Robust Permanence and Impermanence for the Stochastic Replicator Dynamic*

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Abstract

Garay and Hofbauer (2003) propose sufficient conditions for robust permanence and impermanence of the deterministic replicator dynamic. We reconsider these conditions in the context of the stochastic replicator dynamic, which is obtained from its deterministic analog by introducing Brownian perturbations of payoffs. When the deterministic replicator dynamic is permanent and the noise level small, the stochastic dynamic admits a unique ergodic distribution whose mass is concentrated near the maximal interior attractor of the unperturbed system; thus, permanence is robust against small unbounded stochastic perturbations. When the deterministic dynamic is impermanent and the noise level small or large, the stochastic dynamic converges to the boundary of the state space at an exponential rate.

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1 Introduction

The deterministic replicator dynamic of Taylor and Jonker (1978) provides a fundamental model of natural selection in biological systems. One basic question that can be addressed using this model is to determine conditions under which a group of interacting species can coexist indefinitely.

A simple sufficient condition for long term coexistence is the existence of a globally asymptotically stable equilibrium. Such an equilibrium exists, for example, when the underlying game admits an interior ESS: Hofbauer et al. (1979) and Zeeman (1980) show that such states are (interior) globally asymptotically stable under the replicator dynamic.

While the existence of a globally stable equilibrium is a sufficient condition for long term coexistence, it is certainly not necessary. A more general criterion is provided by the notion of *permanence* of Schuster et al. (1979), which requires that the boundary of the state space be a repeller. When the replicator dynamic is permanent, solution trajectories from all interior initial conditions maintain boundedly positive proportions of all species indefinitely. Hofbauer (1981) and Hutson (1984) were among the first to establish general sufficient conditions for permanence; see Hutson and Schmitt (1992) and Hofbauer and Sigmund (1998) for surveys of work on this question.

Since any mathematical model only provides an approximate description of the population under study, it is important to know whether small changes to a model's specification would lead to large changes in results. With this motivation, Schreiber (2000) and Garay and Hofbauer (2003) introduce sufficient conditions for robust permanence: that is, permanence of all small deterministic perturbations of the original system.

In this paper, we consider the question of permanence in the context of Brownian perturbations of the replicator dynamic. The first stochastic differential equation analogue of the replicator dynamic was introduced by Foster and Young (1990). Later, Fudenberg and Harris (1992) offered a biologically more natural model, known as the *stochastic replicator dynamic*, based on Brownian perturbations of the underlying fitness functions. As we shall see, the analysis in this paper applies not just to Fudenberg and Harris's (1992) dynamic, but to more general Brownian perturbations of the replicator dynamic as well.

As in the deterministic case, the initial results on long term coexistence for the stochastic replicator dynamic concerned settings with a single globally attracting state. Using tools specific to one-dimensional diffusions, Fudenberg and Harris (1992) showed that the stochastic replicator dynamic is recurrent in two-strategy Hawk-Dove games, and demonstrated that the unique stationary distribution of the process places nearly all mass near the ESS when the noise level is small. This result has since been generalized by Imhof (2005), who extends it to games with an interior ESS and an arbitrary finite number of strategies. In light of the developments in the deterministic setting, it is natural to ask whether similar results for the stochastic replicator dynamic can be established whenever the underlying deterministic system is known to be permanent. Doing so is the main goal of the present study.

In Section 2, we introduce the deterministic and stochastic replicator dynamics, and we review Garay and Hofbauer's (2003) sufficient conditions for permanence for the deterministic setting. In Section 3, we prove that if the replicator dynamic for a game satisfying Garay and Hofbauer's (2003) conditions is subjected to small Brownian perturbations, then the resulting stochastic process is recurrent, and that its unique stationary distribution places nearly all mass near the interior attractor of the unperturbed system.

To supplement these results, we characterize settings in which the stochastic replicator dynamic is "impermanent", in the sense that its solutions converge to the boundary of the state space at an exponential rate with probability one. In Sections 4 and 5, we show that this is the case if Garay and Hofbauer's (2003) conditions for impermanence hold and if the noise level is sufficiently small or sufficiently large. Section 6 closes the paper with some concluding discussion.

2 Preliminaries

2.1 The replicator dynamic

The replicator dynamic describes natural selection among individuals programmed to play *strategies* from the set $\{1, \ldots, n\}$. In models of animal conflict, a strategy corresponds to a phenotype; in population ecology, a strategy corresponds to a species. If we let x_i represent the proportion of individuals playing strategy i, then our state variable x is an element of $\Delta = \{x \in \mathbb{R}^n : x_i \geq 0, \sum_i x_i = 1\}$, the unit simplex in $\mathbb{R}^n$. We let

$T\Delta = \{x \in \mathbb{R}^n : \sum_i x_i = 0\}$ denote the tangent space of Δ, and we let $\partial\Delta$ and $\mathrm{int}(\Delta)$ denote the boundary and interior of Δ, respectively.

The *fitness* of strategy i is described by a function $F_i : \Delta \to \mathbb{R}$ of the state variable x. In many applications, fitness is determined through random pairwise interactions to play a symmetric normal form game with fitness matrix $U \in \mathbb{R}^{n\times n}$; in such cases the function $F : \Delta \to \mathbb{R}^n$ takes the linear form $F(x) = Ux$. However, we require only that the function F be Lipschitz continuous (and later C^2).

