

Full Length Article



Revisiting deterministic evolution: Robustness of cooperation under stochastic mutations and delayed feedback

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ARTICLE INFO

Keywords:

Evolutionary game
Replicator equation
Stochastic mutation
Delayed system

ABSTRACT

Stochastic mutations are intrinsic to evolutionary processes, reflecting both random genetic variation and broader uncertainties in strategic behavior. Here we extend our previous work on delayed evolutionary dynamics in a two species system by introducing Gaussian stochastic mutations into replicator equations with time delays. This framework captures both intra and interspecific interactions, with delays representing inevitable lags in feedback and response in biological and social systems. Using Lyapunov based stability analysis and numerical simulations, we show that while stochasticity mutations transient trajectories, cooperative equilibria remain robust even under very strong noise, with only extreme perturbations leading to divergence. These findings demonstrate that deterministic models retain strong predictive power for long term evolutionary outcomes across realistic conditions, offering new insights into how memory and randomness jointly shape the evolution of cooperation.

1. Introduction

Collaboration is a crucial feature of both biotic and social systems, spanning microbial consortia, plant-pollinator networks, and human societies [1–3]. These interactions, from mutualism to symbiosis, involve an inherent conflict between cooperative behavior and exploitative strategies, a central theme in evolutionary dynamics [4–6].

Evolutionary game theory presents a formidable and analytical lens to decode how cooperation emerges and persists within competitive settings [7–12]. A key analytical tool in this framework is the replicator equation, which describes how strategy frequencies evolve in response to relative payoff changes within an infinitely large and well-mixed population [13–15]. Central to this dynamic is the idea of the Evolutionary Stable Strategy, which identifies strategies resilient to invasion by rare mutants and ensures the dynamic stability of populations [7,16,17]. The utility of this approach is evidenced across biological and social systems. In public goods games, for instance, the introduction of voluntary participation [18] produces cyclic dominance among cooperators, defectors, and loners, a dynamic reminiscent of ‘rock-paper-scissors’ [19]. Building on this, strategies such as punishment [20–22], reward [23], and exclusion

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[24–26] have been mathematically formalized within replicator systems, each offering pathways to reinforce cooperation [27,28]. However, these models typically regard strategies as proxies for discrete species or genotypes, often overlooking the interactions that unfold within and between species. Recent studies have further illuminated how populations not only compete and cooperate with one another but also reshape the very environments they inhabit [29]. For example, Weitz et al. revealed that overexploitation of shared resources can entrench feedback loops of environmental depletion and recovery, mirrored by oscillations between cooperation and defection [30]. Similarly, Liu et al. integrated environmental feedbacks into replicator dynamics, demonstrating how investments in ecosystem protection modulate collective risks and sustain cooperation under threat [31].

Despite the significant advances, the replicator equation, rooted in deterministic assumptions, often overlooks crucial sources of stochasticity inherent in real world systems. Environmental fluctuations and imperfect information can all shape evolutionary trajectories, occasionally destabilizing otherwise robust evolutionarily stable strategies [32,33]. To address these gaps, stochastic approaches have gained increasing attention. The Moran process, for example, captures the role of random drift in finite populations, providing valuable insights into the probabilistic fixation of strategies and the emergence of cooperation [34,35]. Similarly, spatial games incorporate structured populations and localized interactions, naturally embedding stochastic factors such as probabilistic imitation and exploration in strategy updates [36–40]. Importantly, these stochastic frameworks complement rather than replace replicator dynamics. Indeed, under certain conditions, qualitative agreement has been observed between predictions from replicator equations and outcomes of network simulations [14,40,41], underscoring the enduring relevance of the replicator framework in modeling complex evolutionary processes.

To better understand how uncertainty shapes evolutionary dynamics, we build on our earlier model of two species evolutionary games with time delays [42]. By introducing stochastic mutation processes into the replicator framework, we construct a system that captures the combined effects of random mutations and delayed feedback on cooperation. Leveraging Lyapunov based stability analysis [43,44], we systematically examine how varying noise intensities and temporal delays reshape evolutionary trajectories, revealing conditions under which cooperation can be stabilized or disrupted.

