

From Rule-Taking to Rule-Making Chemistry: A Minimal Population-Environment Feedback Model

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Abstract

A key step toward life is the shift from chemistry that merely adapts to its surroundings to chemistry that actively reshapes them. Using a coupled population-environment feedback model, we identify the conditions under which environment-modifying activity, once present, can become self-sustaining in mixed chemical populations. When environmental conditions adjust instantaneously to population composition, environmental influence leaves no lasting trace and modifiers can spread only if initially common. By contrast, when environmental modification persists over the timescale of population change, production and decay generate heritable local conditions that give rise to bistability and alternative long-term outcomes. This persistence enlarges the basin leading to sustained environmental control, suggesting that even simple feedbacks could have allowed early chemical systems to move beyond passive adaptation and begin constructing the conditions that support their own propagation.

1 Introduction

The origin of life is often described as the emergence of chemical systems capable of sustaining organisation, reproduction, and adaptive change. Classical models illuminate different ways in which such organisation might arise and persist. For example, autocatalytic sets show how reaction networks can collectively maintain and propagate themselves Kauffman [1986]; hypercycle models demonstrate how cooperating replicators can overcome parasitic alternatives once template-based heredity is present Eigen and Schuster [1977]; and protocell constructs illustrate how compartmentalisation can couple metabolism, growth, and division into integrated units Szostak et al. [2001]. Despite capturing essential features of early evolution, these frameworks typically focus on the dynamics of replicating entities themselves and treat reaction conditions as externally imposed and fixed, rather than shaped or stabilised by the chemical systems in which replication occurs.

However, life is distinguished by its capacity to modify the conditions under which it operates Odling-Smee et al. [2003]. Niche construction Laland et al. [1999] and ecological scaffolding Black et al. [2020] show that living systems shape aspects of their environment in ways that influence subsequent evolutionary dynamics. Origins of life research likewise suggests that early chemistries may

have begun to stabilise favourable local conditions rather than merely endure externally imposed ones. In particular, recent work on autocatalytic chemical ecosystems emphasises the continuity between ecological and evolutionary dynamics in open chemical systems, showing how feedback between reaction networks and their environments can support persistence and adaptive change prior to genetic inheritance [Baum et al. \[2023\]](#), [Kalambokidis and Travisano \[2024\]](#).

This convergence suggests that two broad classes of constraints are central to the emergence of life. The first concerns reliable replication and information preservation, including fidelity, stability, and protection of replicating structures. The second concerns the ability of chemical systems to modify or stabilise the conditions under which replication occurs. Much of the origin-of-life literature has focused on the former, developing detailed accounts of how inheritance and replication might become robust. By contrast, the latter has received comparatively less attention, particularly in pre-genetic contexts where regulation and environmental coupling must precede encoded heredity. This emphasis aligns with discontinuist perspectives, which argue that the transition from molecular evolution to biological organisation is marked not by replication alone, but by the emergence of regulatory mechanisms that integrate system and environment [Bich and Damiano \[2012\]](#). Understanding when and how such endogenous feedback can first arise in chemical populations is therefore essential for explaining the transition from rule-taking to rule-making chemistry.

Here we develop a minimal population-environment feedback model to examine when environment-modifying activity, once present, can become self-sustaining and reshape the conditions governing chemical propagation. We analyse the conditions under which such rule-making strategies can spread, how their fate depends on initial abundance and environmental state, and how even a single dynamical environmental variable reshapes the phase structure governing long-term outcomes.

2 Model

We consider a well-mixed population composed of two types of chemical replicators: rule-takers (R), which reproduce under external physicochemical conditions they do not modify, and rule-makers (M), which incur a cost to alter those conditions (Fig. 1). Let y denote the frequency of rule-makers and $1 - y$ the frequency of rule-takers (implicitly assuming that the total population is regulated on a faster timescale than changes in composition, as in chemostat-like or dilution-balanced settings).

The local environment is represented by a scalar variable E , which acts as a coarse-grained descriptor of catalytic, buffering, or stabilizing factors that influence replication rates. The variable E is shared by both types, with rule-makers increasing it while paying a cost, and rule-takers benefiting from it without contributing to its production. Rule-makers are thus the source of environmental change, and the resulting environmental state feeds back on replication.

Each chemical species replicates at a per-capita rate, denoted by a fitness π , which determines its rate of increase. Rule-maker fitness includes three components—a baseline performance s relative to rule-takers, a cost $c > 0$ for modifying the environment, and a feedback benefit pE that increases with environmental quality. Thus,

$$\pi_M = s - c + pE, \quad \pi_R = 1, \tag{1}$$

where the rule-taker's fitness is normalized to unity.

