Quantifying robustness in a spatial model of metabolism-boundary co-construction

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Abstract

We introduce a spatial model of autopoiesis that demonstrates boundary-metabolism co-construction, disintegration following harsh perturbations, and self-repair in response to lighter perturbations. The system’s continued maintenance is equated with robustness and quantitatively investigated. This investigation highlights several important operational dependencies for robustness including spatiality, identity, stability, and appropriate specification of perturbations in the types of environments to which an entity must be robust.

Introduction

Autopoiesis is a proposed formal property of living systems, defined as “a network of processes of production (synthesis and destruction) of components, such that these components: 1) continuously regenerate and realize the network of processes that produces them, and 2) constitute the system as a distinguishable unity in the domain in which they exist” (Weber and Varela, 2002). This provides a unique characterization of life, which shifts the focus from the material properties of living systems to their systemic organization. Living systems retain an autopoietic organization despite material and energetic exchange with the environment, but with death this organization is lost and the system disintegrates into its respective components. A key attribute of such autopoietic systems is their robustness, or their ability to maintain their organization and repair their structure following environmental perturbations.

Elaborations on this concept in the field of enaction have argued that behaviors instantiated by autopoietic systems, which help sustain the basic organization, are equivalent to the processes of cognition. This leads to a radical reconceptualization of cognition, claiming that the inherent precariousness of autopoietic systems provides an intrinsic source of normativity (Weber and Varela, 2002) and an autopoietic system’s ability to evade its impending disintegration is the foundation for adaptivity (Di Paolo, 2005).

However, the original criteria of autopoiesis are highly abstract, and their consequences cannot be verified until we understand the more basic premises. Minimal computational models have been used to ground the study of autopoiesis by observing the emergence of self-constructing systems out of a simulated environment, and to demonstrate the autopoietic logic through the analysis of these systems. Several models of autopoiesis have been developed over the last 40 years (McMullin, 2004). Different modeling approaches highlight different aspects of autopoiesis, but all of them share the assumption that abstractions of molecular interactions are the appropriate setting for studying autopoiesis.

In this paper, we put forth a lattice-based model of concentration dynamics. We demonstrate several properties of autopoiesis that arise in this model, including the roles of containment and metabolism, the precariousness of these systems, and their capacity for self-repair. We then transition to a systematic study of the system’s robustness. We propose robustness as a fundamental property of successful autopoietic systems; they survive contact with the world despite their vulnerability to disintegration. We implement several types of perturbations on the virtual autopoietic systems, and through systematic study we observe how the space of possible perturbations can lead to these system’s disintegration, robust self-repair, or transformation to new configurations.

Computational Autopoiesis

Current models of autopoiesis can be divided into four broad classes: the first type accounts for reaction kinetics but not spatiality, the second accounts for basic spatiality but not boundary construction, the third has an explicitly-defined boundary, and the fourth class consists of spatial models with distinct constructed boundaries.

We begin with arguably the most minimal type of model, which emphasizes reaction kinetics and ignores the spatial dimensions of molecular systems. This is seen in the hypercycle (Eigen, 1978), autocatalysis (Kauffman, 1986), chemical organization theory (Dittrich and Di Fenizio, 2007), and lambda calculus models (Fontana and Buss, 1994). These models implicitly assume homogeneity, such that all reactants interact equally with all other reactants. Reaction-based models are often more interested in the catalytic closure of a given chemical organization, which emphasizes
how molecular sets can synthesize themselves through the reactions of their molecular components. A type of precariousness (the capacity to fall apart) and robustness has been suggested by [Barandiaran and Egbert, 2014] in a non-spatial model composed of ordinary differential equations. For this class of models, death is simply a stable attractor at which all relevant molecular concentrations are zero, and viable spaces are those that have a stable equilibrium at non-negative values of the relevant molecular concentrations.

