dy = -\alpha y e^{-\alpha y} \Big|_0^z + \int_0^z \alpha e^{-\alpha y} dy = 1 - e^{-z\alpha} (1 + z\alpha).$$
(S20)

As the c.d.f.s of both are C^{∞} and exhibit the pointwise convergence above, we have the distributional convergence $\frac{m}{\alpha}Z_{2,m} \stackrel{d}{\to} Y_{2,\alpha}$.

Lemma I.3 (Memoryless characterization of the exponential). The only continuous random variable X which (i) possesses a cumulative distribution function F_X such that $F'_X(0)$ exists and (ii) satisfies the memoryless property

$$P[X > x + y \mid X > x] = P[X > y]$$
(S21)

is the exponential.

Proof. By Bayes' theorem, (S21) is equivalent to

$$P[X > x + y] = P[X > x]P[X > y] \iff 1 - F(x + y) = (1 - F(x))(1 - F(y)).$$
(S22)

Let G = 1 - F; then (S22) is G(x + y) = G(x)G(y). Then for all z,

$$G'(z) = \lim_{h \to 0} \frac{G(z)G(h) - G(z)G(0)}{h} = G(z)G'(0).$$
(S23)

Since by hypothesis (i) F'(0) exists, (S23) implies F' exists everywhere. Let u be such that F(u) < 1. Since F is nondecreasing, this implies G > 0 for $w \in (-\infty, u]$. Then, letting G'(0) = -F'(0) = c,

$$c = \frac{G'(w)}{G(w)} = \frac{d}{dw} \log G(w).$$
(S24)

Integrating, we obtain $G(x) = b \exp(cx)$ for some b. By the conditions F(0) = 0, $\lim_{t\to\infty} F(x) = 1$, we have b = 1, c < 0. Letting $c = -\lambda$ for $\lambda > 0$ we obtain $F_X(x) = 1 - \exp(-\lambda x)$. Hence, $f_X(x) = F'_X(x) = \lambda \exp(-\lambda x)$, and X is an exponential random variable of rate λ .

Lemma I.4 (Maximum-entropy characterization of the exponential). The only nonnegative continuous random variable X with density f_X which maximizes the entropy with fixed mean $\mu > 0$ is the exponential.

Proof. By hypothesis, f_X is a critical point of the functional

$$J[f] = \int_0^\infty L(f(x), \lambda_0, \lambda_1) dx,$$
(S25)

with Lagrange multipliers λ_0 and λ_1 constraining the 0th and 1st moments in the Lagrangian density

$$L(f(x), \lambda_0, \lambda_1) = f(x) \log f(x) + \lambda_0 f(x) + \lambda_1 x f(x).$$
(S26)

Since for all test functions φ , the Fréchet derivative vanishes,

$$0 = \langle DJ[f], \varphi \rangle = \int_0^\infty \frac{\partial L}{\partial f(x)} \varphi(x) dx, \qquad (S27)$$

by the fundamental lemma of the calculus of variations,

$$0 = \frac{\partial L}{\partial f(x)} = 1 + \log f(x) + \lambda_0 + x\lambda_1, \tag{S28}$$

hence $f(x) = \exp(-1 - \lambda_0 - x\lambda_1)$. Applying the total probability constraint,

$$1 = \int_0^\infty \exp(-1 - \lambda_0 - x\lambda_1) dx = \frac{1}{\lambda_1} \exp(-1 - \lambda_0), \tag{S29}$$

where $\lambda_1 > 0$ necessarily. Then, $f_X(x) = \lambda_1 \exp(-\lambda_1 x)$ is the density of an exponential random variable with rate λ_1 .

Theorem I.5 (Characterization of gamma random variables, Lukacs 1955 [S1]). Let Y_1, Y_2 be independent random variables. Then

$$A = Y_1 + Y_2, \qquad B = \frac{Y_1}{Y_1 + Y_2} \tag{S30}$$

are independent if and only if Y_1, Y_2 are gamma random variables of the same rate λ .

Proof (\implies). Consider the map

$$g(Y_1, Y_2) = \left(Y_1 + Y_2, \frac{Y_1}{Y_1 + Y_2}\right) =: (A, B).$$
(S31)

Then for $a \neq 0$,

$$g^{-1}(a,b) = (ab, a - ab).$$
 (S32)

Therefore

$$\left|\det\frac{\partial g^{-1}}{\partial(a,b)}\right| = \left|\det\begin{bmatrix}b & 1-b\\a & -a\end{bmatrix}\right| = a.$$
(S33)

By (S4), the pushforward density is

$$f_{g(Y_1,Y_2)}(a,b) = af_{Y_1}(ab)f_{Y_2}(a-ab)$$
(S34)

$$=\frac{a(ab)^{k_1-1}(a-ab)^{k_2-1}}{\Gamma(k_1)\Gamma(k_2)}\lambda^{k_1+k_2}e^{-\lambda a}$$
(S35)

$$=\frac{b^{k_1-1}(1-b)^{k_2-1}}{\Gamma(k_1)\Gamma(k_2)}a^{k_1+k_2-1}\lambda^{k_1+k_2}e^{-\lambda a}.$$
(S36)

The total A and fraction B are therefore independent. Substituting the Beta function (S11),

$$(S34) = \frac{b^{k_1 - 1}(1 - b)^{k_2 - 1}}{B(k_1, k_2)} \frac{a^{k_1 + k_2 - 1}\lambda^{k_1 + k_2}e^{-\lambda a}}{\Gamma(k_1 + k_2)} =: f_B(b)f_A(a).$$
(S37)

Then $f_A(a)$ is a gamma distribution (as expected, I.1) and $f_B(b)$ is a beta distribution. Therefore,

$$B = \frac{Y_{1;k_1,\lambda}}{Y_{1;k_1,\lambda} + Y_{2;k_2,\lambda}} = Z_{k_1,k_2}$$
(S38)

is beta-distributed for $k_1, k_2 \in \mathbb{R}_{\geq 0}$.

Note that (S38) is independent of the rate λ of Y_1, Y_2 . The converse (\Leftarrow), that gamma distributions are unique in possessing this independence property, is not proven here, but we refer the reader to a proof [S2] using the fact that the gamma distribution is uniquely determined by its moments (3.3.25, [S3]).

Corollary (Beta-thinned gamma random variable). If $Y_{1;k_1+k_2,\lambda}$ and $Z_{1;k_1,k_2}$ are independent gamma and beta random variables, respectively, then

$$Y_{2;k_1,\lambda} = Z_{1;k_1,k_2} Y_{1;k_1+k_2,\lambda} \tag{S39}$$

is an independent gamma random variable of the same rate λ and lower shape parameter k_1 .

The *thinning* here refers to the fact that Z_1 is supported on [0, 1], hence decreasing the number of events occurring in a section of a 1D Poisson process.

Lemma I.6 (Differential entropy of a fixed-mean gamma random variable is strictly decreasing in $k \in (1, \infty)$).

Proof. Let $Y_{k,\lambda}$ be a gamma random variable of shape parameter k and rate λ . Its differential entropy is

$$H(Y) = k + \log \Gamma(k) + (1 - k)\psi(k) - \log \lambda, \tag{S40}$$

where $\psi(k) = \frac{d}{dk} \log \Gamma(k)$ is the digamma function. Hence, at fixed mean $\mu = k/\lambda$, using the hypothesis k > 1 and the trigamma inequality $\psi'(k) > 1/k$ [S3], we have the k-monotonicity

$$\frac{\partial H}{\partial k} = 1 + \psi'(k)(1-k) - \frac{1}{k} < 1 + \frac{1}{k}(1-k) - \frac{1}{k} = 0.$$
(S41)

Note furthermore that $H(Y) \ge 0$ for $k \le 1$, so one recovers the maximum-entropy property of the exponential random variable I.4.

A note on maximum likelihood estimation. Throughout, we use standard methods for maximum-likelihood estimation of the shape and scale parameters (k, λ) of the gamma distribution at fixed offset 0, as implemented in Python's *scipy.stats.gamma.fit* function. As the maximum likelihood estimate of λ is given by the k/\overline{x} where k is given and \overline{x} is the empirical mean, we estimate 95% confidence intervals for the shape parameter k at fixed scale λ using N = 1000 parametric bootstraps as follows. Each sample of size n, where n is the size of the original dataset to be fit, is produced from a gamma distribution with $(\hat{k}, \hat{\lambda})$, the estimated parameters from the original empirical distribution. Then, at fixed $\hat{\lambda}$, a new \tilde{k} is maximum-likelihood estimated from these samples. From this set $\{\tilde{k}_i\}_{i=1}^N$, the values corresponding to the (2.5, 97.5) percentiles are reported as the 95% CIs.

