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URN MODELS, REPLICATOR PROCESSES, AND RANDOM GENETIC DRIFT*

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Abstract. To understand the relative importance of natural selection and random genetic drift in finite but growing populations, the asymptotic behavior of a class of generalized Polya urns is studied using the method of ordinary differential equation (ODE). Of particular interest is the *replicator process*: two balls (individuals) are chosen from an urn (the population) at random with replacement and balls of the same colors (strategies) are added or removed according to probabilities that depend only on the colors of the chosen balls. Under the assumption that the expected number of balls being added always exceeds the expected number of balls being removed whenever balls are in the urn, the probability of nonextinction is shown to be positive. On the event of nonextinction, three results are proven: (i) the number of balls increases asymptotically at a linear rate, (ii) the distribution $x(n)$ of strategies at the nth update is a "noisy" Cauchy–Euler approximation to the mean limit ODE of the process, and (iii) the limit set of $x(n)$ is almost surely a connected internally chain recurrent set for the mean limit ODE. Under a stronger set of assumptions, it is shown that for any attractor of the mean limit ODE there is a positive probability that the limit set for $x(n)$ lies in this attractor. Theoretical and numerical estimates for the probabilities of nonextinction and convergence to an attractor suggest that random genetic drift is more likely to overcome natural selection in small populations for which pairwise interactions lead to highly variable outcomes, and is less likely to overcome natural selection in large populations with the potential for rapid growth.

Key words. Markov chains, random genetic drift, urn models, replicator equations

AMS subject classifications. 92D15, 60J10, 60F99

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1. Introduction.

A successful approach to the study of the Darwinian process of natural selection has been evolutionary game theory, whose starting point can be traced back to the seminal work of Maynard Smith [17, 18, 20]. Recent accounts about the progress in this field exist in books by Weibull [27] and Hofbauer and Sigmund [15]. Unlike noncooperative game theory in which [27] "a game is played exactly once by fully rational players who know all the details of the game... evolutionary game theory... imagines that the game is played over and over again by biologically or socially conditioned players who are *randomly drawn* from *large* populations. More specifically, each player is 'pre-programmed' to some behavior—formally a strategy of the game—and one assumes that some evolutionary selection process operates over time on the population distribution of behaviors." Under the assumptions of an infinite randomly mixing population with overlapping generations whose individuals engage in pairwise contests and reproduce asexually without mutations (i.e., "like begets like") one arrives at the replicator equations [15]

$$\frac{dx_i}{dt} = x_i \left(\sum_{j=1}^{k} A_{ij} x_j - \sum_{j,l=1}^{k} A_{jl} x_j x_l \right), \qquad i = 1, \ldots, k, \tag{1.1}$$

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where x_i is the proportion of the population playing the strategy i and A_{ij} is the *payoff* to an individual playing strategy i following an encounter with an individual playing strategy j. Under these assumptions, the terms $\sum_{j=1}^{k} A_{ij}x_j$ and $\sum_{j,l=1}^{k} A_{jl}x_jx_l$ represent the expected payoff to an individual playing strategy i and the expected payoff for the entire population, respectively.

While this modeling approach has lead to many important insights, the underlying assumption of an "infinite population" ignores the role of chance at the population level. In the words of Maynard Smith [19]:

> The basic problem is as follows. In an infinite population, if one can imagine such a thing, natural selection would always determine which of two types would be established and which eliminated. But real populations are finite, and for a finite population it is quite possible for the fitter of two types to be eliminated and the less fit to be established provided that fitness differences are small. Such random changes not produced by selection and sometimes contrary to selection are referred to as "genetic drift." There is no question that drift will occur, but deep disagreement about its importance.

Since the founding work of Fisher [12] and Wright [28], the effect of finite population sizes has been studied extensively when the population size is assumed to remain constant [10, 11, 16, 21]. These studies involve Markov chains on a finite state space whose states represent the distribution of strategies (or genotypes) in the population. If the individuals replicate asexually without mutations, then states of the Markov chain corresponding to all individuals playing the same strategy are absorbing. Consequently, all individuals in the population typically fixate on a common strategy after a finite number of updates of the process. For this reason, the analysis of these Markov chain models have focused on mathematically more delicate questions such as the expected time to fixation, the probability of fixating on a particular strategy, and approximations thereof.

In contrast to these studies, our interest lies in understanding the evolutionary behavior of finite populations with the potential for growth. With this objective in mind, we study in section 2 the asymptotic behavior of generalized Polya urns: a Markov chain whose state space is the nonnegative cone of the integer lattice and whose states represent the distribution and number of colored balls in an urn. The relevance of these models to evolutionary processes is readily apparent if we view a ball as an individual and its color as the individual's strategy. In the case when new balls are added to the urn at a constant rate, generalized Polya urns have been studied extensively [1, 3, 4, 6, 13, 22, 24]. However, since the number of progeny produced by an individual may vary and individuals may die, we study generalized Polya urns where balls may be removed as well as added at varying rates. For these generalized Polya urns we prove three results. First, on the event of nonextinction, the distribution $x(n)$ of colors (strategies) at update n can be viewed as a "noisy" Cauchy–Euler approximation to a "mean limit" ordinary differential equation (ODE) on the simplex (i.e., the space of all possible distributions of the strategies) where the step size of the approximation is inversely proportional to the population size. Second, on the event that the total number of balls grows asymptotically at a linear rate, the limit set for $x(n)$ is almost surely an invariant, compact, connected, internally chain recurrent set for the mean limit ODE. This linear growth assumption corresponds to exponential population growth with respect to the natural time scale of the process. Since the chain recurrent set is a well-studied set in dynamics [8], this result significantly narrows down the possibilities for the limiting behavior of the stochastic process. Third, under the stronger assumption that more balls are being added than removed at every update of the process, we provide a condition that ensures that the limit set of $x(n)$ is with positive probability contained in an attractor of the mean limit ODE.

In section 3, we formulate a generalized Polya urn that we call the replicator process. In this process two balls are selected at random with replacement and new balls are added or removed according to probabilities that depend only on the colors of the chosen balls. Biologically, the random selection of the balls corresponds to pairwise interactions between individuals, the addition of balls corresponds to replication of an individual, and the removal of balls to the death of individuals. The mean limit ODE for this process is a replicator equation (1.1). We show that if the population expects to exhibit growth whenever individuals are present, then with positive probability the population grows at an exponential rate with respect to the natural time scale of the process. Hence, the first result of section 2 implies that on the event of nonextinction the limit set of the distribution $x(n)$ of strategies is almost surely a connected internally chain recurrent set for the mean limit ODE. Under the stronger assumptions that the population is constantly growing and any strategy present in the population replicates with positive probability, the second result of section 2 is shown to imply that the limit set of $x(n)$ is contained with positive probability in any attractor of the mean limit ODE. We illustrate the results with a stochastic analog of the evolutionary game of rock-scissors-paper [18, 26].

We conclude in section 4 by discussing the relevance of our results to the roles of random genetic drift and natural selection in the evolutionary process.

2. Generalized Polya urns. In this section we develop tools to analyze a class of generalized Polya urns. We follow the approach of Benaïm and Hirsch [2, 3, 4, 6] for studying processes of this type. These models involve an urn that contains balls of up to k different colors. At discrete time intervals, anywhere between 0 to m balls are added or removed according to probabilities that depend only on the number of balls and their distribution at that point in time.

Let $\mathbb{Z}^k$ denote the space of k-tuples of integers. Given a vector $w \in \mathbb{R}^k$ define

$$|w| = |w_1| + \cdots + |w_k| \text{ and } \alpha(w) = w_1 + \cdots + w_k.$$

To avoid confusing the L^1 norm $|\cdot|$ with the Euclidean norm, we shall always write $\|\cdot\|$ for the Euclidean norm on $\mathbb{R}^k$. Let $\mathbb{Z}^k_+$ denote the space of k-tuples of nonnegative integers and $\mathbb{R}^k_+ = \{x \in \mathbb{R}^k : x_1 \geq 0, \ldots, x_k \geq 0\}$ denote the nonnegative cone of $\mathbb{R}^k$. Let $\Delta^{k-1} \subset \mathbb{R}^k$ denote the $k-1$ simplex, i.e.,

$$\Delta^{k-1} = \left\{ x \in \mathbb{R}^k_+ : \sum x_i = 1 \right\}.$$

We say a Markov process $z(n) = (z_1(n), \ldots, z_k(n)) \in \mathbb{Z}^k_+$, where $z_i(n)$ is the number of balls of color i, at time step n is a *generalized Polya urn* provided that

(A1) There exists a positive integer m such that $|z(n+1) - z(n)| \leq m$ for all n.

(A2) There exists a map $F : \mathbb{Z}_+ \times \Delta^{k-1} \to \mathbb{R}^k$ such that

$$F(|z(n)|, z(n)/|z(n)|) = E[z(n+1) - z(n)|z(n)]$$

whenever $z(n) \neq 0$.

(A3) There exists a Lipschitz map $f : \Delta^{k-1} \to \mathbb{R}^k$ such that $F(N, \cdot)$ converges uniformly to $f(\cdot)$ as $N \to \infty$.

