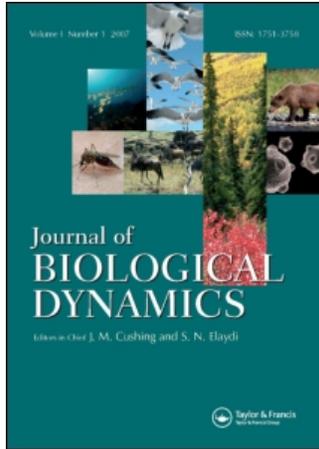


This article was downloaded by:[Hofbauer, Josef]  
On: 19 May 2008  
Access Details: [subscription number 793186641]  
Publisher: Taylor & Francis  
Informa Ltd Registered in England and Wales Registered Number: 1072954  
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Journal of Biological Dynamics

Publication details, including instructions for authors and subscription information:  
<http://www.informaworld.com/smpp/title~content=t744398444>

### Robust permanence and impermanence for stochastic replicator dynamics

Michel Benaïm<sup>a</sup>; Josef Hofbauer<sup>b</sup>; William H. Sandholm<sup>c</sup>

<sup>a</sup> Institut de Mathématiques, Université de Neuchâtel, Switzerland

<sup>b</sup> Fakultät für Mathematik, Universität Wien, Nordbergstrasse, Wien, Austria

<sup>c</sup> Department of Economics, University of Wisconsin, Madison, WI, USA

Online Publication Date: 01 April 2008

To cite this Article: Benaïm, Michel, Hofbauer, Josef and Sandholm, William H. (2008) 'Robust permanence and impermanence for stochastic replicator dynamics', Journal of Biological Dynamics, 2:2, 180 — 195

To link to this article: DOI: 10.1080/17513750801915269

URL: <http://dx.doi.org/10.1080/17513750801915269>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

## Robust permanence and impermanence for stochastic replicator dynamics

Michel Benaim<sup>a</sup>, Josef Hofbauer<sup>b\*</sup> and William H. Sandholm<sup>c</sup>

<sup>a</sup>*Institut de Mathématiques, Université de Neuchâtel, Rue Emile-Argand, Neuchâtel, Switzerland;*  
<sup>b</sup>*Fakultät für Mathematik, Universität Wien, Nordbergstrasse, Wien, Austria;* <sup>c</sup>*Department of Economics, University of Wisconsin, Madison, WI, USA*

(Received 15 July 2007; final version received 13 January 2008)

Garay and Hofbauer (SIAM J. Math. Anal. 34 (2003)) proposed sufficient conditions for robust permanence and impermanence of the deterministic replicator dynamics. We reconsider these conditions in the context of the stochastic replicator dynamics, which is obtained from its deterministic analogue by introducing Brownian perturbations of payoffs. When the deterministic replicator dynamics is permanent and the noise level small, the stochastic dynamics 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 dynamics is impermanent and the noise level small or large, the stochastic dynamics converges to the boundary of the state space at an exponential rate.

**Keywords:** permanence; replicator dynamics; stochastic differential equation; recurrence; transience

*AMS 2000 Mathematics Subject Classification:* 92D25; 60H10

### 1. Introduction

The deterministic replicator dynamics of Taylor and Jonker [26] 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 (or traits within one 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 (evolutionarily stable strategy): Hofbauer *et al.* [12] and Zeeman [27] show that such states are (interior) globally asymptotically stable under the replicator dynamics.

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.* [24], which requires that the boundary of the state space be a repeller. When the replicator dynamics is permanent, solution trajectories from all interior initial conditions maintain proportions of all species that are positive and bounded away from zero.

---

\*Corresponding author. Email: josef.hofbauer@univie.ac.at

Hofbauer [9] and Hutson [14] were among the first to establish general sufficient conditions for permanence; see [15] and [13] 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 [21] and Garay and Hofbauer [8] introduced 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 dynamics. The first stochastic differential equation analogue of the replicator dynamics was introduced by Foster and Young [6]. Later, Fudenberg and Harris [7] offered a biologically more natural model, known as the *stochastic replicator dynamics*, 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 [7] dynamics, but to more general Brownian perturbations of the replicator dynamics as well.