II. 1-DIMENSIONAL MODELS OF CELLS WITHIN AN ECM

Recall that the configuration of a sequence of cellular positions $\{R_i\}$ in a one-dimensional ECM (e.g. $[0, \infty)$ or the circle \mathbb{S}^1) is uniquely defined, up to relabeling, by the intercellular spacings $L_i = R_{i+1} - R_i$. In the following models, we let L_i be given (up to appropriate scaling) by the steady-state protein concentration P_i^* referred to in the main text. Realizing random 1D configurations in different ways by applying constraints analogous to the ensembles of statistical physics, we obtain the same k = 2b-gamma distribution governing the Voronoi lengths in a regime analogous to the thermodynamic limit. These models are named by the ECM dimension d (I or II) and described by the particular ensemble considered. as summarized in Table I.

Notation. We denote random variables by capital letters $X_{i;\alpha,\beta,\ldots}$ accompanied by indices i and parameters α, β, \cdots . Variables $i \neq j$ are independent unless otherwise noted. The letters $W_{i;\mu,\sigma^2}, X_{i;\lambda}, Y_{i;k,\lambda}, Z_{i;\alpha,\beta}$, and $N_{i;\lambda}$, and are reserved for Gaussian, exponential, gamma, beta, and Poisson random variables respectively. $X \stackrel{\text{pdf}}{\sim} f_X(x)$ indicates that X has the probability density function $f_X(x)$, with $X \stackrel{\text{cdf}}{\sim} F_X(x)$ indicating the same for the cumulative density. $X_i \stackrel{\text{d}}{\to} Y$ indicates that X_i converges to Y in distribution. For example, we would say that $Y_{k,\frac{k}{\overline{v}-v_c}} + v_c \stackrel{\text{pdf}}{\sim} p(v)$, where p(v) is the distribution (1).

As in the Gibbs, microcanonical, and grand canonical ensembles, we consider three types of random configurations of cells in the ECM: (i) fixed cell counts N = n, with random intercell spacings and circumferences; (ii) fixed circumferences C = c and counts N = n, with random positions $\{R_i\}_{i=1}^N$; and (iii) fixed circumferences C = c, with random cell counts N and positions. Like the convergence of the ensembles in the thermodynamic limit, we show that the same gamma distribution arises in the large-n, c limits of these cases.

TABLE I. Models in 1D and 2D

Model	Description
I.0	on the half-line
I.1	circular Gibbs
I.2	circular canonical
I.3	circular grand canonical
I.4	circular canonical, finite size
I.D.1	circular canonical, Brownian motion
I.D.2	circular canonical, noncolliding Brownian motion
I.D.3	noncolliding Brownian motion on a growing circle
I.D.4	maximum-entropy growth rates
II.1	canonical on periodic unit square

Model I.0 (on the half-line) —Consider a semi-infinite Volvox modelled as a sequence of cellular positions $\{R_i\}_{i=1}^{\infty}$ on the half-line $[0, \infty)$ as in Fig. 1(c). In the special case of b = 1 protein bursts, R_i are the cumulative sums of i i.i.d. exponential random variables:

$$R_i = \sum_{j=1}^{i} X_{j,i;\lambda},\tag{S42}$$

and therefore occur on the half-line $[0, \infty)$ as a Poisson process [S4]. This is the configuration of the ideal gas—or the maximum-entropy configuration—in which the number of cells observed in any interval of length ℓ is a Poisson random variable $N_{\lambda\ell}$ whose positions are i.i.d. uniform random variables [S4]. This is the case of class (i) configurations.

The Voronoi lengths $V_i = (L_i + L_{i+1})/2 = (X_{i;\lambda} + X_{i+1;\lambda})/2$ are therefore gamma-distributed with k = 2,

$$V_i = \frac{X_{i;\lambda} + X_{i+1;\lambda}}{2} = \frac{1}{2} Y_{i;2,\lambda} \overset{\text{pdf}}{\sim} 4\lambda^2 v e^{-2\lambda v}.$$
(S43)

This result already shows explicitly the deep link between the Voronoi construction and gamma distributions. More generally, for burst count b, the resulting Voronoi lengths, by the same argument, are k = 2b-gamma random variables.

In the opposite limit, holding the mean spacing $\mathbb{E}[L_i] = b/\lambda$ fixed while taking the burst count $b \to \infty$, the variance $\sigma^2 = b/\lambda^2 = \mathbb{E}[L_i]^2/b$ vanishes while the central limit theorem ensures the convergence of the shifted and rescaled lengths $\sqrt{b} \left(\frac{L_i}{\mathbb{E}[L_i]} - 1\right) \to W_{i;0,1}$ to a Gaussian. This is the perfectly spaced lattice of cellular positions occurring as the natural numbers \mathbb{N} on $[0, \infty)$ —the "crystalline," or class (i) configuration.

Model I.1 (circular Gibbs) —Consider a circular Volvox, constructed by selecting a fixed number $N_{;\lambda} = n + 1$ of successive points $\{R_i\}_{i=0}^{n+1}$ from the half-line in I.0 and identifying the first and last points, as in Fig. 1(c). This circle has a random circumference C ("Gibbs ensemble") which is *nb*-gamma distributed, with resulting Voronoi lengths $V_i = Y_{i;2b,2\lambda}$ governed by k = 2b-gamma distributions by an identical argument as in I.0. Fig. 1(d) shows an empirical distribution of V_i from 10⁴ samples.

Model I.2 (circular canonical)—Consider a fixed-N, fixed-C configuration as follows. Let us take the intercellular spacings L_i to be b-gamma random variables $Y_{i;b,\lambda}$ as in I.1, conditional on their sum $\sum_i Y_i = C$. That is, if $A = Y_{1;b,\lambda}$ is one spacing and $B = \sum_{j=2}^{n} Y_{j;b,\lambda} = Y_{B;(n-1)b,\lambda}$ is the rest, then the distribution of A given A + B = C is

$$f_{A|C}(a|c) = \frac{a^{b-1}(c-a)^{(n-1)b-1}}{B(b,(n-1)b)c^{nb-1}}$$
(S44)

which one shows by the fraction-sum independence property of gamma random variables I.5, where $B(\alpha, \beta)$ is the Beta function. Then, by inspection of (S44) and scaling laws for r.v.s, L_i is the beta random variable $A|C = cZ_{i;b,b(n-1)}$ with C = c now the fixed circumference.

Once more, in the special case of protein burst count b = 1, $L_i = cZ_{i;1,n-1}$, which is simply the first order statistic of (n + 1) i.i.d. uniform random variables on the interval [0, c] (with n + 1 arising from identifying the ends of the interval to form a circle). Then, this is the distribution of *uniform spacings* of the interval [0, c], which is precisely the distribution of waiting times for n events in a Poisson process conditional on a total wait time C = c (see §4.1, [S5]), as shown in Fig. 1(c).

Since $Z_{i;b,b(n-1)}$ can be expressed as the fraction $Y_{i;b,\lambda} / \sum_{j=1}^{n} Y_{j;b,\lambda}$ I.5, this allows us to compute the corresponding

Voronoi lengths V_i as

$$V_i = \frac{c}{2} \frac{Y_i + Y_{i+1}}{\sum_{j=1}^n Y_j} = \frac{c}{2} Z_{j;2b,(n-2)b},$$
(S45)

with subscript Z_j indicating that Z_j is a distinct (though not independent) random variable from the earlier Z_i . In the Poisson case b = 1, this is now simply one-half the *second* order statistic of i.i.d. uniform r.v.s. on [0, c].

Taking the large-cell count and ECM circumference limits $n, c \to \infty$ limit at fixed cell number density $\rho = m/c = (n-2)/c$ (analogous to the thermodynamic limit of statistical mechanics) and per-cell burst count b, one obtains I.2 the convergence in distribution of the Voronoi segments,

$$V_i = \frac{mb}{2\rho} Z_{;2b,mb} \xrightarrow{m \to \infty} \frac{1}{2} Y_{;2b,\rho}, \tag{S46}$$

whose limit is once again the k = 2b gamma random variable (with rate ρ) in I.0 and the Gibbs ensemble I.1.

Model I.3 (circular grand canonical)—Let the circumference C = c now be fixed with the count N a random variable. In the case of b = 1 bursts, $N = N_{;c\lambda}$ is Poisson-distributed. Using a similar argument to I.2, the Voronoi length distribution p_{V_i} can be determined by marginalizing the joint distribution $p_{Z_{;2,n-1},N_{;\lambda}}$ over n, giving the compound beta-Poisson distribution which is once again a k = 2 gamma distribution, shown as follows.