To study the long-term behavior of these generalized Polya urns $z(n)$, it is useful to relate its dynamics to an appropriately chosen ODE. To this end, we define

$$x(n) = \begin{cases} \frac{z(n)}{|z(n)|} & \text{if } z(n) \neq 0, \\ 0 & \text{if } z(n) = 0, \end{cases} \tag{2.1}$$

and prove the following lemma which expresses $x(n)$ as a stochastic algorithm.

LEMMA 2.1. *Let $z(n)$ be a generalized Polya urn and $\mathcal{F}_n$ be the σ-algebra generated by $z(1), \ldots, z(n)$. Define $G : \mathbb{Z}_+ \times \Delta^{k-1} \to \mathbb{R}^k$ and $g : \Delta^{k-1} \to \mathbb{R}^k$ by*

$$G(N, x) = F(N, x) - x\alpha(F(N, x)), \qquad g(x) = f(x) - x\alpha(f(x)). \tag{2.2}$$

Then for all $z(n) \neq 0$,

$$x(n+1) - x(n) = \frac{1}{|z(n)|} \left(g(x(n)) + U(n+1) + b(n+1) \right), \tag{2.3}$$

where $U(n)$ and $b(n)$ are random variables adapted to $\mathcal{F}_n$ satisfying

(i) $E[U(n+1)|z(n)] = E[U(n+1)|\mathcal{F}_n] = 0$,

(ii) $\|U(n)\| \leq 4m(m+1)$, *and*

(iii) $\|b(n+1)\| \leq \frac{2m^2}{|z(n)|} + \|G(|z(n)|, x(n)) - g(x(n))\|$ *whenever* $|z(n)| > m$.

Proof. Define the random variables

$$\begin{aligned} U(n+1) &= (x(n+1) - x(n) - E[x(n+1) - x(n)|z(n)])|z(n)|, \\ b(n+1) &= |z(n)|E[x(n+1) - x(n)|z(n)] - g(x(n)). \end{aligned}$$

From these definitions and the fact that $z(n)$ is a Markov chain, it follows that U_n and b_n are adapted to $\mathcal{F}_n$, $E[U(n+1)|z(n)] = E[U(n+1)|\mathcal{F}_n] = 0$, and (2.3) is valid whenever $z(n) \neq 0$.

For the remainder of the proof, we write $z = z(n)$ and $x = x(n)$. To prove (ii), notice that if $z(n+1) \neq 0$, then

$$\begin{aligned} \|(x(n+1) - x)|z|\| &= \left\| \frac{z(n+1)|z| - z|z(n+1)|}{|z(n+1)|} \right\| \\ &\leq \left\| \frac{z(n+1)|z| - z|z|}{|z(n+1)|} \right\| + \left\| \frac{z|z| - z|z(n+1)|}{|z(n+1)|} \right\| \\ &\leq m \left(\frac{|z|}{|z(n+1)|} + \frac{\|z\|}{|z(n+1)|} \right) \\ &\leq 2m(m+1), \end{aligned} \tag{2.4}$$

where the last two lines follow from the fact that no more than m balls are being added or removed at any update. Alternatively if $z(n+1) = 0$, then it must be that $|z(n)| \leq m$ since no more than m balls can be removed at a single update. In which case, $x(n+1) = 0$ and $\|(x(n+1) - x(n))|z(n)|\| = \|z(n)\| \leq m$. Thus, we get that $\|U(n+1)\| \leq 4m(m+1)$.

To prove (iii), notice that if $z \neq 0$ and $z(n+1) - z = w$, then $|z(n+1)| = |z| + \alpha(w)$. Consequently,

$$(x(n+1) - x)|z| = \begin{cases} \frac{|z|(w - \alpha(w)x)}{|z| + \alpha(w)} & \text{if } w \neq -z, \\ -z & \text{if } w = -z. \end{cases}$$

Therefore, for $z \neq 0$

$$\begin{aligned}|z|E[x(n+1)-x|z(n)=z] = &\sum_{w\neq -z} \frac{|z|(w-\alpha(w)x)}{|z|+\alpha(w)} P[z(n+1)-z=w|z(n)=z]\\ &-zP[z(n+1)=0|z(n)=z].\end{aligned} \tag{2.5}$$

Notice that $P[z(n+1)=0|z(n)=z]>0$ only when $|z|\leq m$. Assume that $|z|>m$. Under this assumption, (2.2) and (2.5) and assumption (A2) imply

$$\begin{aligned}\|b(n+1)\| &= \left\|\sum_w \frac{|z|}{|z|+\alpha(w)} P[z(n+1)-z=w|z(n)=z](w-\alpha(w)x)-g(x)\right\|\\
&\leq \left\|\sum_w \frac{|z|}{|z|+\alpha(w)} P[z(n+1)-z=w|z(n)=z](w-\alpha(w)x)-G(|z|,x)\right\|\\
&\quad +\|G(|z|,x)-g(x)\|\\
&= \left\|\sum_w \left(\frac{|z|}{|z|+\alpha(w)}-1\right) P[z(n+1)-z=w|z(n)=z](w-\alpha(w)x)\right\|\\
&\quad +\|G(|z|,x)-g(x)\|\\
&\leq \frac{m}{|z|}\|E[z(n+1)-z-\alpha(z(n+1)-z)x|z(n)=z]\| + \|G(|z|,x)-g(x)\|\\
&\leq \frac{2m^2}{|z|} + \|G(|z|,x)-g(x)\|,\end{aligned}$$

where the third line follows from the definition of G and the linearity of $\alpha(\cdot)$. $\square$

Equation (2.3) can be considered to be a "noisy" Cauchy–Euler approximation scheme for the *mean limit ODE*

$$\frac{dx}{dt} = f(x) - x\alpha(f(x)). \tag{2.6}$$

In particular, whenever $z(n)\neq 0$ we can view $\frac{1}{|z(n)|}$ as the step size of the Cauchy–Euler approximation, $U(n+1)$ as an unbiased noise, and $b(n+1)$ as an additional (possibly biased) noise that goes to zero. On the event $\{\lim_{n\to\infty}|z(n)|=\infty\}$, the step size of the approximation is decreasing and it is natural to compare the sample paths of $x(n)=\frac{z(n)}{|z(n)|}$ with the flow of (2.6). To this end, we rescale time. Let $\tau(0)=0$ and for $n\geq 0$ define

$$\tau(n+1) = \begin{cases} \tau(n)+\frac{1}{|z(n)|} & \text{if } z(n)\neq 0,\\ \tau(n)+1 & \text{if } z(n)=0.\end{cases}$$

We view $\tau(n)$ as representing the amount of time that has elapsed when the generalized Polya urn has been updated n times. This rescaling gives the natural time scale of the process as in a population of $|z(n)|$ individuals, we expect the number of interactions occurring in an interval of time to be proportional to $|z(n)|$. Notice that assumption (A1) implies that $\tau(n)\geq \sum_{i=0}^{n-1}\frac{1}{|z(0)|+m\,i}$. Therefore, $\lim_{n\to\infty}\tau(n)=\infty$.

Using this new time scale, we define a continuous-time version of $x(n)$, namely, the *piecewise constant interpolation* $X:\mathbb{R}_+\to\Delta^{k-1}$ defined by

$$X(t) = x(n), \qquad t\in[\tau(n),\tau(n+1)). \tag{2.7}$$

$X(t)$ is the urn distribution at time t and is constant between updates of the urn.

Prior to stating the main result of this section, we recall a few definitions from dynamical systems theory. Let $\phi : \mathbb{R} \times \Delta^{k-1} \to \Delta^{k-1}$ denote the flow of (2.6). Let $\phi_t(x) = \phi(t, x)$. A set $K \subseteq \mathbb{R}^k$ is said to be *invariant* if for all $t \in \mathbb{R}$, $\phi_t(K) = K$. A point $x \in \mathbb{R}^k$ is said to be *chain-recurrent* provided that for all $T > 0$ and $\epsilon > 0$ there exists points $y(1), \dots, y(n)$ and times $t_1, \dots, t_{n-1}$ greater than T such that $y(1) = y(n) = x$ and $\|y(i+1) - \phi(t_i, y(i))\| < \epsilon$ for all $1 \le i \le n-1$. A subset K is said to be *internally chain-recurrent* if K is a nonempty compact invariant set of which every point is chain-recurrent for the restricted flow $\phi|K$. The chain recurrent set was introduced by Conley [8] and is an extremely well-behaved set as it does not "explode" under small perturbations of the differential equation. Given a sequence $\{w(n)\}_{n\ge 0}$ in $\mathbb{R}^k$, the *limit set* $L(\{w(n)\}_{n\ge 0})$ of the sequence is the set of $x \in \mathbb{R}^k$ such that $\lim_{i\to\infty} w(n_i) = x$ for some sequence $n_i \uparrow \infty$. Similarly, given a function $W : \mathbb{R}_+ \to \mathbb{R}^k$, the *limit set* $L(W)$ of W is the set of points $x \in \mathbb{R}^k$ such that $\lim_{n\to\infty} W(t_n)$ for some sequence $t_n \uparrow \infty$.