To derive the replicator dynamic, let y_i represent the *number* of individuals playing strategy i, and suppose that the per capita growth rate of y_i is given by the fitness of strategy i: in particular,

$$\dot{y}_i = y_i F_i(x), \tag{1}$$

where x is the state variable obtained from y via $x_i = y_i / \sum_j y_j$. Then

$$\dot{x}_i = x_i \hat{F}_i(x),$$

where

$$\hat{F}_i(x) = F_i(x) - \sum\nolimits_j x_j F_j(x)$$

is the *excess fitness* of strategy i over the average fitness in the population. This equation defines the *replicator dynamic* for the fitness function F. To ease future comparisons, we express the replicator dynamic in matrix form:

$$\dot{x} = R(x) \equiv \mathrm{diag}(x)\hat{F}(x). \tag{R}$$

By Lipschitz continuity and standard results, (R) induces a flow $\Phi : \mathbb{R} \times \Delta \mapsto \Delta$ which leaves both $\partial\Delta$ and $\mathrm{int}(\Delta)$ invariant. The flow maps each pair $(t, x) \in \mathbb{R} \times \Delta$ to some $\Phi_t(x) \in \Delta$, the position of the solution with initial condition x at time t. Thus, the map $t \mapsto \Phi_t(x)$ is the solution trajectory of (R) with initial condition $\Phi_0(x) = x$.

2.2 Permanence and impermanence

The notions of permanence and impermanence for the dynamic (R) are defined in terms of its attractors. A set $A \subset \Delta$ is *invariant* under (R) if $\Phi_t(A) = A$ for all $t \in \mathbb{R}$. An invariant set A is an *attractor* of (R) if it is nonempty, compact, and admits a neighborhood $\mathcal{U}$ such that

$$\lim_{t\to\infty} \mathsf{dist}(\Phi_t(x), A) = 0$$

uniformly over $x \in \mathcal{U}$. If A is an attractor, its *basin of attraction* is the open set consisting of all states $x \in \Delta$ for which $\lim_{t\to\infty} \mathsf{dist}(\Phi_t(x), A) = 0$.

Following Schuster et al. (1979) and Hofbauer and Sigmund (1998), we call the dynamic (R) *permanent* if it admits an attractor $A \subset \mathrm{int}(\Delta)$ whose basin of attraction is all of $\mathrm{int}(\Delta)$. Equivalently, (R) is permanent if $\partial\Delta$ is a repeller under (R). If instead $\partial\Delta$ is an attractor under (R), we say that (R) is *impermanent*.

We illustrate these concepts using a well-known class of examples.

Example 1. *The hypercycle equation.* Suppose that fitness is given by the linear function

$$F(x) = Ux = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & k_1 \\ k_2 & 0 & 0 & \cdots & 0 & 0 \\ 0 & k_3 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & k_n & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ \vdots \\ x_{n-1} \\ x_n \end{pmatrix} = \begin{pmatrix} k_1 x_n \\ k_2 x_1 \\ k_3 x_2 \\ \vdots \\ k_{n-1} x_{n-2} \\ k_n x_{n-1} \end{pmatrix}$$

for some $k_1, \ldots, k_n > 0$. In words, the fitness of strategy i depends positively on the proportion of individuals playing strategy $i - 1$, where the indices are counted mod n. The dynamic (R) corresponding to this fitness function,

$$\dot{x}_i = x_i \left(k_i x_{i-1} - \sum_j k_j x_j x_{j-1} \right). \tag{H}$$

is known as the *hypercycle equation*. This equation was introduced by Eigen and Schuster (1979) as a model of prebiotic evolution—in particular, of cyclical catalysis in a collection of polynucleotides.

Equation (H) has a unique interior rest point x^* for all numbers of strategies n. When n equals 2, 3, or 4, rest point x^* is interior globally asymptotically stable, so system (H) is permanent. When $n \geq 5$, x^* is unstable. Nevertheless, Schuster et al. (1979) show that (H) remains permanent. In fact, Hofbauer et al. (1991) use techniques from the theory of monotone dynamical systems to show that when $n \geq 5$, the dynamic (H) admits a stable periodic orbit. For further discussion, see Chapter 12 of Hofbauer and Sigmund (1998).

Schreiber (2000) and Garay and Hofbauer (2003) provide conditions for permanence and impermanence of (R) that are stated in terms of ergodic measures for (R) with supports contained in $\partial\Delta$. Let $\mathcal{M}_\Phi(\partial\Delta)$ denote the collection of Φ-invariant Borel probability measures whose supports are contained in $\partial\Delta$, and let the subset $\mathcal{M}_\Phi^E(\partial\Delta) \subset \mathcal{M}_\Phi(\partial\Delta)$ contain only the ergodic measures: thus, $\mathcal{M}_\Phi^E(\partial\Delta)$ is the set of extreme points of $\mathcal{M}_\Phi(\partial\Delta)$.

The following result is due to Garay and Hofbauer (2003).

Theorem 2 (Garay and Hofbauer (2003))**.** *Let $p_1, \ldots, p_n > 0$. If*

$$\sum_{i=1}^{n} p_i \int_{\partial\Delta} \hat{F}_i(x) d\mu(x) > 0 \tag{P}$$

for all $\mu \in \mathcal{M}_\Phi^E(\partial\Delta)$, then system (R) *is permanent. If instead*

$$\sum_{i=1}^{n} p_i \int_{\partial\Delta} \hat{F}_i(x) d\mu(x) < 0 \tag{I}$$

for all $\mu \in \mathcal{M}_\Phi^E(\partial\Delta)$, then system (R) *is impermanent.*

The integrals in equations (P) and (I) represent the expected excess fitness of strategy i, where the expectation is taken with respect to the ergodic measure μ. Thus, permanence condition (P) requires that for some positive vector $p = (p_1, \ldots, p_n)$, the p-weighted average of these μ-expected excess fitnesses is positive for every ergodic measure μ on $\partial\Delta$. Since $\hat{F}_i(x) = F_i(x) - \sum_j x_j F_j(x)$, condition (P) can be described loosely as requiring unused strategies to tend to outperform the population average. In contrast, impermanence condition (I) requires unused strategies to tend to underperform the population average.

Garay and Hofbauer (2003) provide other conditions that are equivalent to (P) and (I), and they show that these conditions imply permanence and impermanence for small C^0 perturbations of (R). For future reference, we note that their Theorem 4.4 and Sections 12.2-12.3 of Hofbauer and Sigmund (1998) together imply that the hypercycle equation (H) satisfies permanence condition (P) for all $n \geq 2$.