As in I.2, let us consider the kth order statistic of N uniform random variables (representing the fixed-circumference constraint), with N_{λ} now a Poisson-distributed random variable conditioned to be minimum k. The marginal distribution of the order statistic given λ is (a particular) compound beta-Poisson distribution, given by

$$P(Z_{k,N-k+1} = x | \lambda, N \ge k) = \sum_{n=k}^{\infty} P(Z_{k,n-k+1} = x | N = n) P(N = n | \lambda, N \ge k).$$
(S47)

To see the parametrization more clearly, let m = n - k + 1; then,

$$(S47) = \frac{1}{1 - P(N < k)} \sum_{m=1}^{\infty} \frac{x^{k-1}(1-x)^{m-1}}{B(k,m)} \frac{\lambda^{m-1+k}e^{-\lambda}}{\Gamma(m+k)}$$
(S48)

$$= \frac{1}{1 - P(N < k)} \frac{\lambda^k x^{k-1} e^{-\lambda}}{\Gamma(k)} \sum_{m=1}^{\infty} \frac{(\lambda(1-x))^{m-1}}{\Gamma(m)}$$
(S49)

$$= \frac{1}{1 - P(N < k)} \frac{\lambda^k x^{k-1} e^{-\lambda x}}{\Gamma(k)}$$
(S50)

$$=: \frac{1}{Z} \frac{\lambda^k x^{k-1} e^{-\lambda x}}{\Gamma(k)}, \qquad x \in [0, 1].$$
(S51)

Recognizing the second factor as the gamma distribution, the first factor Z is simply a normalizing constant restricting the support to [0, 1]. Here we see the emergence of gamma distributions from the order statistics of a Poissondistributed number of uniform random variables. This may be viewed as a roundabout method of constructing the 1D Poisson process. As we take the support of this distribution (the circumference C) to infinity, we have $P(N_{C\lambda} < k) \rightarrow 0$ for any fixed k, hence $Z \rightarrow 1$ and we recover the true gamma distribution.

For the general b case, we note that this construction is equivalent to placing an observation window [x, x + c] at random on the half-line process I.0, in which case the spacings L_i follow a truncated b-gamma distribution:

$$L_i \stackrel{\text{pdf}}{\sim} \frac{\lambda^b x^{b-1} e^{-\lambda x}}{\gamma(b, \lambda c)}, \qquad x \in [0, c]$$
(S52)

with γ the lower incomplete gamma function. Taking $c \to \infty$ with rate λ fixed (thermodynamic limit), we have $\gamma(b, \lambda c) \to \Gamma(b)$, hence $L_i \stackrel{d}{\to} Y_{i;b,\lambda}$ and $V_j \stackrel{d}{\to} Y_{j;2b,2\lambda}$, giving the same k = 2b-gamma distribution for Voronoi lengths. *Model I.4 (circular canonical, finite size)*—This refers to the fixed-cell size model discussed and analyzed in the main text.

Model I.D.1 (Brownian motion on the circle)—Let $\{R_t^{(i)}\}_{i=1}^n$ be n Brownian motions (BMs) on a circle of radius r given by

$$R_t^{(j)} = r \exp(i\theta_t^{(j)}),\tag{S53}$$

with $\theta_t^{(j)}$ standard BMs on \mathbb{R} and initial conditions for the probability density $p^{(j)}(0) = \delta_{R_0^{(j)}}$. The time-dependent probability density $p^{(i)}(t)$ tends exponentially in L^2 to the uniform distribution, hence $R_t^{(i)}$ converge in distribution



FIG. S1. Dynamic models of cellular positions during growth converge to gamma distributions in various limits. (a1,a2) Standard Brownian motion in angular coordinates converges to beta-distributed segments in large t, and gamma-distributed segments in large n. (b1,b2) Dyson Brownian motion in angular coordinates converges to gamma-distributed segments at large t and n. Non-conformance to gamma distributions is observed at low n due to pair-repulsion. (c1,c2) Dyson Brownian motion on a growing domain satisfying particular growth constraints converges in large-t and n to gamma-distributed segments.

to i.i.d. uniform r.v.s. and the configuration approaches that of Model I.2. V_i are therefore beta-distributed (S45) in large t and gamma-distributed in large t, n (S46)—see Fig. S1(a1,a2). Yet, the sample paths of (S53) almost surely intersect, unphysically reordering the cells.

Model I.D.2 (noncolliding Brownian motion)—Let $\{R_t^{(i)}\}_{i=1}^n$ be samples of the conditional distributions of n circular Brownian motions whose angles are in ascending order modulo 2π , thereby lying in the set

$$D_n = \{ x \in \mathbb{R}^n \mid x_1 < \dots < x_n < x_1 + 2\pi \},$$
(S54)

a construction known as noncolliding Brownian motion or Brownian motion within the Weyl chamber D_n [S6]. In [S7] eq. 4.1, it is shown that the conditional fluctuations are Gaussian plus a singular r^{-1} pair-repulsion,

$$d\theta_t^{(i)} = \sigma dB_t^{(i)} + \frac{\sigma^2}{2} \sum_{j \neq i} \cot\left(\frac{\theta_t^{(i)} - \theta_t^{(j)}}{2}\right) dt.$$
(S55)

A physical interpretation of (S55) is that of a gas confined to the unit circle with the pair-potential

$$U = -\sum_{j < k} \log |\exp(i\theta_k) - \exp(i\theta_j)|, \qquad (S56)$$

constituting a simple model of non-colliding cell motion. Eq. S55 is precisely the eigenvalue dynamics $\lambda_t^{(j)} = \exp(i\theta_t^{(j)})$ of a Brownian motion U_t on the unitary group $\mathbb{U}(n)$, known as Dyson Brownian motion [S8].

Being confined to D_n (S54), the positions $R_t^{(i)}$ do not converge to uniform r.v.s on the circle as in I.5—compare Figs. S1(a1) and S1(b1). The stationary distribution of (S55) is the circular unitary ensemble (CUE) [S8],

$$\rho_*(\theta_1, \cdots, \theta_n) = \frac{1}{Z_n} \prod_{j < k} |\exp(i\theta_j) - \exp(i\theta_k)|^\beta,$$
(S57)

where $\beta = 2$ is the inverse temperature. We use this result to derive the Voronoi length distribution in the large-t, n limits. Let $\{\theta^{(i)}\}_{i=1}^n$ be a sample of the stationary distribution (S57), the spectrum of a uniform sample of $\mathbb{U}(n)$; the

empirical distribution $\mu_{\theta}(n) = n^{-1} \sum_{i=1}^{n} \delta_{\theta^{(i)}}$ converges almost surely in large *n* (Theorem 3, [S9]) to the uniform distribution on the unit circle. Thus, the spacings $\theta_t^{(i+1)} - \theta_t^{(i)}$ converge in large-*t* and *n* to the spacings of the order statistics of *n* uniform random variables as in IS.2. Taking $n \to \infty$ with density $\rho = (n-2)/c$ fixed, V_i converge to k = 2 gamma random variables as in (S46).

Convergence to gamma laws depending on particle count n is shown for BM and DBM in Figs. S1(a2,b2); in contrast to BM, DBM spacings lose the long tail at low n due to repulsion (S57).

Model I.D.3 (noncolliding Brownian motion, growth)—To account for growth of the ECM, let the radius r(t) in A.I.1 be time-dependent, scaling the configuration as $R_t^{(i)} = r(t) \exp(i\theta_t^{(i)})$ with $\theta_t^{(i)}$ given by (S55) as shown in Fig. S1(c1). Applying Itô's lemma, $R_t^{(i)}$ satisfies the stochastic differential equation

$$dR_t^{(i)} = \dot{r} \exp(i\theta_t^{(i)})dt + iR_t^{(i)}d\theta_t^{(i)} - \frac{r}{2}\theta_t^{(i)}dt.$$
 (S58)

Substituting $d\theta_t^{(i)}$ from (S55), the diffusion constant for (S58) is $D = r^2 \sigma^2/2$. Requiring that the lateral diffusion is time invariant implies $\dot{D} = 0$, and thus that the standard deviation of the radius-normalized dynamics (S55) should decay as $\sigma(t) \propto r(t)^{-1}$. Exponential convergence of (S55) to the stationary solution (S57) is ensured by a growth condition on r(t). By standard Fourier arguments (e.g. §2.2, [S10]), solutions to the time-dependent diffusion equation for the probability density of p(t) of the unitary Brownian motion U_t satisfy, for some Poincaré-like constant $C_n > 0$ depending only on n,

$$d(p(t),\nu) \le d(p(0),\nu) \exp\left(-C_n \int_0^t \sigma(s)^2 ds\right),\tag{S59}$$

with d the L^2 metric and ν the uniform (Haar) measure on the unitary group $\mathbb{U}(n)$. Therefore, if r(t) satisfies:

$$\lim_{t \to \infty} \int_0^t \frac{1}{r(s)^2} ds = \infty, \qquad r(0) > 0$$
(S60)

the RHS in (S59) vanishes in large t, and global exponential stability is assured. Then, as in ID.2, the positions $R_t^{(i)}$ approach a random uniform spacing of a circle of radius r(t) in large n, resulting in gamma-distributed Voronoi segments V_i . Rapid convergence in t to a gamma law (with $D = 0.1, n = 1000, \dot{r} = 1$) is shown in Fig. S1(c2). Formally, (S60) is not satisfied by such a linear growth law, yet we observe empirical convergence to a gamma law on the order of a unit of (scaled) time.

