A stochastic model of evolutionary dynamics with deterministic large-population asymptotics

Burton Simon*

Department of Mathematical Sciences, University of Colorado Denver, Campus Box 170, P.O. Box 173364, Denver, CO 80217-3364, USA

A R T I C L E   I N F O

Article history:
Received 29 November 2007
Received in revised form 23 June 2008
Accepted 24 June 2008
Available online 5 July 2008

Keywords:
Evolutionary games
Adaptive dynamics
Replicator equation
Evolutionary birth–death process
Fitness-diffusion equation
Reactive strategies
Iterated prisoner’s dilemma

A B S T R A C T

An evolutionary birth–death process is proposed as a model of evolutionary dynamics. Agents residing in a continuous spatial environment X, play a game G, with a continuous strategy set $S$, against other agents in the environment. The agents’ positions and strategies continuously change in response to other agents and to random effects. Agents spawn asexually at rates that depend on their current fitness, and agents die at rates that depend on their local population density. Agents’ individual evolutionary trajectories in $X$ and $S$ are governed by a system of stochastic ODEs. When the number of agents is large and distributed in a smooth density on $(X,S)$, the collective dynamics of the entire population is governed by a certain (deterministic) PDE, which we call a fitness-diffusion equation.

1. Introduction

A spatial environment, $X$, contains agents that play a game, $G$, with strategy space, $S$, against each other. Individual agents should not be thought of as distinct organisms, but instead should be thought of as moving and evolving colonies of genetically (nearly) identical organisms. At a given point in time, an agent (living) occupies a single point in the environment $x \in X$ (its position) and uses a particular strategy $s \in S$ in games it plays against other agents. During their lifetimes, agents may spawn. Reproduction is asexual, so a newly spawned agent, at time $t$, inherits the exact position and strategy that its parent has at time $t$, and then moves and evolves on its own after that. Every agent eventually dies. Mutant agents, genetically independent of the general population, appear at random, and then move and evolve like everybody else.

In the most general form of this model, the agents’ positions and strategies continuously change in response to the positions and strategies of the other agents present in the environment, and also to random effects; and the spawning rates of the agents and the lengths of their lives likewise depend on the positions and strategies of the other agents, as well as random effects. Our model of agent dynamics, therefore, allows us to analyze the long-term evolution of frequency (or density) dependent traits, since an agent’s life history in $X$ and $S$ depends (statistically) on the constantly changing state of the system. In an important special case of the model, called pure Darwinian selection, individual agent’s positions and strategies change due to random effects only. Only the birth and death rates depend on the system state, but this is sufficient for meaningful evolution to take place. The position and strategy spaces $(X,S)$ in our model are continuums and the evolutionary changes are gradual, so the dynamical equations of the agents’ individual and collective evolutions are differential equations.

Every model of Darwinian selection requires a measure of fitness, which determines the propensity of a given agent to successfully reproduce in a given environment. Evolutionary game dynamics use game payoffs from game competitions between agents to construct the “fitness landscape”, which drives the evolutionary processes. In the present context, each living agent is endowed with a position $x \in X$ and a game strategy $s \in S$ at each point in time during its life, so each agent’s (instantaneous) fitness can be calculated in terms of its game payoffs when paired against its contemporaries. Agents with positions and strategies that, on the average, get better payoffs, are fitter and tend to increase their numbers relative to other agents.

Within the evolutionary game paradigm there are many ways that one can model the evolution of agents in an environment that features interactions with other evolving agents. Most models of evolutionary dynamics involve systems of ODEs, like the Lotka–Volterra equation (Hofbauer and Sigmund, 1998), or the replicator
The fitness-diffusion equation appears to be amenable to simulation. It is relatively easy to simulate an evolutionary birth–death process, as long as the number of agents is not too large. From a numerical perspective, the fitness diffusion equation is usually better suited for higher dimensional models, or models with relatively small equilibrium populations.

Many interesting mathematical models of evolutionary dynamics have no explicit spatial variable. For example, under perfect mixing (Nowak, 2006) an agent’s fitness at time \( t \) is the average game payoff it receives against the other agents present at time \( t \). The positions of the agents, if they are defined at all, play no role in calculations of agent fitness. Under perfect mixing we can simply ignore \( X \), or more precisely, set \( X = \{0\} \) so that it plays no role in the analysis.

The evolutionary birth–death model allows agents to move in \( X \) and evolve in \( S \) in directions that depend on the state of the system (subject to noise), so, for example, agents can be endowed with an ability to move along their fitness gradients (subject to noise). The fitness-diffusion equation has terms allowing an analogous capability. We call this capability (deterministic) drift.

Many interesting mathematical models of evolutionary dynamics have no drift terms. We refer to an evolutionary birth–death process or fitness-diffusion equation with no drift terms as a model of pure Darwinian selection. Without drift, individual agents move and evolve as independent Brownian motions (at random, and without regard to the system state), yet the population as a whole undergoes meaningful evolution. This is possible because agents that become fitter, due to simply fortuitous random events, spawn at a higher rate than their peers, and therefore increase the fraction of agents in the environment that are fit in that environment.

The evolutionary birth–death process studied here is related to other stochastic processes that have been proposed as models in biology and other fields. The term “evolutionary birth–death process” is meant to describe the class of discrete population models developed in this paper. The standard birth–death process is a Markov process taking non-negative integer values, where state transitions are either plus one (a birth) or minus one (a death), and the state can be interpreted as the number of agents of some sort, e.g., Karlin and Taylor (1975). In the basic model, only the total population is kept track of, since individual agents have no distinguishing characteristics. There have been many modifications and extensions of the basic birth–death model. In a spatial birth–death model, the individual agents possess distinguishing characteristics, such as a position in a spatial field. The theory of spatial birth–death processes was developed by Preston (1975) and extended by Garcia and Kurtz (2006).

Mathematically, the evolutionary birth–death process described here is an example of a measure-valued Markov processes. Certain measure-valued Markov processes have been
proposed as models of evolutionary processes, such as the Fleming–Viot process (Fleming and Viot, 1979; Ethier and Kurtz, 1993) used to model allele drift. The fitness-diffusion equation is closely related to reaction-diffusion equations, but the fitness-diffusion equation allows non-local effects in the “reaction” term, e.g., the outcomes of games against distant and dissimilar opponents.