Under the replicator equation, the frequency of rule-makers changes according to

$$\dot{y} = y(\pi_M - \bar{\pi}), \quad (2)$$

where the mean fitness is

$$\bar{\pi} = y\pi_M + (1 - y)\pi_R. \quad (3)$$

Substituting Eqs. (1) and (3) into Eq. (2) gives

$$\dot{y} = y(1 - y)(s - c + pE - 1), \quad (4)$$

a cubic vector field in y whose coupling to the environmental dynamics in E determines the qualitative behaviour of the system.

Environmental conditions evolve according to

$$\dot{E} = \alpha y - \beta E, \quad (5)$$

where α quantifies the rate at which rule-makers improve the environment and β the rate at which environmental conditions relax back toward baseline.

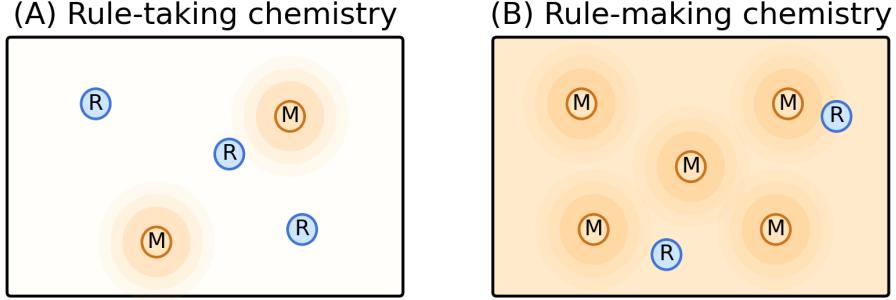


Figure 1: Conceptual illustration of the feedback model. (A) The environment remains tightly coupled to population composition, either because relaxation is fast or because rule-makers are rare, producing effectively instantaneous feedback. (B) Environmental modification accumulates when relaxation is slow or rule-makers are sufficiently abundant, allowing changes in environmental quality to persist over the timescale of population dynamics. Both panels represent different parameter regimes of the same underlying dynamical system.

3 Results

3.1 Stability analysis

The coupled population-environment system defined by Eqs. (4) and (5) admits two natural boundary equilibria. The first (\mathbf{A}_1) corresponds to extinction of rule-makers, so that the population is entirely rule-taking and the environment remains at its baseline level. The second (\mathbf{A}_2) corresponds to full dominance of rule-makers, in which environmental quality is maintained at a steady state set by the balance between production and relaxation. In addition to these boundary states, an interior equilibrium (\mathbf{S}) may exist in which rule-takers and rule-makers coexist at fixed frequencies together with a nontrivial environmental state (see Appendix A). These three equilibria are given by

$$\mathbf{A}_1 = (0, 0), \quad \mathbf{A}_2 = (1, \alpha/\beta), \quad \mathbf{S} = (y_s, E_s) = \left(\frac{p_c}{p_{\text{eff}}}, \frac{\alpha}{\beta} \frac{p_c}{p_{\text{eff}}} \right).$$

The appearance of the interior equilibrium is governed by the threshold condition

$$p_{\text{eff}} > p_c = c + 1 - s,$$

where c is the cost of environmental modification and $1 - s$ is the baseline disadvantage of the modifying strategy, and

$$p_{\text{eff}} = p \frac{\alpha}{\beta} \quad (6)$$

is the effective strength of feedback relative to environmental decay.

For $p_{\text{eff}} \leq p_c$, the only admissible equilibrium is the rule-taking state \mathbf{A}_1 , which is globally stable. For $p_{\text{eff}} > p_c$, \mathbf{A}_1 and \mathbf{A}_2 are both stable, whereas \mathbf{S} is a saddle whose stable manifold forms the separatrix in the (y, E) plane that divides the basins of attraction of the two boundary states (see Appendix A).

