Supporting Information for Stochastic game dynamics under demographic fluctuations

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1 Relating payoffs to birth

If payoffs affect birth instead of competition, the corresponding reactions can be written as

$$\begin{array}{ll} X+X & \xrightarrow{a} X+X+X\\ X+Y & \xrightarrow{b} X+Y+X\\ X+Y & \xrightarrow{c} X+Y+Y\\ Y+Y & \xrightarrow{d} Y+Y+X. \end{array}$$

Using the same principle as in the main text, i.e. individuals with higher payoffs have advantages in pairwise interactions, the birth rates should be an increasing function of the payoff elements a, b, c, and d. The simplest choice is that birth rates equal payoffs. We assume constant intrinsic death rate λ_d for both types, which implies

$$X \xrightarrow{\lambda_d} 0$$
 and $Y \xrightarrow{\lambda_d} 0$

Following a logistic growth model, we assume neutral competition

$$\begin{array}{ccc} X + X & \xrightarrow{\lambda_c} X \\ X + Y & \xrightarrow{\lambda_c} X \\ X + Y & \xrightarrow{\lambda_c} Y \\ Y + Y & \xrightarrow{\lambda_c} Y \end{array}$$

Combining the ten reactions above, we obtain the deterministic rate equations

$$\dot{x} = x (a x + b y - \lambda_c (x + y) - \lambda_d),$$

$$\dot{y} = y (c x + d y - \lambda_c (x + y) - \lambda_d),$$
 (1)

where x and y are the densities of individuals of type X and type Y. We denote the frequencies by u = x/(x + y) and v = y/(x + y). With Eqs. (1), we obtain the change of the frequency of type X as

$$\dot{u} = \frac{\dot{x} y - \dot{y} x}{(x+y)^2}$$

=
$$\underbrace{(x+y)}_{N} \underbrace{u(1-u)[(a-b-c+d)u+b-d]}_{\text{Replicator dynamics}}.$$
 (2)

The dynamics is equivalent to the replicator dynamics scaled by the total population size N. As N changes over time, this can be considered as a dynamical, non-linear rescaling of time without changing the trajectories or equilibria from the standard replicator dynamics [1].

If we now focus on a homogenous population with type X individuals only, i.e. y = 0, in Eqs. (1), we have

$$\dot{x} = x \left((a - \lambda_c) x - \lambda_d \right). \tag{3}$$

This equation has two equilibria, x = 0 and $x = \frac{\lambda_d}{a - \lambda_c}$. The first equilibrium x = 0, corresponding to extinction, is stable. The second equilibrium $x = \frac{\lambda_d}{a - \lambda_c}$ exists when $a > \lambda_c$. However it is always unstable as $\dot{x} > 0$ for $x > \frac{\lambda_d}{a - \lambda_c}$ and $\dot{x} < 0$ for $x < \frac{\lambda_d}{a - \lambda_c}$. In this alternative model where interactions affect birth, a homogenous population either goes extinct or explodes, depending on the initial population size. Although, the deterministic equations Eqs. (1) and (2) appear to be reasonable, their ecological meaning remains unclear [2].

2 Master equation and the diffusion approximation

The microscopic process is a two dimensional Markov process in continuous time which can described by its master equation [3],

$$\frac{\partial P(x, y, t)}{\partial t} = T_{x-1}^{+} P(x-1, y, t) + T_{y-1}^{+} P(x, y-1, t)
+ T_{x+1}^{-} P(x+1, y, t) + T_{y+1}^{-} P(x, y+1, t)
- (T_{x}^{+} + T_{y}^{+} + T_{x}^{-} + T_{y}^{-}) P(x, y, t),$$
(4)

where P(x, y, t) is the probability that there are x individuals of type X and y individuals of type Y at time t, and T is the transition rate of the population from one state to its neighbouring state. The subscript of T refers to the type whose density changes, and the superscript denotes whether its density increases by one or decreases by one. For example, T_x^+ is rate that the number of type X increases from x to x + 1 and the number of type Y remains constant and T_y^+ is rate that the number of type Y increases from y to y + 1 and the number of type X remains constant. The transition rates can be deduced from the reaction rates and the number of individuals of those types involved in the corresponding reactions,

$$T_{x}^{+} = \lambda_{x \to xx} x$$

$$T_{y}^{+} = \lambda_{y \to yy} y$$

$$T_{x}^{-} = \lambda_{x \to 0} x + \frac{x^{2}}{aM} + \frac{x y}{bM}$$

$$T_{y}^{-} = \lambda_{y \to 0} y + \frac{y^{2}}{dM} + \frac{x y}{cM}.$$
(5)

Here, M is a scaling term which determines the frequency of competition compared to intrinsic growth. As we have shown in the main text, it controls the size of the system. When M is larger, the density of individuals in the deterministic equilibria is larger.