Condition (S60) can be understood by a Péclet number relating drift and diffusion timescales in growth. Considering the radial drift velocity v_r in (S58), let

$$Pe = \frac{\tau_d}{\tau_{v_r}} = \frac{2L\dot{r}}{r^2\sigma^2} \propto L\dot{r}$$
(S61)

with L a test length section. In the limit $\text{Pe} \to 0$, condition (S60) is satisfied; when $\text{Pe} \to \infty$, the exponential multiplier in the bound (S59) approaches 1, "freezing" the angles $\theta_t^{(i)}$ to initial conditions. Finally, conditions $\dot{D} = 0$, $\dot{\text{Pe}} = 0$, and (S60) cannot simultaneously be satisfied.

Model I.D.4 (maximum-entropy growth rates)—Let the segments grow linearly in time as $\dot{L}_i = G_{i;\mu}$, with i.i.d. growth rates G_i which are positive continuous random variables with some common mean growth rate μ . If the distribution of G_i maximizes entropy subject to the mean and nonnegativity constraint—perhaps more interpretable as uncertainty about cellular behavior than global maximum-entropy assumptions [S11]—then $G_{i;\mu} = X_{i;1/\mu}$ is an exponential random variable of rate $\lambda = 1/\mu$. Then, for any time t, the normalized configuration

$$\frac{L_i(t)}{\sum_{j=1}^n L_j(t)} = \frac{L_i(0) + tG_i}{\sum_{j=1}^n L_j(0) + tG_j} \stackrel{\mathrm{d}}{\to} \frac{X_{i;1/\mu}}{\sum_{j=1}^n X_{j;1/\mu}}$$
(S62)

converges in large t to a uniform spacing as in I.2, and therefore has beta-distributed Voronoi lengths converging to gamma-distributed lengths in large n (S46).

III. DEFINING POINT PROCESSES IN d DIMENSIONS

Many of the following definitions are standard and recalled here for a self-contained reference.

A. Definitions in \mathbb{R}^d

The familiar Poisson process of rate λ on the half-line $[0, \infty)$ is constructible as the cumulative sum of i.i.d. exponential random variables $X_{i;\lambda}$. The construction of general point processes on a domain $K \subseteq \mathbb{R}^d$, however, is more technical, formalizing the notion of a "random almost-surely finite subset," for which we recall several standard definitions [S4]. Throughout, we assume K is a complete separable metric space (c.s.m.s.), e.g. a closed subset of \mathbb{R}^n .

Definition III.1 (Finite point process -2.2-2.4, [S4]). A finite point process N on a complete separable metric space K is a family of random variables N(E) for each Borel set $E \in \mathcal{F}_K$, such that, for every bounded E,

$$\mathbf{P}[N(E) < \infty] = 1. \tag{S63}$$

Formally, N is a random measure (see e.g. 5.1 [S4] or Chapter 9 [S4]). Without delving too deeply into this formalism, let us introduce the following definition based upon samples of N.

Definition III.2 (Simple point process). A *simple* point process N is one whose points are non-overlapping. In other words, every sample of N can be written as the counting measure

$$\nu = \sum_{i \in I} \delta_{x_i} \tag{S64}$$

where I is an index set, δ denotes the Dirac measure, and $P[x_i = x_j] = 0$ for all $i \neq j$.

Definition III.3 (Non-atomic point process). A *nonatomic* point process N is one for whom the probability of realizing any particular point $x \in K$ is zero. That is,

$$P[N(\{x\}) > 0] = 0.$$
(S65)

These definitions are sufficient to define and analyze the Poisson point process.

Definition III.4 (Poisson point process). A Poisson point process N on a c.s.m.s. K is defined by an *intensity* measure $\Lambda(E)$ such that, for all Borel sets $E \in \mathcal{F}_K$, N(E) is a Poisson random variable, i.e.

$$N(E) \stackrel{\text{pdf}}{\sim} \frac{\Lambda(E)^k \exp(-\Lambda(E))}{k!}.$$
(S66)

Example III.1 (Stationary Poisson process). A stationary Poisson process of rate λ is given by the intensity measure $\Lambda(E) = \lambda \mu(E)$, where μ is the Lebesgue measure and $\lambda > 0$ is a positive rate.

Definition III.5 (Independent scattering / complete independence). A point process N satisfies the *independent* scattering or complete independence property if, for all n > 1 and disjoint Borel sets $E_1, \ldots, E_n \in \mathcal{F}_K$, the variables $N(E_1), \ldots, N(E_n)$ are mutually independent.

B. Characterizing Poisson point processes

Immediately, we see that Poisson point processes are simple and finite if the intensity measure $\Lambda(E)$ is given by

$$\Lambda(E) = \int_{E} \lambda(x) dx \tag{S67}$$

for some function $\lambda : K \to \mathbb{R}_+$. Poisson point processes III.4 satisfy the complete independence property III.5—but remarkably, these properties are not logically independent.

Theorem III.1 (Prekopa 1957, Theorem 2.4.V [S4]). A point process N is a non-atomic Poisson point process if and only if it is finite III.1, simple III.2, non-atomic III.3, and completely independent III.5.

The characterization theorem III.1 motivates and justifies the use of Poisson processes (i.e. Poisson-distributed count variables) in any scenario where points in realizations are non-interacting.

C. Sampling

Lemma III.2. The conditional distribution of a Poisson point process of intensity $\lambda(x)$ on a domain K is $\frac{1}{\Lambda(K)}\lambda(x)$.

Lemma III.2 allows one to sample a homogeneous Poisson point process of rate λ by first sampling a Poisson random variable $N_{\lambda\mu(K)} = n$, and scattering the *n* as points as i.i.d. uniform random variables in *K*. Point processes with a hard-core repulsion (such as the Matérn Type-II point process [S12]) can often be realized as a *thinning* of a Poisson point process.

Definition III.6 (Matérn type-II hard-core point process, [S12]). Let N be a homogeneous Poisson point process of rate λ . To each point X_i of N, assign a mark M_i which is an i.i.d. uniform random variable on (0, 1). Then, construct the Matérn process N' with hard-core repulsion distance r as

$$N' = \{X_i \in N \mid M_i < M_j \ \forall M_j \in B(X_i, r), \ i \neq j\}.$$
(S68)

The points of N' are situated at a minimum distance r from one another.

1. Poisson and Matérn processes on \mathbb{S}^d

Recall that a zero-mean multivariate Gaussian $W_{0,\Sigma}$ with Σ a $d \times d$ symmetric positive-definite covariance matrix has the ellipsoids $\{x \mid x^{\intercal}\Sigma^{-1}x = r^2\}$ as level sets of constant density. When $\Sigma = I$, this is the property of *spherical* symmetry. Combined with the fact that the map $x \mapsto x ||x||^{-1}$ is surface-area-preserving up to a constant multiple, this yields a computationally efficient and numerically stable method for generating iid uniform random variables U_i on \mathbb{S}^d : $U_i = W_{i;0,I} ||W_{i;0,I}||^{-1}$.

Lemma III.2 then allows the realization of homogeneous Poisson processes on *d*-spheres of radius r as $N_{\lambda Ar^d} = n$, $\{U_i\}_{i=1}^n$, with A the surface area of the unit sphere \mathbb{S}^d and λ the intensity per unit area. Conveniently, the parametrization of U_i in Cartesian coordinates allows the realization of Matérn processes (III.6) using the geodesic (great-circle) distance $d(U_i, U_i) = r \arccos(U_i^{\mathsf{T}}U_i)$.