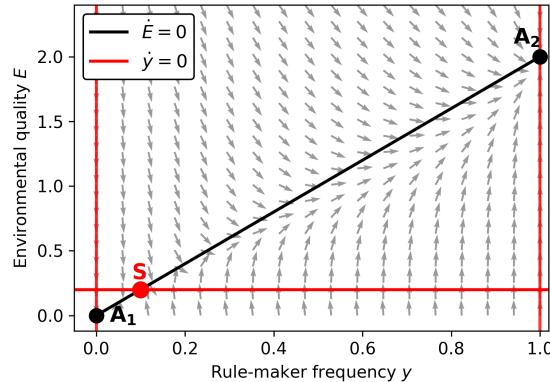


Figure 2: Nullcline structure and flow of the population-environment feedback model (Fig. 1). Black solid line: environmental nullcline $\dot{E} = 0$ with $E = (\alpha/\beta)y$. Red solid lines: population nullclines $\dot{y} = 0$, including the interior nullcline $E = (1 - s + c)/p$ and the invariant boundaries $y = 0$ and $y = 1$. The fixed points are $\mathbf{A}_1 = (0, 0)$, $\mathbf{A}_2 = (1, 2.0)$, and the interior saddle $\mathbf{S} = (y_s, E_s) = (0.1, 0.2)$. Gray arrows indicate the normalized direction field. Parameters: $s = 1.0$, $c = 0.2$, $p = 1.0$, $\alpha = 1.0$, $\beta = 0.5$, giving $p_c = c + 1 - s = 0.2$ and $p_{\text{eff}} = p\alpha/\beta = 2.0$.

The geometry of these coupled dynamics can be visualized through the nullclines and direction field of the (y, E) system, which illustrate how trajectories are guided through phase space (Fig. 2). The vector field points toward the environmental nullcline $\dot{E} = 0$ from both above and below, indicating that it acts as an attracting manifold in the vertical direction. Once close to this curve, further evolution is dominated by changes in the population composition y . In other words, deviations of the environmental modifier from its production-decay balance relax automatically, after which the remaining evolution reflects changes in the relative abundance of rule-makers and rule-takers. This two-dimensional population-environment system, in which environmental modification persists over the same timescale as population change, defines what we refer to as the dynamic-environment regime.

Within the bistable region of the dynamic-environment regime, the two boundary attractors are separated in phase space by a curved separatrix in the (y, E) plane, whose geometry determines how initial conditions are partitioned between rule-taking and rule-making outcomes. The boundary between these regimes is linear in (c, p_{eff}) for fixed s (Fig. 3), reflecting the analytic condition for the appearance of the interior saddle. This linear frontier encodes a direct trade-off between cost and feedback strength. Increasing the energetic or functional cost of rule-making can be compensated by proportionally stronger environmental feedback, thereby preserving bistability.

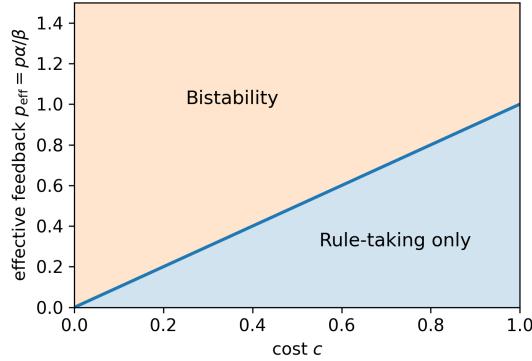


Figure 3: Binary phase diagram of dynamical regimes as a function of cost c and effective feedback strength $p_{\text{eff}} = p\alpha/\beta$ for $s = 1$. At and below the threshold line $p_{\text{eff}} = p_c$, only the rule-taking equilibrium \mathbf{A}_1 exists and is globally stable. Above the line, the system is bistable, with coexistence of the rule-taking equilibrium \mathbf{A}_1 and the rule-making equilibrium \mathbf{A}_2 separated by the interior saddle \mathbf{S} .

Environmental history strongly shapes long-term population outcomes within the bistable regime. Fig. 4 shows trajectories of the coupled system across a uniform range of initial rule-maker frequencies y_0 for two contrasting initial environmental states. When the initial environment is poor ($E_0 = 0$), only sufficiently large initial rule-maker fractions cross the separatrix and approach the rule-making attractor, while smaller populations decay toward the rule-taking state. By contrast, when the environment is initially favorable ($E_0 = 2$), even rare rule-makers reliably grow and invade, and almost all trajectories converge to the rule-making attractor. This demonstrates that pre-existing environmental conditioning can drastically alter the basin structure, lowering the threshold for rule-makers to establish themselves. The same feedback parameters therefore support radically different evolutionary outcomes depending solely on the environmental state from which the system is initialized.