2. Model

2.1. Deterministic baseline model

We examine a two species evolutionary game involving two species, A and B, each with infinitely large, well-mixed populations ($N_{A,B} \rightarrow +\infty$). Individuals engage in pairwise interactions, either with members of their own species (intraspecific interaction, probability p) or with those of the other species (interspecific interaction, probability $1 - p$). Each individual adopts one of two strategies: cooperation or defection. The corresponding payoff matrix can be described as:

$$\begin{aligned}
 M_1 &= \begin{matrix} & C_A & D_A \\ C_A & \begin{pmatrix} R_1 & S_1 \\ T_1 & P_1 \end{pmatrix} \\ D_A & \end{matrix}, & M_2 &= \begin{matrix} & C_B & D_B \\ C_A & \begin{pmatrix} R_2 & S_2 \\ T_2 & P_2 \end{pmatrix} \\ D_A & \end{matrix}, \\
 M_3 &= \begin{matrix} & C_A & D_A \\ C_B & \begin{pmatrix} R_3 & S_3 \\ T_3 & P_3 \end{pmatrix} \\ D_B & \end{matrix}, & M_4 &= \begin{matrix} & C_B & D_B \\ C_B & \begin{pmatrix} R_4 & S_4 \\ T_4 & P_4 \end{pmatrix} \\ D_B & \end{matrix},
 \end{aligned}$$

where M_1 and M_4 are used to describe the intraspecific interactions of species A and B, and M_2 and M_3 indicate the interspecific interactions. The elements of the payoff matrix, R_i (P_i), represent the reward for mutual cooperation (and the penalty for mutual defection), whereas S_i (T_i) denote the payoff to cooperators (or defectors) when interacting with individuals adopting the opposite strategy, with $i = 1, 2, 3, 4$.

The replicator dynamics in two species can be represented by the following differential equation:

$$\begin{cases} dx_1(t) = x_1(t)(1 - x_1(t))(P_A^C(t) - P_A^D(t))dt, \\ dx_2(t) = x_2(t)(1 - x_2(t))(P_B^C(t) - P_B^D(t))dt, \end{cases} \tag{1}$$

where $x_1(t)$ and $x_2(t)$ denote the frequency of cooperation of species A and B at time t , respectively; and $P_A^C(t)$, $P_A^D(t)$, $P_B^C(t)$, $P_B^D(t)$ denote the expected payoff gains of the two species adopting different strategies at time t , respectively. These expected returns can be expressed simply as:

$$\begin{aligned}
 P_A^C(t) &= p[R_1x_1(t - \tau_1) + S_1(1 - x_1(t - \tau_1))] \\
 &\quad + (1 - p)[R_2x_2(t - \tau_2) + S_2(1 - x_2(t - \tau_2))], \\
 P_A^D(t) &= p[T_1x_1(t - \tau_1) + P_1(1 - x_1(t - \tau_1))] \\
 &\quad + (1 - p)[T_2x_2(t - \tau_2) + P_2(1 - x_2(t - \tau_2))], \\
 P_B^C(t) &= (1 - p)[R_3x_1(t - \tau_3) + S_3(1 - x_1(t - \tau_3))] \\
 &\quad + p[R_4x_2(t - \tau_4) + S_4(1 - x_2(t - \tau_4))], \\
 P_B^D(t) &= (1 - p)[T_3x_1(t - \tau_3) + P_3(1 - x_1(t - \tau_3))] \\
 &\quad + p[T_4x_2(t - \tau_4) + P_4(1 - x_2(t - \tau_4))].
 \end{aligned} \tag{2}$$

Table 1
Model parameters and the expressions.

Parameter	Expression
a_1	$p(R_1 + P_1 - S_1 - T_1)$
a_2	$(1 - p)(R_2 + P_2 - S_2 - T_2)$
a_3	$(1 - p)(R_3 + P_3 - S_3 - T_3)$
a_4	$p(R_4 + P_4 - S_4 - T_4)$
b_1	$p(S_1 - P_1) + (1 - p)(S_2 - P_2)$
b_2	$(1 - p)(S_3 - P_3) + p(S_4 - P_4)$

Eq. (2) shows that the payoffs of each species depend on delayed interactions. For species A, the intraspecific interaction payoff is determined by the frequency $x_1(t - \tau_1)$, while the interspecific interaction payoff depends on $x_2(t - \tau_2)$. Similarly, the payoffs of species B depend on the delayed frequencies $x_2(t - \tau_4)$ (intraspecific) and $x_1(t - \tau_3)$ (interspecific). Thus, τ_1 and τ_4 represent the delays within each species, whereas τ_2 and τ_3 capture the delays associated with cross-species interactions. When all delays vanish, i.e., $\tau_1 = \tau_2 = \tau_3 = \tau_4 = 0$, the system reduces to the classical replicator dynamics without temporal memory.

