# Will a large complex system form Turing patterns?

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From atomic spins in magnets to galaxies, and from embryonic development to patchy vegetation in arid environments, the physical world is filled with complex systems that spontaneously form spatial patterns. In the context of reaction-diffusion systems, pattern formation can be explained by the Turing mechanism, which postulates that diffusion can destabilise spatially uniform steady states. However, the resulting Turing patterns have only been analyzed in systems with a small number of diffusing variables, even though the physical systems they aim to describe are highly complex. In this study, we utilize ideas from random matrix theory to explore how spontaneously formed Turing patterns emerge in random complex systems with many variables. Crucially, we find that diffusion-driven instability is not sufficient to explain pattern formation. Nevertheless, modifications of the Turing mechanism that include various forms of local and non-local attraction and repulsion are shown to reliably promote pattern formation in large complex systems. Altogether, this study assesses the robustness of multiple pattern-forming mechanisms in large complex systems, providing a guide for recognising which mechanisms might be important for pattern formation in empirical studies.

Spatial patterns emerge across all scales of the physical world and their spontaneous formation provides a central theme of scientific study. The spins of atoms self-organize in magnetic materials [1, 2], reacting chemicals spontaneously form patterns [3], bacterial cells create spatially heterogeneous biofilms [4], animals develop patterned skin pigmentation [5], vegetation is patchily distributed in arid environments [6], and planets, solar systems and galaxies spontaneously emerged from a relatively homogeneous bulk of energy and matter after the Big Bang [7]. Even though different mechanisms drive pattern formation at different scales, the spontaneous formation of spatial patterns in all these examples shares a common feature. The spatially homogeneous steady state of the system is unstable to spatial perturbations.

Reaction-diffusion systems provide an ideal prototype for the theoretical exploration of spontaneous pattern formation [8], with a long history tracing back to Alan Turing. In 1952, Turing showed that the diffusion of two interacting variables ($N = 2$) might destabilise their spatially homogeneous distribution, even though the diffusion of a single self-interacting variable ($N = 1$) cannot do this [9]. In particular, for patterns to form, one variable must diffuse slowly and activate the dynamics, while the other must diffuse quickly and inhibit the dynamics [8].

Despite the simplicity of the proposed Turing mechanism, observing Turing patterns in experimental and natural systems took several decades [10]. Moreover, those systems that admit Turing patterns are often more complex than can be described with two variables, a slow activator and a fast inhibitor. For example, the chemical reactions that admit Turing patterns involve multiple reactants [3, 11, 12] with similar diffusivities [13]. Biofilm patterns are composed of bacteria that interact with complex chemical environments, secrete multiple extracellular polymeric substances and are capable of biased non-diffusive motility [14]. In zebrafish, pigment cells - melanophores and xanthophores - interact with various chemical factors [5] and perform a non-diffusive movement [15] to produce stripes and spots on the zebrafish skin. Finally, the patterns of vegetation in the arid environment are affected by various biotic and abiotic factors [6] and plant seeds can be dispersed nonlocally [16], for example by rodents [17].

The complexity of these systems has influenced the mathematical modelling of pattern formation. In particular, the Turing mechanism has been generalised to include biased movement, such as advection [18], chemotaxis [19] or cross-diffusion [20], and various forms of nonlocal movement have been considered [21, 22], with a key conclusion that such forms of generalised movement commonly promote pattern formation. Furthermore, the Turing mechanism has been examined in complex systems with more than two interacting variables. Recently, general conditions for Turing instability for the case of three interacting variables ($N = 3$) were derived [23] and necessary conditions on the structure of reactions with an arbitrary number of variables $N$ were provided [24]. Since these analytical conditions are difficult to interpret, several authors investigated the formation of Turing pat-

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terns with $N \geq 2$ variables numerically [13, 25, 26]. Inspired by Robert May's idea to examine the stability of large complex systems with a random matrix theory approach [27], these works [13, 26] suggest that the probability of observing Turing patterns rapidly decreases with increasing number of variables $N$. This observation has also been supported by an analytical argument based on Gershgorin's circle theorem [28]. Yet, this argument requires several simplifying assumptions that may also be unrealistic, such as the uniform and independent distribution of eigenvalues within Gershgorin's circles.