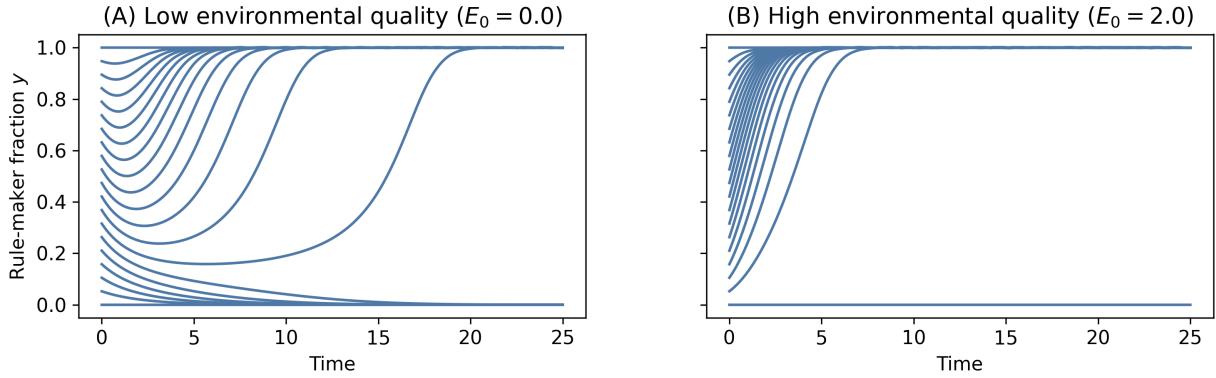


Figure 4: Time evolution of rule-maker frequency $y(t)$ for a uniform range of initial population compositions y_0 under two different initial environmental conditions within the bistable regime. (A) Low initial environmental quality (modifier concentration) ($E_0 = 0$). (B) High initial environmental quality ($E_0 = 2$). Parameters: $s = 1.0$, $c = 0.5$, $p = 0.8$, $\alpha = 1.0$, $\beta = 0.2$, giving $p_c = c + 1 - s = 0.5$ and $p_{\text{eff}} = p\alpha/\beta = 4.0$. For low E_0 , only sufficiently large initial rule-maker fractions overcome decay and approach the rule-making attractor, whereas for high E_0 even initially rare rule-makers reliably invade.

3.2 Quasi-steady environment limit

To isolate the role of environmental persistence, it is instructive to consider the limit in which environmental dynamics are slaved to population composition. In this quasi-steady environment limit, deviations of the environmental variable relax rapidly compared to changes in population composition, so that the system remains close to the environmental nullcline $\dot{E} = 0$ throughout its evolution. The environmental state is therefore no longer an independent dynamical degree of freedom but is approximately determined by the instantaneous rule-maker frequency according to

$$E \approx \frac{\alpha}{\beta} y.$$

Substituting this quasistatic relation into the population equation (4) reduces the coupled two-dimensional dynamics to an effective one-dimensional replicator equation with instantaneous frequency-dependent feedback,

$$\dot{y} = y(1 - y)(s - c + p_{\text{eff}} y - 1),$$

where $p_{\text{eff}} = p\alpha/\beta$ is the effective feedback strength defined in Eq. (6).

The reduced dynamics admits equilibria at the same values of the rule-maker fraction y as in the full system: a rule-taking state at $y = 0$, a rule-making state at $y = 1$, and an interior equilibrium at $y = p_c/p_{\text{eff}}$ when $p_{\text{eff}} > p_c = c + 1 - s$. However, the phase-space geometry is fundamentally altered. In the quasi-steady environment limit, the curved separatrix present in the dynamic-environment case collapses onto a single, sharp threshold at $y = y_s = p_c/p_{\text{eff}}$, so that long-term outcomes depend exclusively on the initial rule-maker frequency. Trajectories with $y_0 < y_s$ converge to the rule-taking state, whereas those with $y_0 > y_s$ converge to the rule-making state, independent of the initial environmental condition.

The consequences of this reduction are illustrated in Fig. 5, which shows trajectories of the reduced one-dimensional dynamics across a uniform range of initial rule-maker frequencies for effective feedback strengths below and above the threshold. For subcritical effective feedback ($p_{\text{eff}} < p_c$), all trajectories relax to the rule-taking state. For supercritical effective feedback ($p_{\text{eff}} > p_c$), a sharp threshold separates trajectories that decay from those that grow toward the rule-making state. Unlike in the dynamic-environment regime analyzed above, environmental history plays no role in this limit; only the initial population composition determines the outcome.