As in the deterministic case, the initial results on long-term coexistence for the stochastic replicator dynamics concerned settings with a single globally attracting state. Using tools specific to one-dimensional diffusions, Fudenberg and Harris [7] showed that the stochastic replicator dynamics 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 [17], who extended 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 dynamics 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 [8] sufficient conditions for permanence for the deterministic setting. In Section 3, we prove that if the replicator dynamics for a game satisfying Garay and Hofbauer's [8] 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 dynamics is 'impermanent', in the sense that its solutions converge to the boundary of the state space at an exponential rate with probability 1. In Sections 4 and 5, we show that this is the case if Garay and Hofbauer's [8] 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 dynamics

The replicator dynamics describes natural selection among individuals programmed to play *strategies* from the set  $\{1, \dots, n\}$ . 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  $\Delta$ , and we let  $\partial\Delta$  and  $\text{int}(\Delta)$  denote the boundary and interior of  $\Delta$ , respectively.

The *fitness* of strategy  $i$  is described by a function  $F_i : \Delta \rightarrow \mathbb{R}$  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  $F : \Delta \rightarrow \mathbb{R}^n$  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 dynamics, 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

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

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

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

By Lipschitz continuity and standard results, (R) induces a flow  $\Phi : \mathbb{R} \times \Delta \rightarrow \Delta$  which leaves both  $\partial\Delta$  and  $\text{int}(\Delta)$  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 system (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 non-empty, compact and admits a neighbourhood  $\mathcal{U}$  such that

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

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  $\lim_{t \rightarrow \infty} \text{dist}(\Phi_t(x), A) = 0$ .

Following Schuster *et al.* [24] and Hofbauer and Sigmund [13], we call the dynamics (R) *permanent* if it admits an attractor  $A \subset \text{int}(\Delta)$  whose basin of attraction is all of  $\text{int}(\Delta)$ . Equivalently, (R) is permanent if  $\partial\Delta$  is a repeller under (R). In this case,  $A$  and  $\partial\Delta$  form an attractor–repeller pair, see [2], and  $A$  is the *dual attractor* of the repeller  $\partial\Delta$ . 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 2.1* 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  $k_1, \dots, k_n > 0$ . 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 dynamics (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 [5] 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, the rest point  $x^*$  is interior globally asymptotically stable, so system (H) is permanent. When  $n \geq 5$ ,  $x^*$  is unstable. Nevertheless, Schuster *et al.* [24] showed that (H) remains permanent. In fact, Hofbauer *et al.* [11] used techniques from the theory of monotone dynamical systems to show that when  $n \geq 5$ , the interior attractor  $A$  of (H) contains a minimal attractor which is a periodic orbit. For further discussion, see Chapter 12 of [13].

Schreiber [21] and Garay and Hofbauer [8] provided 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  $\Phi$ -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 proved in Hofbauer [8].

**THEOREM 2.1** *Let  $p_1, \dots, p_n > 0$ . If*

$$\sum_{i=1}^n p_i \int_{\partial\Delta} \hat{F}_i(x) \mu(dx) > 0, \quad \forall \mu \in \mathcal{M}_\Phi^E(\partial\Delta) \tag{P}$$

*then system (R) is permanent. If instead*

$$\sum_{i=1}^n p_i \int_{\partial\Delta} \hat{F}_i(x) \mu(dx) < 0, \quad \forall \mu \in \mathcal{M}_\Phi^E(\partial\Delta) \tag{I}$$

*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  $\mu$ . Thus, the permanence condition (P) requires that for some positive vector  $p = (p_1, \dots, p_n)$ , the  $p$ -weighted average of these  $\mu$ -expected excess fitnesses is positive for every ergodic measure  $\mu$  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, the impermanence condition (I) requires unused strategies to tend to underperform the population average.

Garay and Hofbauer [8] provided 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 [13] 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 [7] proposed the following stochastic analogue of the replicator dynamics (R). In place of the deterministic Equation (1), Fudenberg and Harris [7] assumed 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  $B_i(t)$ :

$$dY_i(t) = Y_i(t) (F_i(X(t)) dt + \sigma_i dB_i(t)), \quad (2)$$

where  $X_i(t) = Y_i(t) / \sum_j Y_j(t)$  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 the  $\sigma$ -adjusted fitness of strategy  $i$  by

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

and let

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

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

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

where  $I$  denotes the  $n \times n$  identity matrix,  $\mathbf{1} \in \mathbb{R}^n$  is the (column) vector of ones and  $^T$  denotes transposition. This equation defines the *stochastic replicator dynamics*.