The second type of autopoietic model incorporates space but does not demonstrate the construction and maintenance of a boundary. For example, [Virgo, 2011] argues that spots seen in the Gray-Scott reaction diffusion system have the property of individuation. Gray-Scott spots are spatial patterns, seen in a narrow band of system parameter values. They demonstrate how spatiality allows stable patterns to arise through reactions that occur at different rates within a heterogeneous system. However, these spots have no distinct spatial boundary, making it difficult to argue that the spots define themselves as distinct unities in space, and that they are self-regulating with regards to a medium. Similarly, gliders in the game of life are members of this second class because they construct themselves as spatial entities without explicitly different boundary components [Bourgine and Stewart, 2004].

The third type of model includes spatial boundaries that have their own unique physics explicitly defined in the model [Bourgine and Stewart, 2004]. As an example, the model presented by [Egbert and Di Paolo, 2009] has a membrane that is predefined as a circle of connected springs. The sections of this boundary can grow or shrink based on the local number of membrane molecules. This demonstrates boundary-metabolism co-regulation: the boundary contains the require metabolic molecules and keeps them from spilling into the environment, and the boundary requires metabolism because metabolism constructs the membrane molecules. However, the boundary is not something that arises naturally out of the lower-level physics.

The fourth type consists of spatial models that demonstrate constructed membranes. This includes the original particle-based model of autopoiesis [Varela et al., 1974], which defines a two-dimensional lattice, for which each position can be occupied by one particle at a time, or remain empty. Three types of molecules are included: substrates, catalysts, and links (membrane molecules). Through these molecules’ reactions, a spatial boundary arises and contains the internal metabolism that continues to construct it. Similar models have demonstrated growth, change of shape, oscillation, and self-reproduction [Zeleny, 1977], the formation of flexible membranes, and movement [Breyer et al., 1998]. The fourth class of models has been extended by modeling particle interactions in a continuous space, and by taking a macroscopic perspective on concentration dynamics rather than modeling the movement of individual molecules [Ono, 2001]. The model presented in this paper falls into this class of models.

There are many lessons we can learn from these past efforts to model autopoiesis. In this paper, we emphasize that, for a model to address how an autopoietic organization can distinguish itself from an environment, none of the properties on which that distinction is based should be hardcoded into the model. We suggest that most models of autopoiesis to date have various shortcomings with regards to this requirement. The first type of model, which focuses on stoichiometric relations but ignores spatiality, implicitly hardcodes the distinction between system and environment. The second type of model does not account for a spatial boundary, and so the spatial patterns being studied cannot regulate their own boundary conditions and therefore do not make themselves distinct. The third type of model hardcodes the membrane’s properties into the model, and so it does not arise naturally from the underlying physics. The fourth type of model, if implemented carefully, is the only class that has the potential to demonstrate both catalytic closure and maintenance of an emergent boundary. In addition to careful implementation that avoids hardcoding desired organizational properties, resulting models should be systematically investigated to enhance our theoretical understanding of their underlying processes. Most of the described models were provided purely as proofs of concept for the autopoietic logic, and were not examined further.

### Anisotropic Spatial Model

We consider a minimal autocatalytic model consisting of three parts: 1) a set of molecules $M$ and the corresponding set of constructive and destructive reactions, 2) spatial diffusion dynamics biased by repulsion, and 3) an anisotropic repulsion potential. These components are combined in a 2-dimensional lattice model derived from a previous model investigated by [Ono, 2001]. We have simplified the reaction kinetics, moved it to a rectangular lattice, and implemented continuous orientation fields. In addition, our model is completely deterministic.

For each of the molecular types $m \in M$ and at each point in space $x_{ij}$, the equations of motion take the form of a system of coupled differential equations:

$$\frac{\partial m(x_{ij})}{\partial t} = R_m(x_{ij}, t) + D_m^i(x_{ij}, t) + \Gamma_m(x_{ij}, t) \tag{1}$$

where $R_m(x_{ij}, t)$ indicates rate contributions due to the mass-action assumptions of our chemical reactions, $D_m^i(x_{ij}, t)$ indicates a diffusive term biased by repulsion and orientation field $\theta$, and $\Gamma_m(x_{ij}, t)$ denotes potential external contributions to the system. Each of these terms will be addressed below.