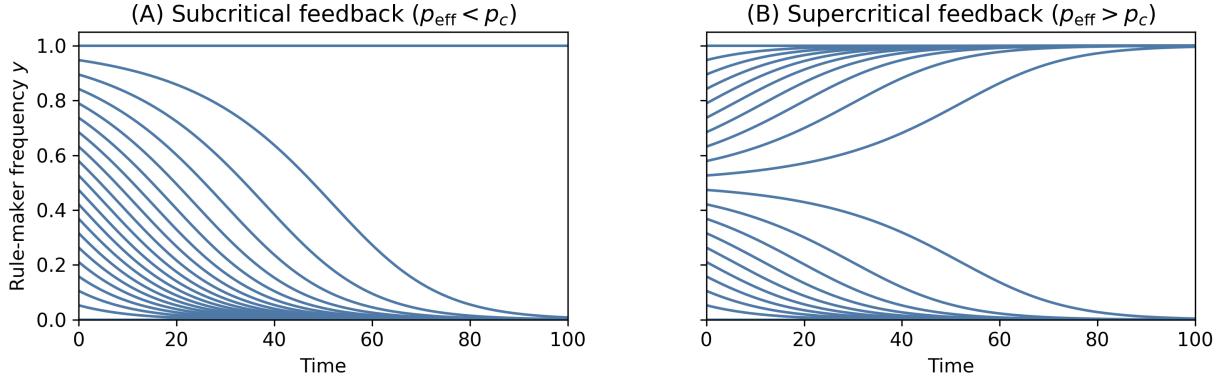


Figure 5: Dynamics in the quasi-steady environment limit. Time evolution of the rule-maker frequency $y(t)$ for a uniform range of initial conditions y_0 under the one-dimensional reduced dynamics obtained by eliminating the environmental variable via the quasi-steady relation $E \approx (\alpha/\beta)y$. (A) Subcritical effective feedback ($p_{\text{eff}} < p_c$), for which all trajectories converge to the rule-taking state $y = 0$. (B) Supercritical effective feedback ($p_{\text{eff}} > p_c$), for which a sharp threshold at $y = y_s = p_c/p_{\text{eff}}$ separates trajectories that decay toward the rule-taking state from those that converge to the rule-making state $y = 1$. Parameters: $s = 1.0$, $c = 0.1$, with $p_c = c + 1 - s = 0.1$.

3.3 Minimal chemical realization of rule-making feedback

The population-environment feedback model admits a direct realization as a minimal chemical reaction network. This construction clarifies how the abstract environmental variable E corresponds to a physically meaningful modifier species and shows that the feedback structure encoded in Eqs. (4)-(5) arises naturally from standard mass-action kinetics under well-defined assumptions.

We consider four chemical species: a rule-taking replicator R , a rule-making replicator M , a generic substrate S supplying material or free energy for replication, and an environmental modifier B . The modifier B represents any chemical factor produced by M that enhances the local replication rate of M , for example through catalysis, buffering, metal chelation, or stabilization of reaction conditions. The reaction network is defined by the following elementary processes:



Here, Eqs. (7) and (8) describe baseline replication of R and M from a common substrate S . Eq. (9) represents enhanced, feedback-mediated replication of M in the presence of the modifier B , which acts catalytically and is regenerated in the process. Eq. (10) captures the costly production of the environmental modifier by M . Eqs. (11)-(13) describe first-order loss of each species due to degradation, dilution, or outflow.

We assume that the substrate S is maintained at an approximately constant concentration S_0 by external supply, as in a chemostat or continuously driven prebiotic reactor. Under this assumption, the mass-action dynamics for the concentrations $R(t)$, $M(t)$ and $B(t)$ take the form

$$\frac{dR}{dt} = (k_R S_0 - \mu_R) R, \quad (14)$$

$$\frac{dM}{dt} = (k_M S_0 - \mu_M + k_{fb} S_0 B) M, \quad (15)$$

$$\frac{dB}{dt} = \alpha M - \beta B. \quad (16)$$

This assumption implies regulation of total replicator abundance on a faster timescale than changes in population composition, consistent with the frequency-based formulation used above.

The reaction scheme induces per-capita growth rates

$$\pi_R = k_R S_0 - \mu_R, \quad \pi_M = k_M S_0 - \mu_M + k_{fb} S_0 B,$$

which determine exponential replication rates and correspond directly to the growth coefficients used in the population-level description. Writing the dynamics in terms of the rule-maker frequency $y = M/(R + M)$ yields the standard replicator form

$$\dot{y} = y(1 - y)(\pi_M - \pi_R).$$

Grouping parameters shows that the intrinsic advantage of rule-makers corresponds to $s - c = k_M S_0 - \mu_M$, while the strength of environmental feedback corresponds to $p = k_{fb} S_0$, with the environmental variable identified chemically as $E \equiv B$. Under these identifications the chemical model reduces exactly to Eq. (4) (see Appendix B).