To perform a diffusion approximation of the master equation, we scale the numbers x and y by M, $\tilde{x} = x/M$ and $\tilde{y} = y/M$. The new variables \tilde{x} and \tilde{y} are approximately continuous for

sufficiently large M. We also rescale time as $\widetilde{t}=t/M.$ This leads to

$$\frac{\partial P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{t}} = T^{+}_{\tilde{x} - \frac{1}{M}} P(\tilde{x} - \frac{1}{M}, \tilde{y}, \tilde{t}) + T^{+}_{\tilde{y} - \frac{1}{M}} P(\tilde{x}, \tilde{y} - \frac{1}{M}, \tilde{t}) \\
+ T^{-}_{\tilde{x} + \frac{1}{M}} P(\tilde{x} + \frac{1}{M}, \tilde{y}, \tilde{t}) + T^{-}_{\tilde{y} + \frac{1}{M}} P(\tilde{x}, \tilde{y} + \frac{1}{M}, \tilde{t}) \\
- (T^{+}_{\tilde{x}} + T^{+}_{\tilde{y}} + T^{-}_{\tilde{x}} + T^{-}_{\tilde{y}}) P(\tilde{x}, \tilde{y}, \tilde{t}),$$
(6)

Note when we rescale the time, we also need to rescale the transition rates accordingly. Thus in the same time unit, the transition rate from, for example, from state (x, y) to state (x + 1, y), equals to the transition rate from the scaled state (\tilde{x}, \tilde{y}) and the scaled state $(\tilde{x} + \frac{1}{M}, \tilde{y})$. This leads to

$$T_{\widetilde{x}}^{+} = M\lambda_{x \to xx} \widetilde{x}$$

$$T_{\widetilde{y}}^{+} = M(\lambda_{y \to yy} \widetilde{y})$$

$$T_{\widetilde{x}}^{-} = M(\lambda_{x \to 0} \widetilde{x} + \frac{\widetilde{x}^{2}}{aM} + \frac{\widetilde{x} y}{bM})$$

$$T_{\widetilde{y}}^{-} = M(\lambda_{y \to 0} \widetilde{y} + \frac{\widetilde{y}^{2}}{dM} + \frac{\widetilde{x} \widetilde{y}}{cM}).$$
(7)

Now we expand the transition rates and probability densities in Eq. (6) in a Taylor series at \tilde{x} or \tilde{y} , and we obtain

$$P(\tilde{x} \pm \frac{1}{M}, \tilde{y}, \tilde{t}) \approx P(\tilde{x}, \tilde{y}, \tilde{t}) \pm \frac{\partial P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^2 P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{x}^2} \frac{1}{2M^2},$$

$$P(\tilde{x}, \tilde{y} \pm \frac{1}{M}, \tilde{t}) \approx P(\tilde{x}, \tilde{y}, \tilde{t}) \pm \frac{\partial P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^2 P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{y}^2} \frac{1}{2M^2},$$

$$T_{\tilde{x} - \frac{1}{M}}^+ \approx T_{\tilde{x}}^+ - \frac{\partial T_{\tilde{x}}^+}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^2 T_{\tilde{x}}^+}{\partial \tilde{x}^2} \frac{1}{2M^2},$$

$$T_{\tilde{x} + \frac{1}{M}}^- \approx T_{\tilde{x}}^- + \frac{\partial T_{\tilde{x}}^-}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^2 T_{\tilde{x}}^-}{\partial \tilde{x}^2} \frac{1}{2M^2},$$

$$T_{\tilde{y} - \frac{1}{M}}^+ \approx T_{\tilde{y}}^+ - \frac{\partial T_{\tilde{y}}^+}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^2 T_{\tilde{y}}^-}{\partial \tilde{y}^2} \frac{1}{2M^2},$$

$$T_{\tilde{y} + \frac{1}{M}}^- \approx T_{\tilde{y}}^- + \frac{\partial T_{\tilde{y}}^-}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^2 T_{\tilde{y}}^-}{\partial \tilde{y}^2} \frac{1}{2M^2}.$$
(8)