By substituting the expected payoffs from Eq. (2) into Eq. (1), it is derived as follows:

$$\begin{cases} \frac{dx_1(t)}{dt} = x_1(t)(1 - x_1(t)) \left[a_1 x_1(t - \tau_1) + a_2 x_2(t - \tau_2) + b_1 \right], \\ \frac{dx_2(t)}{dt} = x_2(t)(1 - x_2(t)) \left[a_3 x_1(t - \tau_3) + a_4 x_2(t - \tau_4) + b_2 \right], \end{cases} \tag{3}$$

where the parameters are shown in Table 1.

A brief calculation reveals that there is an internal equilibrium point $(x_1^*, x_2^*) = \left(\frac{a_4 b_1 - a_2 b_2}{a_2 a_3 - a_1 a_4}, \frac{a_3 b_1 - a_1 b_2}{a_1 a_4 - a_2 a_3} \right)$ in the above dynamical system (3). In addition, there are other four vertex fixed points, namely $(x_1^*, x_2^*) = (0, 0), (0, 1), (1, 0), (1, 1)$, and four boundary fixed points, which are $(x_1^*, x_2^*) = (0, -\frac{b_2}{a_4}), (1, -\frac{a_3 + b_2}{a_4}), (-\frac{b_1}{a_1}, 0), (-\frac{a_2 + b_1}{a_1}, 1)$. In the following content, we centrally explore the stability of the internal equilibrium point in order to provide analysis of the long-term evolutionary dynamics of the strategies.

2.2. Stochastic extension

Building upon the deterministic model, we introduce stochastic mutations based on previous studies and incidentally discuss the effect of time delays. Specifically, this mutation is modeled as two independent Brownian motions, denoted by $\omega_1(t)$ and $\omega_2(t)$, where each process has increments that follow a normal distribution with zero mean and variance proportional to the time difference. Then, the following stochastic time delay differential system is obtained by expanding Eq. (1):

$$\begin{cases} dx_1(t) = x_1(t)(1 - x_1(t)) \left(a_1 x_1(t - \tau_1) + a_2 x_2(t - \tau_2) + b_1 \right) dt + \sigma_1 \left(x_1(t) - x_1^* \right) d\omega_1(t), \\ dx_2(t) = x_2(t)(1 - x_2(t)) \left(a_3 x_1(t - \tau_3) + a_4 x_2(t - \tau_4) + b_2 \right) dt + \sigma_2 \left(x_2(t) - x_2^* \right) d\omega_2(t). \end{cases} \tag{4}$$

here, σ_1 and σ_2 denote the intensities of the stochastic mutations, reflecting the strength of fluctuations in each species. The mutations of the state variables near their steady states are modeled as Wiener processes, with magnitudes proportional to the deviations of $x_1(t)$ and $x_2(t)$ from the equilibrium point $\mathbf{X}^* = (x_1^*, x_2^*)$. To examine the dynamical implications of these stochastic perturbations, our subsequent analysis focuses on the stability properties of \mathbf{X}^* . We employ a Lyapunov functional approach to establish sufficient conditions for stochastic asymptotic stability, complemented by numerical simulations to illustrate the system's behavior under varying parameter regimes. The complete derivation process and proof supporting these results are detailed in the supplementary materials.

3. Results and numerical simulations

In this section, we employ numerical simulations to investigate the evolutionary dynamics of the two-species game and to validate the accuracy of the proposed stability criterion. To solve the stochastic delay differential equations, we use the Euler-Maruyama method, a well-established numerical technique for simulating stochastic processes. This method is particularly suitable for handling both the stochastic noise and time delays in our system.