THEOREM 2.2. *Let $z(n)$ be a generalized Polya urn. Let ϕ be the flow of the mean limit ODE, $x(n)$ be the distribution of balls at update n as defined in* (2.1), *and $X(t)$ be the piecewise constant interpolation defined by* (2.7). *On the event* $\{\liminf_{n\to\infty} \frac{z(n)}{n} > 0\}$,

1. $X(t)$ *is almost surely an* asymptotic pseudotrajectory *for ϕ: in other words, for any $T > 0$*

$$\lim_{t\to\infty} \sup_{0\le h\le T} \|X(t+h) - \phi_h(X(t))\| = 0;$$

2. $L(X) = L(\{x(n)\}_{n\ge 0})$ *is almost surely a connected compact internally chain recurrent set for ϕ.*

Remark. The assertions of Theorem 2.2 hold more generally on the event

$$\left\{ \liminf_{n\to\infty} \frac{|z(n)|}{n^\alpha} > 0 \text{ for some } \alpha > 1/2 \right\}.$$

However, since for the generalized Polya urns of interest the event of nonextinction and the event of linear growth are almost surely the same (see, e.g., Theorem 3.1), we restrict ourselves to linear growth.

The assumption of linear growth with respect to updates in Theorem 2.2 implies exponential growth with respect to the natural time scale as $\liminf_{n\to\infty} \frac{|z(n)|}{n} = \alpha$ implies $\liminf_{n\to\infty} \frac{\log(|z(n)|)}{\tau(n)} = \alpha$. The first assertion of Theorem 2.2 can be thought of as follows: On finite time intervals far into the future the interpolated process $X(t)$ tracks the flow ϕ_t with arbitrarily small error. The notion of an asymptotic pseudotrajectory was introduced by Benaïm and Hirsch [6] and studied in the context of stochastic algorithms by Benaïm [2].

Prior to proving Theorem 2.2, we discuss one of its corollaries. Further corollaries follow in the spirit of Benaïm and Hirsch [3, 6]. Using Theorem 2.2 it is possible to give a complete description of the candidate limit sets for $x(n)$ when $z(n)$ is an urn process involving balls of two or three colors. To this end, recall that for a flow ϕ_t on Δ^{k-1}, the *α-limit set* of a point $x \in \Delta^{k-1}$ equals the set of points $y \in \Delta^{k-1}$ such that $\phi_{t_k} x \to y$ for some sequence of times $t_k \to -\infty$. The *ω-limit set* of a point $x \in \Delta^{k-1}$ equals the set of points $y \in \Delta^{k-1}$ such that $\phi_{t_k} x \to y$ for some sequence of times

$t_k \to \infty$. A *cycle of equilibria* for ϕ is a union

$$\bigcup_{j=1}^{n} (\{e_j\} \cup \gamma_j)$$

consisting of equilibria e_j and connecting orbits γ_j such that the α-limit set of $\gamma_j = e_{j-1}$ and the ω-limit set of $\gamma_j = e_j$ for all $j = 1, \dots, n$ with the convention that $e_0 = e_n$. An equilibrium x for ϕ is called *isolated* if there is an open neighborhood of x that contains no other equilibria. Benaïm and Hirsch [5] proved the following characterization of compact connected internally chain recurrent sets for planar flows.

THEOREM 2.3 (see [5]). *Let ϕ be a flow on a open subset U of $\mathbb{R}^2$ with isolated equilibria and $L \subseteq U$ be a connected compact internally chain-recurrent set for ϕ. Then L is a connected union of equilibria, periodic orbits, and cycles of equilibria.*

Combining Theorems 2.2 and 2.3, we get the following corollary.

COROLLARY 2.4. *Suppose $z(n)$ is a generalized Polya urn with $k = 3$. Assume that the equilibria of the mean limit ODE are isolated. Then on the event $\{\lim_{n\to\infty} |z(n)|/n > 0\}$, the limit set of $x(n) = z(n)/|z(n)|$ almost surely is a connected union of equilibria, periodic orbits, and cycles of equilibria of the mean limit ODE.*

Proof of Theorem 2.2. We need to invoke Theorem 1.2 and Lemma 4.2 of [2] about *deterministic* difference equations. We restate these results as follows.

THEOREM 2.5 (see [2]). *Let $g : \mathbb{R}^k \to \mathbb{R}^k$ be a Lipschitz vector field and let $\{x(n)\}_{n\geq 0}$ be a solution to the recursion*

$$x(n+1) - x(n) = \gamma(n+1)\left(g(x(n)) + U(n+1) + b(n+1)\right),$$

where $\gamma(n)$, $U(n)$, and $b(n)$ are sequences such that

(i) $\lim_{n\to\infty} \gamma(n) = 0$ *and* $\sum_{n\geq 0} \gamma(n) = \infty$,
(ii) $\lim_{n\to\infty} b(n) = 0$,
(iii) $\{x(n)\}_{n\geq 0}$ *is bounded, and*
(iv) *for all* $T > 0$,

$$\lim_{n\to\infty} \sup \left\{ \left\| \sum_{i=n}^{l-1} \gamma(i) U(i) \right\| : 0 \leq \tau(l) - \tau(n) \leq T \right\} = 0,$$

where $\tau(n) = \gamma(1) + \cdots + \gamma(n)$.

Then

(a) $L(\{x(n)\}_{n\geq 0})$ *is a connected, compact, internally chain-recurrent set for the flow generated by* $\dot{x} = g(x)$;
(b) *the interpolated process* $\bar{X}$ *defined by*

$$\bar{X}(t) = x(n) + \frac{t - \tau(n)}{\gamma(n+1)}(x(n+1) - x(n)), \qquad t \in [\tau(n), \tau(n+1)),$$

is an asymptotic pseudotrajectory for the flow ϕ_t generated by $\dot{x} = g(x)$, i.e., for all $T > 0$

$$\lim_{t\to\infty} \sup_{0\leq h\leq T} \|\bar{X}(t+h) - \phi_h(\bar{X}(t))\| = 0. \tag{2.8}$$

To employ Theorem 2.5, we set

$$g(x) = f(x) - x\alpha(f(x))$$

and

$$\gamma(n+1) = \begin{cases} \frac{1}{|z(n)|} & \text{if } z(n) \neq 0, \\ 1 & \text{if } z(n) = 0. \end{cases}$$

Let $U(n)$ and $b(n)$ as defined in Lemma 2.1. We need to verify that these three sequences of random variables satisfy assumptions (i)–(iv) of Theorem 2.5 almost surely on the event $\mathcal{G} = \{\liminf_{n\to\infty} \frac{|z(n)|}{n} > 0\}$. Assumption (A1) implies that assumption (i) of Theorem 2.5 holds on the event $\mathcal{G}$. Assumption (A3) and assertion (iii) of Lemma 2.1 imply that assumption (ii) of Theorem 2.5 holds on the event $\mathcal{G}$. Assumption (iii) of Theorem 2.5 follows from the fact that $x(n)$ either equals 0 or lies in Δ^{k-1}. To verify assumption (iv) of Theorem 2.5, we define

$$M(n) = \sum_{i=1}^{n} \gamma(i)U(i)$$

and $\mathcal{F}_n$ to be the σ-algebra generated by $z(1), \ldots, z(n)$. To prove that assumption (iv) of Theorem 2.5 holds almost surely on the event $\mathcal{G}$, it suffices to show that $M(n)$ converges almost surely on the event $\mathcal{G}$. Since $E[U(n+1)|\mathcal{F}_n] = 0$ and $\gamma(n+1) \in \mathcal{F}_n$, $M(n)$ is a martingale. Given $l \in \mathbb{Z}_+$, define the stopping time

$$T_l = \inf\left\{ n : \sum_{i=1}^{n} \gamma(i)^2 > l \right\}.$$

By orthogonality of the increments of $M(n \wedge T_l)$,

$$\begin{aligned} E[M(n\wedge T_l)^2] &= E\left[\sum_{i=1}^{n\wedge T_l} \gamma(i)^2 U(i)^2\right] \\ &\leq 16m^2(m+1)^2 E\left[\sum_{i=1}^{n\wedge T_l} \gamma(i)^2\right] \leq 16m^2(m+1)^2(l+1), \end{aligned}$$

where the second line follows from assertion (ii) of Lemma 2.1 and the definition of T_l. Therefore by Doob's L^2 convergence theorem, $M(n \wedge T_l)$ converges almost surely to a limit X_l. Since $M(n \wedge T_l) = M(n)$ on the event $\mathcal{G}_l = \{\sum_{i=1}^{n} \gamma(i)^2 \leq l \text{ for all } n\}$ and $\mathcal{G} \subseteq \bigcup_{l=1}^{\infty} \mathcal{G}_l$, $M(n)$ converges almost surely on the event $\mathcal{G}$.