In the next section we discuss the replicator equation for evolutionary dynamics and compare it to the evolutionary birth–death process and the fitness-diffusion equation. In Section 3 we describe the evolutionary birth–death process in detail and propose the agent dynamical equations. In Section 4 we derive the large-population asymptotics for the evolutionary birth–death process, which leads to the fitness-diffusion equation. To keep notational complexities to a minimum, we derive the equations in Sections 3 and 4 for the case where both $X$ and $S$ are real valued, i.e., $(X,S) = \mathbb{R}^2$. This is not a restriction of the method; higher dimensional spaces, with and without boundaries, can be handled as well, as will be illustrated in Section 5. In Section 5 we study reactive strategies for the iterated prisoner’s dilemma under perfect mixing and pure Darwinian selection, comparing Nowak’s analysis (Nowak, 2006) using the replicator equation to an analysis based on an evolutionary birth–death process and the corresponding fitness-diffusion equation. Finally, in Section 6 we summarize our results, discuss numerical issues in solving our equations, and point to some interesting avenues for future work.

2. The replicator equation

The replicator equation has been used extensively to study evolutionary dynamics (e.g., Nowak, 2006), so it will serve nicely as a point of comparison with the evolutionary birth–death process and fitness-diffusion equation introduced here. Models based on the replicator equation assume a fixed collection of game strategies, $\{s_1, s_2, \ldots, s_n\}$, that compete against each other for survival. There are no explicit spatial variables in the replicator equation, or in other words, the replicator equation assumes perfect mixing. The replicator equation is a system of (deterministic) non-linear ODEs,

$$\frac{d}{dt} z_t(i) = \bar{f}_t(i) - \bar{f}_t \mathbf{z}_t(i), \quad i = 1, 2, \ldots, n$$

where $z_t(i)$ is a measure of the population of strategy $s_i$ at time $t$, $f_t(i)$ is the fitness of strategy $s_i$ at time $t$, and

$$\bar{f}_t = \frac{1}{n} \sum_{i=1}^{n} f_t(i) z_t(i).$$

An important feature of the replicator equation is that $d/dt \sum_{i=1}^{n} z_t(i) = 0$, where

$$\sum_{i=1}^{n} z_t(i),$$

so the total population size does not change. Typically, the population is set to unity, so $z_t(i)$ is the fraction of the population using strategy $s_i$ at time $t$ and $\bar{f}_t$ is the average fitness of the entire population at time $t$. The interactions between the strategies are completely random (perfect mixing), so

$$f_t(i) = \frac{1}{n} \sum_{j=1}^{n} \phi(s_i, s_j) z_t(j),$$

where $\phi(s_i, s_j)$ is the payoff to strategy $s_i$ when paired against strategy $s_j$. The replicator equation does not model individual agents directly; evolution is observed as changes in the relative frequencies of a fixed set of strategies. However, the fixed set of strategies can (in principle) be as large and closely packed as the modeler wishes. One can, therefore, imagine a (probability) density function $\mathbf{z}(s), s \in S$ for the population so that the fraction of the population using a strategy from the set $B \subset S$ at time $t$ is $\int_B \mathbf{z}(s) ds$. Clearly, at each $s \in S$, the density would change following

$$\frac{d}{dt} \mathbf{z}(s) = (f_t(s) - \bar{f}_t) \mathbf{z}(s),$$

where $f_t(s) = \int \phi(s, s') \mathbf{z}(s') ds'$, and $\bar{f}_t = \int f_t(s) \mathbf{z}(s) ds$. Eq. (2) is valid as long as the initial density $\mathbf{z}(s)$ is integrable over $S$. There are no differentiability (or even continuity) requirements. Evolutionary dynamics in continuous models like (2) are studied in Oechssler and Riedel (2002) and some of the references cited therein.

The replicator equation keeps the population fixed by tying the growth rate of each strategy to its fitness relative to the average fitness of the population. Another way to regulate the population is to tie the growth rate of each strategy to its fitness and to the population level. For example,

$$\frac{d}{dt} \mathbf{z}(i) = m(i) + (f_t(i) - c N_t) \mathbf{z}(i), \quad i = 1, 2, \ldots, n$$

is another model of evolutionary dynamics for a fixed set of strategies $\{s_1, s_2, \ldots, s_n\}$. Summing over the strategies, we obtain

$$\frac{d}{dt} N_t = m + \bar{f}_t - c N_t^2,$$

where $m = \sum_{i=1}^{n} m(i)$, so Eq. (3) does not have a fixed population and, therefore, differs qualitatively from the replicator equation. If the payoffs $\phi(s_i, s_j)$ are constrained to the non-negative interval $[a, b]$, then $\bar{f}_t$ is likewise constrained to $[a, b]$, and the total population $N_t$ is constrained to the interval

$$a + \sqrt{a^2 + 4mc} \leq N_t \leq b + \sqrt{b^2 + 4mc}.$$  

(once it is in it), since the population increases when $N_t < (a + \sqrt{a^2 + 4mc})/2c$ and decreases when $N_t > (b + \sqrt{b^2 + 4mc})/2c$.

The salient feature of the evolutionary birth–death model is the individual agent’s ability to evolve on its own. The evolutionary dynamics that emerge from an evolutionary birth–death model are, therefore, different in kind from those of the replicator equation and similar models, like (3), where the set of strategies is fixed. In the evolutionary birth–death model, the set of strategies currently in use is constantly changing as the agents evolve. During their lifetimes, the agents’ evolutionary trajectories are governed by a system of stochastic ODEs that branch and die at random (e.g., Fig. 1). The total number of agents living at time $t$ is a Markov process, where the (instantaneous) birth and death rates depend on the always-changing positions and strategies used by the living agents. Fitter agents spawn more often than less fit agents, and since agents spawn asexually, fitter strategies and positions become more numerous. Some agents are born without being spawned by another agent. These “mutants” appear at random, choose an initial position and strategy at random, and then move and evolve like everybody else.

Another difference between the replicator equation and the evolutionary birth–death equations becomes apparent when the population is very large and diverse. The limit of the replicator equation as the population diversifies into a probability density is given by (2). Eq. (3) has a similar large-diversity limit

$$\frac{d}{dt} \mathbf{z}(s) = m(s) + (f_t(s) - c N_t) \mathbf{z}(s), \quad s \in S.$$  

(4)
As the population grows, the stochastic nature of the individual agent trajectories is washed away by laws of large numbers, so the large-population limit is, in fact, deterministic. However, the stochastic nature of the individual agent trajectories as well as any deterministic drift in the model, causes the time derivative of the population density function to involve derivatives with respect to $x$ and $s$, so the result is qualitatively different than (2) or (4). Neither (2) nor (4) is a PDE, but the large-population asymptotics for the evolutionary birth–death process yields a PDE: the fitness–diffusion equation (23).