In this Letter, we complement the numerical work of [13, 26] with an analytical investigation of general random systems in the limit of many variables, $N \gg 1$, formalizing the result about large reaction-diffusion systems from [28] and extending it to more complex non-diffusive transport mechanisms. In particular, we focus on the near-equilibrium analysis of spontaneous pattern formation in these systems and use the general term "Turing patterns" to describe such spatiotemporal patterns.

To formalise this idea, we consider a system with $i = 1, \ldots, N$ interacting variables that are arranged in a vector $\mathbf{n} = (n_1, \ldots, n_i, \ldots, n_N)$. In a well-mixed system without diffusion, we assume that the dynamics is described by the reaction functions $f_i(\mathbf{n})$:

$$\frac{\mathrm{d}n_i(t)}{\mathrm{d}t} = f_i(\mathbf{n}(t)) \tag{1}$$

and the variables approach a unique stable steady state $\mathbf{n}^*$. Turing patterns form if the homogeneous steady state $\mathbf{n}(t, \mathbf{x}) = \mathbf{n}^*$ of the reaction-diffusion system,

$$\partial_t n_i(t, \mathbf{x}) = d_i \nabla^2 n_i(t, \mathbf{x}) + f_i(\mathbf{n}(t, \mathbf{x})) \tag{2}$$

with diffusivities $d_i > 0$ and infinite domain $\mathbf{x} \in \mathbb{R}^D$, becomes unstable to spatial perturbations. Standard linear stability analysis [8] shows that whether or not Turing patterns form is determined by the eigenvalues of the matrix

$$J(\boldsymbol{k}) = J - k^2 \mathrm{diag}(d_1, \ldots, d_N), \tag{3}$$

where the matrix $J = \partial \mathbf{f} / \partial \mathbf{n}|_{\mathbf{n}^*}$ is the Jacobian for the reaction system (1) evaluated at $\boldsymbol{n}^*$ and $\boldsymbol{k}$ is the wavenumber vector of the perturbation, with magnitude $|\boldsymbol{k}| = k$. In particular, the steady-state $\mathbf{n}^*$ is unstable to spatial perturbations with wavenumber $k$ precisely if some eigenvalue of $J(k^2)$ has a positive real part. Since the steady state of the reaction system (1) is stable, the eigenvalues of $J(0) = J$ are assumed to have negative real parts. Therefore, Turing patterns form precisely if some eigenvalue $\lambda$ of $J(k^2)$ crosses the boundary $\mathrm{Re}\lambda = 0$ as $k^2$ increases.

Inspired by previous studies [13, 26, 27], we utilize random matrix theory to study a complex system with many variables ($N \gg 1$) and randomly sample the Jacobian interactions $J_{ij}$ between different variables at a homogeneous stationary state. Specifically, we assume that the Jacobian matrix is given by

$$J_{ij} = -\mu \delta_{ij} + j_{ij}, \tag{4}$$

where $\mu$ is a characteristic return rate of a single variable to its steady state, $\delta_{ij}$ is the Kronecker delta function and $j_{ij}$ are independent and identically distributed random variables with mean 0 and variance $\sigma^2$. If the complex system contains many variables, $N \gg 1$, a recent generalisation of the circle law in random matrix theory [29] can be used to predict that the eigenvalues of the matrix

$$J_{ij}(k) = J_{ij} - k^2 d_i \delta_{ij} = -(\mu + k^2 d_i)\delta_{ij} + j_{ij}, \tag{5}$$

are confined in the subset of the complex plane $S(k) = \{z | f(z, k^2) \geq \frac{1}{\sigma^2}\}$, where

$$f(z, k^2) = \sum_{i=1}^{N} \frac{1}{|z + \mu + k^2 d_i|^2}. \tag{6}$$

In particular, the eigenvalues of $J(0) = J$ are distributed on the circle $|z + \mu| \leq \sigma\sqrt{N}$ (Fig. 1a). For Turing patterns to form, we assume that the eigenvalues of $J(0) = J$ describe a stable system, which requires that the interactions between variables are sufficiently weak, hence

$$0 < \sigma\sqrt{N} < \mu, \tag{7}$$

that is we assume that the interactions $\sigma$ scale with the number of variables $N$ as $O(N^{-1/2})$. Crucially, for any $z$ with a positive real part, $\mathrm{Re}(z) > 0$, it is the case that

$$\frac{\partial f}{\partial k^2} = -2 \sum_{i=1}^{N} d_i \frac{\mathrm{Re}(z) + \mu + d_i k^2}{|z + \mu + d_i k^2|^4} < 0, \tag{8}$$

which implies that, for any $k^2 \geq 0$,

$$f(z, k^2) \leq f(z, 0) = \frac{N}{|z + \mu|^2} < \frac{N}{\mu^2} < \frac{1}{\sigma^2}. \tag{9}$$