Fig. 6 shows the feedback dynamics expressed as normalized concentrations of rule-takers, rule-makers, and modifier species, obtained by integrating Eqs. (4) and (5). For bistable parameters,

these trajectories illustrate the same regime structure identified at the population level. When the initial modifier concentration is low, modifier decay prevents sustained feedback and the system relaxes to the rule-taking state. When the modifier concentration is initially high, feedback between M and B is maintained, allowing rule-makers to increase in abundance and stabilize a persistent environmental state.

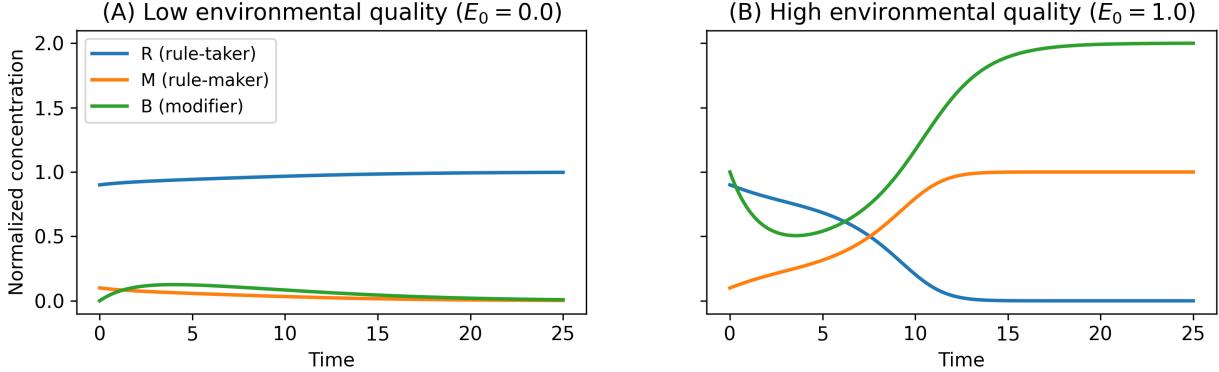


Figure 6: Dynamics of a chemically interpreted population-environment feedback model. Time series of normalized concentrations of the rule-taker R (blue), rule-maker M (orange), and modifier B (green) for the bistable parameter set $s = 1.0$, $c = 0.2$, $p = 0.8$, $\alpha = 1.0$, and $\beta = 0.5$, so that $p_c = c + 1 - s = 0.2$ and $p_{\text{eff}} = p\alpha/\beta = 1.6$. In both panels the initial rule-maker fraction is $y_0 = 0.1$; the two panels differ only in the initial environmental quality. (A): low initial environmental quality ($E_0 = 0$) leads to extinction of rule-makers and decay of the modifier concentration. (B): high initial environmental quality ($E_0 = 1.0$) allows rule-makers to increase in abundance, maintain a positive modifier concentration, and drive the system to the rule-making attractor.

In this chemically grounded formulation, the environmental variable E corresponds to the concentration of a modifier species that is produced by rule-makers at a cost, enhances their own replication, and decays on a characteristic timescale β^{-1} . The effective feedback strength $p_{\text{eff}} = p\alpha/\beta$ therefore admits a direct chemical interpretation as the ratio between the catalytic enhancement rate of modifier-assisted replication and the lifetime of the modifier in the environment.

This minimal reaction network shows explicitly how population-environment feedback can arise from chemically plausible processes without invoking preexisting genetic information or complex metabolic organization. Environmental modification persists only when supported by sufficient population abundance, reproducing the same bistable transition between externally constrained and self-stabilizing regimes identified in the population-level analysis.

Discussion

The results identify a sharp threshold separating qualitatively distinct regimes of chemical organisation, consistent with the broader role of thresholds as organising principles in origin-of-life scenarios. In many prebiotic contexts, small and continuous changes in parameters can produce discontinuous changes in system-level behaviour, marking transitions between regimes with funda-

mentally different modes of persistence and control [Jeancolas et al. \[2020\]](#). In the present model, the relevant threshold concerns the persistence of population–environment feedback. Below a critical strength, environmental modification remains transient and does not alter long-term outcomes. Above it, modifier-producing populations can collectively stabilise the conditions that support their own persistence.