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

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

where (i)  $B(t) = (B_1(t), \dots, B_m(t))^T$  is an  $m$ -dimensional standard Brownian motion defined on some probability space  $(\Omega, \mathcal{F}, \mathbb{P})$ , and (ii)  $\tilde{F} : \Delta \rightarrow \mathbb{R}^n$  and  $\Sigma : \Delta \rightarrow \mathbb{R}^{n \times m}$  are Lipschitz continuous maps with the property that for each  $x \in X$ , the drift vector

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

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

$$S(x) = \text{diag}(x) \Sigma(x) \quad (4)$$

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

Generalizing the terminology in [8], we call (S') a *random  $\delta$ -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  $\delta$ -perturbation of (R) on  $\partial\Delta$*  if this inequality holds whenever  $x \in \partial\Delta$ . In the latter case, the nature of the perturbation outside a neighbourhood 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 is denoted 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  $\bigcap_{s \geq t} \{X_s^x \in \text{int}(\Delta)\}$  coincide  $\mathbf{P}$  – 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') *non-degenerate* if for all  $x \in \text{int}(\Delta)$ , the column vectors  $S^1(x), \dots, S^m(x)$  span  $T\Delta$ . A direct calculation reveals that this requirement is satisfied by the stochastic replicator dynamics (S). For our impermanence results, even weaker non-degeneracy 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 [17] showed that in such cases, the permanence of the deterministic system extends to its stochastic analogues: in particular, he proved that if the underlying game  $F$  has an interior ESS  $x^*$ , the stochastic replicator dynamics (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.

A probability measure  $\mu$  on  $\text{int}(\Delta)$  is called *invariant* under (S') provided  $X(t)$  has law  $\mu$  whenever  $X(0)$  has law  $\mu$  and is chosen independently on  $\{B_t, t \geq 0\}$ . Equivalently

$$\int \mathbf{P}(X_t^x \in A) \mu(dx) = \mu(A),$$

for all Borel sets  $A \subset \text{int}(\Delta)$  and all times  $t > 0$ .

**THEOREM 3.1** *Assume that  $R$  is  $C^2$  and that Condition (P) holds. Then for every  $r > 0$ , there exists a  $\delta > 0$  such that for all  $\delta \in (0, \delta)$ , every non-degenerate random  $\delta$ -perturbation of (R) on  $\partial\Delta$  enjoys the following properties:*

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

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

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

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

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

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

$\mathbf{P}$  – almost surely.

- (iv) Let  $A \subset \text{int}(\Delta)$  be the dual attractor of  $\partial\Delta$  for the dynamics  $(\mathbb{R})$ , and suppose that  $r < 1$ . Then for any neighbourhood  $\mathcal{N}$  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 [3], or from Theorem 15.0.1 in [19].

LEMMA 3.1 Let  $U$  be an open subset of  $\mathbb{R}^d$ , and let  $p : U \times U \rightarrow \mathbb{R}^+$  be a positive continuous Markov transition kernel. For any bounded or non-negative Borel function  $\Psi : U \mapsto \mathbb{R}$ , define

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

and

$$P^n\Psi = P(P^{n-1})(\Psi)$$

for all  $n \geq 1$  with the convention that  $P^0\Psi = \Psi$ . For any Borel set  $A \subset U$ , set

$$P^n(x, A) = P^n\mathbf{1}_A(x).$$

Assume that there exists a non-negative continuous function  $H : U \rightarrow \mathbb{R}^+$  such that

- (a)  $\lim_{x \rightarrow \partial U} H(x) = \infty$ , and  
 (b)  $PH(x) \leq aH(x) + b$  for all  $x \in U$ , where  $0 < a < 1$  and  $b \in \mathbb{R}$ .

Then

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

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

$\mathbb{P}$  – almost surely.