Put differently, the confining sets $S(k)$ cannot intersect with the positive half-plane $\{z | \mathrm{Re}(z) > 0\}$ at any wavenumber $k$, implying that all eigenvalues have negative real parts and the spatial perturbations with wavenumber $k$ always decay (Fig. 1). In summary, diffusion cannot drive the formation of Turing patterns in complex random systems with many variables $N \gg 1$, in agreement with the numerical findings in [13, 26] that the probability of observing Turing patterns rapidly decays with a large number of variables $N \gg 1$.

As diffusion cannot explain Turing patterns in complex systems with many variables, a key question arises. What mechanisms could drive Turing patterns? As mentioned above, such mechanisms could either include generalised local interactions (e.g., advection [18], chemotaxis [19] and cross-diffusion [20]) or generalised non-local interactions [21, 22]. The most general model with local interactions is given by

$$\partial_t n_i = d_i \nabla^2 n_i + f_i(\mathbf{n}) - \nabla \cdot \mathbf{F}_i(\mathbf{n}, \nabla \mathbf{n}), \tag{10}$$

where $\mathbf{F}_i$ describes the non-diffusive flux of variable $i$. In this case, the linear stability of the steady state $\mathbf{n}^*$ is determined by the eigenvalues of the matrix

$$J_{ij}(\mathbf{k}) = J_{ij} - k_\alpha k_\alpha d_i \delta_{ij} - i k_\alpha A_{ij}^{\alpha} + k_\alpha k_\beta C_{ij}^{\alpha\beta}, \tag{11}$$

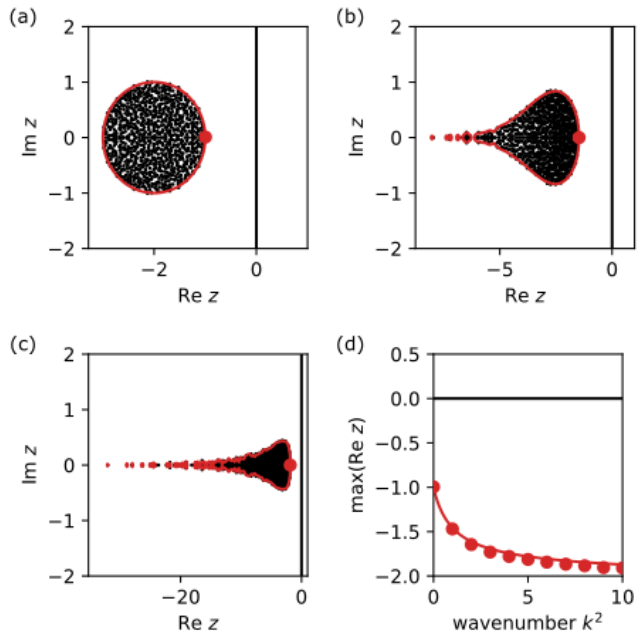


FIG. 1. Diffusion cannot induce Turing patterns in a large random system. The random system with $N = 1000$ variables is simulated by a Jacobian matrix $J_{ij} = -2\delta_{ij} + j_{ij}$ with independently sampled entries $j_{ij} \sim \mathcal{N}(0, 0.001)$. The diffusivities $d_i$ of all variables are sampled independently from an exponential distribution with scale 1. Eigenvalues of the spatially perturbed Jacobian $J_{ij}(k)$ are found numerically and plotted (black dots) for $k^2 = 0$ (a), $k^2 = 1$ (b), and $k^2 = 5$ (c). The eigenvalue of the maximal real part is emphasised by a red dot and the analytically predicted boundary is plotted as a red line. In panel (d), the eigenvalues of the maximal real part (red dots) and their analytically predicted values (red line) are plotted for a range of wavenumbers $k^2$. The analytically predicted values were obtained by a Newton-Rapshon method for the equation $0 = 1/f(\lambda + i0, k^2) - \sigma^2$ with the initial value of $\lambda = 0$.