Eq. (4) is, in fact, the fitness–diffusion equation minus the drift and diffusion terms. Eq. (3), is therefore, more closely analogous to the evolutionary birth–death equations than the replicator equation. As with the replicator equation, the equilibrium or limiting behavior of $z_i$ is of particular interest. Equilibrium solutions $z^*$ of (4) must satisfy

$$m(s) + (f^*(s) - Cn^*)z^*(s) = 0,$$

where $f^*(s) = \int f(s, s') z^*(s') ds'$ is the equilibrium fitness function and $N' = \int f(s, s) ds$ is the equilibrium population. A mathematical study of (3)–(5) along the lines of Pressman (1988) or Pressman and Garay (2003) will be left for future research.

3. The evolutionary birth–death model

Agent $i \in \{1, 2, 3, \ldots\}$ is born at time $\tau_i$ and dies at time $T_i$, where $0 < \tau_i < T_i < \infty$. Let $A_t$ be the set of indices of the agents alive at time $t$, and let $N_t$ be the number of agents alive at time $t$. The original population consists of agents $A_0 = \{1, 2, \ldots, N_0\}$. At time $t$, the position of agent $i \in A_t$, is denoted $x_i(t)$, and the game strategy used by agent $i \in A_t$ is denoted $s_i(t)$. The evolutionary birth–death process is the point-set valued stochastic process,

$$\Theta_t = \{(x_i(t), s_i(t)), i \in A_t\}, \quad t > 0.\tag{6}$$

Agents spawn asexually, and at random, yielding new agents with identical positions and strategies. The new agents then move and evolve on their own (Fig. 1). The instantaneous rate at which an agent spawns is constantly changing, and depends on its current fitness. Fitness is a measure of how well the agent plays the game $G$ against its contemporaries. Agent $i$ plays against all its contemporaries, but typically a larger share of the games are played against close neighbors, including itself. The fractions of agent $i$'s games played against the other agents are determined by the values of $\psi(x(t) - x_i(t)), j \in A_t$, where $\psi$ is a weighting function chosen by the modeler. Mathematically, we only need to assume $\psi$ is non-negative, bounded, and twice differentiable, but in practice $\psi$ will typically give less weight to agents far away. An agent's death rate depends on its local population density, which is calculated in terms of the values of $\psi(x_i(t) - x_j(t)), j \in A_t$, where $\psi$ is a nonnegative, bounded, and twice differentiable weighting function chosen by the modeler. The shapes of the weighting functions $\psi$ and $\psi$ determine some important qualitative aspects of the model, such as the likely fate of isolated agents. Sums of Weibull density functions, for example, offer a wide and useful range of possible shapes for the weighting functions. The payoff to an agent using strategy $s$ against an opponent using $s'$ is denoted $\phi(s, s'), s, s' \in S$. The payoff function is assumed to be twice differentiable in both variables, non-negative, and bounded.

3.1. The agent dynamical equations

In this section we will define several (random) variables whose values depend on the system state, $\Theta_t$. Variables subscripted with $t$ are understood to be functions of $\Theta_t$. Let $F_t(x, s)$ be the fitness of a hypothetical agent at position $x$ using strategy $s$ at time $t$, which we define to be

$$F_t(x, s) = \sum_{i \in A_t} \phi(s, s_i(t)) \psi(|x - x_i(t)|) / \sum_{i \in A_t} \psi(|x - x_i(t)|).$$

Eq. (7) can be written

$$F_t(x, s) = \sum_{i \in A_t} \phi(s, s_i(t)) \rho_i(t)$$

where $\rho_i(t) = \psi(|x - x_i(t)|) / \sum_{i \in A_t} \psi(|x - x_i(t)|)$. If we interpret $\rho_i(t)$ as the probability that the (hypothetical) agent $(x, s)$ chooses agent $i$ to play a game at time $t$, then $F_t(x, s)$ is the resulting expected value of $\phi(s, s_i(t))$. Note that if $\psi(0) = 0$ (for example, if $\psi(d) = e^{-dy}$) then agents do not play against themselves. If agent $i$ does not have any close neighbors, its fitness will be approximately $\phi(s_i(t), s_i(t))$ (as long as $\psi(0) > 0$), so isolated agents that play well against themselves can prosper. There are many ways to define fitness, so (7) is just one example. Under perfect mixing, $\psi = 1$, so (7) reduces to

$$F_t(x, s) = N_t \sum_{i \in A_t} \phi(s, s_i(t)),\tag{8}$$

which is the standard fitness function for non-spatial models, e.g., Nowak (2006). The fitness of agent $i \in A_t$ at time $t$ is $F_t(x_i(t), s_i(t))$, which we will denote by

$$F_t(i) = F_t(x_i(t), s_i(t)).$$

Let $o(u)$ denote a function that satisfies $\lim_{u \to 0} o(u)/u = 0$. If $i \in A_t$ then agent $i$ spawns in the time interval $[t, t + dt]$ with probability $F_t(i) dt + o(dt)$, i.e., agent $i$'s instantaneous birth rate is equal to its fitness. New agents may also suddenly appear in the population as a result of a "mutation". A mutant appears in the time interval $[t, t + dt]$ with probability $mdt + o(dt)$ (independent of $\Theta_t$) and assumes position and strategy $(x, s)$ randomly from a probability density $h(x, s)$ on $(X, S)$. Agent $i$ dies in $[t, t + dt]$ with probability $d_i(i) dt + o(dt)$, where $d_i(i)$ is (typically) an increasing function of the local population density, such as

$$d_i(i) = c \sum_{j \neq i} \psi(|x_i(t) - x_j(t)|),\tag{9}$$

where $c > 0$. There are many other ways to define the death rate, so (9) is just one example. Under perfect mixing, $\psi = 1$, so (9) reduces to $d_i(i) = CN_i$.