To finish the proof of the theorem, we translate Theorem 2.5's statement about the piecewise affine process $\bar{X}(t)$ to a statement about the piecewise constant process $X(t)$. To this end, given $t \geq 0$ define $c = c(t) = \sup\{n : t \geq \tau(n)\}$. Notice that $X(t) = x(c) = \bar{X}(\tau(c))$. If $z(c+1) \neq 0$, then (2.4) implies that

$$\begin{aligned} \|X(t) - \bar{X}(t)\| &= \|(t-\tau(c))|z(c)|(x(c+1) - x(c))\| \\ &\leq (t-\tau(c))2m(m+1) \\ &\leq \frac{2m(m+1)}{|z(c)|}. \end{aligned} \tag{2.9}$$

Since for any $h > 0$

$$\|X(t+h) - \phi_h(X(t))\| \leq \|X(t+h) - \bar{X}(t+h)\| + \|\bar{X}(t+h) - \phi_h(\bar{X}(t))\| + \|\phi_h(\bar{X}(t)) - \phi_h(X(t))\|$$

(2.9) implies that on the event $\mathcal{G}$, $X(t)$ is an asymptotic pseudotrajectory whenever $\bar{X}(t)$ is an asymptotic pseudotrajectory. ∎

A question arising from Theorem 2.2 is, To what internally chain-recurrent sets of the mean limit flow ϕ does $x(n)$ converge with positive probability? A natural candidate is an attractor for the mean limit flow. For a compact set $K \subset \mathbb{R}^{k-1}$ and point in $x \in \mathbb{R}^{k-1}$ define $\operatorname{dist}(x, K) = \min_{y \in K} \|x - y\|$. Recall that a compact invariant set $\mathcal{A} \subseteq \Delta^{k-1}$ is called an *attractor* for ϕ if there exists an open neighborhood U of $\mathcal{A}$ such that $\operatorname{dist}(\phi_t x, \mathcal{A}) \to 0$ as $t \to \infty$ uniformly in $x \in U$. The basin of attraction $B(\mathcal{A})$ of $\mathcal{A}$ is the positively invariant open set consisting of all points x such that $\operatorname{dist}(\phi_t x, \mathcal{A}) \to 0$ as $t \to \infty$. Benaïm [3, sect. 7] provides a useful approach to this question via the notion of *attainability*. If $z(n)$ is a generalized Polya urn and $X(t)$ is the piecewise constant process defined by (2.7), then a point $x \in \Delta^{k-1}$ is called *attainable* if $P[\exists s \geq t : X(s) \in U] > 0$ for each $t \in \mathbb{R}_+$ and every open neighborhood U of x. Let $\operatorname{Att}(X)$ denote the set of attainable points.

THEOREM 2.6. *Let $z(n)$ be a generalized Polya urn and $X(t)$ be the piecewise constant process defined by* (2.7). *Assume that there exist $a, \beta > 0$ such that $P[|z(n)| \geq a\,n$ for all $n \geq 0] = 1$ and*

$$\|F(N,x) - x\alpha(F(N,x)) - f(x) + x\alpha(f(x))\| \leq \frac{\beta}{N} \tag{2.10}$$

for all $N \geq 1$. Let $\mathcal{A}$ be an attractor for the mean limit ODE with basin of attraction $B(\mathcal{A})$. If $U \subseteq \Delta^{k-1}$ is an open set such that $\overline{U} \subset B(\mathcal{A})$, then there exists a $K > 0$ such that for all $z(0) \neq 0$ and $t \in \mathbb{R}_+$

$$P[L(X) \subseteq \mathcal{A}] \geq \left(1 - \frac{K}{|z(0)| \exp(a\,t)}\right) P[\exists s \geq t \text{ such that } X(s) \in U].$$

In particular, if $B(\mathcal{A}) \cap \operatorname{Att}(X) \neq \emptyset$, then $P[L(X) \subseteq \mathcal{A}] > 0$.

Proof. Let $z(n)$ be an urn process satisfying (A1)–(A3). Assume there is an $a > 0$ such that $|z(n)| \geq a\,n$ almost surely and $\beta > 0$ such that (2.10) holds. Let $x(n) = z(n)/|z(n)|$ and $X(t)$ be the process defined by (2.7). Define $c(t) = \sup\{n \in \mathbb{Z}_+ : t \geq \tau(n)\}$ and $\mathcal{F}_t$ as the σ-algebra generated by $z(1), \dots, z(c(t))$.

The next lemma is a straightforward adaptation of a theorem due to Benaïm [3, Thm. 7.3] but for the reader's convenience we supply a proof.

LEMMA 2.7 (adapted from [3]). *Assume there exists $w : \mathbb{R}_+^3 \to \mathbb{R}_+$ such that*

$$P\left[\sup_{n \geq 1} \|X(t+nT) - \phi_T X(t+(n-1)T)\| \geq \delta | \mathcal{F}_t\right] \leq w(t,T,\delta)$$

and for all $T > 0$ and $\delta > 0$, $w(t,T,\delta) \downarrow 0$ as $t \uparrow \infty$. If $U \subseteq \Delta^{k-1}$ is an open set such that $\overline{U} \subset B(\mathcal{A})$, then there exists $T > 0$ and $\delta > 0$ (depending on U) such that for all $t \in \mathbb{R}_+$

$$P[L(X) \subseteq \mathcal{A}] \geq (1 - w(t,T,\delta))\, P[\exists s \geq t \text{ such that } X(s) \in U].$$

Proof of Lemma 2.7. Pick $\delta > 0$ such that $N(\mathcal{A}, 2\delta) = \{x \in \Delta^{k-1} : \operatorname{dist}(x, \mathcal{A}) \leq 2\delta\}$ is contained in $B(\mathcal{A})$. Since $\mathcal{A}$ is an attractor and $W = N(A, 2\delta) \cup \overline{U}$ is contained in its basin, there is a $T > 0$ such that $\phi_T(W) \subset N(\mathcal{A}, \delta)$. Suppose that $X(t)$ is a sample path such that $L(\{X(t)\}_{t\geq 0})$ is an internally chain recurrent set for ϕ, $X(s) \in U$ for some $s \in \mathbb{R}_+$, and

$$\sup_{n\geq 1} \|X(s+nT) - \phi_T X(s+(n-1)T)\| \leq \delta. \tag{2.11}$$

We will show for this sample path that $L(\{X(t)\}_{t\geq 0}) \subseteq \mathcal{A}$. Since $X(s) \in U$, our choice of T implies that $\phi_T X(s) \in N(\mathcal{A}, \delta)$. Equation (2.11) implies that $X(s+T) \in N(\mathcal{A}, 2\delta)$. Proceeding inductively, we get that $X(s+nT) \in N(\mathcal{A}, 2\delta)$ for all $n \geq 1$. Hence, for this sample path, $L(\{X(t)\}_{t\geq 0}) \cap B(\mathcal{A}) \neq \emptyset$. Since $L(\{X(t)\}_{t\geq 0})$ is an internally chain recurrent set for ϕ, a standard result about chain recurrence (see, e.g., [3, Cor. 5.4]) implies that $L(\{X(t)\}_{t\geq 0}) \subseteq \mathcal{A}$.

Given $t_0 \in \mathbb{R}_+$, define $S = \inf\{s \geq t_0 : X(s) \in U\}$. Since Theorem 2.2 implies that $L(\{X(t)\}_{t\geq 0})$ is almost surely an internally chain recurrent set for ϕ, we have just shown that the following inclusion of events holds:

$$\{S < +\infty\} \cap \left\{\sup_{n\geq 1} \|X(S+nT) - \phi_T X(S+(n-1)T)\| \leq \delta\right\} \subseteq \{L(X) \subseteq \mathcal{A}\}.$$

Since $\{S < +\infty\} = \{S = t_0\} \cup (\bigcup_{i>c(t_0)} \{S = \tau(i)\})$, it follows that

$$\begin{aligned} P[L(X) \subseteq \mathcal{A}] \geq E&\left[P\left[\sup_{n\geq 1} \|X(t_0+nT) - \phi_T X(t_0+(n-1)T)\| \leq \delta | \mathcal{F}_{t_0}\right] 1_{\{S=t_0\}}\right] \\ &+ \sum_{i>c(t_0)} E\left[P\left[\sup_{n\geq 1} \|X(\tau(i)+nT) - \phi_T X(\tau(i)+(n-1)T)\| \right.\right. \\ &\qquad\qquad \left.\left. \leq \delta | \mathcal{F}_{\tau(i)}\right] 1_{\{S=\tau(i)\}}\right] \\ &\geq (1 - w(t_0, T, \delta)) P[\exists s \geq t_0 \text{ such that } X(s) \in U]. \qquad \square \end{aligned}$$