#### Autocatalytic stoichiometry.

Our model captures the concentration dynamics of four distinct molecular types $M = \{A, M, F, W\}$: the autocatalyst $A$, the membrane $M$,
the food $F$, and water $W$. Each of these molecular types reacts as follows. Autocatalyst $A$ catalyses the replication of additional $A$ and consumes $F$ in the process, with a rate $k_{AA}$. Autocatalyst $A$ also catalyzes membrane $M$ from $F$ at a rate $k_{AM}$. Both $A$ and $M$ decay at rates $k_{A}$ and $k_{M}$ respectively. Water $W$ is an inert substance. These reactions are summarized by the following stoichiometric equations:

$$
2A + F \xrightarrow{k_{AA}} 3A \quad 2A + F \xrightarrow{k_{AM}} 2A + M \quad (2)
$$

with all reverse reaction rates set to 0. Conservation of mass can be assumed via the introduction of an inert waste product which is instantaneously removed from the system. Finally, instead of modeling each individual molecule, we course-grain over space and consider positive concentrations of molecules. The mass-action assumptions allow us to convert these stoichiometric relations into dynamical equations:

$$
R_A(x_{ij}, t) = k_{AA}F(x_{ij}, t)A(x_{ij}, t)^2 - k_{A}A(x_{ij}, t)
$$
$$
R_M(x_{ij}, t) = k_{AM}F(x_{ij}, t)A(x_{ij}, t)^2 - k_{M}M(x_{ij}, t)
$$
$$
R_F(x_{ij}, t) = -(k_{AA} + k_{AM})F(x_{ij}, t)A(x_{ij}, t)^2
$$
$$
R_W(x_{ij}, t) = 0 \quad (3)
$$

Unlike the aforementioned Ono [2001] model, the reaction rates are all constant.

**Diffusion and repulsion.** The above reactions take place on a $N_x \times N_y$ lattice. Each molecular concentration $m \in M$ follows diffusive dynamics resulting in conserved concentration flows between the lattice sites:

$$
D_m^\theta(x_{ij}, t) = d_m \sum_{x_{\alpha\beta} \in N_{ij}} m(x_{\alpha\beta}) g_m^\theta(x_{\alpha\beta} \rightarrow x_{ij}, t) - m(x_{ij}) g_m^\theta(x_{ij} \rightarrow x_{\alpha\beta}, t) \quad (4)
$$

where $d_m$ is the diffusion constant for the $m$-th molecular concentration, $N_{ij}$ is the Moore neighborhood of each lattice site $x_{ij}$, and $g_m^\theta(x_{ij} \rightarrow x_{\alpha\beta})$ is the diffusive bias of concentration $m$ from site $x_{ij}$ to site $x_{\alpha\beta}$. This diffusive bias is given as a function of the gradient of a repulsion potential $P_m^\theta$, between the sites:

$$
g_m^\theta(x_{ij} \rightarrow x_{\alpha\beta}, t) = \frac{\Delta P_m^\theta(x_{ij} \rightarrow x_{\alpha\beta}, t)}{1 - e^{-\Delta P_m^\theta(x_{ij} \rightarrow x_{\alpha\beta}, t)}} \quad (5)
$$

where $\Delta P_m^\theta(x_{ij} \rightarrow x_{\alpha\beta}, t) = P_m^\theta(x_{ij}, t) - P_m^\theta(x_{\alpha\beta}, t)$ is the gradient of the repulsion potential $P_m^\theta$ in the direction of $x_{\alpha\beta}$. Finally, the repulsion potential $P_m^\theta(x_{ij}, t)$ for molecular concentration type $m$ at lattice site $x_{ij}$ takes the form:

$$
P_m^\theta(x_{ij}, t) = \sum_{\mu \in M} \sum_{x_{\alpha\beta} \in N_{ij}} \mu(x_{ij}, t) f_m^\theta(x_{\alpha\beta}, x_{ij}) \quad (6)
$$

which has contributions from all $\mu$-type concentrations in the inclusive Moore neighborhood $N_{ij}^\mu$ of $x_{ij}$. Within this framework, the specific interactions between concentration types $m$ and $\mu$ are determined by the interaction strength $f_m^\theta(x_{\alpha\beta}, x_{ij})$. In general, these interactions can have different values depending on the relative location within the neighborhood (including self interactions). In the next section, we will explain how those interactions involving $M$ are dependent on the orientation field $\theta$.