From a chemical perspective, this threshold reflects a balance between production and dissipation of environmentally active species. The environmental variable represents the concentration of a modifier produced by rule-makers and removed by background processes such as dilution, degradation, or buffering. When production exceeds dissipation, the modifier accumulates and reshapes the effective growth conditions experienced by the population. When dissipation dominates, environmental improvements fail to persist. The transition therefore marks a shift from environments that merely respond to chemistry to environments that are actively stabilised by it.

Importantly, this transition does not concern the fidelity of replication, the closure of reaction networks, or the stability of specific molecular structures. Instead, it concerns the stability of environmental influence itself. In threshold-based frameworks for the origin of life, this corresponds to a system–environment coupled transition, in which persistence depends jointly on internal population dynamics and environmental timescales [Jeancolas et al. \[2020\]](#). The emergence of rule-making chemistry thus represents a qualitative change in how chemical systems relate to their surroundings, from passive dependence to partial environmental control. This interpretation becomes explicit in the chemically grounded formulation of the model. There, the environmental variable corresponds to the concentration of a concrete modifier species produced by rule-makers and removed by background processes. The effective feedback strength reflects the balance between how strongly the modifier enhances replication and how long it persists in the environment. When production outpaces loss, the modifier accumulates to levels that feed back to enhance the replication of its producers. When loss dominates, environmental effects remain short-lived. The minimal reaction network therefore provides a concrete chemical mechanism by which replicators can create, maintain, and transmit enabling environmental conditions without requiring genetic encoding or complex metabolism.

Recent work has shown that the emergence of Darwin-like evolutionary dynamics may itself require crossing a threshold separating degradation-dominated chemistry from sustained propagation [Kocher and Dill \[2024\]](#). In that work, cooperative autocatalysts are shown to overcome such a barrier and enter a growth-dominated regime in which evolutionary invasion becomes possible. Related perspectives argue more broadly that ecological and evolutionary dynamics form a continuum even in purely chemical systems, with selection acting on persistence and dispersal prior to genetic encoding [Baum et al. \[2023\]](#). The transition identified here is conceptually distinct. Replication is assumed to be already possible, but the results show that replicating populations may nevertheless remain confined to a rule-taking regime unless population–environment feedback persists strongly enough to stabilise favourable conditions. In this sense, rule-making chemistry represents a subsequent threshold, marking the shift from propagation under given conditions to partial control over the conditions that govern propagation itself.

The model also connects naturally to niche-construction and constraint-inheritance frameworks [Laland et al. \[1999\]](#). Modifier-producing replicators generate environmental conditions that persist long enough to influence the selective environment of subsequent generations, providing a minimal example of non-genetic inheritance. Once established, these conditions stabilise the modifier-dominated regime, much as niche construction stabilises organism–environment couplings in bi-

ological systems. In this sense, the model illustrates how chemical populations can acquire a rudimentary form of autonomy by reinforcing the constraints that favour them.

A central consequence of the threshold is strong history dependence. Initial conditions jointly determine whether the system crosses the separatrix into the modifier-dominated state or relaxes to the rule-taking state. Such sensitivity to initial conditions may have been important on the early Earth, where heterogeneous microenvironments would have intermittently supported the accumulation of environmental modifiers. Only locales that crossed the threshold would have supported self-maintaining chemical organisation, potentially seeding the emergence of more complex evolutionary dynamics. At the same time, the model clarifies why such transitions should be rare rather than inevitable. Environmental modification is widespread in chemistry, but most modifications are too weak, too transient, or too costly to persist long enough to reshape selection. In the present framework, modifiers that decay rapidly are erased before they can influence population composition, while modifiers that enhance replication only weakly fail to offset their production costs. Even when bistability exists, successful transition into the modifier-dominated state requires crossing a separatrix that depends jointly on population composition and environmental state. The model therefore does not imply that feedback generically produces autonomy. Instead, it shows that autonomy emerges only under restricted conditions of sufficient feedback strength, persistence, and favourable history.

Despite its simplicity, the model suggests qualitative experimental predictions. In laboratory reactors or serial-dilution experiments, one could compare a resource-consuming replicator with a variant that also produces a stabilising modifier. The theory predicts bistability when environmental modification is strong relative to cost, with hysteresis under controlled perturbations providing evidence for the predicted feedback threshold. More generally, the framework highlights population–environment feedback as a distinct axis along which chemical systems can transition from passive adaptation to partial environmental control.