IV. RESULTS FOR TWO-DIMENSIONAL POISSON-VORONOI TESSELLATIONS

In dimension $d \ge 2$, known analytical results concerning Voronoi tessellations of point processes are limited to lower-dimensional facets, such as edge (2D) and face (3D) distributions (see [S13] and §4.4, [S14]). The difficulty in higher dimensions arises primarily from the loss of uniqueness for shapes satisfying geometric properties—such as fixed measure (length, area, volume)—for which one must first consider distributions over shapes, then marginalize over the level-sets satisfying a scalar geometric property, such as aspect ratio. For this reason, in the following models we present primarily numerical results (with partial analytical arguments where applicable), and present a validation of the numerical method in IV A.

Model II.1 (periodic unit square)—Consider a homogeneous Poisson point process on the unit square $[0,1]^2$ with periodic boundary conditions, denoted \mathbb{T}^2 . On general *d*-dimensional domains, the point process is specified by an intensity measure $\lambda(A)$ for subsets $A \subseteq \mathbb{T}^2$ in which the count $N_{A;\lambda(A)}$ is a Poisson random variable of rate $\lambda(A)$. A homogeneous Poisson process —one whose intensity λ is constant on sets A of constant measure—is realizable by sampling the total count $N_{;\lambda(\mathbb{T}^2)}$ and assigning the positions $\{R_i\}_{i=1}^n$ conditional on N = n as i.i.d. uniform random variables. Figure S2 shows numerical simulations for k = 1000 trials with intensity $\lambda(\mathbb{T}^2) = 10^3$, which is on the order of the number of somatic cells in Volvox carteri.

The periodic Voronoi tessellation on \mathbb{T}^2 , shown in the small-*n* example in Figure S2(a1)-(d1), is constructed by copying $\{R_i\}$ in four quadrants around \mathbb{T}^2 and selecting the sub-tessellation corresponding to the original points. Areas a, nondimensionalized as λa , conform to a gamma random variable with $k \approx 3.5$, as in Fig. S2(a2). The isoperimetric deficit $D = L/\sqrt{4\pi a} - 1$ with L the perimeter, conforms after an appropriate rescaling to a log-normal random variable with $\sigma \approx 0.6$, shown in Fig. S2(c2). The aspect ratio AR of a Poisson-Voronoi tessellation does not conform to a gamma distribution (Fig. S2(b2)), in contrast to confluent tissue [S15] in which gamma-distributed aspect ratios appear in a diverse range of densely-packed cell types and inert matter. Instead, AR conforms approximately to a beta-prime distribution, which naturally arises as the ratio of independent gamma random variables. Figure S2(d2-e2) shows that the major and minor axis lengths are approximate gamma-distributed; while we do not in general expect the major and minor axis to be independent random variables, the beta-prime distribution governs the aspect ratio in the event that they are, with shape parameter k_1/k_2 .

Aspect ratio Isoperimetric deficit Major axis Minor axis Area (c1) 0.283Y_{3.534} (b2) 10° (d2) 10° (e2) 0.065Y_{25.087,1} - 0.61 10- 10^{-} 10 10 10 10-10 $\lambda_1/\overline{\lambda_1}$ 2.0 $(AR - 1)/(\overline{AR} - 1)$ $(D - D_{\min})/(\overline{D} - D_{\min})$ $\lambda_2/\overline{\lambda_2}$ λα

FIG. S2. Poisson-Voronoi tessellation on the periodic unit square. Panels (a1) - (e1) show the Voronoi cells colored by four geometric quantities defined from the *n*th moments of area and perimeter. Panels (a2) - (e2) show empirical and maximum-likelihood estimations of gamma (denoted Y), lognormal (denoted $\exp(W)$), and beta prime (denoted Z') distributions where applicable. Poisson-Voronoi tessellations do not have gamma-distributed aspect ratios, instead following an approximate beta-prime law.

A. Validating Poisson-Voronoi simulations

Let V_i be the measure (area, volume, etc.) of the typical Poisson-Voronoi cell. While the distribution of V_i is presently unknown, numerically integrated second moments of V_i in \mathbb{R}^2 and \mathbb{R}^3 have been reported [S16], facilitating comparison with numerical study. Large simulations [S17, S18] with $n > 10^6$ cells have found that gamma distributions, and in particular a 3-parameter generalization [S17]

$$f_{Y_{;k,\lambda,a}}(v) = \frac{a\lambda^{k/a}v^{k-1}e^{-\lambda v^a}}{\Gamma(k/a)}$$
(S69)

achieve good maximum-likelihood fit to data with < 1% error relative to the analytical second moment. In Fig. S3, the estimated second moment $\langle V_i^2 \rangle$, shape parameter k, and CDF root mean square error are displayed for 500 trials of $N \stackrel{\text{pdf}}{\sim}$ Poisson(10³) points. The average empirical, gamma, and beta second moments show good agreement with Gilbert's [S16] numerically integrated value of 1.280 and are within 1% relative error, validating the numerical method. The estimated value of $k \approx 3.7$ for gamma on the torus T is consistent with prior results finding $k \approx 3.6$ [S19] in the plane \mathbb{R}^2 . On the other hand, the estimated value of $k \approx 3.2$ for beta is lower than gamma and closer to Tanemura's [S17] generalized-gamma (S69) fit finding k = 3.315, suggesting that a beta hypothesis is a good substitute for the generalized gamma distribution. Lastly, we observe that the beta RMSE is slightly decreased compared to gamma.

B. A conjecture for the distribution of Poisson-Voronoi areas

In dimension $d \ge 2$, exact distributions for the cell measures (areas, volumes, and so on) of Delaunay triangulations (denoted D_i) of a Poisson point process are known [S20], with the distribution in \mathbb{R}^2 given by a modified Bessel function of the second kind,

$$f_{D_i}(v) = c_1 v^{\alpha_1} K_n(c_2 v^{\alpha_2}), \tag{S70}$$

with parameters c_i, α_j, n . On the other hand, exact distributions for their vertex-cell duals—the Voronoi tessellations—are presently unknown. We conjecture, however, that (S70) should also govern the Voronoi areas V_i based on the following heuristic argument. Conditional independence of the volume of the *fundamental region* (a particular set containing the vertices of a Voronoi cell and the origin) and its shape (see [S13]) suggests that one may assume a particular approximate shape for the typical Voronoi cell, say, an approximately elliptical region. If, as seen in Fig. S2, the principal axes are gamma-distributed, and additionally they are independent, then V_i is proportional to their



FIG. S3. Gamma- and Beta-maximum likelihood fits for Poisson-Voronoi tessellations of the flat torus \mathbb{T}^2 . The numerically integrated value of the second moment $\mathbb{E}[V_i^2] = 1.280$ found by [S16] is plotted as a dashed line in the left plot, indicating good agreement with our numerical simulations. The experimentally determined shape parameter k = 3.315 of the generalized-gamma fit found by [S17] is plotted as a dashed line in the middle plot.

product and has a distribution precisely of the form (S70) (see [S21]). A possible route to proving this claim is to show that the desired independence holds in a thermodynamic limit.

V. THE VORONOI LIQUID

Let $\Omega \subset \mathbb{R}^d$ be a compact connected measurable set with positive *d*-dimensional Lebesgue measure $|\Omega| > 0$ as in the main text. For a finite set of points $\{x_i\}_{i=1}^n = \mathcal{X} \subset \Omega^d$ and associated partitions $\{D_i\}_{i=1}^n = \mathcal{D}$ with $D_i \cap D_j = \emptyset$, $\bigcup_i D_i = \mathbb{T}^d$, the quantization problem is to minimize the cost

$$E(\mathcal{X}, \mathcal{D}) = \sum_{i=1}^{n} E_{i}, \quad E_{i} = \int_{D_{i}} \|x_{i} - y\|_{2}^{2} dy,$$
(S71)

which is the approximation error of points $y \in \Omega^d$, and therefore the domain Ω^d itself, by the partitions $\{x_i, D_i\}$. This illustrates the origin of (S71) in meshing problems [S22].