We denote $P = P(\tilde{x}, \tilde{y}, \tilde{t})$ and insert Eqs. (8) into Eq. (6), then we obtain

$$\frac{\partial P}{\partial \tilde{t}} \approx \left(T_{\tilde{x}}^{+} - \frac{\partial T_{\tilde{x}}^{+}}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^{2} T_{\tilde{x}}^{+}}{\partial \tilde{x}^{2}} \frac{1}{2M^{2}} \right) \left(P - \frac{\partial P}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^{2} P}{\partial^{2} \tilde{x}} \frac{1}{2M^{2}} \right) \\
+ \left(T_{\tilde{y}}^{+} - \frac{\partial T_{\tilde{y}}^{+}}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^{2} T_{\tilde{y}}^{+}}{\partial \tilde{y}^{2}} \frac{1}{2M^{2}} \right) \left(P - \frac{\partial P}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^{2} P}{\partial^{2} \tilde{y}} \frac{1}{2M^{2}} \right) \\
+ \left(T_{\tilde{x}}^{-} + \frac{\partial T_{\tilde{x}}^{-}}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^{2} T_{\tilde{x}}^{-}}{\partial \tilde{x}^{2}} \frac{1}{2M^{2}} \right) \left(P + \frac{\partial P}{\partial \tilde{x}} \frac{1}{M} + \frac{\partial^{2} P}{\partial^{2} \tilde{x}} \frac{1}{2M^{2}} \right) \\
+ \left(T_{\tilde{y}}^{-} + \frac{\partial T_{\tilde{y}}^{-}}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^{2} T_{\tilde{y}}^{-}}{\partial \tilde{y}^{2}} \frac{1}{2M^{2}} \right) \left(P + \frac{\partial P}{\partial \tilde{y}} \frac{1}{M} + \frac{\partial^{2} P}{\partial^{2} \tilde{y}} \frac{1}{2M^{2}} \right) \\
- \left(T_{\tilde{x}}^{+} + T_{\tilde{y}}^{+} + T_{\tilde{x}}^{-} + T_{\tilde{y}}^{-} \right) P.$$
(9)

If we consider only the terms of the first order M^{-1} and the second order M^{-2} in Eq. (9), we obtain the Fokker-Planck equation

$$\frac{\partial P}{\partial \tilde{t}} = -\frac{1}{M} \left(\frac{\partial}{\partial \tilde{x}} \left(\left(T_{\tilde{x}}^{+} - T_{\tilde{x}}^{-} \right) P \right) + \frac{\partial}{\partial \tilde{y}} \left(\left(T_{\tilde{y}}^{+} - T_{\tilde{y}}^{-} \right) P \right) \right)
+ \frac{1}{2M^{2}} \left(\frac{\partial^{2}}{\partial^{2} \tilde{x}} \left(\left(T_{\tilde{x}}^{+} + T_{\tilde{x}}^{-} \right) P \right) + \frac{\partial^{2}}{\partial^{2} \tilde{y}} \left(\left(T_{\tilde{y}}^{+} + T_{\tilde{y}}^{-} \right) P \right) \right).$$
(10)

From Eqs. (7), we have $T_{\widetilde{x}}^+ - T_{\widetilde{x}}^- = M((\lambda_{x \to xx} - \lambda_{x \to 0})\widetilde{x} - \frac{\widetilde{x}^2}{aM} - \frac{\widetilde{x}\widetilde{y}}{bM}), T_{\widetilde{y}}^+ - T_{\widetilde{y}}^- = M((\lambda_{y \to yy} - \lambda_{y \to 0})\widetilde{y} - \frac{\widetilde{y}^2}{dM} - \frac{\widetilde{x}\widetilde{y}}{cM}), T_{\widetilde{x}}^+ + T_{\widetilde{x}}^- = M((\lambda_{x \to xx} + \lambda_{x \to 0})\widetilde{x} + \frac{\widetilde{x}^2}{aM} + \frac{\widetilde{x}\widetilde{y}}{bM}), \text{ and } T_{\widetilde{y}}^+ + T_{\widetilde{y}}^- = M((\lambda_{y \to yy} + \lambda_{y \to 0})\widetilde{y} + \frac{\widetilde{y}^2}{dM} + \frac{\widetilde{x}\widetilde{y}}{cM}).$ Putting these into Eq. (10), we can rewrite the Fokker-Planck equation as