If $\psi$ is bounded away from zero, i.e., $\psi > \epsilon$, then the total death rate for the population at time $t$ is $d_t = \sum_{i \neq i} d_i(i) > CN_t^2 \epsilon$. Since the total birth rate is $b_t = \sum_{i \in A_t} F_t(i) = O(N_t)$, the population level will stay finite and will fluctuate around an equilibrium level until such a time that global extinction occurs. Global extinction occurs with probability one, but the expected time until extinction occurs may be extremely large. For example, under perfect mixing, $d_t = CN_t^2$ and $b_t = \sum_{i \in A_t} F_t(i)$. If we define $b_t = b_t/N_t$ to be the average fitness of the population at time $t$, then the equilibrium population at time $t$ is

$$N_t = b_t/c.\tag{10}$$

We now propose the stochastic equations for the evolutionary birth–death process for the case $(X, S) = \mathbb{R}^2$. The general case is analogous and the equations can be constructed at the cost of more cumbersome notation. Let $f_{1 MAX} = \max(n: \tau_n < t)$ be the largest agent index used up to time $t$. A new agent born at time $t$ gets index $j = j + 1$. The new agent's initial position and strategy is denoted $(x_j, s_j)$. If agent $i$ spawns at time $t$ then the offspring assumes agent $i$'s position and strategy exactly, i.e., $x_j = x_i(t)$ and $s_j = s_i(t)$, although the two agents evolve independently after that. A mutant appearing at time $t$ is assigned a random position and strategy, i.e., $P(x_j, s_j) = R_{\text{mut}} = h(x, s) dx ds + o(dx ds)$, where $h(x, s)$ is a fixed probability density function on $(X, S)$ and $R_{\text{mut}}$ is the
Let $\sigma_x$ and $\sigma_t$ be non-negative constants, $(W_t^i, i \geq 1)$ and $(W_t^j, i \geq 1)$ be independent sequences of independent Brownian motions, and let $\beta_i(x,s)$ and $\gamma_i(x,s)$ be functions of the system state that are differentiable in $x$ and $s$. Define $\beta_i(t) = \beta_i(x_i(t), s_i(t))$ and $\gamma_i(t) = \gamma_i(x_i(t), s_i(t))$. Then, agent $i$’s evolutionary trajectory satisfies

$$
\begin{bmatrix} x_i(t) \\ s_i(t) \end{bmatrix} = \begin{bmatrix} x_i(0) \\ s_i(0) \end{bmatrix} + \int_{t_0}^{t} \begin{bmatrix} dx_i(t) \\ ds_i(t) \end{bmatrix}, \quad t \in [t_0, T_i]
$$

where

$$
dx_i(t) = \beta_i(t) \ dt + \sigma_x \ dW_i^x(t), \quad ds_i(t) = \gamma_i(t) \ dt + \sigma_t \ dW_i^s(t). \quad (11)
$$

A new agent is born around time $t$ with probability satisfying

$$
P(t_j \in [t, t + dt]| j = j_i + 1) = \left( \frac{m + \sum_{i \in A} F_i(t)}{m} + \alpha dt \right),
$$

so the birth process satisfies

$$
P(t_j \in [t, t + dt]| j = j_i + 1) = \sum_{i \in A} \delta_{(i, d_i)}(j_i) = d_i(t) dt + \alpha dt. \quad (13)
$$

Eqs. (11)–(13) uniquely specify the probabilities of events associated with the evolutionary birth–death process, $\Theta_t$, $t \geq 0$, and are in a form that can be easily simulated.

3.2. Discussion

In order to make sense of our proposed model, it is important to be able to interpret the equations in evolutionary terms. The key is to think of an agent as a colony of genetically (almost) identical organisms that move and evolve together. An individual organism cannot evolve on its own, but a colony can. If a colony is sufficiently fit and lucky, it will spawn new colonies with probability satisfying

$$
P(T_j \in [t, t + dt]| i \in A_j) = d_i(t) dt + \alpha dt. \quad (13)
$$

Eqs. (11)–(13) uniquely specify the probabilities of events associated with the evolutionary birth–death process, $\Theta_t$, $t \geq 0$, and are in a form that can be easily simulated.

The life span of a population, the survival rate of a species, and the average number of offspring produced per individual are all important evolutionary parameters. These parameters can be used to infer the evolutionary trajectory of a species, and to predict its future population size.

4. Large-population asymptotics

In the previous section we developed the stochastic equations for the evolutionary birth–death model of evolutionary dynamics in the case $(X, S) = \mathbb{R}^2$. The equations are valid, in principle, for any finite initial population. As $N_0 \to \infty$ and/or $d_i(t) \to 0$, it becomes impractical to solve the resulting system of equations, so we look to an asymptotic analysis. In this section we will argue that if the initial population is very large, and is spread out...
"smoothly" in a density, and the death rate is small enough so that the population remains large, then:

(a) the stochastic components of the individual agents’ evolutionary trajectories average out so that the population density evolves deterministically, and,

(b) the stochastic nature of the individual agents’ trajectories shows up as a diffusion term in the asymptotic form of the dynamical equations governing the evolution of the population density: a second-order PDE we call a fitness-diffusion equation.

For a measurable set $B \subset \mathbb{R}^2$, define

$$
\mu_t(B) = \sum_{i \in N} \int_{B} \theta_i(x, t) dx ds.
$$

to be the counting measure for the agents’ positions and strategies at time $t$ in an evolutionary birth–death process. The counting measure contains the same aggregate information as $\theta_t$, so it can be considered as another form of the system state at time $t$. Suppose that a scaled version of the initial population measure can be approximated by a twice differentiable (population density function, $\theta_0(x, t), x \in X, s \in S$, i.e.,

$$
N_0^{-1} \mu_0(B) \approx \int_B \theta_0(x, s) dx ds.
$$

Then we can study the population dynamics in our model by working with the (continuous) density functions, $\mu_t, t \geq 0$, instead of the (discrete) measures, $\mu_t, t \geq 0$. The population density function $\mu_t$ plays the role of the initial state in the continuous model, so we expect $\mu_t, t \geq 0$ to be analogous to $\theta_t, t \geq 0$. If $N_0^{-1}$, is constant through time. The fitness function at time $t \geq 0$ will, therefore, be analogous to (7) but in an integral form

$$
F_t(x, s) = \int_x \int_{s'} \phi(s, s') \psi((x-x')) \theta_t(x', s') dx' ds' \int_x \int_{s'} \phi((x-x')) \theta_t(x', s') dx' ds'.
$$

Since $F_t(i)$ is the instantaneous birth rate at $(x(t), s(t))$ in the evolutionary birth–death model, $F_t(x, s)$ is interpreted as a per-agent birth rate at $(x, s)$ in the continuous model. Likewise, the death rate, $d_t(x)$ in the evolutionary birth–death model is a death rate at $(x(t), s(t))$, so a function $d_t(x, s)$ takes the role of a per-agent death rate in the continuous model. For example, if $d_t(x)$ satisfies (9) then

$$
d_t(x, s) = c \int_x \int_{s'} \psi((x-x')) \theta_t(x', s') dx' ds'.
$$

Mutant births in the continuous model are spread out continuously in the shape of the density function, $h(x, s)$, and arrive at a continuous rate of $m$ per unit time, so the number of mutant births in the set $B \subset \mathbb{R}^2$ in the interval $[t, t+d]$ is exactly $m \int_B h(x, s) dx ds$.