We now proceed with the proof of Theorem 3.1. Let the constants  $p_i, i = 1, \dots, n$ , be as in Equation (P) of Theorem 2.1. 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 in [8] that there exists a constant

$\alpha > 0$ , a neighbourhood  $\mathcal{U}$  of  $\partial\Delta$ , and a  $C^2$  map  $W : \Delta \rightarrow \mathbb{R}$  such that

$$\sum_i p_i \hat{F}_i(x) + \langle \nabla W(x), R(x) \rangle > \alpha, \tag{5}$$

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

$$V(x) = \sum_i p_i \log x_i + W(x) \tag{6}$$

satisfies

$$\langle \nabla V(x), R(x) \rangle > \alpha, \tag{7}$$

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

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

$$\mathcal{L}\psi(x) = \langle \nabla\psi(x), R(x) \rangle + \mathcal{A}\psi(x), \tag{8}$$

where

$$\mathcal{A}\psi(x) = \frac{1}{2} \sum_{i,j} x_i x_j a_{ij}(x) \frac{\partial^2 \psi}{\partial x_i \partial x_j}(x) \tag{9}$$

and

$$a(x) = \Sigma(x)\Sigma(x)^T. \tag{10}$$

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  $\delta$  small enough, we can assume that

$$\mathcal{L}V(x) \geq \alpha, \tag{11}$$

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

Set  $\lambda = r/\inf_i p_i$  and define

$$H = \exp(-\lambda V). \tag{12}$$

Then,  $H$  is  $C^2$ , positive, and satisfies

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

and

$$H(x) \geq \frac{K}{\text{dist}(x, \partial\Delta)^r}, \tag{13}$$

for some constant  $K > 0$ . On the other hand, recalling Equation (4),

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

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

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

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

$$\mathcal{L}H \leq -\beta H + \gamma \tag{14}$$

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

$$\begin{aligned} e^{\beta t} H(X_t^x) - H(x) &= \int_0^t e^{\beta s} (\beta H(X_s^x) + \mathcal{L}H(X_s)) ds + N_t \\ &\leq \frac{\gamma}{\beta} e^{\beta t} + N_t, \end{aligned} \tag{15}$$

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

$$\begin{aligned} dM_t &= \langle \nabla V(X_t^x), \sum_j S^j(X_t^x) dB_t^j \rangle \\ &= \sum_{j=1}^m \left[ \sum_{i=1}^n (p_i \Sigma_{ij}(X_t^x) + S_{ij}(X_t^x) \frac{\partial W}{\partial x_i}(X_t^x)) \right] dB_t^j. \end{aligned} \tag{16}$$

Let  $\tau_N = \inf\{t \geq 0 : H(X_t^x) > N\}$ . Then,  $N_{t \wedge \tau_N}$  is a martingale, and so  $E(N_{t \wedge \tau_N}) = 0$ . Replacing  $t$  by  $t \wedge \tau_N$  in Equation (15), taking the expectation, and letting  $N \rightarrow \infty$  yields

$$E(H(X_t^x)) \leq e^{-\beta t} H(x) + \frac{\gamma}{\beta}. \tag{17}$$

Let  $\{P_t\}_{t \geq 0}$  denote the Markov semigroup induced by  $(S')$  on  $\text{int}(\Delta)$ . Then, Equation (17) can be rewritten as

$$P_t H \leq a(t)H + b \tag{18}$$

with  $0 < a(t) < 1$ . On the other hand, by the non-degeneracy 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 [4]). Therefore, Lemma 3.1 applies to  $P_t$  for any  $t > 0$ .

Applying this lemma, let  $\mu$  denote the unique invariant probability measure of  $P_1$ . Then,  $\mu$  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 (13).

Let  $\mu\psi$  be shorthand for  $\int \psi d\mu$  and let  $P_n(x, \cdot)$  denote the measure defined by  $P_n(x, A) = P_n \mathbf{1}_A(x)$  for all Borel sets  $A$ .

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

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

where  $|\cdot|_{VT}$  stands for the total variation norm. Hence, by Lemma 3.1(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  $u(x) = P(\lim_{t \rightarrow \infty} 1/t \int_0^t \Psi(X_s^x) ds = \mu\Psi)$  is clearly harmonic for  $P_1$  (that is,  $P_1 u = u$ ). Hence, by Lemma 3.1 (iii) and Theorem 17.1.5 [19],  $u$  is a constant. On the other hand, by the Birkhoff ergodic theorem,  $u(x) = 1$  for  $\mu$  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  $K$  denotes the Lipschitz constant of  $R$  and set  $\lambda = K/(1 - r)\alpha$ . By Gronwall's inequality, with  $\Phi_t(x)$  the flow of (R),