2.3 Stochastically perturbed replicator dynamics

Fudenberg and Harris (1992) propose the following stochastic analog of the replicator dynamic (R). In place of the deterministic equation (1), Fudenberg and Harris (1992) assume that the per capita growth rate of the number of individuals playing strategy i is stochastic, given by the sum of the fitness of strategy i and a standard Brownian motion $B_i(t)$:

$$dY_i(t) = Y_i(t)\left(\hat{F}_i(X(t)) + \sigma_i dB_i(t)\right), \tag{2}$$

where $X_i(t) = Y_i(t)/\sum_j Y_i(t)$ and $\sigma_i > 0$. The resulting law of motion for the state $X(t)$ can be obtained via a straightforward application of Ito's formula. Define strategy i's *σ-adjusted fitness* by

$$F_i^\sigma(x) = F_i(x) - \sigma_i^2 x_i,$$

and let

$$\hat{F}_i^\sigma(x) = F_i^\sigma(x) - \sum_j x_j F_j^\sigma(x) = \hat{F}_i(x) - \sigma_i^2 x_i + \sum_j x_j^2 \sigma_j^2 \tag{3}$$

be strategy i's *excess σ-adjusted fitness*. Applying Ito's formula to equation (2) reveals that the law of motion for $X(t)$ is

$$dX(t) = \mathrm{diag}(X(t))\left(\hat{F}^\sigma(X(t))dt + (I - \mathbf{1}X(t)^T)\mathrm{diag}(\sigma)dB(t)\right), \tag{S}$$

where $\mathbf{1} \in \mathbb{R}^n$ is the vector of ones. This equation defines the *stochastic replicator dynamic*.

Our results apply to more general stochastic perturbations of equation (R). We consider stochastic equations of the form

$$dX(t) = \mathrm{diag}(X(t))\left(\tilde{F}(X(t))dt + \Sigma(X(t))dB(t)\right), \tag{S$'$}$$

where *(i)* $B_t = (B_t^1, \ldots, B_t^m)$ is an m-dimensional standard Brownian motion, and *(ii)* $\tilde{F} : \Delta \to \mathbb{R}^n$ and $\Sigma : \Delta \to \mathbb{R}^{n\times m}$ are Lipschitz continuous maps with the property that for each $x \in X$, the drift vector

$$\tilde{R}(x) = \mathrm{diag}(x)\tilde{F}(x)$$

and the columns $S^1(x), \ldots, S^m(x)$ of the diffusion coefficient

$$S(x) = \mathrm{diag}(x)\Sigma(x)$$

are elements of $T\Delta$. Note that equation (S$'$) can be written component by component as

$$dX_i(t) = X_i(t)\left(\tilde{F}_i(X(t))dt + \sum_{j=1}^{m} \Sigma^j(X(t))dB^j(t)\right),$$

where $\Sigma^1(x), \ldots, \Sigma^m(x)$ are the columns of $\Sigma(x)$.

Generalizing the terminology of Garay and Hofbauer (2003), we call (S$'$) a *random δ-perturbation of* (R) if

$$\sum_i |\hat{F}_i(x) - \tilde{F}_i(x)| + \sum_{i,j} |\Sigma_{ij}(x)|^2 \leq \delta$$

for all $x \in \Delta$, and a *random δ-perturbation of* (R) *on* $\partial\Delta$ if this inequality holds whenever $x \in \partial\Delta$. In the latter case, the nature of the perturbation away from a neighborhood of $\partial\Delta$ is unrestricted.

By standard results, the Cauchy problem associated with (S$'$) and with initial condition $X_0 = x$ admits a unique (strong) solution, which we denote by $(X_t^x, t \geq 0)$. The set $\text{int}(\Delta)$ is invariant under (S$'$), in the sense that for any $t \geq 0$ the events $\{X_t^x \in \text{int}(\Delta)\}$ and $\cap_{s\geq 0}\{X_s^x \in \text{int}(\Delta)\}$ coincide almost surely. The set $\partial\Delta$ is invariant in this same sense.

To prove our permanence result, we require the following full rank condition on the random perturbations in equation (S$'$). We call system (S$'$) *nondegenerate* if for all $x \in \text{int}(\Delta)$, the column vectors $S^1(x), \ldots, S^m(x)$ span $T\Delta$. A direct calculation reveals that this requirement is satisfied by the stochastic replicator dynamic (S). For our impermanence results, even weaker nondegeneracy conditions will suffice—see Section 4.

3 Stochastic Permanence

We now turn to the question of permanence under stochastically perturbed replicator dynamics. As we noted at the onset, permanence obtains most simply in a deterministic system when there is a globally attracting interior equilibrium—for instance, an interior ESS. Imhof (2005) shows that in such cases, the permanence of the deterministic system extends to its stochastic analogues: in particular, he proves that if the underlying game F has an interior ESS x^*, the stochastic replicator dynamic (S) is recurrent, with a stationary distribution that places nearly all mass close to

x^*. Of course, this result does not apply to permanent systems without an interior ESS—including, for example, the hypercycle equation with $n \geq 4$.

Our main result, Theorem 3, addresses this more general question. It shows that when the level of noise is small, random perturbations of permanent replicator dynamics—in particular, replicator dynamics satisfying condition (P)—are "stochastically permanent" in a variety of senses.