4.1. The fitness-diffusion equation

We now derive the dynamical equations for $\theta_t(x, s), t \geq 0$, somewhat informally, for the case $(X, S) = \mathbb{R}^2$. A formal theorem specifying the precise mathematical conditions for convergence of a sequence of evolutionary birth–death processes satisfying (11)–(13), to a deterministic continuous process satisfying (23), will be left for future work.

When $N_0$ is large, laws of large numbers allow us to treat the collective evolution of the agents as a deterministic process, even though individual agents and family lines evolve randomly. Consider the small rectangle $R_{ost} \subset \mathbb{R}^2$ with one corner at $(x, s)$ and the opposite corner at $(x + dx, s + ds)$. Since the agents in the scaled model are distributed approximately in a density, $\theta_t(x, s, t)$, at time $t$ the number of agents in $R_{ost}$ is $\theta_t(x, s, t) dx ds + o(dx ds)$ and at time $t + dt$ it is $\theta_t(x, s, t) dx ds + o(dx ds)$. The change in the population of $R_{ost}$ in $[t, t + dt]$ is, therefore,

$$
\frac{d\theta_t}{dt}(x, s) dx ds dt = (A_{birth/death} + A_{drift} + A_{diffusion}) dx ds dt + o(dx ds dt),
$$

where the right side takes account of three factors:

1. births and deaths in $R_{ost}$, including proper offspring and mutants,
2. migration to and from $R_{ost}$ due to drift,
3. migration to and from $R_{ost}$ due to diffusion.

From (12) the number of proper offspring and mutants born in $R_{ost}$ in the interval $[t, t + dt]$ is $(mh(x, s) + \theta_t(x, s)F_t(x, s)) dx ds dt + o(dx ds dt)$, and the number of deaths in $R_{ost}$ in $[t, t + dt]$ is $d_t(x, s)\theta_t(x, s) dx ds dt + o(dx ds dt)$, so

$$
A_{birth/death} = mh(x, s) + (F_t(x, s) - d_t(x, s))\theta_t(x, s).
$$

From (11) it follows that in the scaled model, the number of agents moving out of $R_{ost}$ to the “left” in $[t, t + dt]$ due to spatial drift is $\beta_t(x, s)\theta_t(x, s) dx ds + o(dx ds)$, and the number of agents moving into $R_{ost}$ from the “right” in $[t, t + dt]$ due to spatial drift is $\beta_t(x + dx, s)\theta_t(x + dx, s) dx ds + o(dx ds)$, so the population change in $R_{ost}$ in $[t, t + dt]$ due to spatial drift is $\beta_t(x, s)\theta_t(x, s) dx ds + o(dx ds)$, likewise, the population change in $R_{ost}$ in $[t, t + dt]$ due to strategic drift is $\beta_t(x, s)\theta_t(x, s) dx ds + o(dx ds)$, so

$$
A_{drift} = \frac{1}{c} \int_{\mathbb{R}^2} \beta_t(x, s)\theta_t(x, s) dx ds + o(dx ds),
$$

To handle the stochastic part of Eq. (11) we note that the probability that a Brownian motion starting at $(x', s')$ at time $t'$ is in $R_{ost}$ at time $t$ has the form $P_{x', s'}(x', s', x, s) dx ds + o(dx ds)$, where

$$
P_{x', s'}((x', s'), (x, s)) = \frac{1}{2\pi \sigma^2} \exp \left(-\frac{(x-x')^2}{2\sigma^2}\right) \times \exp \left(-\frac{(s-s')^2}{2\sigma^2}\right).
$$

If random motion was the only dynamical force (no births/deaths or drift) then as $N_0 \to \infty$, with statistical certainty,

$$
\theta_t(x, s) = \int_x \int_{s'} \theta_t(x, s') P_{x', s'}((x', s'), (x, s)) dx' ds'.
$$

A direct calculation yields

$$
\frac{d\theta_t}{dt} = \frac{\alpha_T^2}{2} \frac{\partial^2 \theta_t}{\partial x^2} + \frac{\alpha_S^2}{2} \frac{\partial^2 \theta_t}{\partial s^2}.
$$

From (20) and (21) it follows that

$$
A_{diffusion} = \frac{\alpha_T^2}{2} \frac{\partial^2 \theta_t}{\partial x^2} + \frac{\alpha_S^2}{2} \frac{\partial^2 \theta_t}{\partial s^2}.
$$

Adding (18), (19) and (22) strongly suggests that if the birth, death, drift, and mutant rates are scaled properly as $N_0 \to \infty$, the evolutionary birth–death process, $\theta_t$, can be closely approximated by a density, $\theta_t$, governed by a PDE we call the fitness-diffusion equation:

If $N_0^{-1} \mu_t \approx \theta_t$, where $\theta_t$ is twice differentiable then $N_0^{-1} \mu_t \approx \theta_t$, where $\theta_t$ satisfies

$$
\frac{\partial \theta_t}{\partial t} = mh + (F_t - d_t)\theta_t + \frac{\partial}{c} \left[ \beta_t(x, s) \theta_t \right] + \frac{\partial}{c} \left[ \beta_t(x, s) \theta_t \right]
$$

$$
+ \frac{\sigma_T^2}{2} \frac{\partial^2 \theta_t}{\partial x^2} + \frac{\sigma_S^2}{2} \frac{\partial^2 \theta_t}{\partial s^2}, \quad t \geq 0,
$$

where $F_t(x, s)$ is given by (16) and $d_t(x, s)$ is given by (17).
Of particular interests are equilibrium population density functions, \( \theta^*(x, s) = \lim_{t \to \infty} \theta_t(x, s) \), which satisfy

\[
mh + (F^* + d*) \theta^* + \frac{\partial [\alpha^{\gamma^*}]_{x}}{\partial x} + \frac{\partial [\gamma^*, \theta^*]}{\partial x} + \frac{\partial^2 \gamma^*}{\partial x^2} + \frac{\partial^2 \theta^*}{\partial x^2} = 0, \quad (24)
\]

where \( F^* \), \( d^* \), \( \gamma^* \), and \( \alpha^* \) are the corresponding equilibrium fitness, death, and drift functions. Note that in a model with perfect mixing and no drift or diffusion terms, (23) reduces to (4) and (24) reduces to (5).