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

Let  $0 \leq \psi \leq 1$  be a smooth function on  $\Delta$  which is 1 on a neighbourhood of  $A$  and 0 outside  $\mathcal{N}$ . Thus by Lipschitz continuity of  $\psi$ ,

$$|P_t \psi(x) - \psi \circ \Phi_t(x)| \leq Cst e^{Kt} t \delta.$$

Integrating the last inequality gives

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

by the invariance of  $\mu$ . It follows that

$$\mu\psi \geq \int_{\{V \geq -v\}} \psi \circ \Phi_t d\mu - Cst e^{Kt} t \delta$$

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  $t \geq t_v$  and  $V(x) > -v$ . Therefore, Markov's inequality implies that

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

Now, using the fact that  $V(\Phi_t(x)) \geq \alpha t + V(x)$  on a neighborhood of  $\partial\Delta$  (since  $\langle \nabla V, F \rangle \geq \alpha$ ) 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  $v \geq v_0$ . Thus,

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

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

$$1 - \mu\psi \leq Cst \delta + Cst \delta^r \log(\delta). \quad \blacksquare$$

In some cases, the invariant measure  $\mu$  can be explicitly computed. Fudenberg and Harris [7] found beta distributions for  $n = 2$  and Hofbauer and Imhof [10] found Dirichlet distributions for  $n$  strategy games that are close to zero-sum games.

#### 4. Stochastic impermanence

Our next result, Theorem 4.1, 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 fast with high probability.

This result requires a weaker non-degeneracy condition than that used in Theorem 3.1. Rewrite Equation (S') using the Stratonovich formalism, so that

$$dX_t = J(X_t) dt + S(X_t) \circ dB_t^j, \quad (19)$$

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 exists a non-negative number  $u$  and smooth maps  $\eta_i : [0, \infty) \rightarrow \mathbb{R}, i = 1, \dots, m$ , that allow one to 'steer' the solution of the ordinary differential equation

$$\frac{dy}{dt} = uJ(y(t)) + \sum_{j=1}^m \eta_j(t) S^j(y(t)), \quad (20)$$

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 neighbourhood of  $A$  is accessible from  $x$ , and *weakly accessible* if it is weakly accessible from all  $x \in \text{int}(\Delta)$ .

By Chow's [1] theorem (see, e.g., [20]), a sufficient condition for every subset of  $\Delta$  to be weakly accessible is given by Hörmander's condition:

$$\text{Lie}(S^1, \dots, S^m)(x) = T\Delta, \quad \text{for all } x \in \text{int}(\Delta), \quad (21)$$

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

*Remark 4.1* Hörmander's condition is satisfied if (S') is non-degenerate, as assumed in Theorem 3.1. In fact, the non-degeneracy assumption in Theorem 3.1 can be weakened to the assumption that Hörmander's condition holds for every random  $\delta$ -perturbation of (R).

**THEOREM 4.2** *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  $\delta$ -perturbation of (R) on  $\partial\Delta$  with  $\delta \in (0, \bar{\delta})$  satisfies the following property: given any  $0 < \beta < 1$ , there exists a neighbourhood  $\mathcal{U}$  of  $\partial\Delta$  such that*

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

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

$$\mathbb{P} \left( \limsup_{t \rightarrow \infty} \frac{\log(\text{dist}(X_t^x, \partial\Delta))}{t} \leq -\alpha \right) = 1,$$

for all  $x \in \Delta$ .

*Proof* Let  $V$  be Function (6) introduced in the proof of Theorem 3.1. A variation of the argument we used there shows that for  $\delta$  small enough,

$$\mathcal{L}V \leq -\alpha < 0,$$

on a neighbourhood  $\tilde{\mathcal{U}}$  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 (16).

Equation (16) implies that the quadratic variation of  $M_t$  satisfies  $\langle M \rangle_t \leq Ct$  for some  $C > 0$ . Hence, by the strong law of large numbers for martingales, we have that

$$\lim_{t \rightarrow \infty} M_t/t = 0, \tag{22}$$

$\mathbb{P}$  – almost surely. Let  $\tau = \inf\{t \geq 0 : X_t^x \in \partial\tilde{\mathcal{U}}\}$  be the exit time from  $\tilde{\mathcal{U}}$ . It follows from Equations (11) and (22) that

$$\limsup_{t \rightarrow \infty} \frac{V_t}{t} \leq -\alpha,$$

$\mathbb{P}$  – almost surely on the event  $\{\tau = \infty\}$ . Hence,

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

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

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

To conclude the proof of the first assertion, it remains to show that for any  $0 < \beta < 1$ , there exists a neighbourhood  $\mathcal{U}$  of  $\partial\Delta$  such that  $\mathbb{P}(\{\tau = \infty\}) \geq \beta$  whenever  $x \in \mathcal{U}$ . Let  $\lambda$  be a positive constant (to be chosen later), and let  $G$  be the map defined by  $G(x) = e^{\lambda V(x)}$  for  $x \in \text{int}(\Delta)$  and by  $G(x) = 0$  for  $x \in \partial\Delta$ . On  $\text{int}(\Delta)$