where the Einstein summation convention is used, $\alpha, \beta$ denote the indices of the spatial dimensions, $A^{\alpha}_{ij} = \partial F^{\alpha}_i / \partial n_j|_{\mathbf{n}^*}$ describes linearised advection and $C^{\alpha\beta}_{ij} = \partial F^{\alpha}_i / \partial(\nabla_\beta n_j)|_{\mathbf{n}^*}$ describes linearised cross-diffusion. As before, we consider a random system with the Jacobian matrix $J_{ij}$ given by equation (4), and matrices $A^{\alpha}_{ij}$ (resp. $C^{\alpha\beta}_{ij}$) with independent and identically distributed entries of mean 0 and variance $s_A^2$ (resp. $s_C^2$). Furthermore, since diffusion cannot generate Turing patterns, we simplify the analysis by assuming that all variables have the same diffusivity $d_i = d$. With these assumptions, the circle law [29] dictates that a system with many variables $N \gg 1$ described by the matrix $J_{ij}(\mathbf{k})$ in equation (11) has eigenvalues that are distributed uniformly in a circle given by

$$|z + \mu + k^2 d|^2 \leq N(\sigma^2 + k^2 s_A^2 + k^4 s_C^2). \tag{12}$$

In particular, the eigenvalue with maximal real part is real and given by

$$\lambda(k) = -\mu - k^2 d + \sqrt{N(\sigma^2 + k^2 s_A^2 + k^4 s_C^2)}. \tag{13}$$

If the cross-diffusion is stronger than the self-diffusion ($s_C\sqrt{N} > d$), then $\lambda(k) \to \infty$ as $k \to \infty$, suggesting that Turing patterns can form (Fig. 2a,b,g). However, in this case, the spatial perturbations grow increasingly quickly with increasing wavenumbers $k$, which might indicate that the original problem in equation (10) is ill-posed. Therefore, we assume that the self-diffusion is stronger than the cross-diffusion ($s_C\sqrt{N} < d$) so that $\lambda(k) \to -\infty$ as $k \to \infty$. In this case, the dominant eigenvalue $\lambda(k)$ achieves a maximum at the wavenumber

$$k^2 = \frac{N s_A^2 - 2\mu d}{2(d^2 - N s_C^2)}, \tag{14}$$

provided $N s_A^2 > 2\mu d$, and is positive at this maximum, provided

$$|N s_A^2 - 2\mu d| > 2\sqrt{(\mu^2 - N\sigma^2)(d^2 - N s_C^2)}. \tag{15}$$

Therefore, there is an intermediate range of wavenumbers $k$ corresponding to growing perturbation modes precisely if

$$N s_A^2 > 2\left(d\mu + \sqrt{(\mu^2 - N\sigma^2)(d^2 - N s_C^2)}\right). \tag{16}$$

Put differently, a sufficiently strong advection $s_A$ can always introduce Turing patterns in a complex system with many variables $N \gg 1$ (Fig. 2c,d,g).

In addition to generalised local interactions, we can also consider complex systems with non-local interactions [21, 22], such as cell-cell interactions via pseudopodia in the context of developmental biology [30, 31] or long-range seed dispersal in the context of plant ecology [16, 32]. The authors in [22] consider a general model for non-local interactions of the form

$$\begin{aligned}\partial_t n_i =& d_i \nabla^2 n_i + f_i(\mathbf{n}) \\ &- \nabla \cdot \left( G_i(\mathbf{n}) \frac{1}{\zeta^D} \int_{\mathbb{R}^D} \Omega\left(\frac{s}{\zeta}\right) H_i(\mathbf{n}) \hat{\mathbf{s}} \mathrm{d}\mathbf{s}^D \right),\end{aligned} \tag{17}$$