5. A case study: reactive strategies for the iterated prisoner’s dilemma

For the iterated prisoner’s dilemma there is a class of strategies, specified by two continuous parameters, that contains always-cooperate, always-defect, tit-for-tat and other generic strategies as special cases. These are the reactive strategies, specified by \((p, q) \in [0, 1]^2\), where \(p \) is the probability of cooperating in the \(n+1\)st game if the opponent cooperated in the \(n\)th game and \(q\) is the probability of cooperating in the \(n+1\)st game if the opponent defected in the \(n\)th game. Nowak (2006) analyzes the evolution of reactive strategies (under Axelrod’s payoffs) using the replicator equation (1) and reports some very interesting evolutionary dynamics. If (say) 100 strategies are randomly selected from the unit square, more often than not the strategies near (0,0) (always-defect) increase in frequency at the expense of all the others, until only those strategies are left. However, if there are strategies close enough to (1,0) (tit-for-tat) then a strange thing happens. Just when it looks like the always-defect strategies are about to drive all the others extinct, the tit-for-tat strategies suddenly start growing until they begin to dominate. After that, strategies close to (1,1/3) (generous tit-for-tat) take over and the evolution finally settles down.

5.1. An evolutionary birth–death model of evolving reactive strategies

To compare the evolutionary trajectories from the evolutionary birth–death model to the trajectories from the replicator equation, we construct an evolutionary birth–death model as close to Nowak’s model as possible. The strategy space, \( S \), is the unit square, \([0, 1]^2\). The variable \( X \) will not play a role, so we set \( X = 0 \) and ignore it in the subsequent calculations. Eq. (7) becomes

\[
F_t(p, q) = N_t^{-1} \sum_{i \in \mathcal{A}} \phi((p, q), (p_i(t), q_i(t))),
\]

where \(\phi((p_1, q_1), (p_2, q_2))\), specified below, is the payoff function. Perfect mixing also implies that the death rate should depend on the entire population, so \(d_i(t) = cN_i\) for each \(i \in \mathcal{A}\). Nowak defines \(\phi((p_1, q_1), (p_2, q_2))\) to be the stationary per-game payoff in the iterated game, which can be derived by a Markov chain analysis. Nowak used Axelrod’s prisoner’s dilemma payoffs: three for mutual cooperation, one for mutual defection, zero for cooperating against a defector, and five for defecting against cooperation. In that case,

\[
\phi((p_1, q_1), (p_2, q_2)) = 3r_1r_2 + 5(1 - r_1)r_2 + (1 - r_1)(1 - r_2),
\]

where

\[
r_1 = \frac{q_2(p_1 - q_1) + q_1}{1 - (p_1 - q_1)p_2 - q_2}, \quad r_2 = \frac{q_1(p_2 - q_2) + q_2}{1 - (p_1 - q_1)p_2 - q_2}
\]

are the stationary probabilities of players 1 and 2 cooperating. (Eq. (26) is not defined if \((p_1 - q_1)p_2 - q_2) = 1, but this has no effect on the subsequent analysis.) There is no “drift” in the replicator equation, so the model is pure Darwinian selection. The resulting agent evolutionary trajectories, \( s(t) \), \( t \in [t, T] \), \( i = 1, 2, \ldots \) are, therefore, two-dimensional Brownian motions when they are in the interior of \( S \), i.e.,

\[
\frac{dp_i}{dt} = \sigma \frac{dW_i^p}{dW_i^p}.
\]

In this model we are free to choose the boundary behavior of the Brownian motion from several possibilities: we choose orthogonal reflection for its simplicity.

Brownian motion on \([0, 1]^2\) with orthogonal reflection can be understood by noting how it is simulated. Time is discretized into time steps of length \(dt\). To determine \((p(t + dt), q(t + dt))\) from \((p(t), q(t))\), we first generate \((dp_i(t), dq_i(t))\) as two independent Normal variates with mean 0 and variance \(\sigma^2 dt\). If \((p(t) + dp_i(t), q(t) + dq_i(t))\) remains inside the unit square then we set \((p(t + dt), q(t + dt)) = (p(t) + dp_i(t), q(t) + dq_i(t))\). However, if it is outside the unit square then it “reflects” back in, e.g., if \(p(t) + dp_i(t) = 1 + \varepsilon\) then we set \(p(t + dt) = 1 - \varepsilon\). See Harrison (1985) for a precise definition and analysis of reflected (regulated) Brownian motion.

The agent trajectories in the evolutionary birth–death process are governed by a system of stochastic ODEs, and, therefore, can be numerically simulated using the Euler–Maruyama method (Higham, 2001). (Milstein’s higher order method reduces to the Euler–Maruyama Method in our model because \(\sigma\) is a constant.) In each time step the probability that each agent spawns or dies and the probability of a mutant birth is given by (12) and (13), so the branching and dying aspect of the simulation is very simple. The bottleneck in the simulation is evaluating the fitness of each agent (25). This calculation uses \(O(N_t^2)\) computations at each time step. Populations of a few hundred or even a few thousand agents pose no insurmountable computational difficulties, but there is a limit to how large a model can be realistically simulated.

In the replicator equation, the total population does not change. In the evolutionary birth–death formulation, the population fluctuates, but remains fairly stable automatically. This is an intrinsic difference between the two approaches. There are also no “mutants” in the replicator equation, so we do not want too many in our model. However, in the evolutionary birth–death model, “species” can literally go extinct, so large regions of \( S \) may be completely uninhabited during long stretches of the simulation. The time until a species re-emerges due to random fluctuations alone could be prohibitively large, but a small stream of mutants allows every species to occasionally get a chance to compete in the environment. For simplicity we set \(h(p, q) = 1\), \(0 < p, q < 1\), so mutants choose a strategy uniformly from the square.

The model parameters can be varied in many ways, and the resulting simulations have many interesting features. Fig. 1 illustrates the \(p_i(t)\) component of the evolutionary birth–death process, \(\Theta_t\), for a single family line. The death rate is very low when \(N_t\) is small, so most sample paths look like Fig. 1. In the absence of mutants, the population will eventually reach an equilibrium. (Technically, there is no equilibrium since the probability of eventual extinction is one; but the expected time until extinction can be extremely large.) If the mutant rate \(m > 0\) then individual family lines have to compete with other family lines, and their lifetimes are much shorter.