To simplify the analysis, all simulations were performed using fixed parameters: $R_i = 1, P_i = 0$ for $i = 1, 2, 3, 4$; $S_1 = S_3 = 0.1, S_2 = S_4 = 0.4$; $T_1 = T_3 = 1.5, T_2 = T_4 = 1.3$; and $p = 0.8$. Under these conditions, the internal equilibrium of Eq. (4) is located at $\mathbf{X}^* \approx (0.167, 0.571)$. The remaining parameters associated with delay and random effects significantly affect the stability of the equilibrium and determine the evolution of cooperation.

We first explore the role of stochastic mutations on system stability in the absence of delays ($\tau_i = 0$ for all i). Fig. 1 illustrates the time evolution of cooperation levels in both species for increasing noise intensities ($\sigma_1 = \sigma_2 = 0, 0.1, 0.3, 0.5, 1, 10$). All theoretical results related to this figure are provided in the Supplementary Information. From theory, parameter settings in the first row are guaranteed to be stable, whereas those in the second row cannot be ensured to meet the stability conditions. Nevertheless, simulations

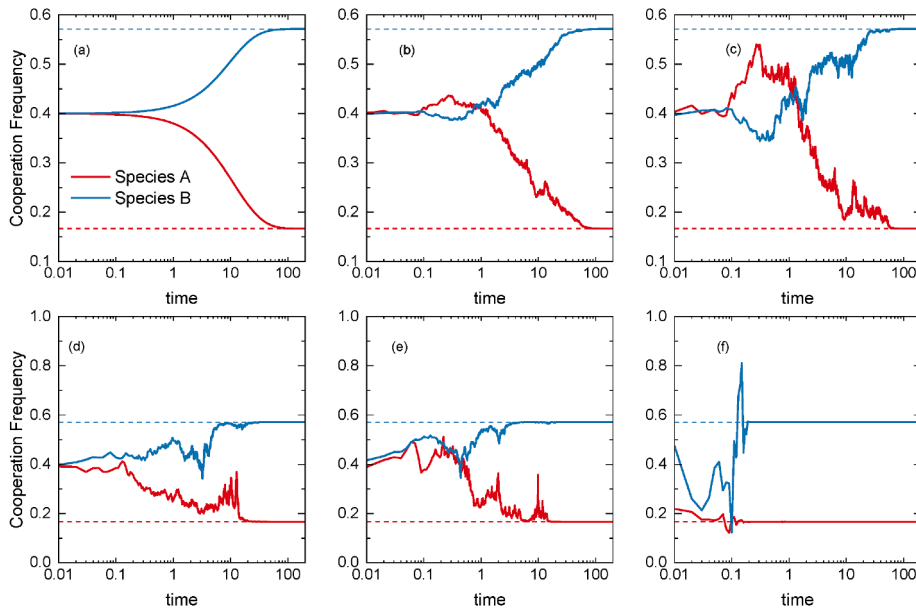


Fig. 1. Evolutionary dynamics under stochastic effects. All panels assume $\tau_i = 0$ for $i = 1, 2, 3, 4$. Noise intensities are set to $\sigma_1 = \sigma_2 = 0, 0.1, 0.3, 0.5, 1, \text{ and } 10$ in panels (a)–(f), respectively, illustrating increasing levels of stochasticity. In the first row, parameter settings lie within the range where stability can be established by theoretical analysis (Table S1 in Supplementary Information), whereas those in the second row exceed this range. Blue and red dashed lines mark the equilibrium point (X^*) across all panels, with convergence of trajectories to these lines indicating stability. As stochastic noise increases, fluctuations in cooperation rates within a single time step become more pronounced; however, the overall system stability is preserved and may even exhibit accelerated convergence, highlighting the robustness of the deterministic model.

consistently demonstrate convergence to the deterministic equilibrium (X^*) across all cases, in line with the predictions derived from Eqs. (S6, S7) whenever applicable. The associated stability coefficients, Ψ_1 and Ψ_2 , remain negative throughout the theoretically admissible range, thereby satisfying the stability conditions of Theorem 1 (Table S1). Strictly speaking, this corresponds to stochastic asymptotic stability; however, for conciseness, we hereafter use stable and unstable to denote this property.