**Anisotropic membrane potentials.** With isotropic interaction potentials, the membrane molecules behave like oil in water, forming large symmetric clumps without any containment properties, thus we turn to anisotropic interaction potentials to generate a boundary layer. Motivated by the dynamics of lipid sheets that form in water, we focus on an important property of boundaries; they are lower dimensional surfaces embedded in a higher-dimensional space. A natural consequence of this embedding is the introduction of an orientation field that describes the local orientation $\theta(x_{ij}, t) \in [0, \pi)$ of the membrane concentration at each lattice site $x_{ij}$. This specifies the orientation of the major axis for an elliptical repulsion potential between the membrane concentration $M$ and any other $\mu$-type concentration as shown in Figure 1. The interaction strength $f_{M,\mu}^\theta(x_{\alpha\beta}, x_{ij}) = f_{M,\mu}(x_{\alpha\beta} - x_{ij})$ in each of the 8 neighboring cells $x_{\alpha\beta} \in N_{ij}$ is calculated as the normalized area $C^\theta(x_{\alpha\beta} - x_{ij})$ of the directionally appropriate $\pi/4$ octant of the ellipse, with the $-\pi/8$ to $\pi/8$ octant directed towards the central right neighbor $x_{i+1,j}$. The lengths of the major and minor axes of this ellipse are given by $r_{M}^{major}$ and $r_{M}^{minor}$ respectively.

Further mimicking the behavior of lipid sheets, the orientation of membrane concentrations $\theta(x_{ij}, t)$ at lattice site

![Figure 1: Anisotropic repulsive interaction ellipse. The ellipse is centered at lattice site $x_{ij}$ with the major axis oriented at angle $\theta_{ij}$ with respect to the horizontal. Each of the 8 lattice sites in the Moore neighborhood $N_{ij}$ of $x_{ij}$ (orange) is subject to an interaction proportional to the normalized area of the corresponding $\pi/4$ octant of the ellipse (blues). Darker shades of blue signify stronger repulsion.](image-url)
where $\psi(x) = \sin(2x)$ was chosen so as to stabilize aligned orientations and destabilize anti-aligned ones in a smooth manner.

**Full model.** The full model consists of four differential equations in the form of equation (1) (one for each molecular concentration type $m \in M$) and one differential equation for the orientation in the form of equation (7) for each site $x_{ij} \in N_x \times N_y$ the lattice. Thus, the model is technically a $5N_xN_y$ dimensional coupled, nonlinear dynamical system. Since many of the phenomena we are interested in occur in non-equilibrium, the $\Gamma_m(x_{ij}, t)$ term allows for general flows of concentrations in or out of the system. This will be particularly useful for modifying the food concentration $F$ which plays the role of an energy supply for the chemical reactions, but does not participate in repulsive interactions. Additionally, we note that while the water concentration $W$ is reactively inert, it contributes to repulsive interactions and fills what would otherwise be empty space. The spatial distributions of the autocatalyst $A$ and membrane $M$ concentrations are of primary interest to the following analysis.