When the populations get larger and the time frame of the simulation longer, the individual agent trajectories and family lines run together and can no longer be easily discerned. Fig. 2 shows the trajectories of \(p_i(t)\) and \(q_i(t)\) of a model similar in size to the ones Nowak (2006) described. The initial population level is \(N_0 = 100\), and \((p_i, q_i), i \in \mathcal{A}\) are chosen uniformly in the unit square. From (26) we can guess that the average per-agent birth rate will be between 1.0 and 2.0, so if we set the death rate
The population switches back to always-defect. This shifting between always defect and tit-for-tat seems to continue indefinitely with the transition times quite random. The simulation in Fig. 2. Only the (almost) successful mutants can be seen.

**Fig. 2.** Simulated trajectories of $p_i(t)$ and $q_i(t)$, $0 < t < 1500$, for a model with parameters, $N_0 = 100$, $c = 0.02$, $\sigma = 0.01$, and $m = 2.0$. The initial population, $(p_i(0), q_i(0)), i \in A_t$ is randomly and evenly spread out on the unit square, but there is a mass extinction during the first stages of the process (Fig. 3). The remaining agents are clustered around $p = 0$ and $q = 0$ (always-defect). At about $t = 300$ we see a shift from $p = 0$ to 1, corresponding to a take over by agents playing tit-for-tat. However, at about $t = 400$ the population switches back to always-defect. It appears that the shifts from always-defect to tit-for-tat and vice-versa are usually due to a mutant whose family line takes over the population. Note that when a dominant tit-for-tat colony persists for long enough, the $q$ values of the colony tend to move from 0 to 1/3, which is generous tit-for-tat.

**Fig. 3.** A close-up of the mass extinctions at the beginning ($0 < t < 100$) of the simulation in Fig. 2. Only $p_r(t)$ is shown, since $q_r(t)$ is very similar. By $t = 10$ most of the population is near always defect. At this time scale, the family lines of some of the (almost) successful mutants can be seen.

The basic evolutionary tendencies can be seen clearly through the haze of mutant strains. Fig. 4 shows the population trajectory, $N_t$, and the fitness trajectories, $F_t(i)$. Comparing Fig. 4 with Fig. 2 it is apparent that when the population is concentrated near always-defect $(0, 0)$, the average fitness is often less than 1.0, and when it is concentrated near tit-for-tat $(1, 0)$ or generous tit-for-tat $(1, 1/3)$ the average fitness is often more than 2.0. The difference in the population levels resulting from the two configurations can be clearly seen.

If the death rate is decreased, then (10) shows that the equilibrium population levels will increase proportionately. Fig. 5 shows $p_i(t)$ and $q_i(t)$ for a model with populations in the 300–600 range. The collective evolution is clearly "smoother" than that shown in Fig. 2, but the same tendency to alternate between defection and cooperation is apparent.

### 5.2. A fitness-diffusion equation for evolving reactive strategies

The fitness-diffusion equation corresponding to our evolutionary birth–death model has the form

$$\frac{\partial \theta_i}{cP} = m + (F_t - cN_t)\theta_i + \frac{\sigma^2}{2} \left( \frac{\partial^2 \theta_i}{cP^2} + \frac{\partial^2 \theta_i}{cQ^2} \right)$$  \hspace{1cm} (27)$$

with boundary conditions (corresponding to orthogonal reflection; Harrison, 1985)

$$\frac{\partial \theta_i}{cP}(0, q') = \frac{\partial \theta_i}{cP}(1, q') = \frac{\partial \theta_i}{cQ}(p', 0) = \frac{\partial \theta_i}{cQ}(p', 1) = 0, \quad 0 < p', q' < 1,$$  \hspace{1cm} (28)$$
Fig. 4. The population level, \( N_t \), and the agent fitness levels, \( F_t(i) \), for the simulation of Fig. 2. Note the almost perfect correlation between the two. The fitness and population levels are high when the population is dominated by tit-for-tat players, and low when it is dominated by always defect players.

Fig. 5. Simulated trajectories of \( p_t(i) \) and \( q_t(i) \), \( 0 \leq t \leq 5000 \) for a model with parameters \( N_0 = 400, c = 0.004, \sigma = 0.01 \), and \( m = 1.0 \). Comparing Fig. 5 with Fig. 2, it is apparent that the larger average population leads to a more predictable outcome, but the transition times from always-defect to (generous) tit-for-tat and back again are still random and appear to continue indefinitely. The gradual adaptation from tit-for-tat to generous tit-for tat when \( p \approx 1 \) is more apparent here than in Fig. 2.
where
\[ N_t = \int_0^1 \int_0^1 \theta_t(p,q) \, dp \, dq \]
is the population at time \( t \) and
\[ F_t(p,q) = N_t^{-1} \int_0^1 \int_0^1 \phi((p,q),(p',q')) \theta((p',q')) \, dp' \, dq' \]
is the fitness of strategy \((p,q)\) at time \( t \).

It is relatively simple to solve the fitness-diffusion equation numerically by finite differences (LeVeque, 2007). The numerical bottleneck is calculating the fitness function (29), which in the present case uses \( O(n^4) \) computations per time-step, where \( n \) is the grid size.

As expected, the fitness-diffusion equation (27) with boundary conditions (28) appears to have two stable equilibria; one concentrated near \((0,0)\) (always-defect) and the other concentrated near \((1,1/3)\) (generous tit-for-tat). The equilibrium solutions satisfy (24), which for this problem takes the form
\[ m + (F^* - cN^*)0^* + \frac{\sigma^2}{2} \left( \frac{\partial^2 \theta^*}{\partial p^2} + \frac{\partial^2 \theta^*}{\partial q^2} \right) = 0 \]
with boundary conditions
\[ \frac{\partial \theta^*}{\partial p}(0,q^*) = \frac{\partial \theta^*}{\partial q}(1,q^*) = \frac{\partial \theta^*}{\partial q}(p^*,0) = \frac{\partial \theta^*}{\partial q}(p^*,1) = 0, \quad 0 < p^*, q^* < 1. \]
The two basins of attraction (the set of parameter settings and initial population densities that converge to each equilibrium) have not been mapped out in any detail, but it is a simple matter to find parameter settings and initial densities from each basin.