In summary, the model isolates a key ingredient in the emergence of autonomy. Early evolutionary dynamics may have depended not only on replication with variation and selection, but also on the capacity of chemical systems to stabilise the constraints enabling their own persistence. The results suggest that the transition from rule-taking to rule-making chemistry is neither inevitable nor ubiquitous, but rare and conditional, arising only when feedback is strong enough to persist across the timescales that shape population change.

Data availability

Code used for model implementation, simulation, and figure generation is available at <https://github.com/celiablanco/GameTheoryOoL>

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Appendix A: Fixed-point and stability analysis

The fixed points for the coupled system defined by Eqs. (4) and (5) satisfy $\dot{y} = 0$ and $\dot{E} = 0$ simultaneously. From $\dot{E} = 0$ we obtain the environmental nullcline

$$E = \frac{\alpha}{\beta} y. \quad (17)$$

Substituting (17) into $\dot{y} = 0$ yields the three equilibria

$$(y_0, E_0) = (0, 0), \quad (y_1, E_1) = (1, \alpha/\beta), \quad (y^*, E^*) = \left(\frac{p_c}{p_{\text{eff}}}, \frac{\alpha}{\beta} \frac{p_c}{p_{\text{eff}}} \right), \quad (18)$$

where

$$p_c = c + 1 - s, \quad p_{\text{eff}} = \frac{p\alpha}{\beta}. \quad (19)$$

The interior equilibrium exists in the admissible region only when $0 < y^* < 1$, or what is the same, when $p_{\text{eff}} > p_c$.

Linear stability is determined from the Jacobian of the two-dimensional flow,

$$J(y, E) = \begin{pmatrix} (1 - 2y)(s - c + pE - 1) & p y(1 - y) \\ \alpha & -\beta \end{pmatrix}. \quad (20)$$

Evaluating (20) at the boundary equilibria in (18) and using Eq.(19), gives

$$J(0, 0) = \begin{pmatrix} -p_c & 0 \\ \alpha & -\beta \end{pmatrix}, \quad J(1, \alpha/\beta) = \begin{pmatrix} p_c - p_{\text{eff}} & 0 \\ \alpha & -\beta \end{pmatrix}, \quad (21)$$

Hence $(y_0, E_0) = (0, 0)$ is stable whenever $p_c > 0$, and $(y_1, E_1) = (1, \alpha/\beta)$ is stable when $p_{\text{eff}} > p_c$.

At the interior equilibrium (y^*, E^*) , direct evaluation of the trace and determinant shows that

$$\det J(y^*, E^*) = -\alpha p y^*(1 - y^*) < 0,$$

whenever it exists. The determinant is therefore always negative in the admissible regime, implying one positive and one negative eigenvalue and confirming that (y^*, E^*) is a saddle point.

Appendix B: Derivation of the Reduced Replicator–Environment System

The deterministic mass-action equations for the three variables are

$$\frac{dR}{dt} = (k_R S_0 - \mu_R) R, \quad (22)$$

$$\frac{dM}{dt} = (k_M S_0 - \mu_M + k_{\text{fb}} S_0 B) M, \quad (23)$$

$$\frac{dB}{dt} = \alpha M - \beta B. \quad (24)$$

The coefficients in front of R and M define the per-capita growth rates

$$\pi_R = k_R S_0 - \mu_R, \quad \pi_M = k_M S_0 - \mu_M + k_{\text{fb}} S_0 B.$$

Let $N = R + M$ and $y = M/N$. Differentiating y yields

$$\dot{y} = \frac{N \dot{M} - M \dot{N}}{N^2}.$$

Using $\dot{M} = \pi_M M$ and $\dot{R} = \pi_R R$, we obtain

$$\dot{N} = \pi_M M + \pi_R R.$$

Substituting into the expression for \dot{y} and simplifying gives the standard replicator form

$$\dot{y} = y(1-y)(\pi_M - \pi_R).$$

To connect this with the reduced notation in the main text, we rescale time so that $\pi_R = 1$ and define the parameter combinations

$$s - c = k_M S_0 - \mu_M, \quad p = k_{\text{fb}} S_0.$$

Under this rescaling,

$$\dot{y} = y(1-y)(s - c + pB - 1),$$

which matches the functional form of Eq. (4) once we identify the environmental variable as $E \equiv B$.

The environmental dynamics follow directly from (24). Under chemostat-like conditions the total abundance N remains approximately constant, allowing $M = yN$ and therefore

$$\dot{E} = \alpha y N - \beta E = \tilde{\alpha} y - \beta E,$$

where $\tilde{\alpha} = \alpha N$ is absorbed into the effective production rate. This reproduces the environmental equation used in the main text.

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