**Model parameters.** The general model supports a plethora of possible behaviors for the spatial distribution of the molecular concentrations. Although a systematic study of these parameters was not performed, our parameter selection was informed by two criteria: repulsion should allow membranes to form stable sheets, and the tradeoff between diffusion and production rates should support the requirement of containment for ongoing catalysis. The following parameter values were used: $k_{AA} = 0.09$, $k_{AM} = 0.1$, $k_A = k_M = 0.001$, $k_{dA} = 0.0125$, $d_A = d_M = d_F = d_W = 0.29$. For the repulsion interactions, we assume all interactions are symmetric with respect to molecular type (i.e. $f_{m\mu}^\theta = f_{\mu m}^\theta$), and take values: $f_{AA}^\theta(|x_{i\alpha\beta} - x_{ij}| = 1) = 0.875$, $f_{MM}^\theta(|x_{i\alpha\beta} - x_{ij}| = 1) = 1.5 \times C^\theta(x_{i\alpha\beta} - x_{ij})$, $f_{MA}^\theta(|x_{i\alpha\beta} - x_{ij}| = 1) = f_{MW}^\theta(|x_{i\alpha\beta} - x_{ij}| = 1) = 7.0 \times C^\theta(x_{i\alpha\beta} - x_{ij})$, where $C^\theta(x_{i\alpha\beta} - x_{ij})$ is the orientation-dependent ellipsoidal area with radii $r_M^{\text{minor}} = 20$ and $r_M^{\text{major}} = 1$. All other parameters were set to 0.

The system we consider unfolds on a $N_x = N_y = 50$ square lattice with toroidal boundary conditions, making a total of 12,500 ordinary differential equations. To keep a steady supply of food entering the system, the concentration of $F$ is driven towards a saturation value of $s_F$ at a rate $k_F$ via the additional linear term $\Gamma_F(x_{ij}, t) = k_F(s_F - F(x_{ij}, t))$, where we set $k_F = 0.8$ and $s_F = 0.18$. This only applied outside of a circle of radius 9 cell units. This area of food resupply does not overlap with the self-constructing configurations that we will explore, food can only reach the central area surrounding these configurations by diffusion. No additional interactions with an external source are assumed, thus $\Gamma_A(x_{ij}, t) = \Gamma_M(x_{ij}, t) = \Gamma_W(x_{ij}, t) = 0$.

**Model Behavior**

**Initiation and time evolution.** Given any initial spatial configuration for the molecular concentrations and orientation field, the system unfolds deterministically, most often towards a uniform state in which $A$ and $M$ concentrations have been depleted. To facilitate finding a viable stable configuration, with non-zero values of $A$ and $M$, the system was initialized in the convenient configuration shown in Figure 2 at $t = 0$. This configuration consists of a small circle of autocatalyst with a diameter of five lattice cells across and a uniform concentration of 0.6. The circle of autocatalyst is surrounded by a ring of membrane that is 3 lattice cells thick and has a concentration of 0.8. The membrane orientation field is initiated as concentric circles around the lattice's center. Food is initiated as a uniform field with a concentration of 0.18, and water fills the environment to bring the summed concentrations of all molecules at each lattice cell to a value of 1.0. This cell-like initial configuration, with autocatalyst contained by a membrane boundary, facilitates the subsequent unfolding towards a viable configuration. No systematic study of initial configurations was performed.

We are primarily interested in the first stable configura-
tion (shown in greater detail in Figure 3), which arises from the initial configuration after a short transient, and then persists practically unaltered from \( t = 5000 \) to \( t = 27000 \). This timescale is much longer than the timescale of typical cell processes and death events, so we treat the structure as stable given the processes of interest. The configuration of the system at \( t = 10000 \) will be resimulated and tested for the remainder of this paper. This configuration will be called the stable configuration, or \( SC \). In \( SC \), the membrane is thinner than the initial configuration, and there is an interesting bridge formation of membrane cutting across the center of the cell and splitting the autocatalyst into two regions. Cells with low molecular concentration appear directly to the left and the right side of the bridge, this is due to the directional repulsion of the anisotropic membrane molecules.

\( SC \) eventually destabilizes due to small changes in concentrations that accumulate over time. The destabilized structure goes through a short transient before restabilizing at a different configuration.

**Containment and metabolism.** Of particular importance to models of autopoiesis is the establishment of metabolism-boundary co-construction. While the boundary’s dependence on metabolism is explicitly made through the reactions in our model, the other direction needs a bit more justification. Figure 4 demonstrates the role of containment and metabolism by pulling apart the membrane and autocatalyst fields of \( SC \). The membrane field is displaced upwards by 25 lattice cells from its original position and the membrane orientation is copied. Everything else is kept equal. Whereas the stable configuration would have lasted for approximately 25000 time steps, the displaced configuration is clearly disintegrating after 500 time steps, and the final vestiges of the relevant molecules disintegrate around \( t = 3000 \).