To prove Theorem 2.6 we need to find a function $w(t, T, \delta)$ that satisfies the hypotheses of Lemma 2.7. To this end, let $g(x) = f(x) - \alpha(f(x))x$, where $f(x)$ is given by (A3), $L > 0$ be the Lipschitz constant for g, $\|g\|_0 = \sup_{x\in\Delta^{k-1}} \|g(x)\|$, ϕ_t denote the flow of g, and $U(n+1)$ and $b(n+1)$ be as in Lemma 2.1. We begin by proving the following inequality for any $t > 0$ and $T > 0$:

$$\|\phi_T(X(t)) - X(t+T)\| \leq e^{LT} \left(\Gamma_1(t,T) + \Gamma_2(t,T) + \Gamma_3(t,T)\right), \tag{2.12}$$

where

$$\Gamma_1(t,T) = \sup_{c(t)\leq l\leq c(t+T)} \frac{2\|g\|_0}{|z(l)|},$$

$$\Gamma_2(t,T) = \sup_{c(t)\leq l\leq c(t+T)-1} \left\| \sum_{i=c(t)}^{l} \frac{b(i+1)}{|z(i)|} \right\|,$$

and

$$\Gamma_3(t,T) = \sup_{c(t)\le l\le c(t+T)-1} \left\| \sum_{i=c(t)}^{l} \frac{U(i+1)}{|z(i)|} \right\|.$$

To prove (2.12), notice that for any $h \ge 0$

$$\begin{aligned} X(t+h) - X(t) = x(c(t+h)) - x(c(t)) &= \sum_{i=c(t)}^{c(t+h)-1} x(i+1) - x(i) \\ &= \sum_{i=c(t)}^{c(t+h)-1} \frac{g(x(i)) + U(i+1) + b(i+1)}{|z(i)|} \\ &= \int_{\tau(c(t))}^{\tau(c(t+h))} g(X(s))\,ds + \sum_{i=c(t)}^{c(t+h)-1} \frac{U(i+1)+b(i+1)}{|z(i)|} \\ &= \int_{\tau(c(t))-t}^{\tau(c(t+h))-t} g(X(t+s))\,ds + \sum_{i=c(t)}^{c(t+h)-1} \frac{U(i+1)+b(i+1)}{|z(i)|}. \end{aligned}$$

Since $\phi_h X(t) = X(t) + \int_0^h g(\phi_s X(t))\,ds$, the previous equalities imply that

$$\begin{aligned} \|\phi_h(X(t)) - X(t+h)\| &\le \int_0^h \|g(\phi_s(X(t)) - g(X(t+s))\| ds \\ &\quad + \int_{\tau(c(t))-t}^{0} \|g(X(t+s))\| ds \\ &\quad + \int_{\tau(c(t+h))-t}^{h} \|g(X(t+s))\| ds \\ &\quad + \left\| \sum_{i=c(t)}^{c(t+h)-1} \frac{U(i+1)+b(i+1)}{|z(i)|} \right\| \\ &\le L\int_0^h \|\phi_s(X(t)) - X(t+s)\| ds + \frac{\|g\|_0}{|z(c(t))|} \\ &\quad + \frac{\|g\|_0}{|z(c(t+h))|} + \left\| \sum_{i=c(t)}^{c(t+h)-1} \frac{U(i+1)+b(i+1)}{|z(i)|} \right\|. \end{aligned}$$

Applying Gronwall's inequality (see, e.g., [23]) to the previous inequality over the interval $0 \le h \le T$ gives us (2.12).

Next, we find upper bounds on $\Gamma_1(t,T)$, $\Gamma_2(t,T)$, and $P[\sup_{n\ge 0} \Gamma_3(t+nT,T) \ge \delta|\mathcal{F}_t]$. Our assumption that $|z(n)| \ge a\,n$ and the definition of $c(t)$ imply that

$$t \le \sum_{n=0}^{c(t)} \frac{1}{|z(0)| + a\,n} \le \frac{1}{|z(0)|} + \int_0^{c(t)} \frac{dx}{|z(0)| + a\,x}.$$

Consequently,

$$|z(0)| + a\,c(t) \ge |z(0)| \exp(a(t-1)). \tag{2.13}$$

The definition of $\Gamma_1(t,T)$ and (2.13) imply that

$$\Gamma_1(t,T) \leq \frac{2\|g\|_0}{|z(0)| + a\,c(t)} \leq \frac{2\|g\|_0}{|z(0)|\exp(a(t-1))}. \tag{2.14}$$

Assertion (iii) of Lemma 2.1, (2.10), and (2.13) imply that for $|z(0)| + a\,c(t) \geq m$,

$$\begin{aligned}\Gamma_2(t,T) &\leq \sum_{i=c(t)}^{\infty} \frac{|b(i+1)|}{|z(i)|} \leq \sum_{i=c(t)}^{\infty} \frac{2m^2+\beta}{(|z(0)|+a\,i)^2}\\ &\leq \int_{c(t)-1}^{\infty} \frac{2m^2+\beta}{(|z(0)|+a\,x)^2}dx \leq \frac{4m^2+2\beta}{a|z(0)|\exp(a(t-1))}.\end{aligned} \tag{2.15}$$

The definition of Γ_3, Doob's inequality, assertion (ii) of Lemma 2.1, and (2.13) imply that for any $\delta > 0$, $t \geq 0$, and $T > 0$

$$\begin{aligned}P\left[\sup_{n\geq 0}\Gamma_3(t+nT,T) \geq \delta|\mathcal{F}_t\right] &\leq \sum_{n\geq 0} P[\Gamma_3(t+nT,T)\geq \delta|\mathcal{F}_t]\\ &\leq \frac{16m^2(m+1)^2}{\delta^2}\sum_{i=c(t)}^{\infty}\frac{1}{|z(i)|^2}\\ &\leq \frac{16m^2(m+1)^2}{\delta^2}\int_{c(t)-1}^{\infty}\frac{dx}{(|z(0)|+a\,x)^2}\\ &\leq \frac{32m^2(m+1)^2}{a\delta^2|z(0)|\exp(a(t-1))}.\end{aligned} \tag{2.16}$$

Equations (2.14)–(2.16) imply that for any $T > 0$, and $\delta > 0$, there exists a $K_0(\delta,T) > 0$ such that for all $t \geq 0$ and $z(0) \neq 0$,

$$\sup_{n\geq 0} e^{LT}(\Gamma_1(t+nT,T) + \Gamma_2(t+nT,T)) \leq \frac{K_0(\delta,T)}{|z(0)|\exp(a\,t)} \tag{2.17}$$

and

$$P\left[\sup_{n\geq 0} e^{LT}\Gamma_3(t+nT,T) \geq \delta/3|\mathcal{F}_t\right] \leq \frac{K_0(\delta,T)}{|z(0)|\exp(a\,t)}. \tag{2.18}$$

These upper bounds and (2.12) imply that if $|z(0)|\exp(a\,t) \geq 3K_0(\delta,T)/\delta$, then

$$\begin{aligned}P\left[\sup_{n\geq 1}\|X(t+nT) - \phi_T X(t+(n-1)T)\| \geq \delta|\mathcal{F}_t\right] &\leq P\left[\sup_{n\geq 0} e^{LT}\Gamma_3(t+nT,T) \geq \delta/3|\mathcal{F}_t\right]\\ &\leq \frac{K_0(\delta,T)}{|z(0)|\exp(a\,t)}.\end{aligned}$$

Define $K(\delta,T) = \max\{K_0(\delta,T), 3K_0(\delta,T)/\delta\}$. Since $\frac{K(\delta,T)}{|z(0)|\exp(a\,t)} \geq 1$ whenever $|z(0)|\exp(a\,t) \leq 3K_0(\delta,T)/\delta$, we get that

$$P\left[\sup_{n\geq 1}\|X(t+nT) - \phi_T X(t+(n-1)T)\| \geq \delta|\mathcal{F}_t\right] \leq \frac{K(\delta,T)}{|z(0)|\exp(a\,t)}$$

for all $t \in \mathbb{R}_+$. Setting $w(t,T,\delta) = \frac{K(\delta,T)}{|z(0)|\exp(a\,t)}$ and applying Lemma 2.7 completes the proof of the first assertion of Theorem 2.6. To prove the second assertion, it suffices to pick an attainable point $p \in B(\mathcal{A})$, pick an open neighborhood U of p such that $\overline{U} \subset B(\mathcal{A})$, and apply the first assertion of the theorem. $\square$

3. Replicator processes. We consider a system consisting of a finite population of individuals playing k different strategies. At each update of the population, pairs of individuals are chosen randomly with replacement from the population. These chosen individuals replicate and die according to probabilities that depend only on the strategies of the chosen individuals. More precisely, let m be a nonnegative integer that represents the maximum number of progeny that any individual can produce in one update. Let $\{R(n)\}_{n\geq 0}$ and $\{\tilde{R}(n)\}_{n\geq 0}$ be sequences of independent identically distributed random $k\times k$ matrices whose entries take values in the set $\{-1,0,1,\dots,m\}$. Let $\{r(n)\}_{n\geq 0}$ be a sequence of independent identically distributed random $k\times 1$ matrices whose entries take values in the set $\{-1,0,1,\dots,m\}$. Define a *replicator process* with respect to $R(n)$, $\tilde{R}(n)$, and $r(n)$ to be a Markov chain $z(n)\in\mathbb{Z}_+^k$ which is updated at time step n according to the following rules:

1. If there are no balls (i.e., individuals) in the urn (i.e., the population), then the process stops else choose two balls at random with replacement from the urn.
2. If the same ball is chosen twice and it is of color i (i.e., strategy i), then add $r_i(n)$ balls of color i.
3. If two different balls are chosen, say the first ball has color i and the second ball has color j, then add $R_{ij}(n)$ balls of color i and add $\tilde{R}_{ji}(n)$ balls of color j.