As the level of stochasticity increases, all trajectories ultimately converge to the same equilibrium, underscoring the robustness of the deterministic model. Interestingly, noise may even accelerate convergence in certain cases, suggesting that stochastic mutations can reinforce long term stability rather than undermine it. Nevertheless, cooperation frequencies exhibit larger transient fluctuations within a finite time window, particularly evident at higher noise intensities (e.g., $\sigma_1 = \sigma_2 = 10$), where short term variability during the evolutionary process becomes more pronounced. These results indicate that, in the absence of delays, even relatively strong stochastic mutations are insufficient to fundamentally alter system stability.

Having examined the system without delays, we now turn to the role of time delays and the impact of stochastic mutations. To assess whether weak noise can alter system stability, we consider parameter values close to the Hopf bifurcation threshold in the deterministic setting, where stability is most sensitive to perturbations. The critical values of the delay parameters can be rigorously derived with complete theoretical proof and explicit criteria, as established in our previous work [42]. In Fig. 2, we fix $\tau_1 = \tau_2 = 1$ across all panels. For comparison, in the absence of stochasticity, setting $\tau_3 = \tau_4 = 11$ would yield oscillations that eventually converge to equilibrium, whereas $\tau_3 = \tau_4 = 12$ would instead produce sustained periodic oscillations. Against this deterministic backdrop, the figure illustrates the effect of weak stochastic perturbations ($\sigma_1 = \sigma_2 = 0.05$): trajectories follow the deterministic tendencies but with small amplitude fluctuations superimposed. The qualitative outcomes remain unchanged, systems that converge in the deterministic case still converge, while oscillatory regimes persist in oscillation. Together, these results show that weak stochastic mutations do not fundamentally alter the stability of equilibrium points, but merely introduce minor variability around deterministic trajectories.

Whereas weak stochastic perturbations leave the qualitative behavior of delayed dynamics essentially unchanged (Fig. 2), stronger mutations reveal a different picture. As shown in Fig. 3, the left column ($\tau_3 = \tau_4 = 11$) largely preserves the deterministic trend: trajectories fluctuate with greater amplitude over finite windows but eventually converge, maintaining the stability observed under weaker noise. In contrast, the right column ($\tau_3 = \tau_4 = 12$) departs markedly from expectations. In the deterministic setting, this parameter choice yields sustained periodic oscillations, and under weak noise it produces quasi periodic behavior, yet with strong mutations the system can instead converge toward the internal equilibrium. Although this convergence does not occur in every simulation, its appearance highlights an intriguing phenomenon: the combined influence of delay and stochastic mutations, typically destabilising on their own, can under certain conditions reinforce stability. Overall, these results indicate that noise and delay, although often destabilising when considered separately, can in combination sometimes promote stability.

To move beyond single trajectory evidence, our aim here is to quantify how noise and delay jointly shape stability at the ensemble level. Fig. 4 presents heat maps of the probability of convergence to equilibrium, estimated from 100 independent simulations for

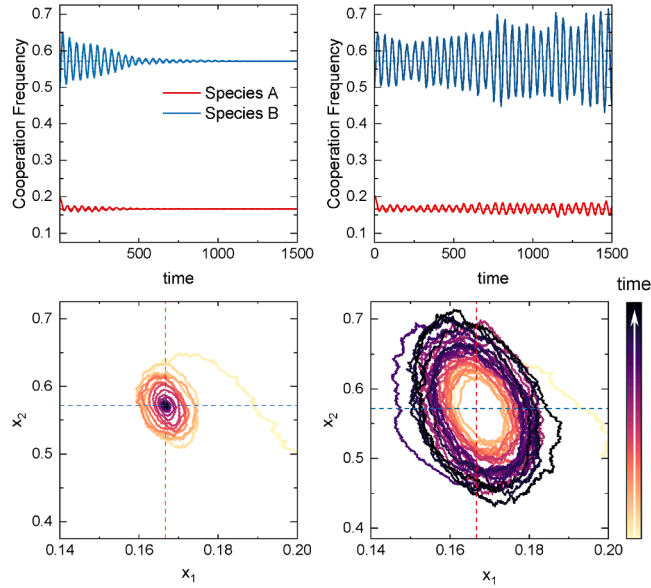


Fig. 2. Delayed evolutionary dynamics under weak stochastic mutations. The upper panels show the temporal evolution of cooperation rates, while the lower panels depict the corresponding evolutionary trajectories, with color indicating temporal progression. In all panels, $\tau_1 = \tau_2 = 1$ and the noise intensity is uniform ($\sigma_1 = \sigma_2 = 0.05$). In the left column, $\tau_3 = \tau_4 = 11$, yielding stable convergence; in the right column, a slight increase to $\tau_3 = \tau_4 = 12$ destabilises the system, producing quasi-periodic oscillations. Theoretical analysis cannot guarantee stability for all parameter choices, yet prior work without stochastic mutations shows that these near critical delays yield one convergent and one oscillatory regime. Consistently, the introduction of weak mutations here does not alter the stability of the equilibrium points.