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

so that for  $\lambda$  small enough,

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

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

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

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  $t \rightarrow \infty$ , the Lebesgue-dominated convergence theorem implies that

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

Hence,

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

We now pass to the proof of the second assertion. Fix  $T > 0$  (to be chosen later) and let  $\mathcal{W}$  denotes the space of all continuous paths  $w : [0, T] \rightarrow \Delta$  equipped with the topology of uniform convergence and the associated Borel  $\sigma$ -field. Let  $\mathcal{W}_x = \{w \in \mathcal{W} : w(0) = x\}$ , and let

$\mathbb{P}_x$  denotes the probability law of  $\{X_t^x\}_{0 \leq t \leq T}$  on  $\mathcal{W}_x$ . Let  $\underline{D} : \mathcal{W} \mapsto \mathbb{R}$  be the function defined by  $\underline{D}(w) = \inf_{0 \leq t \leq T} \text{dist}(w(t), \partial \Delta)$ .

LEMMA 4.1 *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  $\eta = (\eta_1, \dots, \eta_m)$ , let  $y^{u, \eta, x}$  denote the solution to Equation (20) with initial condition  $x$ . Since  $\partial \Delta$  is weakly accessible, there exist  $u_x \geq 0$  and  $\eta_x$  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,  $t \rightarrow y^{1, \tilde{\eta}_x, x}(t) = y^{u_x, \eta_x, x}(t/u_x)$  enters  $N_\epsilon(\partial \Delta)$ . If  $u_x = 0$ , then by continuity of  $u \rightarrow y^{u, \eta_x, x}(t)$ ,  $y^{u, \eta_x, x}$  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  $\eta_x$  and  $t_x \geq 0$  such that  $y^{1, \eta_x, x}(t_x) \in N_\epsilon(\partial \Delta)$ .

Now, by the continuity of  $z \rightarrow y^{1, \eta_x, z}(t_x)$  and the compactness of  $\Delta$ , we can assume in addition that  $t_x \leq T$  for some  $T$  independent of  $x$ . The claim now follows from the support theorem [25] (see also [16], 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  $\{y^{1, \eta, x}|_{[0, T]} : \eta \text{ is smooth}\}$ . ■

We continue with the proof of Theorem 4.2. Let  $h_\epsilon : \mathbb{R}^+ \rightarrow [0, 1]$  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,  $h_\epsilon(x) = (1 - (x - \epsilon)^+/\epsilon)^+$ ). 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  $\Delta$  then imply that

$$\mathbb{P}_x(w \in \mathcal{W} : \underline{D}(w) < 2\epsilon) \geq \gamma, \tag{23}$$

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

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

and let  $\tau(w) = \inf\{0 \leq t \leq 1 : \text{dist}(w(t), \partial \Delta) < 2\epsilon\}$ . Using the strong Markov property, combined with Equation (23) 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,  $\lim_{t \rightarrow \infty} \mathbf{E}(\mathbf{1}_{\mathcal{E}} | \mathcal{F}_t) = \mathbf{1}_{\mathcal{E}}$   $\mathbb{P}$ -almost surely, where  $\mathcal{F}_t$  is the  $\sigma$ -field generated by  $\{w(s) : s \leq t\}$ . On the other hand, the Markov property implies that  $\mathbf{E}(\mathbf{1}_{\mathcal{E}} | \mathcal{F}_t) = \mathbb{P}_{w(t)}(\mathcal{E}) \geq \beta \delta$ , completing the proof of the theorem. ■

COROLLARY 4.1 Assume that  $R$  is  $C^2$  and that condition (I) holds. Then there exist  $\delta, \alpha > 0$  such that for every parameter  $\sigma$  satisfying

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

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

$$\limsup_{t \rightarrow \infty} \frac{\log(\text{dist}(X_t^x, \partial\Delta))}{t} \leq -\alpha$$

$\mathbb{P}$  – almost surely.