These results illustrate the strong symmetrical dependence of boundary and metabolism in the processes of co-construction. The processes of containment and molecular synthesis counter the effects of diffusion and decay. The autocatalyst needs to be contained by the membrane in order to remain at the high concentrations that allow for its reactions of production. Without the membrane, autocatalyst diffuses away and quickly decays. This dependence is shown in Figure 4, as the autocatalyst diffuses away and quickly decays. The boundary’s shape begins to change immediately as it thickens where the autocatalyst once was, and begins to decay. Within several hundred time steps, only vestiges of the boundary survive and soon after they are gone. Only through coupled co-constructive processes can either molecular species survive.

**Self-repair and disintegration.** Figure 4 illustrates \( SC \)’s precariousness and its capacity for self-repair. In the figure, two sequences are shown in which a tear perturbation was applied to the membrane of \( SC \), with a larger tear in the bottom sequence. A tear is a perturbation in which a small section of membrane is removed by setting all the concentrations to a value of 0, and randomizing the orientation of those lattice cells. At \( t = 1 \), we can see the missing membrane section in both sequences.

In the top sequence, which has a smaller tear, the membrane flows back into the removed section and the system fully restabilizes by \( t = 500 \). The orientation, which is not illustrated in the figure, also realigns and allows the membrane concentration to flow around the boundary. Interestingly, this event results in a different stable configuration than before the perturbation. The cell is elongated on the top side where it suffered the perturbation, resembling residual outgrowth.

In the bottom sequence, with the larger tear, the autocatalyst begins to leak out, as shown at \( t = 15 \). Membrane also flows into the tear, but it is repulsed by the autocatalyst and

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Figure 3: Stable configuration \( SC \), showing the central \( 19 \times 19 \) cells of the lattice. \( SC \) is composed of autocatalyst (red) and membrane (blue), and is embedded in an environment that is refilled with food (green). This food field is omitted in all other figures. The membrane’s orientation is shown by the yellow lines. Brighter regions designate reduced molecular concentrations.

Figure 4: The co-dependent roles of containment and metabolism are illustrated by separating membrane from autocatalyst, and showing the system’s rapid disintegration.
cannot repair the hole. By \( t = 500 \), most of the autocatalyst has leaked out, and the membrane is in a distorted form. The leaking autocatalyst creates new membrane molecules, which self-assemble additional strings in the environment. With the containment condition broken, the metabolism cannot persist and the boundary decays. Most of the structure has been depleted by \( t = 1000 \), and soon after the system returns to its terminal, uniform state.

**Perturbation Studies**

In the behavioral studies of the previous section, we observed conditions that allow the membrane and autocatalyst to sustain each other through co-construction, and repair themselves following tear perturbations. We now shift to a more quantitative approach for investigating the limits of the system’s viability and its robustness to perturbation. Here, robustness is simply defined as the capacity to retain configurational stability despite harmful perturbations. We study these properties by systematically applying perturbations and observing which conditions drive the system to disintegration, and which allow it to remain viable.

Quantifying robustness immediately highlights three challenges: 1) How to quantify viable stability, 2) How to characterize a system perturbation, and 3) How to characterize a system’s response to a perturbation.

Given that the death state is a stable attractor for which the relevant concentrations are depleted, viability exists in stable, nonzero configurations of autocatalyst and membrane. We associate stability with extended periods of time in which all of \( A \) and \( M \)’s time derivatives are near zero. Thus, a structural configuration is stable when the sum of the temporal derivatives of \( A \) and \( M \) over the whole system satisfies

\[
\sum_{x_{ij}} |A(x_{ij}, t_k)| < \epsilon \quad \text{and} \quad \sum_{x_{ij}} |M(x_{ij}, t_k)| < \epsilon
\]

for all \( t_k \in [t, t + 5000] \), and a sufficiently small \( \epsilon = 0.01 \).