Theorem 3. *Assume that R is C^2 and that condition* (P) *holds. Then for every $r > 0$, there exists a $\bar{\delta} > 0$ such that for all $\delta \in (0, \bar{\delta})$, every nondegenerate random δ-perturbation of* (R) *on $\partial\Delta$ enjoys the following properties:*

(i) *There exists a unique probability measure μ on $\mathrm{int}(\Delta)$ that is invariant under* (S′). *The measure μ is absolutely continuous with respect to the Lebesgue measure on $\mathrm{int}(\Delta)$ and satisfies*

$$\int \frac{1}{\mathsf{dist}(x, \partial\Delta)^r} \mu(dx) < \infty.$$

(ii) *There exist positive constants $C, \alpha > 0$ such that for all $x \in \mathrm{int}(\Delta)$ and every Borel set $B \subset \mathrm{int}(\Delta)$,*

$$|\mathsf{P}(X_t^x \in B) - \mu(B)| \leq \frac{Ce^{-\alpha t}}{\mathsf{dist}(x, \partial\Delta)^r}.$$

(iii) *For all $x \in \mathrm{int}(\Delta)$ and all $\psi \in L^1(\mathrm{int}(\Delta), \mu)$,*

$$\lim_{t\to\infty} \frac{1}{t} \int_0^t \psi(X_s^x)\, ds = \int \psi(x)\, d\mu$$

almost surely.

(iv) *Let $A \subset \mathrm{int}(\Delta)$ be the dual attractor of $\partial\Delta$ for the dynamic* (R), *and suppose that $r < 1$. Then for any neighborhood $\mathcal{N}$ of A,*

$$\mu(\Delta \setminus \mathcal{N}) = O(\delta^r \log \delta).$$

Proof : Our proof relies on the following lemma, which can be seen as a special case of more general geometric ergodic theorems for discrete time Markov chains. The lemma follows from Theorems 8.1.5, 8.2.16 and 8.3.18 in Duflo (1997), or from Theorem 15.0.1 in Meyn and Tweedy (2005).

Lemma 4. *Let U be an open subset of $\mathbb{R}^d$, and let $p : U \times U \mapsto \mathbb{R}^+$ be a positive continuous Markov transition kernel. For any Borel set $A \subset U$, and any bounded or nonnegative Borel map $\Psi : U \mapsto \mathbb{R}$, define*

$$P(x, A) = \int_A p(x, y)dy$$

and

$$P\Psi(x) = \int p(x, y)\Psi(y)dy.$$

Assume that there exists a nonnegative continuous function $H : U \mapsto \mathbb{R}^+$ such that

(a) $\lim_{x \to \partial U} H(x) = \infty$, *and*

(b) $PH \leq aH + b$ *where* $0 < a < 1$.

Then

(i) *There exists a unique p-invariant probability measure μ. This measure is absolutely continuous with respect to Lebesgue measure and satisfies $\int H(x)\, d\mu < \infty$.*

(ii) *There exist constants $C \geq 0$ and $0 < \rho < 1$ such that*

$$|P^n(x, A) - \mu(A)| \leq C\rho^n(1 + H(x))$$

for any Borel set $A \subset U$.

(iii) *Let (Y_n) be a Markov chain with transition kernel p, and let $f \in L^1(\mu)$. Then for any initial distribution,*

$$\lim_{n \to \infty} \frac{1}{n} \sum_{i=1}^{n} f(Y_i) = \int f(x)\ d\mu$$

almost surely.

We now proceed with the proof of Theorem 3. Let the constants $p_i, i = 1, \ldots, n$, be as in equation (P) of Theorem 2. Without loss of generality, we may assume that $\sum_i p_i = 1$. It follows easily from Theorem 3.4, Remark 3.5, and Theorem 4.4 of Garay and Hofbauer (2003) that there exist a constant $\alpha > 0$, a neighborhood $\mathcal{U}$ of $\partial\Delta$, and a C^2 map $W : \Delta \to \mathbb{R}$ such that

$$\sum_i p_i \hat{F}_i(x) + \langle \nabla W(x), R(x) \rangle > \alpha \tag{4}$$

for all $x \in \mathcal{U}$. It follows that the map $V : \mathcal{U} \setminus \partial\Delta \mapsto \mathbb{R}$ defined by

$$V(x) = \sum_i p_i \log x_i + W(x). \tag{5}$$

satisfies

$$\langle \nabla V(x), R(x) \rangle > \alpha \tag{6}$$

for all $x \in \mathcal{U} \setminus \partial\Delta$.

Consider now a random δ-perturbation of (R) on $\partial\Delta$ given by (S′). It induces a diffusion process on Δ whose infinitesimal generator $\mathcal{L}$ acts on C^2 functions according to the formula

$$\mathcal{L}\psi(x) = \langle \nabla \psi(x), R(x) \rangle + \mathcal{A}\psi(x), \tag{7}$$

where

$$\mathcal{A}\psi(x) = \frac{1}{2} \sum_{i,j} x_i x_j a_{ij}(x) \frac{\partial^2 \psi}{\partial x_i x_j}(x) \tag{8}$$

and

$$a(x) = \Sigma(x)\Sigma(x)^T. \tag{9}$$

Hence, for all $x \in \mathcal{U} \setminus \partial\Delta$

$$\mathcal{L}V(x) = \sum_i p_i \hat{F}_i(x) + \langle \nabla W(x), R(x) \rangle - \frac{1}{2} \sum_i p_i a_{ii}(x) + \mathcal{A}W(x)$$

Therefore, by choosing δ small enough, we can assume that

$$\mathcal{L}V(x) \geq \alpha \tag{10}$$

for all $x \in \mathcal{U} \setminus \partial\Delta$.