A. The intensive energy

Define U to be the energy per unit measure

$$U(\mathcal{X}) = \frac{n^{2/d}}{|\Omega|^{1+2/d}} E(\mathcal{X}, \operatorname{Vor}(\mathcal{X})).$$
(S72)

We argue (S72) is an intensive quantity as follows. First, consider the "tiling" (frozen) phase in which \mathcal{X}, \mathcal{D} is a tiling of Ω with x_i the centroids of congruent cells $D_0 \cong D_i$ and $|\Omega| = n |D_0|$. Then (S72) becomes

$$U_{\text{tiling}}(\mathcal{X}) = \frac{\rho^{2/d}}{|\Omega|} \sum_{i=1}^{n} \int_{D_i} \|x_i - y\|^2 \, dy = \frac{\rho^{2/d}}{d \, |D_0|} \operatorname{tr}(S_i(\mu_i)) = \frac{1}{|D_0|^{1+2/d}} \operatorname{tr}(S_i(\mu_i)), \tag{S73}$$

which is simply the cell's second moment S_i , nondimensionalized by the cell measure. Recall that in 2D, for example, $tr(S_i)$ has units length⁴. More generally, if $\langle E_i \rangle$ is the average partition energy, then U is expressible as

$$U(\mathcal{X}) = \rho^{1+2/d} \langle E_i \rangle. \tag{S74}$$

Now we note that U is scale-invariant as follows. Let $x \mapsto \alpha x$ with $\alpha > 0$, so that $|\Omega| \mapsto \alpha^d |\Omega|$ and $E_i \mapsto \alpha^{2+d} E_i$. Then,

$$U(\mathcal{X}) \mapsto \frac{n^{1+2/d}}{\alpha^{d+2} |\Omega|^{1+2/d}} \cdot \alpha^{d+2} \langle E_i \rangle = U(\mathcal{X})$$
(S75)

Lastly, let us make an informal argument for U being a dimensionless quantity independent of n in the general- \mathcal{X}, \mathcal{D} case. Let $a \sim b$ indicate that a is of the same units and scale as b, such that $|\Omega| \sim V$ is the scale of the system measure. Then,

$$U(\mathcal{X}) = \frac{\rho^{2/d}}{|\Omega|} \sum_{i} E_{i} \sim \left(\frac{n}{V}\right)^{2/d} \cdot \frac{1}{V} \cdot n \cdot E_{i}.$$
(S76)

Let $||x_i - y|| \sim \ell$ be the length scale of the typical partition and note that $E_i \sim \ell^{2+d}$. Assuming further the decomposition $\ell^d \sim V/n$, the generalization from the tiling case, we have

$$\sim (\ell^{-d})^{2/d} \cdot \ell^{-d} \cdot \ell^{2+d} \sim 1, \tag{S77}$$

so that U is dimensionless.

B. Interpreting E as a strain energy

Eq. (S71) is expressible in terms of the second area moment $S_i(x_i)$ about x_i as

$$E(\mathcal{X}, \mathcal{D}) = \sum_{i} \operatorname{tr} S_{i}(x_{i}).$$
(S78)

Since for affine transforms $T_x(y) = F(y-x) + x$ about the point x for some F with $\det(F) > 0$, we have that the second moment maps as $S(x) \xrightarrow{y \mapsto T(y)} FS(x)F^{\intercal} \det F$, and (S78) is further equal to

$$=\sum_{i}m_{i}\operatorname{tr}F_{i}F_{i}^{\mathsf{T}}\operatorname{det}F_{i} \tag{S79}$$

where $\frac{m_i}{p}I$ is the second area moment of an isotropic natural configuration (e.g. a circle or regular *p*-gon) from which F_i is a strain tensor. It was already shown in the main text that the optimal \mathcal{D} for fixed \mathcal{X} is the Voronoi tessellation, hence for convex Ω , D_i are convex polygonal. Then, as argued in [S23] (SM), tr(FF^{\intercal}) is the bulk strain energy, in the small-strain limit, of a deformation from a regular *n*-gon, for any isotropic frame-indifferent constitutive relation (which therefore depends only on the principal tensor invariants of F). Note that, for dilatations $\Omega \mapsto \alpha \Omega$ with $\alpha > 0$,

$$E[\{\alpha x_i, \alpha D_i\}] \mapsto \alpha^{2+d} E[\{x_i, D_i\}].$$
(S80)

C. Gradient flow is a nonlinear diffusion in 1D

When d = 1, for positions $x = (x_1, \ldots, x_n) \in O$ where $O \subset \mathbb{R}^n$ are the ordered vectors (also called *Weyl chamber*)

$$O = \{ y \in \mathbb{R}^n \mid 0 \le y_1 \le \dots \le y_n < 1 \le y_1 + 1 \},$$
 (S81)

we have the Voronoi centroids and lengths

$$\mu_i = \frac{x_{i-1} + 2x_i + x_{i+1}}{4}, \quad v_i = \frac{x_{i+1} - x_{i-1}}{2}, \tag{S82}$$

with $x_{n+1} = x_1$. Thus the energy (S78) becomes the nearest-neighbors cubic potential

$$V(\mathcal{X}) = \sum_{i} \int_{\frac{x_{i-1}-x_i}{2}}^{\frac{x_{i+1}-x_i}{2}} y^2 dy = \frac{1}{24} \sum_{i} \left[(x_{i+1}-x_i)^3 + (x_i-x_{i-1})^3 \right].$$
 (S83)

Moreover, its gradient descent, as we see to be consistent with (S89), is

$$\dot{x}_i = -\frac{\partial U}{\partial x_i} = 2 \left| D_i \right| (\mu_i - x_i) \tag{S84}$$

$$= (x_{i+1} - x_{i-1}) \left(\frac{x_{i-1} + 2x_i + x_{i+1}}{4} - x_i \right)$$
(S85)

$$= \frac{1}{4} \left((x_{i+1} - x_i)^2 - (x_i - x_{i-1})^2 \right),$$
(S86)



FIG. S4. Gradient flow of the quantization energy from Poisson initial conditions on the unit circle have Voronoi lengths which are well-approximated by beta and gamma distributions with increasing shape parameter k.

whose fixed point is the 1D lattice satisfying $(x_{i+1} - x_i)^2 = (x_i - x_{i-1})^2$ for all *i*. The dynamics of the spacings $\ell_i = x_{i+1} - x_i$ are then given by

$$\dot{\ell}_i = \frac{d}{dt}(x_{i+1} - x_i) = \frac{1}{4}(\ell_{i+1}^2 - 2\ell_i^2 + \ell_{i-1}^2) = \frac{1}{4}\sum_{j=i\pm 1}(\ell_j^2 - \ell_i^2).$$
(S87)

We recognize from the final expression that (S87) is a centered-differences discretization of the porous medium equation $\partial_t u = \partial_{xx} u^2$. Moreover, from (S83), we see that the equivalent energy over lengths $(\ell_1, \ldots, \ell_n) = \mathcal{L}$ is

$$V(\mathcal{L}) = \frac{1}{24} \sum_{i} (\ell_i^3 + \ell_{i-1}^3), \tag{S88}$$

with ℓ_i nonnegative and subject to total length constraint $\sum_i \ell_i = L$. For uniformly distributed (Poisson) initial conditions x_i on [0, 1] with periodic boundary conditions, the resulting Voronoi lengths under the dynamics (S87) are well-approximated by beta random variables as shown in Figure S4.

D. Stochastic gradient flow on the torus

Fix now $\Omega = \mathbb{T}^d$. It is shown in [S22] that E is C^2 and

$$\frac{\partial U}{\partial x_i} = \frac{2|D_i|}{|\mathbb{T}^d|} (x_i - \mu_i) = 2|D_i| (x_i - \mu_i)$$

where μ_i is the centroid of D_i . This suggests the continuous-time gradient flow

$$\dot{x}_i = 2 \left| D_i \right| (\mu_i - x_i). \tag{S89}$$

Consider now the Itô process

$$dR_i(t) = \frac{\partial U}{\partial x_i} \bigg|_{R_i(t)} dt + \sigma dW_i(t), \tag{S90}$$

where $W_i(t)$ are independent standard Brownian motions. In the limit $\sigma \to \infty$, $(\mathcal{X}(t), \mathcal{D}(t))$ converges in distribution (in large t) to a Poisson-Voronoi tessellation, while in the limit $\sigma \to 0$ it converges to a centroidal Voronoi tessellation [S22, S24]. The corresponding Fokker-Planck equation for the joint probability density $p(R_1, \ldots, R_n) =: p(R)$ of (S90) is

$$\frac{\partial p}{\partial t} = -\nabla \cdot p\nabla U + \frac{\sigma^2}{2}\Delta p. \tag{S91}$$

$$\frac{d\mu_{\beta}(x)}{dx} = f_{\beta}(x) = \frac{1}{Z_{\beta}} \exp\left(-\beta U(x)\right), \qquad (S92)$$

with Z_{β} the normalizing constant and $\beta^{-1} = \sigma^2/2$ the diffusion constant. Then (S92) minimizes the Gibbs free energy functional

$$G_{\beta} = \mathbb{E}_{f_{\beta}}[U] - \beta^{-1}H[f_{\beta}], \tag{S93}$$

with $\mathbb{E}_{f_{\beta}}$ denoting the expectation with respect to f_{β} and H the differential entropy of f_{β} . The previous limits—Poisson-Voronoi and centroidal Voronoi tessellations—correspond to the infinite- $(\beta \to 0)$ and zero- $(\beta \to \infty)$ temperature limits respectively.