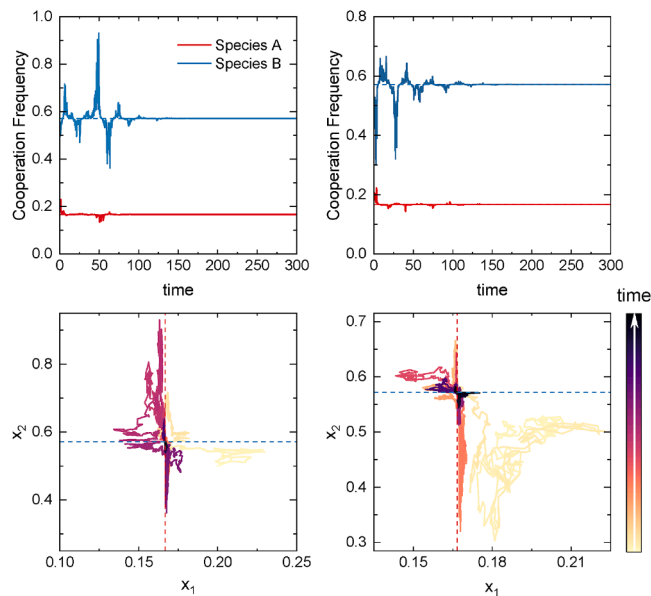


Fig. 3. Delayed evolutionary dynamics under strong stochastic mutations. The upper panels show the temporal evolution of cooperation rates, while the lower panels illustrate the corresponding evolutionary trajectories, with color indicating temporal progression. In all panels, $\sigma_1 = \sigma_2 = 1$ and $\tau_1 = \tau_2 = 1$. In the left column, $\tau_3 = \tau_4 = 11$; in the right column, $\tau_3 = \tau_4 = 12$. Despite differences in fluctuation amplitude and trajectory, both cases converge to the equilibrium point. Although such convergence is not guaranteed in every simulation, comparison with the weak mutation regime suggests that strong stochasticity can, to some extent, enhance system stability. These findings further underscore the influence of stochastic mutations and highlight the resilience of classical replicator dynamics.