Set $\lambda = \frac{r}{\inf_i p_i}$ and define

$$H = \exp(-\lambda V). \tag{11}$$

Then H is smooth, positive, and satisfies

$$\lim_{x \to \partial\Delta} H(x) = \infty$$

and

$$H(x) \geq \frac{K}{\mathsf{dist}(x, \partial\Delta)^r} \tag{12}$$

for some constant $K > 0$. On the other hand,

$$\mathcal{L}H = -\lambda H[\mathcal{L}V + \frac{1}{2}\lambda \sum_{k=1}^{m} \langle \nabla V, S^k \rangle^2]$$

Since $\langle \nabla V, S^k \rangle = \langle p, \Sigma^k \rangle + \langle \nabla W, S^k \rangle$, for δ small we have that

$$\mathcal{L}H \leq -\beta H$$

on $\mathcal{U}$ for some $\beta > 0$, say $\beta = \lambda\alpha/2$. Hence,

$$\mathcal{L}H \leq -\beta H + \gamma \tag{13}$$

on $\mathrm{int}(\Delta)$. It then follows from Ito's formula that

$$\begin{aligned} e^{\beta t} H(X_t^x) - H(x) &= \int_0^t e^{\beta s}(\beta H(X_s^x) + \mathcal{L}H(X_s))ds + N_t \\ &\leq \frac{\gamma}{\beta} e^{\beta t} + N_t, \end{aligned} \tag{14}$$

where

$$N_t = \int_0^t e^{\beta s}(-\lambda H(X_s))dM_s,$$

and $(M_t)_{t \geq 0}$ is the continuous martingale defined by $M_0 = 0$ and

$$\begin{aligned} dM_t &= \langle \nabla V(X_t^x), \sum_j S^j(X_t^x) dB_t^j \rangle \\ &= \sum_{j=1}^{m} [\sum_{i=1}^{n} (p_i \Sigma_{ij}(X_t^x) + S_{ij}(X_t^x) \frac{\partial W}{\partial x_i}(X_t^x))] dB_t^j \end{aligned} \tag{15}$$

Let $\tau_N = \inf\{t \geq 0 : \; H(X_t^x) > N\}$. Then $N_{t \wedge \tau_N}$ is a martingale, and so $\mathsf{E}(N_{t \wedge \tau_N}) = 0$. Replacing t by $t \wedge \tau_N$ in (14), taking the expectation, and letting $N \to \infty$ yields

$$\mathsf{E}(H(X_t^x)) \leq e^{-\beta t} H(x) + \frac{\gamma}{\beta}. \tag{16}$$

Let $\{P_t\}_{t\geq 0}$ denote the Markov semigroup induced by (S′) on $\mathrm{int}(\Delta)$. Then (16) can be rewritten as

$$P_t H \leq a(t)H + b \tag{17}$$

with $0 < a(t) < 1$. On the other hand, by the nondegeneracy assumption there exists a continuous positive kernel $p_t(x, y)$ such that

$$P_t\psi(x) = \int p_t(x, y)\psi(y)dy.$$

(see, e.g., Theorem 7.3.8 of Durrett (1996)). Therefore, Lemma 4 applies to P_t for any $t > 0$.

Applying this lemma, let μ denote the unique invariant probability measure of P_1. Then μ is also the invariant probability measure of P_t for all $t > 0$: the invariant measure for P_t is invariant for $P_{kt} = P_t^k$; thus, the invariant measure for $P_{k/2^n}$ is independent of k and n, and so, by the density of the dyadic rationals in the reals, is an invariant measure of P_t for all $t > 0$. The integrability condition of assertion (i) then follows from inequality (12).

Now, for any continuous bounded function ψ and any $0 \leq s < 1$,

$$|P_{n+s}\psi(x) - \mu\psi| = |P_n(P_s\psi)(x) - \mu(P_s\psi)| \leq |P_n(x, .) - \mu|_{VT}||P_s\psi||_\infty$$

where $|.|_{VT}$ stands for the total variation norm. Hence, by Lemma 4(ii),

$$\begin{aligned}|P_{n+s}(x, \cdot) - \mu|_{VT} &\leq \rho^n||P_s\psi||_\infty(1 + H(x))\\ &\leq \rho^n(1 + H(x))||\psi||_\infty,\end{aligned}$$

so assertion (ii) of the theorem holds.

For $\Psi \in L^1(\mu)$ the function $u(x) = \mathsf{P}(\lim_{t\to\infty} \frac{1}{t}\int \Psi(X_t^x)dt = \mu\Psi)$ is clearly harmonic for P_1 (that is, $P_1u = u$). Hence, by Lemma 4(iii) and Theorem 17.1.5 of Meyn and Tweedy (2005), u is constant. On the other hand, by the Birkhoff ergodic theorem, $u(x) = 1$ for μ almost all x, so that $u(x) = 1$ for all x.

It remains to prove the last assertion of the theorem. To reduce notation, we write Cst to denote a constant that may change from line to line or within a line. Let K denote the Lipschitz constant of R and set $\lambda = \frac{K}{(1-r)\alpha}$. By Gronwall's inequality,

$$\mathsf{E}(|\Phi_t(x) - X_t^x|^2)^{1/2} \leq \mathsf{Cst}\ e^{Kt}t\delta.$$

Let $0 \le \psi \le 1$ be a smooth function on Δ which is 1 on a neighborhood of A and 0 outside $\mathcal{N}$. Integrating the last inequality gives

$$|\mathsf{P}_t\psi(x) - \psi \circ \Phi_t(x)| \le \mathsf{Cst}\ e^{Kt} t\delta,$$

so

$$|\mu\psi - \mu\Psi \circ \Phi_t| \le \mathsf{Cst}\ e^{Kt} t\delta$$

by the invariance of μ. It follows that

$$\mu\Psi \ge \int_{\{V \ge -v\}} \Psi \circ \Phi_t d\mu - \mathsf{Cst}\ e^{Kt} t\delta$$

for all $v > 0$. Since A is a global attractor, we can find for each $v > 0$ a time t_v such that $\psi(\phi_t(x)) = 1$ whenever $t \ge t_v$ and $V(x) > -v$. Therefore, Markov's inequality implies that

$$\mu\psi \ge \mu(V \ge -v) - \mathsf{Cst}\ e^{Kt_v} t_v \delta \ge 1 - e^{-\lambda v} \int H d\mu - \mathsf{Cst}\ e^{Kt_v} t_v \delta.$$

Now, using the fact that $V(\Phi_t(x)) \ge \alpha t + V(x)$ on a neighborhood of $\partial\Delta$ (since $\langle \nabla V, F \rangle \ge \alpha$) one can choose t_v to be

$$t_v = t_{v_0} + \frac{(v - v_0)}{\alpha}$$

for some v_0 large enough and any $v \ge v_0$. Thus

$$\mu\psi \ge 1 - \mathsf{Cst}\ e^{-\lambda\alpha t_v} - \mathsf{Cst}\ e^{Kt_v} t_v \delta.$$

Therefore, choosing v in such a way that $t_v = -\frac{(1-r)}{K} \log(\delta)$, we conclude that

$$1 - \mu\psi \le \mathsf{Cst}\ \delta + \mathsf{Cst}\ \delta^r \log(\delta).$$

QED

4 Stochastic Impermanence

Our next result, Theorem 6, shows that when the level of noise is small, random perturbations of impermanent replicator dynamics—in particular, replicator dynamics satisfying condition (I)—approach $\partial\Delta$ exponentially quickly with high probability.