where $G_i(\mathbf{n})$ and $H_i(\mathbf{n})$ modify the interaction strength, $\zeta$ is the length-scale of the non-local interaction, $\Omega(s)$ is the interaction kernel and $\hat{\mathbf{s}}$ is the unit vector of a specified direction in the $D$-dimensional space $\mathbb{R}^D$. It can be shown that the linear stability of the steady state $\mathbf{n}^*$ is determined by the eigenvalues of the matrix [22]

$$J_{ij}(k) = J_{ij} - k^2 d_i \delta_{ij} + \Lambda_{ij} \frac{K(k\zeta)}{\zeta}, \tag{18}$$

where the strength of the non-local interactions is captured by the matrix

$$\Lambda_{ij} = \frac{2\pi^{D/2}}{\Gamma\left(\frac{D}{2}\right)} G_i(\mathbf{n}^*) \left.\frac{\partial H_i}{\partial n_j}\right|_{\mathbf{n}^*}. \tag{19}$$

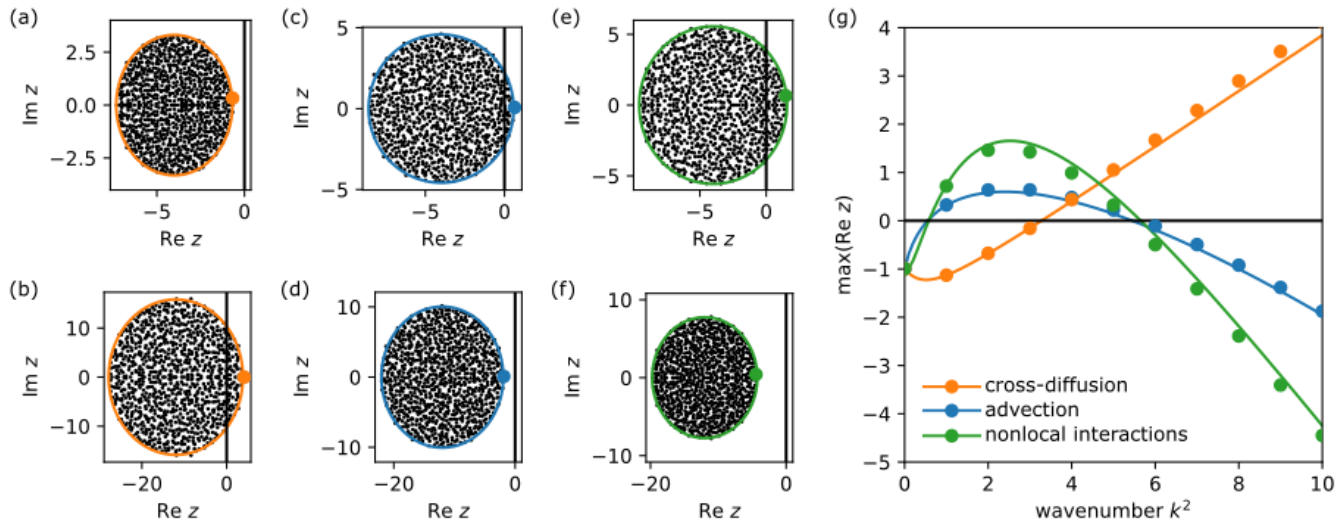


FIG. 2. Cross-diffusion (orange), advection (blue), and nonlocal interactions (green) can induce Turing patterns in a large random system. The random system with $N = 1000$ variables is simulated by a Jacobian matrix $J_{ij} = -2\delta_{ij} + j_{ij}$ with independently sampled entries $j_{ij} \sim \mathcal{N}(0, 0.001)$. In addition to a constant diffusivity $d = 1$ for all variables, cross-diffusion of strength $s_C = 0.05$ (a, b, g), advection of strength $s_A = 0.1$ (c, d, g), and non-local interactions of strength $s_N = 2$ and length-scale $\zeta = 0.5$ (e, f, g) were considered. As in [22], non-local interactions were modelled by a two-dimensional ($D = 2$) interaction kernel $\Omega(s) = e^{-s}/(2\pi)$, which is transformed to $K(q) = q^2/[2\pi(1+q^2)^{3/2}]$. Eigenvalues of the spatially perturbed Jacobian $J_{ij}(\boldsymbol{k})$ are found numerically and plotted (black dots) for $k^2 = 2$ (a, c, e) and $k^2 = 10$ (b, d, f), with the eigenvalue of the maximal real part emphasised as a coloured dot and the analytically predicted boundary plotted as a coloured line. In panel (g), the eigenvalues of the maximal real part (coloured dots) and their analytically predicted values (coloured lines) are plotted for a range of wavenumbers $k^2$.