There are many types of system perturbations that could be systematically explored. We classify the space of possible perturbations by three main dimensions: type, location, and time. Type refers to the five different state variables: the molecular types \( (A, M, F, W) \) and the orientation field of the membrane \( (\theta) \). Perturbations can be applied to any combination of these variables. Location refers to the positions within the lattice at which these molecules are perturbed. Perturbations can be applied to spatially localized regions, or to all points throughout the system. Time refers to the temporal structure of perturbations throughout a simulation.

Ideally, each class of perturbations will have a few parameters which capture the perturbation and allow one to explore the system’s robustness as the parameters are varied. The tear perturbation is an instantaneous, spatially-local perturbation, applied to \( M \) and \( \theta \) and parameterized by the spatial extent of the tear. On the other hand, global noise is an instantaneous perturbation that modifies every variable in the system. The space of possible perturbations is vast.

Finally, we must characterize a system’s response to a perturbation. Here, we measure how long it takes for a system to reach stability following a perturbation. When it stabilizes, we determine its structural distance from the original configuration by taking the summed absolute difference between the two configuration’s states. If this sum is near zero, then the system has restabilized at the original configuration. In contrast, larger values indicate a new configuration has been reached.

**Gaussian blur perturbations.** The Gaussian blur is a global perturbation applied instantaneously to the four molecular species (but not the orientation field \( \theta \)). Gaussian blur is a common technique from image processing used to make an image blurry or reduce image noise. For our model, applying the blurring function is akin to instantaneously shaking the system. More shaking leads to more blurring, as molecules between local regions are mixed. Mathematically, the Gaussian blur is a convolution of the concentration fields with a Gaussian function, resulting in a Gaussian-weighted spatial average. By increasing the variance \( (\sigma^2) \) of the Gaussian function, we can make the blurring increasingly severe.

Figure 6 shows the time to restabilization following a Gaussian blur perturbation as \( \sigma^2 \) is systematically varied. In all instances the system was initialized to \( SC \). The figure shows that the restabilization time varies as the blur becomes more severe until, for \( \sigma^2 > 4.9 \), the system becomes too scrambled and can no longer recover and instead evolves to the stable terminal attractor.

Figure 6 also illustrates four different stable viable configurations that are reached following perturbations. Configuration \( A \), which we observe at small \( \sigma^2 \), is \( SC \). As \( \sigma^2 \) is increased it takes slightly longer to restabilize at \( A \). At \( \sigma^2 > 3.4 \) we see a discrete change occur, in which the system takes much longer to stabilize, and when it stabilizes it

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Figure 5: \( SC \)’s precariousness and capacity for self-repair are illustrated by applying two different-sized tears, pointed to with the red arrows. The upper sequence, which sustains a smaller tear, is able to repair itself. The lower sequence, with the larger tear, ends in disintegration.
is at a new configuration $B$. This configuration looks similar to $A$, but has a diameter 2 cells larger. As we increase $\sigma^2$ beyond 4.1, configuration $C$ is reached, and at 4.5 we see configuration $D$. For configurations $C$ and $D$, we observe small membrane structures that have formed external to the boundary, there are also internal differences from $A$ and $B$. The external points are stable, and are sustained by a slow and constant diffusion of autocatalyst that spreads outside of the boundary. In $D$, we observe a broken symmetry in the internal membrane stripes. Presumably there is another stable configuration identical to this, but with reversed broken symmetry.

**Spatially-localized Gaussian perturbations.** Finally, we explore two variants of a spatially-localized Gaussian perturbation. These are applied in space by using a translated Gaussian function to multiply concentrations of the four molecular species ($A$, $M$, $F$, and $W$) in the region around a given focal point. The function is of the form:

$$G(x_{ij}) = \alpha e^{-(|x_{ij} - x_f|^2)/2\sigma^2} + 1$$

where $|x_{ij} - x_f|$ is the distance from the focal point $x_f$ and the given cell $x_{ij}$, $\alpha \in [-1, \infty)$ is the amplitude of the function, and $\sigma^2$ is the variance. An $\alpha$ of 0 produces no change to the fields because the focal point and the points around it are multiplied by 1. Negative $\alpha$ reduces the field concentration while positive $\alpha$ increases the concentrations of the affected cells surrounding the focal point.