This result requires a weaker nondegeneracy condition than that used in Theorem 3. Rewrite equation (S′) using the Stratonovich formalism, so that

$$dX_t = J(X_t)dt + S(X_t) \circ dB_t^j, \tag{18}$$

where

$$J_i(x) = x_i \tilde{F}_i(x) - \frac{1}{2} \sum_{j=1}^{m} \sum_{k=1}^{n} \frac{\partial S_{ij}}{\partial x_k}(x) S_{kj}(x).$$

We call the set $A \subset \Delta$ *accessible* from $x \in \Delta$ if there exist a nonnegative number u and smooth maps $\eta_i : [0, \infty) \to \mathbb{R}, i = 1, \ldots, m$, that allow one to "steer" the solution of the ordinary differential equation

$$\frac{dy}{dt} = uJ(y(t)) + \sum_{j=1}^{m} \eta_j(t) S^j(y(t)) \tag{19}$$

with initial condition $y(0) = x$ to A, in the sense that $y(t) \in A$ for some $t \geq 0$. We call A *weakly accessible* from x if every neighborhood of A is accessible from x, and *weakly accessible* if it is weakly accessible from all $x \in \text{int}(\Delta)$.

By Chow's (1940) theorem (see e.g. Montgomery (2001)), a sufficient condition ensuring that every subset of Δ is weakly accessible is given by Hörmander's condition:

$$\mathsf{Lie}(S^1, \ldots, S^m)(x) = T\Delta \quad \text{for all } x \in \text{int}(\Delta), \tag{20}$$

where $\mathsf{Lie}(S^1, \ldots, S^m)$ is the Lie algebra generated by $S^1, \ldots, S^m$ and $\mathsf{Lie}(S^1, \ldots, S^m)(x) = \{L(x) : L \in \mathsf{Lie}(S^1, \ldots, S^m)\}$.

Remark 5. Hörmander's condition is satisfied if (S′) is nondegenerate, as assumed in Theorem 3. In fact, the nondegeneracy assumption in Theorem 3 can be weakened to the assumption that Hörmander's condition holds for every random δ-perturbation of (R).

Theorem 6. *Suppose that R is C^2 and that condition* (I) *holds. Then there exist constants $\alpha > 0$ and $\bar{\delta} > 0$ such that every random δ-perturbation of* (R) *on $\partial\Delta$ with $\delta \in (0, \bar{\delta})$ satisfies the following property: Given any $0 < \beta < 1$, there exists a neighborhood $\mathcal{U}$ of $\partial\Delta$ such that*

$$\mathsf{P}\left(\limsup_{t \to \infty} \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \leq -\alpha\right) \geq \beta$$

for all $x \in \mathcal{U}$. If in addition $\partial\Delta$ is weakly accessible, then

$$\mathsf{P}\left(\limsup_{t\to\infty} \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \le -\alpha\right) = 1$$

for all $x \in \Delta$.

Proof : Let V be the function (5) introduced in the proof of Theorem 3. A variation on the argument we used there shows that for δ small enough,

$$\mathcal{L}V \le -\alpha < 0$$

on a neighborhood $\tilde{\mathcal{U}}$ of $\partial\Delta$.

Let (X_t^x) be a solution to (S′) with $x \in \tilde{\mathcal{U}} \setminus \partial\Delta$, and let $V_t = V(X_t^x)$. By Ito's formula,

$$V_t = V(x) + \int_0^t \mathcal{L}V(X_s^x)ds + M_t,$$

where M_t is the martingale given by equation (15).

Equation (15) implies that $\langle M\rangle_t \le Ct$ for some $C > 0$. Hence, by the strong law of large numbers for martingales, we have that

$$\lim_{t\to\infty} M_t/t = 0 \tag{21}$$

almost surely. Let $\tau = \inf\{t \ge 0 :\ X_t^x \in \partial\tilde{\mathcal{U}}\}$ be the exit time from $\tilde{\mathcal{U}}$. It follows from (10) and (21) that

$$\limsup_{t\to\infty} \frac{V_t}{t} \le -\alpha$$

almost surely on the event $\{\tau = \infty\}$. Hence

$$\limsup \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \le -\frac{\alpha}{\sum_i p_i} = -\alpha$$

almost surely on $\{\tau = \infty\}$, since

$$\log(\mathsf{dist}(x, \partial\Delta)) = \log(\inf_i x_i) \le \sum_i p_i \log x_i.$$

To conclude the proof of the first assertion, it remains to show that for any $0 < \beta < 1$, there exists a neighborhood $\mathcal{U}$ of $\partial\Delta$ such that $\mathsf{P}(\{\tau =$