Under these assumptions, $z(n)$ is a generalized Polya urn where no more than $2m$ balls are added or removed at any update, the function $F(N,x)=(F_1(N,x),\dots,F_k(N,x))$ described in (A2) is given by

$$F_i(N,x) = \frac{x_i(x_iN-1)}{N}E[R_{ii}(0)+\tilde{R}_{ii}(0)] + \frac{x_i}{N}E[r_i(0)] + x_i\sum_{j\neq i}x_jE[R_{ij}(0)+\tilde{R}_{ij}(0)], \tag{3.1}$$

and the limiting function $f(x)=(f_1(x),\dots,f_k(x))$ alluded to in (A3) is given by

$$f_i(x) = x_i\sum_{j=1}^k x_jE[R_{ij}(0)+\tilde{R}_{ij}(0)]. \tag{3.2}$$

Therefore, the mean limit ODE for the replicator process is a *mean limit replicator equation*:

$$\begin{aligned}\dot{x}_i &= x_i\sum_{j=1}^k x_jE[R_{ij}(0)+\tilde{R}_{ij}(0)] \\ &\quad -x_i\sum_{j,l=1}^k x_jx_lE[R_{jl}(0)+\tilde{R}_{jl}(0)], \\ i &= 1,\dots,k,\end{aligned} \tag{3.3}$$

with payoff $E[R(0)+\tilde{R}(0)]$. Notice that $E[r(0)]$ does not appear in (3.3). This corresponds to the fact that as the population grows in size, encounters between different individuals become more likely.

In order to apply Theorem 2.2, we need to find conditions that ensure that the number of balls grows asymptotically at a linear rate with positive probability.

THEOREM 3.1. *Let $z(n)$ be a replicator process. Define*

$$a = \min_{i,j}\{E[R_{ij}(0) + \tilde{R}_{ji}(0)], E[r_i(0)]\}. \tag{3.4}$$

If $a > 0$, then

(i) *there is a $\delta > 0$ such that for all $z(0)$*

$$P[z(n) \neq 0 \text{ for all } n \geq 0] \geq 1 - e^{-|z(0)|\delta},$$

(ii) *on the event $\{z(n) \neq 0$ for all $n\}$, $z(n)$ almost surely satisfies*

$$\liminf_{n\to\infty} \frac{|z(n)|}{n} \geq a.$$

Theorems 2.2 and 3.1 imply the following corollary.

COROLLARY 3.2. *Let $z(n)$ be a replicator process and $X(t)$ be defined by* (2.7). *Assume that a as defined in* (3.4) *is strictly positive. Then on the event $\{z(n) \neq 0$ for all $n\}$, the limit set of $X(t)$ is almost surely a connected internally chain recurrent set for the mean limit replicator equation.*

Before proving Theorem 3.1, it is worth noting that even with the restriction $a > 0$ it is possible to realize all replicator dynamics as a mean limit of a replicator process. More specifically, let A be an arbitrary $k \times k$ matrix and consider the change of payoff, given by $\lambda A + b$, where $\lambda, b \in \mathbb{R}$. Under this change of payoff, the replicator equation in (1.1) becomes

$$\dot{x}_i = \lambda x_i \left(\sum_j A_{ij} x_j - \sum_{j,l} A_{jl} x_j x_l \right). \tag{3.5}$$

If $\lambda > 0$, then the dynamics of (1.1) and (3.5) are equivalent up to a rescaling of time. Hence, there are many choices of the random matrices $R(0), \tilde{R}(0)$, and $r(0)$ such that (3.3) realizes the dynamics of (1.1) up to a rescaling of time.

Proof of Theorem 3.1. To prove (i), define $N(0) = 0$ and $N(n) = |z(n)| - |z(n-1)|$ for $n \geq 1$. Let $\mathcal{G}$ be the event $\{z(n) \neq 0$ for all $n \geq 0\}$. We claim that there exists a $\delta > 0$ such that

$$E[\exp(-\delta N(n+1))|z(n)] \leq 1. \tag{3.6}$$

Since $N(n+1) = 0$ whenever $z(n) = 0$, it follows that $E[\exp(-\delta N(n+1))|z(n) = 0] = 1$ for any choice of δ. Let $z \in \mathbb{Z}_+^k \backslash \{0\}$ be given. Define

$$g(\theta) = E[\exp(\theta N(n+1))|z(n) = z].$$

Recall that for the replicator process there is an integer m such that no more than $2m$ balls are being added and no more than 2 balls are being removed at any given update of the process. Therefore,

$$g(\theta) = \sum_{i=-2}^{2m} \exp(\theta i) P[N(n+1) = i|z(n) = z].$$

It follows that $g(0) = 1$, $g'(0) = E[N(n+1)|z(n) = z] \geq a > 0$, and $|g''(\theta)| < e^{2m} 8m^2(1+m)$ for all $\theta \in [-1,1]$. Since $g'(\theta) = g'(0) + \int_0^\theta g''(s)ds$, it follows that $g'(\theta) > 0$ for $\theta \in [-\delta, 0]$, where $\delta = \frac{a}{e^{2m}8m^2(1+m)}$. Hence (3.6) holds for this choice of δ.

Next we define $M(n) = \exp(-\delta(N(1) + \cdots + N(n)))$ and $\mathcal{F}_n$ to be the σ-algebra generated by $z(1), \ldots, z(n)$. Since $z(n)$ is a Markov chain, our choice of δ implies that $E[M(n+1)|\mathcal{F}_n] = M(n)E[\exp(-\delta N(n+1))|z(n)] \leq M(n)$. Therefore $M(n)$ is a supermartingale. Define the stopping time

$$T = \inf\{n : z(n) = 0\}.$$

To use this stopping time, we use the following generalization of Wald's equation (see, e.g., Theorem 7.6 in Chapter 4 of [9]).

THEOREM 3.3. *If $M(n)$ is a nonnegative supermartingale and $T \leq \infty$ is a stopping time, then $E[M(T)] \leq E[M(0)]$, where $M(\infty) = \lim_{n\to\infty} M(n)$ exists by the martingale convergence theorem.*

Applying this theorem to our supermartingale, we get that $E[M(T)] \leq 1$. Since $N(0) + \cdots + N(T) = -|z(0)|$ whenever $T < \infty$, it follows that

$$1 \geq E[M(T)] \geq \exp(\delta|z(0)|)P[T < \infty].$$

Therefore $P[T < \infty] \leq \exp(-\delta|z(0)|)$ and $P[\mathcal{G}] = P[T = \infty] \geq 1 - \exp(-\delta|z(0)|)$.

To prove assertion (ii), we define a new sequence of random variables by $\tilde{N}(0) = 0$ and

$$\tilde{N}(i) = \begin{cases} N(i) & \text{if } z(i) \neq 0, \\ a & \text{if } z(i) = 0 \end{cases}$$

for $i \geq 1$. Notice that on the event $\mathcal{G}$, $\tilde{N}(i) = N(i)$ for all $i \geq 1$. Let

$$\tilde{M}(n) = \sum_{i=1}^{n} \frac{1}{i}(\tilde{N}(i) - E[\tilde{N}(i)|\mathcal{F}_{i-1}]).$$

$\tilde{M}(n)$ is a martingale that satisfies

$$\sup_n E[\tilde{M}(n)^2] \leq 4m^2 \sum_{i\geq 1} \frac{1}{i^2}$$

as $|\tilde{N}(i)| \leq 2m$. Therefore by Doob's convergence theorem $\{\tilde{M}(n)\}_{n\geq 1}$ converges almost surely. By Kronecker's lemma

$$\lim_{n\to\infty} \frac{1}{n} \sum_{i=1}^{n} \tilde{N}(i) - E[\tilde{N}(i)|\mathcal{F}_{i-1}] = 0 \tag{3.7}$$

almost surely. Since $\sum_{i=1}^n \tilde{N}(i) = |z(n)| - |z(0)|$ on the event $\mathcal{G}$ and $E[\tilde{N}(i)|\mathcal{F}_{i-1}] \geq a$, (3.7) implies that $\liminf_{n\to\infty} \frac{|z(n)|}{n} \geq a$ almost surely on the event $\mathcal{G}$. □

Theorem 2.6 implies the following result about convergence to attractors with positive probability.

THEOREM 3.4. *Let $z(n)$ be a replicator process such that*

$$P[R_{ij}(0) + \tilde{R}_{ji}(0) \geq 1] = P[r_i(0) \geq 1] = 1 \tag{3.8}$$

for all i, j. *If* $z_i(0) \geq 1$ *for all* i *and* $\mathcal{A}$ *is an attractor for* (3.3), *then* $P[L(X) \subseteq \mathcal{A}] > 0$ *where* X *is defined by* (2.7).