Figure 7 shows this class of perturbations applied to two different focal points of $SC$. The locations of the focal points are shown by the green dots on the inset configuration diagrams, and the results are shown in the two perturbation figures. In these plots, $SC$ restabilization is shown in green, stabilization to a different configuration is shown in purple, and perturbations that lead to death are shown in red. Time to restabilization is shown by the shade, with darker shading indicates longer time to restabilization. This highlights several features. Since $\alpha = 0$ perturbations have no effect on $SC$, the corresponding light green line indicates zero timesteps to regain stability. The shading also highlights that as a boundary between different configurations is approached, it takes increasingly longer to restabilize.

A qualitative comparison of the two perturbation figures reveals that the location of perturbation significantly alters the systems response. In Figure 7A, there is less red overall, meaning that fewer perturbations lead to $SC$’s disintegration. In fact, we see that the red area from Figure 7B is mostly purple in 7A. For example, perturbations with low $\alpha$ and mid-range $\sigma$ lead to disintegration when applied to the focal point in 7B, but when applied to the focal point in 7A, they merely drive the system to a different configuration.

**Discussion**

Robustness of boundary-metabolism co-construction is a key property of autopoietic systems. Living systems do not exist in perfect conditions, and are prone to environmental perturbation. Because of this, successful autopoietic systems must be able to repair themselves in order to persist. We outlined a minimal spatial model that exhibits metabolism-boundary co-construction and emergent organization. This allowed us to simulate stable, mutually
Spatiality adds an important dimension to our understanding of autopoiesis. Instead of imposing a system/environment distinction upon our model, an identity emerges as a sustained spatial inhomogeneity. Precariousness then becomes the potential for the network of interactions to explicitly dissolve. While we can qualitatively observe the system spatially disintegrate, we currently lack a quantitative measure of precariousness. Therefore, we used the uniform system state as an indicator that dissolution has occurred, rather than its definition. This contrasts with non-spatial models that define disintegration as relevant variables equaling zero (Barandiaran and Egbert, 2014), or as essential variables leaving explicitly-defined viability limits (Ashby, 1952).

Our quantitative analysis of robustness for boundary-metabolism co-construction highlighted several important operational dependencies for the concept. A formalization of robustness is highly dependent on the definition of perturbation to which the configuration must be robust. Here, we laid out a few key dimensions that describe the space of spatial-temporal perturbations and showed quantitatively distinct descriptions of robustness emerged as different perturbations were considered. Robustness is also dependent on the identity criteria used to establish organizational equivalence. For example, should the configuration with a small outgrowth resulting from the small tear perturbation in Figure 5 be considered the same organization as the original stable configuration SC? How about the equivalence between SC and the configurations with differing internal structure following the Gaussian blur in Figure 6B? Finally, our quantitative measure for robustness is dependent on the particular method for evaluating the stability of steady-state configurations. The shortcomings of this definition were particularly evident when we determined the original stable configuration SC eventually transforms into a qualitatively different stable configuration after a significantly long time.

One unexplored phenomenon observed in our model is the emergence of dynamic behavior. Behaviors can arise from heterogeneous environments or from the temporal dependence of a system’s robustness profile. For example, food gradients might result in a form of mobility due to asymmetries in the configuration’s local environment (Egbert and Di Paolo, 2009). As a system is exposed to different perturbations its configuration can be altered, which would change its robustness profile and behavioral responses following future perturbations. Extensions of identity and stability that allow one to characterize spatial configurations engaging in dynamic behaviors are still lacking. Of particular interest are configurations that have a disposition for being perturbed towards increasingly robust configurations, which might relate to the notion of adaptivity in enaction (Di Paolo, 2005).

Computational models, like the one presented here, provide a vehicle for exploring such concepts.

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