$\infty\}) \geq \beta$ whenever $x \in \mathcal{U}$. Let λ be a positive constant (to be chosen later), and let G be the map defined by $G(x) = e^{\lambda V(x)}$ for $x \in \mathrm{int}(\Delta)$ and by $G(x) = 0$ for $x \in \partial\Delta$. On $\mathrm{int}(\Delta)$

$$\mathcal{L}G = \lambda G[\mathcal{L}V - \frac{1}{2}\lambda \sum_{k=1}^{m} \langle \nabla V, S^k \rangle^2] = G[\mathcal{L}V - \frac{1}{2}\lambda \sum_{k=1}^{m} (\langle p, \Sigma^k \rangle + \langle \nabla W, S^k \rangle)],$$

so that for λ small enough,

$$\mathcal{L}G \leq 0$$

on $\tilde{\mathcal{U}}$. This makes the process $G(X^x_{t\wedge\tau})$ a supermartingale. Hence,

$$\mathsf{E}(G(X^x_{t\wedge\tau})\mathbf{1}_{\tau<\infty}) \leq \mathsf{E}(G(X^x_{t\wedge\tau})) \leq G(x).$$

Write $\mathcal{U}_r = \{x \in \Delta : \ G(x) < r\}$ for $r > 0$. Fix r small enough so that $\mathcal{U}_r \subset \tilde{\mathcal{U}}$ and set $\mathcal{U} = \mathcal{U}_{(1-\beta)r}$. Then letting $t \to \infty$, the Lebesgue dominated convergence implies that

$$r\mathsf{P}(\tau < \infty) \leq G(x) \leq (1-\beta)r.$$

Hence

$$\mathsf{P}(\tau = \infty) \geq \beta > 0.$$

We now pass to the proof of the second assertion. Fix $T > 0$ (to be chosen later) and let $\mathcal{W}$ denote the space of all continuous paths $w : [0, T] \to \Delta$ equipped with the topology of uniform convergence and the associated Borel σ-field. Let $\mathcal{W}_x = \{w \in \mathcal{W} : \ w(0) = x\}$, and let $\mathbb{P}_x$ denote the probability law of $\{X^x_t\}_{0\leq t\leq T}$ on $\mathcal{W}_x$. Let $\underline{D} : \mathcal{W} \mapsto \mathbb{R}$ be the function defined by $\underline{D}(w) = \inf_{0\leq t\leq T} \mathsf{dist}(w(t), \partial\Delta)$.

Lemma 7. *The constant T can be chosen such that*

$$\mathbb{P}_x(w \in \mathcal{W} : \ \underline{D}(w) < \epsilon) > 0$$

for all $x \in \Delta$ and $\epsilon > 0$.

Proof : Given $x \in \Delta, u \geq 0$, and a smooth map $\eta = (\eta_1, \ldots, \eta_m)$, let $y^{u,\eta,x}$ denote the solution to (19) with initial condition x. Since $\partial\Delta$ is weakly accessible, there exist $u_x \geq 0$ and η_x such that $y^{u_x,\eta_x,x}$ enters $N_\epsilon(\partial\Delta)$. Let us first show that we can always assume that $u_x = 1$. If $u_x > 0$, set $\tilde{\eta}_x(t) = \eta_x(t/u_x)$. Then $t \to y^{1,\tilde{\eta}_x,x}(t) = y^{u_x,\eta_x,x}(t/u_x)$ enters $N_\epsilon(\partial\Delta)$. If

$u_x = 0$, then by continuity of $u \to y^{u,\eta_x,x}(t)$, $y^{u,\eta_x,x}$ enters $N_\epsilon(\partial\Delta)$ for $u > 0$ small enough and we are back to the preceding case. In summary, we have established the existence of η_x and $t_x \geq 0$ such that $y^{1,\eta_x,x}(t_x) \in N_\epsilon(\partial\Delta)$.

Now, by the continuity of $z \to y^{1,\eta_x,z}(t_x)$ and the compactness of Δ, we can assume in addition that $t_x \leq T$ for some T independent of x. The claim now follows the support theorem of Stroock and Varadhan (1972) (see also Ikeda and Watanabe (1981), Chapter VI, Section 8), according to which the topological support of $\mathbb{P}_x$ (i.e., the smallest closed subset of $\mathcal{W}_x$ having $\mathbb{P}_x$ measure 1) is the closure in $\mathcal{W}_x$ of the set $\{y^{1,\eta,x}|_{[0,T]} : \eta \text{ is smooth}\}$. **QED**

We continue with the proof of Theorem 6. Let $h_\epsilon : \mathbb{R}^+ \to [0,1]$ be a continuous function such that $h_\epsilon(x) = 1$ for $x \leq \epsilon$ and $h_\epsilon(x) = 0$ for $x > 2\epsilon$ (for example, $h_\epsilon(x) = (1 - \frac{(x-\epsilon)^+}{\epsilon})^+$). Then

$$\begin{aligned}\mathbb{P}_x(w \in \mathcal{W} :\ \underline{D}(w) < 2\epsilon) &\geq \int_{\mathcal{W}} (h_\epsilon \circ \underline{D})(w)\ \mathbb{P}_x(dw) \\ &\geq \mathbb{P}_x(w \in \mathcal{W} :\ \underline{D}(w) < \epsilon) > 0.\end{aligned}$$

The continuity of $h_\epsilon \circ \underline{D}$, the weak* continuity of $x \mapsto \mathbb{P}_x$, and the compactness of Δ then imply that

$$\mathbb{P}_x(w \in \mathcal{W} :\ \underline{D}(w) < 2\epsilon) \geq \gamma \tag{22}$$

for some $\gamma > 0$ and all $x \in \Delta$.