E. Specifics of the Langevin simulation

Let us now sample from the Gibbs measure (S92) using Markov Chain Monte Carlo (MCMC). We take $\Omega = \mathbb{T}^d$ to be the unit *d*-cube with periodic boundary conditions. Euler-Maruyama integration of (8) with discrete steps $\varepsilon > 0$ is performed by

$$R_i(t+\varepsilon) = -\varepsilon \frac{\partial V}{\partial x_i} \Big|_{R_i(t)} + \sqrt{2\varepsilon\beta^{-1}}\eta, \ \eta \stackrel{\text{pdf}}{\sim} \mathcal{N}(0,1).$$
(S94)

As (S94) no longer necessarily satisfies detailed balance with respect to (7), we add a Metropolis-Hastings step, a procedure known as the Metropolis-adjusted Langevin algorithm (MALA) [S26]. That is, the transition $R_i(t) \mapsto R_i(t + \varepsilon)$ occurs with probability min(1, α), where

$$\alpha = \exp\left(-V_{\Delta} - \beta \frac{\|\varepsilon \nabla V_{t+\varepsilon} - R_{\Delta}\|_2^2 - \|\varepsilon \nabla V_t + R_{\Delta}\|_2^2}{4\varepsilon}\right)$$
(S95)

and $V_{\Delta} = V_{t+\varepsilon} - V_t$ and $R_{\Delta} = (R_i(t+\varepsilon) - R_i(t))_{i=1}^n$. We iterate (S94), (S95) for n = 1000 particles in the unit square with periodic boundary conditions. For non-Poisson configurations ($\beta > 0$, Fig. 2(b)-(d)), we use the "frozen" initial condition (Fig. 2(d)), computed using a gradient descent of (5), which has a faster mixing time than starting with the infinite-temperature (Poisson) initial condition.

We use the following simulation conditions to produce Fig. 2 in the main text.

- n = 1000 particles
- k = 1000 samples at each temperature β^{-1} in distinct Markov chains
- $\beta \in [10^{-3}, 1]$ at 13 logarithmically spaced intervals and $\beta \in [1, 40]$ at 21 linearly spaced values
- $n_{\rm mix} = 1000$ mixing steps for each chain prior to sampling
- $\varepsilon = 1.0$ time step size
- $n_{\text{freeze}} = 2000$ gradient steps of size $\varepsilon_{\text{freeze}} = 0.1$ to produce the frozen initial condition

The sufficiency of the mixing time n_{mix} is validated by running the same procedure again with double the time $2n_{\text{mix}}$, which produced no measurable differences in the resulting distributions except at high $\beta = 100, k \approx 2000$.

F. Enforcing hard-sphere constraints

We now apply a hard-sphere constraint to samples of the fixed-N, V ensemble (7). One of the simplest methods is the Matérn thinning rule (S68), which filters points from a particular configuration \mathcal{X} to \mathcal{X}' such that a minimum user-specified spacing d_{\min} is satisfied. Fig. S5 shows several such samples at fixed $\beta = 10^4$ and d_{\min} a multiple $\alpha \in \{0, 0.25, 0.5, 1\}$ of the minimum spacing in the frozen phase (Fig 2(d) in the main text). As seen in Fig. S5(e), the hard-sphere thinning shows a transition to gamma-distributed aspect ratios.



FIG. S5. Transition to gamma-distributed aspect ratios under Matérn thinning of the Voronoi liquid at fixed $\beta = 10^4$. Panels (a-c, f) show samples thinned by the Matérn rule (S68) at various distances d_{\min} . Panel (d) shows that partition areas are well-described by k-gamma distributions at all d_{\min} , with k monotone decreasing. Panel (e) shows that partition aspect ratios, calculated from the second area moment, transition from an approximate beta-prime distribution to a gamma distribution with $k \approx 2.4$.

A second method is to add a divergent term to E (5) for invalid configurations for which f_{β} (7) is vanishing. The Langevin diffusion (8) is of course no longer interpretable due to the loss of derivatives. However, we can interpret its discretization (S94) at valid configurations as an arbitrary sequence of proposals (still outperforming the random walk) for which the Metropolis-Hastings step (S95) rejects invalid configurations ($V_{\Delta} = \infty$) and ensures detailed balance with respect to f_{β} . We mention this approach for completeness; however, additional modifications to MALA need to be made to improve the sampling efficiency, as we find this procedure to be computationally intractable at even moderate hard-sphere radii. One possible approach is to use Hamiltonian Monte Carlo [S26] with constraints.

VI. APPROXIMATE VORONOI TESSELLATION OF THE SURFACE OF V. CARTERI

Below are standard data processing procedures recalled for a self-contained reference, which we compose in a pipeline to produce a simplicial Voronoi tessellation about the somatic cells on the surface of *Volvox*.

A. Fitting ellipsoids in *d* dimensions

Let x, v be vectors in some d-dimensional basis. The equation of a (d-1)-sphere S centered at v is

$$\|x - v\|_2^2 = 1 \quad \forall x \in S.$$
(S96)

Applying a rotation P (an orthogonal matrix) of the sphere onto a set of principal axes and stretching along those axes by Λ (a positive diagonal matrix), one generalizes (S96) to an ellipsoid E via a symmetric positive-definite matrix

 $M = P\Lambda P^{\intercal}$ defining a generalized inner product in which x satisfies

$$(x-v)^{\mathsf{T}}M(x-v) = 1 \quad \forall x \in E.$$
(S97)

The elliptic radii r_i are then $r_i = \Lambda_{ii}^{-\frac{1}{2}}$ and the elliptic axes are the columns of P.

1. The minimum volume bounding ellipsoid

Given the volume

$$V = \frac{\pi^{d/2}}{\Gamma(d/2+1)} \prod_{i=1}^{d} r_i \propto \sqrt{\det(M^{-1})},$$
(S98)

it follows that maximizing $\log \det(M)$ minimizes V. Hence for a given dataset $\{x_i\}_{i=1}^n$, the following convex program computes the minimum-volume bounding ellipsoid:

$$\sup_{M,v} \log \det(M) \tag{S99}$$

subject to
$$(x_i - v)^{\mathsf{T}} M(x - v_i) \le 1 \quad \forall i$$
 (S100)

$$M > 0. \tag{S101}$$

Here, M > 0 in the sense of linear matrix inequality (LMI), i.e. M is constrained to lie in the positive-definite cone. However, the offset $x_i - v$ produces a variable-product constraint which is not disciplined convex (DCP). The following reparametrization uses the invertibility of M to convert the constraint to linear least squares:

$$\sup_{A,b} \log \det(A) \tag{S102}$$

subject to
$$||Ax_i - b||_2^2 \le 1 \quad \forall i$$
 (S103)

$$A > 0 \tag{S104}$$

$$M = A^2 = A^{\mathsf{T}}A \tag{S105}$$

$$v = A^{-1}b. (S106)$$

DCP solvers such as CVXOPT [S27] solve this problem. We further reduce the problem size by considering the subset of X lying on the convex hull, computed in $O(n \log n)$.

2. ℓ^2 -minimal projection to ellipsoids

Given a representation of an ellipsoid as (M, v) in the same basis as x, define the following convex program:

$$\inf_{V} \|Y - X\|_{2}^{2} \tag{S107}$$

subject to $||A(x_i - v)||_2^2 = 1 \quad \forall i$ (S108)

$$A^{\mathsf{T}}A = A^2 = M,\tag{S109}$$

with A computed by (Hermitian) eigendecomposition of M. Then Y is the minimum- ℓ^2 -distance projection of X onto (M, v). This problem is not DCP; however, since there are no matrix cone constraints, we can simply use non-DCP solvers compatible with nonlinear constraints, such as SLSQP [S28]. The constraint Jacobian for (S108) is $2M(x_i - v)$.