*Proof* If  $\sigma_i \neq 0$ , every solution to  $\dot{y} = S^i(y)$  converges to  $\partial\Delta$ , since  $\dot{y}_i = \sigma_i y_i(1 - y_i)$ . Hence, every neighbourhood of  $\partial\Delta$  is accessible from all  $x \in \Delta$ , so the result follows from Theorem 4.1. ■

The stochastic impermanence results in this section imply the transience of the stochastic processes (S) and (S') on  $\text{int}(\Delta)$ . For (S) with linear fitness function  $F$ , further conditions implying transience have been found in Khasminskii and Potsepun [18] Hofbauer and Imhof [10].

### 5. Stochastic impermanence at large noise levels

Theorem 4.1 shows that when the noise level is small, the behaviour of the stochastic dynamics (S') agrees with the behaviour of the deterministic dynamics (R): the impermanent deterministic dynamics becomes a stochastic dynamics that approaches  $\partial\Delta$  with high probability. Another way of enforcing convergence to  $\partial\Delta$  is to add large levels of noise to an arbitrary deterministic replicator equation. The noise makes the solutions of the system quickly approach  $\partial\Delta$ ; given the form of equation (S'), a small enough neighbourhood of  $\partial\Delta$  is nearly impossible to leave.

THEOREM 5.1 Suppose that  $R$  is  $C^2$  and that there exist  $p_1, \dots, p_n > 0$  such that for all  $x \in \partial\Delta$ ,

$$\sum_i p_i \left( \tilde{F}_i(x) - \frac{1}{2} \sum_{j=1}^m \Sigma_{ij}(x)^2 \right) < 0. \tag{24}$$

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

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

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

$$\mathbb{P} \left( \limsup_{t \rightarrow \infty} \frac{\log(\text{dist}(X_t^x, \partial\Delta))}{t} \leq -\alpha \right) = 1,$$

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 4.1 shows that  $\mathcal{L}V(x) \leq -\alpha < 0$  on some neighbourhood of  $\partial\Delta$ , and our conclusion follows in a similar fashion. ■

In the stochastic replicator dynamics (S), the role of the function  $\tilde{F}_i$  from dynamics (S') is played by the excess adjusted fitness function  $\hat{F}_i^\sigma$ , which depends directly on the noise level  $\sigma$  (cf Equation (3)). For this reason, to obtain implications of Theorem 9 for the dynamics (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  $\Delta$ .

**COROLLARY 5.1** *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 dynamics (S) where  $\sigma_1 = \dots = \sigma_n = \bar{\sigma}$ . Then, for  $\bar{\sigma}$  large enough, the second conclusion of Theorem 5.1 holds.*

*Proof* In the case of the dynamics (S),

$$\hat{F}_i^\sigma(x) - \frac{1}{2} \sum_j \Sigma_{ij}(x)^2 = \hat{F}_i(x) + \frac{1}{2} \sigma^2 \left( \sum_i x_i^2 - 1 \right),$$

so that Inequality (24) holds true at each vertex and, by continuity, on a neighbourhood  $U$  of the vertices  $e_1, \dots, e_n$ . Outside  $U$ ,  $\sum_i x_i^2 - 1 < 0$ , so for  $\bar{\sigma}$  large enough, Equation (24) holds true in this case as well. ■

## 6. Concluding remarks

In two recent papers, Schreiber [22], [23] considered small *bounded* random perturbations of *discrete time* dynamical systems on a set  $D$  (not necessarily the unit simplex) with closed invariant boundary  $\partial D$ . Under non-degeneracy assumptions similar to ours, Schreiber [23] proved that almost sure convergence to  $\partial D$  occurs if and only if the deterministic dynamics contains no attractor in  $\text{int}(D)$ . Thus, Schreiber [22] proposed 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 behaviours, and so renew the case for permanence. In particular, in view of our Theorem 4.1, almost sure convergence to  $\partial D$  is possible even with the presence of attractors in  $\text{int}(D)$ , as 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.

## Acknowledgements

We are grateful to two referees for their careful reading of the manuscript. We acknowledge financial support under Swiss National Science Foundation Grants 200021-1036251/1 and 200020-11231611 and U.S. National Science Foundation Grant SES-0617753. We also thank Gerard Ben Arous and Patrick Cattiaux for useful discussions.