and $K(q)$ is the transformed interaction kernel

$$K(q) = q \int_0^\infty s^{D-1} \Omega(s) j_1^{(D)}(qs) \mathrm{d}s, \tag{20}$$

with $j_1^{(D)}(s)$ being the $D$-dimensional hyperspherical Bessel function. As before, we consider a random system with equal diffusivities $d_i = d$, the Jacobian matrix $J_{ij}$ given by equation (4) and the matrix of non-local interactions $\Lambda_{ij}^{\alpha}$ that has independent and identically distributed entries of mean 0 and variance $s_N^2$. With these assumptions, the circle law [29] implies that a system with matrix $J_{ij}(k)$ in equation (18) and with many variables $N \gg 1$ has eigenvalues that are distributed uniformly in a circle given by

$$|z + \mu + k^2 d|^2 \leq N \left( \sigma^2 + \frac{K(k\zeta)^2}{\zeta^2} s_N^2 \right). \tag{21}$$

In particular, the eigenvalue with the maximal real part is real and given by

$$\tilde{\lambda}(k) = -\mu - k^2 d + \sqrt{N \left( \sigma^2 + \frac{K(k\zeta)^2}{\zeta^2} s_N^2 \right)}. \tag{22}$$

Since any non-trivial interaction kernel has a transform $K(k\zeta)$ that is not identically zero, there must exist a wavenumber $k$ with $K(k\zeta) \neq 0$ such that the eigenvalue $\tilde{\lambda}(k)$ can be made arbitrarily large by increasing the strength of non-local interactions $s_N$. In particular, non-local interactions can introduce Turing patterns in complex random systems with many interacting variables $N \gg 1$. Overall, non-local interactions foster pattern formation in a similar manner to advective local interactions (Fig. 2e,f,g).

In this Letter, we have analyzed spontaneous pattern formation in complex random systems with a large number of interacting variables, reflecting the properties of many experimental and natural systems where Turing patterns are observed [3–6, 11, 12]. Crucially, we provide rigorous arguments to show that diffusion cannot destabilise a spatially homogeneous steady state of a system with a large number of interacting variables $N \gg 1$, as observed in the numerical simulations [13, 26] and suggested in [26] based on an analytical argument. This result can be interpreted in several ways. Firstly, with an increasing number of variables $N$, equation (7) suggests that stable spatially homogeneous steady states are increasingly rare in large well-mixed systems, implying that complex random systems are unlikely to admit a stable spatially homogeneous steady state of the well-mixed system that could be destabilised by spatial perturbations. Consequently, complex random systems are likely to exhibit highly dynamic spatiotemporal patterns. For example, in predator-prey systems, phenotypic heterogeneity increases the number of variables $N$ and induces predator-prey waves even in regimes where phe-

notypically homogeneous populations remain uniformly distributed in space [33]. Secondly, the inability of diffusion to introduce Turing patterns in random systems could suggest that systems admitting Turing patterns must be highly structured and non-random. This hypothesis aligns with the finding that Turing patterns can only occur in highly structured reaction networks [24, 34] or more structured random systems with non-trivial correlations between variables [35], and it could explain why it took several years to find an appropriate chemical reaction that validates Turing's theory [10]. Thirdly, while diffusion could be inefficient in producing patterns on its own, other forms of non-diffusive interactions might promote spontaneous pattern formation in complex systems with many interacting variables. In this Letter, we proved that generalised local and non-local forces that mediate attraction and repulsion robustly promote pattern formation in complex systems with many interacting variables. This result strengthens the message of previous studies that showed how advection [18], chemotaxis [19], cross-diffusion [20] and non-local interactions [21, 22] facilitate pattern formation in systems with a few variables. Altogether, our work examined the robustness of various pattern-forming mechanisms in realistically complex systems, which might be helpful when identifying appropriate chemical or biological systems that admit Turing patterns discussed in this paper [36].

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