B. Fitting hyperplanes in *d* dimensions

The equation of a hyperplane H in d dimensions is

$$n \cdot (x - v) = 0 \quad \forall x \in H \tag{S110}$$



FIG. S6. Computational pipeline for tessellating the surface of V. carteri. (a) The somatic cell positions, available from [S29], displayed in three-dimensional space. (b) The minimum-volume bounding ellipsoid containing the somatic cells is computed. This establishes the approximate anterior-posterior axis of the spheroid. (c) The ℓ^2 -optimal projection of the somatic cell positions X to this ellipsoid are computed, and the Delaunay tetrahedralization of this projected point cloud \hat{X} is computed. As \hat{X} is now its own convex hull, the index triplets corresponding to the triangular faces lying on the convex hull of the tetrahedral complex are taken to be an approximate Delaunay triangulation of the original point cloud X. (d) A quasi-2D Voronoi tessellation of the surface is computed by taking the ℓ^2 -optimal planar embedding of the simplicial ring around any vertex, and constructing a planar Voronoi face in that embedding using the usual circumcenter rule. If invalid (self-intersecting) polygons are produced by the planar embedding, they are corrected by taking the 2D convex hull, which in the limit of zero curvature is a no-op. This procedure introduces overlapping artifacts near gonidia (as seen) but is otherwise unaffected by the global radius of curvature which is large compared to the size of individual polygons.

for $n, v \in \mathbb{R}^d$. Without loss of generality, we may assume that ||n|| = 1, so that n is a unit normal to H; expressing H in the form

$$n \cdot x - b = 0, \tag{S111}$$

we see that $b = n \cdot v$ is the distance from the origin to H. It further follows that the distance from an arbitrary point $y \in \mathbb{R}^d$ to the plane is

$$d(y,H) = |n \cdot (y-v)| = |n \cdot y - b|.$$
(S112)

Now, let $\{x_i\}_{i=1}^N = X \in \mathbb{R}^{N \times d}$ be a set of data points with $N \ge 3$. The best-fit hyperplane (in the ℓ^2 sense) is

$$\inf_{v \in V} \|(X - v)n\|_2^2 \tag{S113}$$

ubject to
$$||n||_2 = 1.$$
 (S114)

The cost is bi-convex in the parameters v and n. For fixed n, the critical point of the cost in v is given by

$$0 = \frac{\partial}{\partial v} \left\| (X - v)n \right\|_{2}^{2} = 2 \sum_{i=1}^{N} (x_{i} - v).$$
(S115)

Then $v = \frac{1}{N} \sum_{i=1}^{N} x_i$ is the centroid. Letting $\overline{X} = X - v$, the critical point of the cost in n is

S

$$0 = \frac{\partial}{\partial n} \left\| \overline{X}n \right\|_2^2 = 2\overline{X}^{\mathsf{T}}\overline{X}n.$$
(S116)

A common method to estimate n in this LSQ problem is the singular vector of \overline{X} corresponding to the smallest singular value, which of course is 0 if $\{x_i\}$ are coplanar. By (S112) it follows that the ℓ^2 -orthogonal projection of X onto H is

$$Y = X - (X - v)nn^{\mathsf{T}}.$$
(S117)

Let $u \in \mathbb{R}^d$ be a random vector such that $u \times n \neq 0$ (e.g. a Gaussian vector, for which this is almost surely true); then an invertible planar embedding Y_H of a point Y lying in H is defined by the random orthonormal plane basis B:

$$B = \frac{1}{\|v\|} \begin{bmatrix} v & v \times n \end{bmatrix}, \quad v = u \times n, \tag{S118}$$

$$Y_H = YB. (S119)$$

First, 3D meshes and an ellipsoidal approximation of the organism's surface are constructed using the procedure detailed in Figure S6. Then, all Voronoi polygon areas (including those near gonidia, which typically introduce high-aspect-ratio polygons) are converted to solid-angles (4π times the area fraction of total) and are filtered by the cutoff $v_c = 0.007$ specified in [S29]. The empirical area distribution for each organism is shifted by this cutoff and nondimensionalized to empirical mean 1, at which point they are combined across all 6 organisms and shown as a combined histogram in Figure 1.

- [S1] E. Lukacs, A Characterization of the Gamma Distribution, Ann. Math. Stat. 26, 319–324 (1955).
- [S2] P. Findeisen, A simple proof of a classical theorem which characterizes the gamma distribution, Ann. Stat 6, 1165–1167 (1978).
- [S3] R. Durrett, Probability: Theory and Examples, Vol. 49 (Cambridge University Press, 2019).
- [S4] D. J. Daley, D. Vere-Jones, et al., An Introduction to the Theory of Point Processes: Volume I: Elementary Theory and Methods (Springer, 2003).
- [S5] R. Pyke, Spacings, J. R. Stat. Soc. B 27, 395–436 (1965).
- [S6] D. J. Grabiner, Brownian motion in a Weyl chamber, non-colliding particles, and random matrices, Ann. IHP Prob. Stat. 35, 177–204 (1999).
- [S7] D. G. Hobson and W. Werner, Non-Colliding Brownian Motions on the Circle, Bull. Lon. Math. Soc. 28, 643–650 (1996).
- [S8] F. J. Dyson, A Brownian-Motion Model for the Eigenvalues of a Random Matrix, J. Math. Phys. 3, 1191–1198 (1962).
- [S9] P. Diaconis and M. Shahshahani, On the eigenvalues of random matrices, J. Appl. Prob. **31**, 49–62 (1994).
- [S10] T. Kemp, Heat Kernel Empirical Laws on $\mathbb{U}(n)$ and $\mathbb{GL}(n)$, J. Theor. Prob. **30**, 397–451 (2017).
- [S11] T. Aste and T. Di Matteo, Emergence of Gamma distributions in granular materials and packing models, Phys. Rev. E 77, 021309 (2008).
- [S12] D. Stoyan, W. S. Kendall, S. N. Chiu, and J. Mecke, Stochastic Geometry and its Applications (John Wiley & Sons, 2013).
- [S13] J. Møller and S. Zuyev, Gamma-type results and other related properties of Poisson processes, Adv. Appl. Prob. 28, 662–673 (1996).
- [S14] J. Møller, Lectures on random Voronoi tessellations, Vol. 87 (Springer Science & Business Media, 2012).
- [S15] L. Atia, et al., Geometric constraints during epithelial jamming, Nat. Phys. 14, 613–620 (2018).
- [S16] E. Gilbert, Random Subdivisions of Space into Crystals, Ann. Math. Stat. 33, 958–972 (1962).
- [S17] M. Tanemura, Statistical distributions of poisson voronoi cells in two and three dimensions, FORMA-TOKYO- 18, 221 (2003).
- [S18] J.-S. Ferenc and Z. Néda, On the size distribution of Poisson Voronoi cells, Physica A 385, 518–526 (2007).
- [S19] D. Weaire, J. Kermode, and J. Wejchert, On the distribution of cell areas in a Voronoi network, Phil. Mag. B 53, L101–L105 (1986).
- [S20] P. Rathie, On the volume distribution of the typical Poisson–Delaunay cell, J. Appl. Prob. 29, 740–744 (1992).
- [S21] H. J. Malik, Exact Distribution of the Product of Independent Generalized Gamma Variables with the Same Shape Parameter, Ann. Math. Stat. 39, 1751–1752 (1968).
- [S22] Q. Du, V. Faber, and M. Gunzburger, Centroidal voronoi tessellations: Applications and algorithms, SIAM Rev. 41, 637 (1999).
- [S23] R. Li, C. Ibar, Z. Zhou, S. Moazzeni, A. N. Norris, K. D. Irvine, L. Liu, and H. Lin, E² and gamma distributions in polygonal networks, Phys. Rev. Res. 3(4), L042001 (2021).
- [S24] Q. Du and D. Wang, The optimal centroidal Voronoi tessellations and the Gersho's conjecture in the three-dimensional space, Comp. Math. Appl. 49, 1355 (2005).
- [S25] H. Risken, Fokker-Planck Equation, (Springer, 1996).
- [S26] M. Girolami and B. Calderhead, Riemann manifold Langevin and Hamiltonian Monte Carlo methods, J. Roy. Stat. Soc. B 73, 123 (2011).
- [S27] S. Diamond and S. Boyd, CVXPY: A Python-embedded modeling language for convex optimization, J. Mach. Learn. Res. 17, 2909 (2016).
- [S28] D. Kraft, A software package for sequential quadratic programming, Forschungsbericht- Deutsche Forschungs- und Versuchsanstalt fur Luft- und Raumfahrt (1988).
- [S29] T. C. Day, S. S. Höhn, S. A. Zamani-Dahaj, D. Yanni, A. Burnetti, J. Pentz, A. R. Honerkamp-Smith, H. Wioland, H. R. Sleath, W. C. Ratcliff, et al., Cellular organization in lab-evolved and extant multicellular species obeys a maximum entropy law, eLife 11, e72707 (2022).