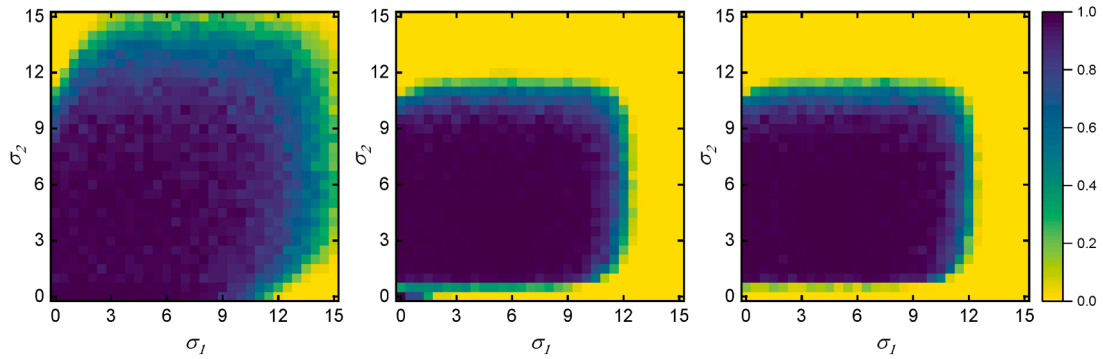


Fig. 4. Convergence probability as a function of stochastic perturbations and time delay. Panels show the probability of convergence to equilibrium, estimated from 100 independent simulations, with color indicating convergence likelihood. Axes denote noise intensities σ_1 and σ_2 . In the left panel, $\tau_i = 0$; in the middle panel, $\tau_1 = \tau_2 = 1, \tau_3 = \tau_4 = 11$; in the right panel, $\tau_1 = \tau_2 = 1, \tau_3 = \tau_4 = 12$. In the absence of noise, the left and middle regimes are stable, though the latter lies near a bifurcation and exhibits transient oscillations before convergence, while the right regime displays sustained periodic oscillations. The simulations reveal that time delays can indeed destabilise the system, whereas the noise free regime without delays withstands even large stochasticity, underscoring the predictive value of deterministic models in two population interactions. Notably, the similarity between the middle and right panels indicates that stochastic perturbations diminish the impact of delay on stability.

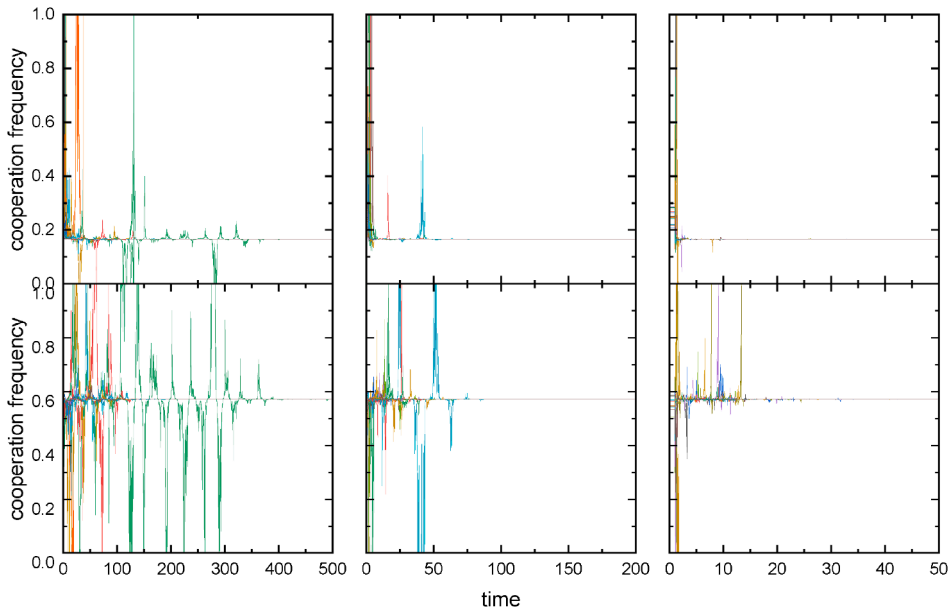


Fig. 5. Acceleration of convergence under strong stochastic mutations. Panels show cooperation levels in species A (top row) and species B (bottom row) for increasing noise intensities $\sigma_1 = \sigma_2 = 1, 2, 5$ (left to right). In all cases, delays are fixed at $\tau_1 = \tau_2 = 1$ and $\tau_3 = \tau_4 = 11$. Coloured trajectories correspond to 20 independent simulations. While occasional divergence is observed, the dominant effect is a pronounced acceleration of convergence: typical trajectories reach equilibrium around 400 steps at $\sigma = 1$, around 100 steps at $\sigma = 2$, and within 20 steps at $\sigma = 5$. These results demonstrate that stronger stochastic mutations, although destabilising in some instances, can substantially enhance the speed of convergence when equilibrium is reached.

each pair of noise intensities (σ_1, σ_2) ; color encodes the convergence likelihood. Panels correspond to the delay-free case (left, $\tau_i = 0$), a near bifurcation regime (middle, $\tau_1 = \tau_2 = 1, \tau_3 = \tau_4 = 11$), and a periodically oscillatory regime in the deterministic setting (right, $\tau_1 = \tau_2 = 1, \tau_3 = \tau_4 = 12$). At sufficiently large mutation intensities the system diverges with high probability, as expected, yet the maps also reveal a marked resilience to stochastic perturbations. In the delay-free panel the convergence domain is substantially larger than in the other two panels, indicating that delays diminish stability. The color distribution in the left panel is nearly symmetric about the diagonal, suggesting broadly similar aggregate effects of noise acting on the two species. By contrast, the middle and right panels display almost identical patterns, implying that stochasticity, rather than delay, predominates in determining the evolutionary outcome; this confirms that the behavior observed in Fig. 3 is not incidental. A closer inspection also exposes subtle asymmetries: convergence probabilities in the middle and right panels are not perfectly diagonal symmetric. In particular, larger values of σ_2 tend to promote convergence to the internal equilibrium, whereas very small (but nonzero) σ_2 are associated with a substantial probability