## References

- [1] W.-L. Chow, *Über Systeme von linearen partiellen Differentialgleichungen erster Ordnung*, Mathematische Annalen 117 (1940), pp. 98–115.
- [2] C. Conley, *Isolated Invariant Sets and the Morse Index*. Conference Board of the Mathematical Sciences 38. American Mathematical Society, 1978.
- [3] M. Duflo, *Random Iterative Models*, Springer, Berlin, 1997.
- [4] R. Durrett, *Stochastic Calculus: A Practical Introduction*, CRC Press, Boca Raton, FL, 1996.
- [5] M. Eigen and P. Schuster, *The Hypercycle: A Principle of Natural Self-Organization*, Springer, Berlin, 1979.
- [6] D. Foster and H.P. Young, *Stochastic evolutionary game dynamics*, Theor. Popul. Biol. 38 (1990), pp. 219–232. Correction, 51 (1997), 77–78.

- [7] D. Fudenberg and C. Harris, *Evolutionary dynamics with aggregate shocks*, J. Econ. Theory 57 (1992), pp. 420–441.
- [8] B.M. Garay and J. Hofbauer, *Robust permanence for ecological differential equations, minimax, and discretizations*, SIAM J. Math. Ana. 34 (2003), pp. 1007–1039.
- [9] J. Hofbauer, *A general cooperation theorem for hypercycles*, Monatshefte für Mathematik 91 (1981), pp. 233–240.
- [10] J. Hofbauer and L. Imhof, *Time averages, recurrence and transience in the stochastic replicator dynamics*, preprint 2007.
- [11] J. Hofbauer, J. Mallet-Paret, and H.L. Smith, *Stable periodic solutions for the hypercycle system*, J. Dyn. Differ. Equ. 3 (1991), pp. 423–436.
- [12] J. Hofbauer, P. Schuster, and K. Sigmund, *A note on evolutionarily stable strategies and game dynamics*, J. Theor. Biol. 81 (1979), pp. 609–612.
- [13] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, 1998.
- [14] V. Hutson, *A theorem on average Lyapunov functions*, Monatshefte für Mathematik 98 (1984), pp. 267–275.
- [15] V. Hutson and K. Schmitt, *Permanence and the dynamics of biological systems*, Math. Biosci. 111 (1992), pp. 1–71.
- [16] N. Ikeda and S. Watanabe, *Stochastic Differential Equations and Diffusion Processes*, North Holland, Amsterdam, 1981.
- [17] L.A. Imhof, *The long-run behavior of the stochastic replicator dynamics*, Ann. Appl. Probab. 15 (2005), pp. 1019–1045.
- [18] R. Khasminskii and N. Potsepun, *On the replicator dynamics behavior under Stratonovich type random perturbations*, Stoch Dyn. 6 (2006), pp. 197–211.
- [19] S.P. Meyn and R.L. Tweedy, *Markov Chains and Stochastic Stability*, 2nd ed., Springer, Berlin, (2005) (posted online).
- [20] R. Montgomery, *A Tour of Subriemannian Geometries, Their Geodesics and Applications*, Providence: American Mathematical Society, 2001.
- [21] S.J. Schreiber, *Criteria for  $C^r$  robust permanence*, J. Differ. Equ. 162 (2000), pp. 400–426.
- [22] ———, *Persistence despite perturbations for interacting populations*, J. Theor. Biol. 242 (2006), pp. 844–852
- [23] ———, *On persistence and extinction for randomly perturbed dynamical systems*, Discrete Contin. Dyn. Syst. B 7 (2007), pp. 457–463.
- [24] P. Schuster, K. Sigmund, and R. Wolff, *Dynamical systems under constant organization. III. Cooperative and competitive behavior of hypercycles*, J. Differ. Equ. 32 (1979), pp. 357–368.
- [25] D.W. Stroock and S.R.S. Varadhan, *On the support of diffusion processes with applications to the strong maximum principle*, in Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability (Berkeley, 1970–1971), Vol. 3, University of California Press, Berkeley, (1972), pp. 333–359.
- [26] P.D. Taylor and L. Jonker, *Evolutionarily stable strategies and game dynamics*, Math. Biosci. 40 (1978), pp. 145–156.
- [27] E.C. Zeeman, *Population dynamics from game theory*, Z. Nitecki and C. Robinson, eds., *Global Theory of Dynamical Systems (Evanston, 1979)*, pages 472–497. Springer, Berlin, 1980.