Now let

$$\mathcal{E} = \{w \in \mathcal{W} :\ \limsup_{t \to \infty} \frac{\log(\mathsf{dist}(w(t), \partial\Delta))}{t} \leq -\alpha\},$$

and let $\tau(w) = \inf\{0 \leq t \leq 1 :\ \mathsf{dist}(w(t), \partial\Delta) < 2\epsilon\}$. Using the strong Markov property, combined with (22) and the first assertion of the theorem, we find that

$$\mathbb{P}_x(\mathcal{E}) = \int_{\mathcal{W}} [\mathbb{P}_{w(\tau(w))}(\mathcal{E}) \mathbf{1}_{\tau(w) < \infty}] \mathbb{P}_x(dw) \geq \beta\delta$$

uniformly in x, from which it follows that $\mathbb{P}_x(\mathcal{A}) = 1$. Indeed, by a standard martingale result, $\lim_{t \to \infty} \mathsf{E}(\mathbf{1}_{\mathcal{E}}|\mathcal{F}_t) = \mathbf{1}_{\mathcal{E}}$ almost surely, where $\mathcal{F}_t$ is the σ-field generated by $\{w(s) : s \leq t\}$. On the other hand, the Markov property implies that $\mathsf{E}(\mathbf{1}_{\mathcal{E}}|\mathcal{F}_t) = \mathbb{P}_{w(t)}(\mathcal{E}) \geq \beta\delta$, completing the proof of the theorem. **QED**

Corollary 8. *Assume that R is C^2 and that condition* (I) *holds. Then there exist $\delta, \alpha > 0$ such that for every parameter σ satisfying*

$$0 < \sup_i |\sigma_i| \le \delta$$

and every $x \in \Delta$, the solution (X_t^x) to the stochastic replicator dynamic (S)*) satisfies*

$$\limsup_{t \to \infty} \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \le -\alpha$$

almost surely.

Proof : If $\sigma_i \neq 0$, every solution to $\dot{y} = \Sigma^i(y)$ converges to $\partial\Delta$, since $\dot{y}_i = \sigma_i y_i(1 - y_i)$. Hence every neighborhood of $\partial\Delta$ is accessible from all $x \in \Delta$, so the result follows from Theorem 6. **QED**

5 Stochastic Impermanence at Large Noise Levels

Theorem 6 shows that when the noise level is small, the behavior of the stochastic dynamic (S′) agrees with the behavior of the deterministic dynamic (R): the impermanent deterministic dynamic becomes a stochastic dynamic that approaches $\partial\Delta$ with high probability. Another way to ensure convergence to $\partial\Delta$ is to introduce large levels of noise to an *arbitrary* deterministic replicator equation. The noise ensures that the system quickly approaches $\partial\Delta$; given the form of equation (S′), a small enough neighborhood of $\partial\Delta$ is nearly impossible to leave.

Theorem 9. *Suppose that R is C^2 and that there exist $p_1, \ldots, p_n > 0$ such that for all $x \in \partial\Delta$,*

$$\sum_i p_i \left(\tilde{F}_i(x) - \frac{1}{2} \sum_{j=1}^{m} \Sigma_{ij}(x)^2 \right) < 0. \tag{23}$$

Then there exists an $\alpha > 0$ such that the following property holds: Given any $0 < \beta < 1$, there exists a neighborhood $\mathcal{U}$ of $\partial\Delta$ such that the solution to (S′) *satisfies*

$$\mathsf{P}\left(\limsup_{t \to \infty} \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \le -\alpha \right) \ge \beta$$

for all $x \in \mathcal{U}$. If we assume in addition that $\partial\Delta$ is weakly accessible, then

$$\mathsf{P}\left(\limsup_{t\to\infty} \frac{\log(\mathsf{dist}(X_t^x, \partial\Delta))}{t} \le -\alpha\right) = 1$$

for all $x \in \Delta$.

Proof : Let $V(x) = \sum_i p_i \log(x_i)$. Then the computation made in the proof of Theorem 6 shows that $\mathcal{L}V(x) \le -\alpha < 0$ on some neighborhood of $\partial\Delta$, and our conclusion follows in a similar fashion. **QED**

In the stochastic replicator dynamic (S), the role of the function $\tilde{F}_i$ from dynamic (S′) is played by the excess adjusted fitness function $\hat{F}_i^\sigma$, which depends directly on the noise level σ (cf equation (3)). For this reason, to obtain implications of Theorem 9 for the dynamic (S) we must assume a weakened form of condition (I), one that only considers the ergodic measures $\mu \in \mathcal{M}_\Phi^E(\partial\Delta)$ that are point masses on the vertices of Δ.

Corollary 10. *Suppose that R is C^2 and that there exist $p_1, \dots, p_n > 0$ such that $\sum_i p_i \hat{F}_i(e_k) < 0$ for each vertex $e_1, \dots, e_n$. Consider the stochastic replicator dynamic* (S) *where $\sigma_1 = \ldots = \sigma_n = \bar{\sigma}$. Then, for $\bar{\sigma}$ large enough, the second conclusion of Theorem 9 holds.*

Proof : In the case of the dynamic (S),

$$\hat{F}_i^\sigma(x) - \tfrac{1}{2}\sum\nolimits_j \Sigma_{ij}(x)^2 = \hat{F}_i^\sigma(x) + \tfrac{1}{2}\sigma\left(\sum\nolimits_i (x_i)^2 - 1\right),$$

so that inequality (23) holds true at each vertex and, by continuity, on a neighborhood U of the vertices $e_1, \dots, e_n$. Outside U, $\sum_i (x_i)^2 - 1 < 0$, so for $\bar{\sigma}$ large enough, equation (23) holds true in this case as well. **QED**

6 Concluding remarks

In two recent papers, Schreiber (2006, 2007) considers small *bounded* random perturbations of *discrete time* dynamical systems on a set D (not necessarily the unit simplex) with closed invariant boundary ∂D. Under nondegeneracy assumptions similar to ours, Schreiber (2007) proves that almost sure convergence to ∂D occurs if and only if the deterministic dynamic contains no attractor in $\mathrm{int}(D)$. Thus, Schreiber (2006) proposes the existence of an interior attractor as the more appropriate notion of "persistence".

The results of the present paper show that unbounded noise may lead to very different behavior, and so renew the case for permanence. In particular, in view of our Theorem 6, almost sure convergence to ∂D is possible even with the presence of attractors in $\text{int}(D)$, and indeed with any deterministic dynamic away from ∂D, so long as the deterministic system is impermanent in the sense of condition (I). On the other hand, permanence of the deterministic system (P) leads to stochastic permanence under small unbounded noise.

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