Proof. Let $z(n)$ be a replicator process such that $z_i(0) \geq 1$ for all $1 \leq i \leq k$ and such that (3.8) holds. Let $x(n) = z(n)/|z(n)|$, $\tau(n) = \sum_{i=0}^{n-1} \frac{1}{|z(i)|}$, and $X(t)$ be defined by (2.7).

First, we show that the set of attainable points is the entire simplex Δ^{k-1}. Since $P[r_i(0) \geq 1] = 1$ for $1 \leq i \leq k$, there exists $w = (w_1, \ldots, w_k) \in \mathbb{Z}_+^k$ such that $w_i \geq 1$ for $1 \leq i \leq k$, and $P[r_i(0) = w_i] > 0$. Since $z_i(0) \geq 1$ for $1 \leq i \leq k$, it follows that for $v \in \mathbb{Z}_+^k$,

$$P\left[x(|v|) = \frac{z(0) + (v_1 w_1, \ldots, v_k w_k)}{|z(0)| + v_1 w_1 + \cdots + v_k w_k}\right] > 0.$$

Since the set

$$\left\{\frac{z(0) + (v_1 w_1, \ldots, v_k w_k)}{|z(0)| + v_1 w_1 + \cdots + v_k w_k} : v \in \mathbb{Z}_+^k\right\}$$

is dense in Δ^{k-1} and $\tau(n) \geq \sum_{i=0}^{n-1} \frac{1}{|z(0)|+i}$, it follows that for any $t \geq 0$ and open set U in Δ^{k-1} there is a $v \in \mathbb{Z}_+^k$ such that $\tau(|v|) \geq t$ and

$$P[\exists s \geq t : X(s) \in U] \geq P\left[x(|v|) = \frac{z(0) + (v_1 w_1, \ldots, v_k w_k)}{|z(0)| + v_1 w_1 + \cdots + v_k w_k}\right] > 0.$$

Therefore, the set of attainable points for X is the entire simplex Δ^{k-1}.

To invoke Theorem 2.6 and thereby complete this proof we verify the initial assumptions of Theorem 2.6. Our assumptions that $z_i(0) \geq 1$ for $1 \leq i \leq k$ and $P[R_{ij}(0) + \tilde{R}_{ji}(0) \geq 1] = P[r_i(0) \geq 1] = 1$ for all $1 \leq i, j \leq k$ imply that $|z(n)| \geq |z(0)| + n$ almost surely for $n \geq 0$. Equations (3.1) and (3.2) imply that

$$|F_i(N, x) - f_i(N, x)| = \frac{x_i}{N} |E[R_{ii}(0) + \tilde{R}_{ii}(0) - r_i(0)]| \leq \frac{3m}{N}$$

for all $N \geq 1$, $x \in \Delta^{k-1}$, and $1 \leq i \leq k$. Therefore (2.10) is satisfied for an appropriate choice of $\beta > 0$. □

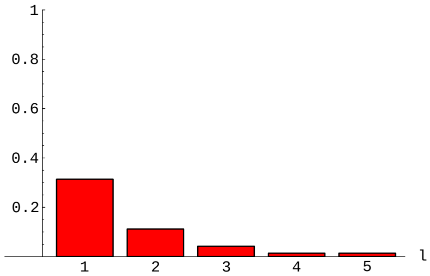
Theorem 3.4 has immediate implications for a *permanent* replicator equation: a replicator equation (3.3) such that there exists a compact attractor $A \subset \mathrm{int}\Delta^{k-1}$ whose basin of attraction equals $\mathrm{int}\Delta^{k-1}$. Biologically, permanence corresponds to the long-term coexistence of all strategies and has been studied extensively for replicator equations [15] which are know to exhibit quite complex dynamics (e.g., the higher dimension hypercycle equations exhibit heteroclinic cycles on the boundary and stable periodic orbits in the interior of the simplex [14]).

COROLLARY 3.5. *Let* $z(n)$ *be a replicator process such that the mean limit flow* (3.3) *is permanent. Assume that* $z_i(0) \geq 1$ *for all* $1 \leq i \leq k$ *and*

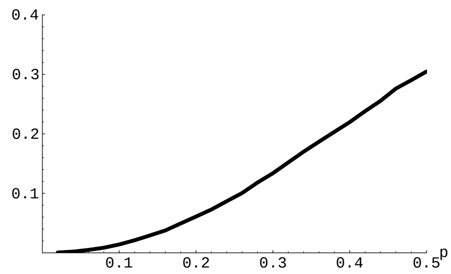
$$P[R_{ij}(0) + \tilde{R}_{ji}(0) \geq 1] = P[r_i(0) \geq 1] = 1 \tag{3.9}$$

for all i, j. *Then* $P[L(X) \subset \mathrm{int}\Delta^{k-1}] > 0$, *where* X *is defined by* (2.7).

3.1. An example: The rock-scissors-paper game. To illustrate what the theory can and cannot tell us, we conclude by studying a replicator process inspired by the children's game in which rock (strategy 1) beats scissors, scissors (strategy 2)



(a)



(b)

FIG. 3.1. *Probability of extinction for the rock-scissors-paper process when* $a(n)$ *and* $\tilde{a}(n)$ *equal* -1, 1, *and* 2 *with probabilities* p, $1-2p$, *and* p, *respectively, while* $b(n)$ *and* $\tilde{b}(n)$ *equal* -1, 4, *and* 9 *with probabilities* p, $1-2p$, *and* p, *respectively. In* (a), $p = 1/2$ *and* $z(0) = (l, l, l)$, *while in* (b), $z(0) = (1, 1, 1)$ *and* p *varies.*

beats paper, and paper (strategy 3) beats rock. This evolutionary game is believed to be played by males of the lizard species *Uta stansburiana* [26] that exhibit color polymorphisms associated with three mating strategies: keeping one female and guarding it closely, keeping several females and guarding each female less closely, and guarding no females and mating with unguarded females.

To define this process, let $m \geq 1$ be an integer, and let $a(n), \tilde{a}(n)$, and $b(n)$ be sequences of independent and identically distributed random variables that take values in the set $\{0, 1, \ldots, m\}$. Define random payoff matrices as follows:

$$R(n) = \begin{pmatrix} a(n) & b(n) & -1 \\ -1 & a(n) & b(n) \\ b(n) & -1 & a(n) \end{pmatrix}, \qquad \tilde{R}(n) = \begin{pmatrix} \tilde{a}(n) & b(n) & -1 \\ -1 & \tilde{a}(n) & b(n) \\ b(n) & -1 & \tilde{a}(n) \end{pmatrix},$$

and

$$r(n) = \begin{pmatrix} a(n) \\ a(n) \\ a(n) \end{pmatrix}.$$

Assume that $E[\tilde{a}(0)] = E[a(0)] = 1$ and $E[b(0)] = 4$. Since the conditions of Theorem 3.1 are satisfied, there is a $\delta > 0$ such that this replicator process goes extinct with a probability less than $\exp(-\delta|z(0)|)$. In Figure 3.1, we numerically estimate the probability of extinction when $a(n)$ and $\tilde{a}(n)$ equal -1, 1, and 2 with probabilities p, $1-p$, and p, respectively, while $b(n)$ and $\tilde{b}(n)$ equal -1, 4, and 9 with probabilities p, $1-2p$, and p, respectively. Consistent with the predictions of Theorem 3.1, Figure 3.1(a) shows that the probability of extinction decreases with initial population size. On the other hand, Figure 3.1(b) shows that the probability of extinction increases as the variance of the payoff matrix increases.

The replicator dynamics for the payoff matrix $A = E[R(0) + \tilde{R}(0)]$ are well known (see, e.g., Theorem 7.7.2 in [15]), and its phase portrait is shown in Figure 3.2. On the event of nonextinction, Corollary 3.2 implies that the limit set of the distribution $X(t)$ of balls is either an equilibrium for the mean limit ODE or the boundary of Δ^2. In Figure 3.3, sample paths of $X(t)$ are shown for the process when $a(n) = \tilde{a}(n) = 1$, $b(n) = \tilde{b}(n) = 4$, and $z(0) = (1, 1, 1)$. Theorem 3.4 predicts that $X(t)$ converges with positive probability to $(1/3, 1/3, 1/3)$ as illustrated in Figure 3.3(a). However,