of instability, largely independent of σ_1 . This asymmetry may be caused by the specific interaction parameters, the delay settings, and the position of the internal equilibrium. Taken together, these findings show that while delays weaken the stability landscape, stochastic perturbations can in some regimes offset delay induced loss of stability and promote convergence, whereas excessively strong noise ultimately drives divergence.

Finally, to directly assess the influence of noise on convergence speed, we examined trajectories under fixed delays ($\tau_1 = \tau_2 = 1$, $\tau_3 = \tau_4 = 11$) with increasing mutation intensities. As shown in Fig. 5, cooperation levels in both species are plotted for $\sigma_1 = \sigma_2 = 1, 2, 5$ (from left to right), with colors indicating 20 independent realizations. Although a subset of trajectories diverges under strong perturbations, the prevailing outcome is a marked acceleration of convergence. At $\sigma = 1$, equilibrium is typically reached after about 400 steps; at $\sigma = 2$, convergence occurs within about 100 steps; and at $\sigma = 5$, equilibrium is attained in as few as 20 steps. This finding complements our earlier results by showing that stochasticity, beyond shaping stability, can also strongly influence the temporal scale of evolutionary dynamics.

These findings reveal how delays and randomness interact to shape cooperative dynamics. In real systems such as biological system or social groups, delays in information transmission often coexist with environmental noise. Our results show that stability persists even under very strong stochastic fluctuations (e.g., $\sigma = 10$), and only extreme noise leads to divergence. This robustness highlights the reliability of deterministic replicator dynamics in capturing core evolutionary outcomes across a broad range of realistic conditions.

4. Conclusion

The replicator dynamics have long provided a foundational framework for understanding the evolution of cooperation, yet they often abstract away stochastic factors, particularly those arising from random mutations that pervade natural and social systems. Overlooking such randomness risks mischaracterizing evolutionary pathways and overestimating system resilience under uncertainty.

Here, we extend our previous work on two species evolutionary games with time delay by incorporating stochastic mutations into the replicator framework. This approach captures both the memory effects embedded in delayed interactions and the unpredictability of mutation driven perturbations. Through Lyapunov based stability analysis and extensive simulations, we show that cooperative equilibria remain robust even under very strong stochastic fluctuations, while only extreme noise levels drive divergence. Delays can erode stability by inducing oscillations, although in some regimes stochasticity partly counteracts these destabilising effects. Together, these results highlight that classical replicator dynamics retain strong predictive power for long term outcomes across a broad and realistic range of conditions.

Our analysis does not identify a precise threshold beyond which stochasticity fundamentally alters stability, and it remains unclear whether such a threshold can be defined. Future work should develop refined methodologies to better approximate these boundaries. Moreover, randomness in evolutionary dynamics extends beyond mutation driven effects, and stochasticity associated with time delays, fluctuating interaction strengths, or environmental variability may play equally important roles. Progress in these directions will be essential for a more comprehensive understanding of how randomness shapes the resilience and adaptability of cooperative systems.

Data availability

No data was used for the research described in the article.

Acknowledgement

We acknowledge the following financial support for this research: Kaipeng Hu from Yunnan Fundamental Research Projects (202401AU070100, 202501AT070450); Zhouhong Li from Key Laboratory of Complex Dynamics System and Application Analysis, Yunnan Provincial Department of Education; Lei Shi from Major Project of National Philosophy and Social Science Foundation of China (22&ZD158), [National Natural Science Foundation of China \(11931015, 12271471\)](#), Yunling Scholar Program of Yunnan Province, and Yunnan Provincial Science and Technology Key Project (202403AC0010); and Matjaž Perc from Slovenian Research Agency (P1-0403, N1-0232).

Supplementary material

Supplementary material associated with this article can be found, in the online version, at [10.1016/j.amc.2026.129994](https://doi.org/10.1016/j.amc.2026.129994)

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