Fig. 6. Dynamics of the population density function, \( \theta_t(p,q) \), \( 0 \leq t \leq 200 \) from the fitness-diffusion equation, for a model with parameters, \( m = 0.01, c = 1.0, \) and \( \sigma = 0.02 \). In this example, the initial population density is approximately uniform over the half of the unit square including the corners \((0,0)\) (always-defect), \((1,0)\) (tit-for-tat), and \((1,1)\) (always-cooperate). The axis on the “left” is \( 0 \leq p < 1 \) and the axis on the “right” is \( 0 \leq q < 1 \). The grid used in the numerical calculation is \( 30 \times 30 \), and the tick marks on the \( p \) and \( q \) axes correspond to the grid. The dynamics here are analogous to the dynamics from the evolutionary birth–death equation, but are deterministic. The population initially move towards always-defect, completing that phase by about \( t = 20 \), then move towards tit-for-tat, completing that phase by about \( t = 100 \), and then move towards generous tit-for-tat, where it settles down. Although it is easy to find initial population densities (like this one) that converge to generous tit-for-tat, most examples seem to converge to a density concentrated near always-defect. The stable densities near always-defect and generous tit-for-tat appear to be the only ones for reactive strategies.
Fig. 6 shows an initial population density, concentrated on the tit-for-tat half of the unit square, morphing into the stable density around generous tit-for-tat. Our experiments show that most initial densities in the always-defect basin move towards their limit very rapidly, so their trajectories are not as interesting. Fig. 7 shows the corresponding $t_t(p, q)$, $t > 0$ trajectories for always-defect, tit-for-tat, and generous tit-for-tat, for three settings of $\sigma$ (the diffusion term) near the boundary of the two basins of attraction. The first two (corresponding to $\sigma = 0.02$ and 0.026) end up dominated by cooperating strategies, while the third ($\sigma = 0.0275$) ends up dominated by defectors. Fig. 8 shows the population level, $\text{N}_t$, for the same three cases. It is difficult to find the precise location of the boundary between the two basins of attraction, but when $m = 0.01$ and $c = 1.0$, it appears that the critical value of $\sigma$ is about 0.0262. The diffusion parameter, $\sigma$, whose precise value often determines which basin of attraction the fitness-diffusion model is in, has no analog in deterministic evolutionary models like the replicator equation.

6. Summary and concluding remarks

In this paper we introduce two new models of evolutionary dynamics. In both models, the evolution occurs in a continuous spatial environment, $X$, and an agent’s fitness in the environment depends on the numbers and locations of its peers, and its game payoffs against them. The space of game strategies, $S$, is also a continuum in both models. In the first model, the agents are discrete. They move, evolve, spawn, and die in $(X, S)$, according to the stochastic equations (11)–(13). We call the resulting stochastic
process an evolutionary birth–death process. The second model is analogous to the first, except that the agents are not discrete. Instead, the agents are spread out in a continuous density over \((X, S)\). The evolution of the population density function is a second order (deterministic) PDE given by equation (23), which we call a fitness-diffusion equation. The nature of the analogy between the two models can be made exact. The fitness diffusion equation is derived, via an asymptotic analysis, as an approximation to the evolutionary birth–death equations when the agents populations are large and smoothly distributed on \((X, S)\). We study both our models when applied to the evolution of reactive strategies for the iterated prisoner’s dilemma, and compare them to Nowak's results using the replicator equation. While the qualitative forms of the evolutionary trajectories produced by our models are quite different from each other, and quite different from those produced by the replicator equation, the same basic behavior is observed in every case when applied to reactive strategies.

At this point it is not clear whether the fitness-diffusion equation or the evolutionary birth–death process should be considered our primary model of evolutionary dynamics. Either can be thought of as an approximation for the other. Typically, if one model is appropriate for a given example, the other model is appropriate as well. Since the solutions of the two models are quite different in form—a branching/dying stochastic ODE for the evolutionary birth–death process (e.g., Fig. 1) and a continuously deforming density function for the fitness-diffusion equation (e.g., Fig. 6)—the modeler can try to employ both models when analyzing an example, as we did for the reactive strategies in the iterated prisoner’s dilemma.

There are trade-offs between numerically solving the fitness-diffusion equation and numerically simulating the evolutionary birth–death process. The numerical bottleneck in solving the fitness-diffusion equation is calculating the fitness function (16), which depends on the grid size used. If \((X, S)\) is \(d\)-dimensional, then the complexity of solving (16) is \(O(n^{2d})\), where \(n\) is the size of the grid. The numerical bottleneck in simulating the evolutionary birth–death process is calculating (7) for each living agent. The complexity is, therefore, \(O(N^n)\), where \(N\) is the average population size. The population size is not an issue in the numerical solution of the fitness-diffusion equation, and the dimension of \((X, S)\) is not an issue in the simulation of the evolutionary birth–death process. An evolutionary birth–death process with a large population may be numerically intractable, even if the dimension of \((X, S)\) is small. In such cases, the fitness-diffusion equation is the preferred model. On the other hand, if moderate population sizes are sufficient for the model, then high dimensional examples can be analyzed by the evolutionary birth–death equations. In any case, the development of efficient algorithms for solving (simulating) the evolutionary birth–death equations and the fitness-diffusion equation will greatly expand the scope of the models. A mathematical study of the basic differential equations introduced here, (3)–(5), (23), and (24) would help in that regard.

By mimicking Nowak's analysis of reactive strategies for the iterated prisoner's dilemma, we found an ideal preliminary study of our two models. In that example, \((X, S)\) is two-dimensional (S is the unit square and X is absent since Nowak's model assumes perfect mixing), so both models can be solved relatively easily and compared to Nowak's results. Most examples of interest are likely to be higher dimensional. For example, it would be interesting to analyze the evolution of reactive strategies for the iterated prisoner's dilemma on a torus. A torus is an ideal spatial environment for our models. It is a finite surface with no boundary and is naturally represented as a unit square. For reactive strategies on a torus, \((X, S)\) is, therefore, the four-cube. Simulating the evolutionary birth–death process in this case is no harder than the perfect mixing case, but the fitness-diffusion equation has become more difficult, i.e., a computational complexity of \(O(n^8)\) vs. \(O(n^4)\). For suitable choices of the weighting functions \(\psi\) and \(\bar{\psi}\), distinct "local ecosystems" (clusters of agents) could emerge and persist on a torus. Distinct clusters would evolve (almost) independently, so a spatial model can feature simultaneous evolutionary processes. Based on our results in Section 5, in the case of reactive strategies some clusters would be dominated by strategies around always-defect and others would be dominated by strategies around tit-for-tat or generous tit-for-tat. Due to the random motion of the clusters, occasionally two of them would come close enough together to interact. The resulting "chaos" would be interesting to study. Models with (deterministic) drift would be interesting to study as well. If we allow the agents to drift in \(X\) along their fitness gradients, i.e., \(\bar{\psi}(i)\) with the form (15), then agents will tend to move towards clusters of agents that they play well against. Likewise, they will tend to move away from clusters of agents that they play poorly against. We will leave these, and other interesting applications of the models introduced here, to future work.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at 10.1016/j.jtbi.2008.06.032.

References