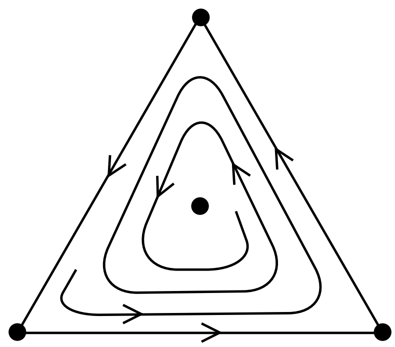
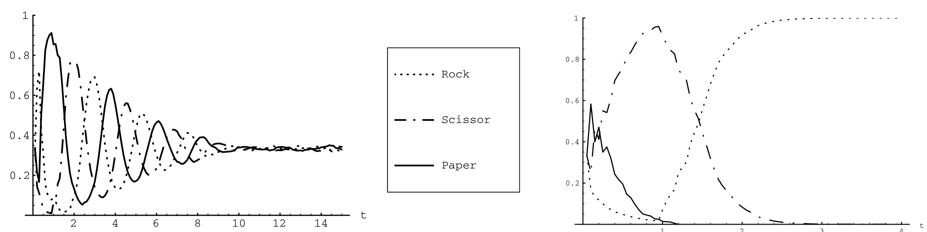
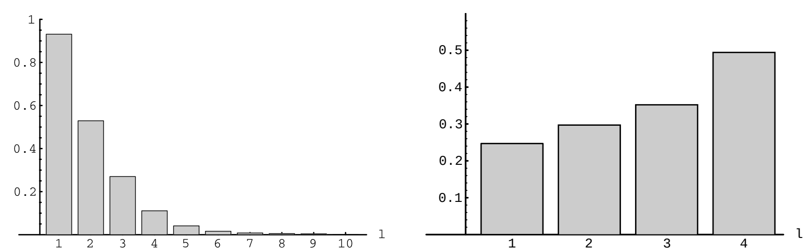


FIG. 3.2. *The phase diagram for the rock-scissors-paper game.*



(a) (b)

FIG. 3.3. *Sample paths of $X(t)$ for the rock-scissors-paper process with $a(n) = \tilde{a}(n) = 1$, $b(n) = \tilde{b}(n) = 4$, and $z(0) = (3, 3, 3)$.*



(a) (b)

FIG. 3.4. *Numerical approximations for the probability of a strategy being removed in finite time for the rock-scissors-paper process. In* (a), *$b(n) = \tilde{b}(n) = 4$, $a(n) = \tilde{a}(n) = 1$, and $z(0) = (l, l, l)$. In* (b), *the process is given by $b(n) = \tilde{b}(n) = 4 + c(n)$, where $c(n)$ takes on values $-l$ and l with equal likelihood, $a(n) = \tilde{a}(n) = 1$, and $z(0) = (3, 3, 3)$.*

if papers initially meet scissors too frequently, then with positive probability the paper strategy is removed in finite time. With no papers left, rocks crush scissors resulting in a rock dominated world as illustrated in Figure 3.3(b). Therefore, unlike its deterministic counterpart, a strategy can be removed in finite time by the rock-scissors-paper process. In Figure 3.4(a), we numerically approximate the probability of a strategy being removed in finite time when $a(n) = \tilde{a}(n) = 1$, $b(n) = \tilde{b}(n) = 4$, and $z(0) = (l, l, l)$ with $l = 1, 2, \ldots, 10$. As suggested by Theorem 3.4, this probability decreases as the initial population size increases. Alternatively, Figure 3.4(b) shows numerical estimates for the probability of a strategy being removed in finite time when $a(n) = \tilde{a}(n) = 1$, $b(n) = \tilde{b}(n) = 4 + c(n)$, where the $c(n)$ are independent and identically distributed random variables that take on the value $-l$ and l with equal likelihood and $z(0) = (3, 3, 3)$. Figure 3.4(b) illustrates that increasing the variance of the payoff matrix increases the likelihood of a strategy being removed in finite time.

4. Conclusions. We introduce a generalized class of urn processes that can be used to model the dynamics of finite populations of interacting individuals. This class of models includes what we call the replicator process for which updates correspond to pairwise interactions between individuals that influence the likelihood of replication and death. It is our contention that these processes provide insight into the relative importance of natural selection and random genetic drift on the evolution of finite populations with the potential for growth. In particular, they may help population geneticists better understand the "founder-effect" in which a new population is established by a few original founders [25].

Like their branching process sisters, these urn processes either go extinct in finite time or grow exponentially with respect to a natural time scale. The probability of growth represents the likelihood a founding population successfully establishes itself and is likely to be of interest to population geneticists. We have shown that if the replicator process expects to exhibit growth whenever individuals are present, then the process exhibits growth with positive probability. Our work suggests that the likelihood of a population establishing itself increases with the initial population size and decreases with the variance of the payoffs for pairwise interactions.

For these models, the effect of random fluctuations is most pronounced when the population numbers remain small. When the populations become sufficiently large, they tend to grow at an exponential rate and evolve in an essentially deterministic way. Consequently, on the event of growth, one associates a mean limit ODE with the process. The mean limit ODE represents the force of natural selection. Namely, if the populations follow the expected, then the distribution of strategies follow the trajectories of the mean limit ODE. However, since the population sizes are finite, the distribution of strategies can deviate from the expected. These deviations correspond to random genetic drift and can have unexpected consequences. For instance, when the initial distribution of strategies lies in the basin of attraction for an attractor of the mean limit ODE, random fluctuations can push the process permanently out of this basin of attraction. Such motions are impossible for solutions of the mean limit ODE, and correspond to random genetic drift overcoming natural selection. Our results suggest that random genetic drift overcoming selection is less likely for large populations or rapidly growing populations, and is more likely for populations for which pairwise interactions lead to highly variable outcomes.

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REFERENCES

[1] B. Arthur, Y. Ermol'ev, and Y. Kaniovskii, *A generalized urn problem and its applications*, Cybernetics, 19 (1983), pp. 61–71.
[2] M. Benaïm, *A dynamical systems approach to stochastic approximations*, SIAM J. Control Optim., 34 (1996), pp. 437–472.
[3] M. Benaïm, *Dynamics of stochastic approximation algorithms*, in Le Seminaire de Probabilites, Lecture Notes in Math. 1709, Springer-Verlag, New York, 1999, pp. 1–68.

[4] M. Benaïm and M. W. Hirsch, *Dynamics of Morse-Smale urn processes*, Ergodic Theory Dynam. Systems, 15 (1995), pp. 1005–1030.
[5] M. Benaïm and M. W. Hirsch, *Chain recurrence in surface flows*, Discrete Contin. Dynam. Systems, 1 (1995), pp. 1–16.
[6] M. Benaïm and M. W. Hirsch, *Asymptotic pseudotrajectories and chain recurrent flows, with applications*, J. Dynam. Differential Equations, 8 (1996), pp. 141–176.
[7] M. Benaïm and S. J. Schreiber, *Ergodic properties of weak asymptotic pseudotrajectories for semiflows*, J. Dynam. Differential Equations, 12 (2000), pp. 579–598.
[8] C. Conley, *Isolated Invariant Sets and the Morse Index*, CBMS Reg. Conf. Ser. Math. 38, AMS, Providence, RI, 1978.
[9] R. Durrett, *Probability: Theory and Examples*, 2nd ed., Duxbury Press, Boston, 1996.
[10] W. J. Ewens, *Mathematical Population Genetics*, Biomathematics 9, Springer-Verlag, Berlin, New York, 1979.
[11] W. Feller, *Diffusion processes in genetics*, in Proceedings of the 2nd Berkeley Symposium on Mathematical Statistics and Probability, J. Neyman, ed., The University of California Press, Berkeley, CA, 1951, pp. 227–246.
[12] R. A. Fisher, *The Genetical Theory of Natural Selection*, Clarendon Press, Oxford, 1930.
[13] B. M. Hill, D. Lane, and W. Sudderth, *A strong law for some generalized urn processes*, Ann. Probab., 8 (1980), pp. 214–226.
[14] J. Hofbauer, J. Mallet-Paret, and H. L. Smith, *Stable periodic solutions for the hypercycle system*, J. Dynam. Differential Equations, 3 (1991), pp. 423–436.
[15] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, UK, 1998.
[16] M. Kandori, G. J. Mailath, and R. Rob, *Learning, mutation and long run equilibria in games*, Econometrica, 61 (1993), pp. 29–56.
[17] J. Maynard Smith, *The theory of games and the evolution of animal conflicts*, J. Theoret. Biol., 47 (1974), pp. 209–221.
[18] J. Maynard Smith, *Evolution and the Theory of Games*, Cambridge University Press, Cambridge, UK, 1982.
[19] J. Maynard Smith, *Did Darwin Get It Right?*, Chapman and Hall, New York, 1988.
[20] J. Maynard Smith and G. R. Price, *The logic of animal conflict*, Nature, 246 (1973), pp. 15–18.
[21] T. Nagylaki, *Models and approximations for random genetic drift*, Theoret. Population Biol., 37 (1990), pp. 192–212.
[22] R. Pemantle, *Nonconvergence to unstable points in urn models and stochastic approximations*, Ann. Probab., 18 (1990), pp. 698–712.
[23] L. Perko, *Differential Equations and Dynamical Systems*, Texts Appl. Math. 7, Springer-Verlag, New York, 1996.
[24] M. Posch, *Cycling in a stochastic learning algorithm for normal form games*, J. Evolutionary Economics, 7 (1997), pp. 193–207.
[25] M. Ridley, *Evolution*, Blackwell Scientific, Boston, 1993.
[26] B. Sinervo and C. M. Lively, *The rock-paper-scissors game and the evolution of alternative male strategies*, Nature, 380 (1996), pp. 240–243.
[27] J. W. Weibull, *Evolutionary Game Theory*, MIT Press, Cambridge, MA, 1995.
[28] S. Wright, *Evolution in Mendelian populations*, Genetics, 16 (1931), pp. 97–159.