$$\frac{\partial P(\tilde{x}, \tilde{y}, \tilde{t})}{\partial \tilde{t}} = - \frac{\partial}{\partial \tilde{x}} \left((\lambda_{x \to xx} - \lambda_{x \to 0}) \tilde{x} - \frac{\tilde{x}^2}{aM} - \frac{\tilde{x}\tilde{y}}{bM} \right) P(\tilde{x}, \tilde{y}, \tilde{t})
- \frac{\partial}{\partial \tilde{y}} \left((\lambda_{y \to yy} - \lambda_{y \to 0}) \tilde{y} - \frac{\tilde{y}^2}{dM} - \frac{\tilde{x}\tilde{y}}{cM} \right) P(\tilde{x}, \tilde{y}, \tilde{t})
+ \frac{1}{2M} \frac{\partial^2}{\partial^2 \tilde{x}} \left((\lambda_{x \to xx} + \lambda_{x \to 0}) \tilde{x} + \frac{\tilde{x}^2}{aM} + \frac{\tilde{x}\tilde{y}}{bM} \right) P(\tilde{x}, \tilde{y}, \tilde{t})
+ \frac{1}{2M} \frac{\partial^2}{\partial^2 \tilde{y}} \left((\lambda_{y \to yy} + \lambda_{y \to 0}) \tilde{y} + \frac{\tilde{y}^2}{dM} + \frac{\tilde{x}\tilde{y}}{cM} \right) P(\tilde{x}, \tilde{y}, \tilde{t}).$$
(11)

The equivalent stochastic differential equations [4], which can often be handled in a numerically

more efficient way, are

$$\frac{\partial \widetilde{x}}{\partial \widetilde{t}} = (\lambda_{x \to xx} - \lambda_{x \to 0})\widetilde{x} - \frac{\widetilde{x}^2}{aM} - \frac{\widetilde{x}\widetilde{y}}{bM} + \sqrt{\frac{\widetilde{x}}{M}} \left(\lambda_{x \to xx} + \lambda_{x \to 0} + \frac{\widetilde{x}}{aM} + \frac{\widetilde{y}}{bM}\right)} \xi,$$

$$\frac{\partial \widetilde{y}}{\partial \widetilde{t}} = (\lambda_{y \to yy} - \lambda_{y \to 0})\widetilde{y} - \frac{\widetilde{y}^2}{dM} - \frac{\widetilde{x}\widetilde{y}}{cM} + \sqrt{\frac{\widetilde{y}}{M}} \left(\lambda_{y \to yy} + \lambda_{y \to 0} + \frac{\widetilde{y}}{dM} + \frac{\widetilde{x}}{cM}\right)} \xi, \quad (12)$$

where ξ is Gaussian white noise with mean 0 and variance 1. Note that the noise term vanishes when the population is close to extinction, but increases approximately linearly in the population density.

3 The stability of the equilibria

The deterministic rate equations for two types are

$$\dot{x} = x \left(r - \frac{1}{a} \frac{x}{M} - \frac{1}{b} \frac{y}{M} \right)$$
(13a)

$$\dot{y} = y \left(r - \frac{1}{c} \frac{x}{M} - \frac{1}{d} \frac{y}{M} \right),$$
 (13b)

where x and y denote the densities of individuals of type X and Y, and r refers to the same intrinsic growth rate for both types. For $\dot{x} = 0$ and $\dot{y} = 0$, we have four equilibria, $E_1 = (0,0)$, $E_2 = (0, dMr)$, $E_3 = (aMr, 0)$, $E_4 = (\frac{ac(b-d)}{bc-ad}Mr, \frac{bd(c-a)}{bc-ad}Mr)$. In the following, we perform a linear stability analysis of the four equilibria. The Jacobian matrix at the equilibrium (x^*, y^*) is

$$J(x^*, y^*) = \begin{bmatrix} r - \frac{2x^*}{aM} - \frac{y^*}{bM} & -\frac{x^*}{bM} \\ -\frac{y^*}{cM} & r - \frac{x^*}{cM} - \frac{2y^*}{dM} \end{bmatrix}.$$
 (14)

- (i) For $E_1 = (0,0)$, $J(0,0) = \begin{bmatrix} r & 0 \\ 0 & r \end{bmatrix}$. Thus, for any r > 0, the two eigenvalues are positive and this equilibrium is unstable.
- (ii) For $E_2 = (0, dMr)$, $J(0, dMr) = \begin{bmatrix} r \frac{d}{b}r & 0 \\ -\frac{d}{c}r & -r \end{bmatrix}$ with eigenvalues -r and -(d-b)r/b. If d > b, the equilibrium is stable. Otherwise, it is unstable.

(iii) For
$$E_2 = (aMr, 0)$$
, $J(aMr, 0) = \begin{bmatrix} -r & -\frac{a}{b}r \\ 0 & r - \frac{a}{c}r \end{bmatrix}$ with eigenvalues $-r$ and $-(a-c)r/c$. If

a > c, the equilibrium is stable. Otherwise, it is unstable.

(iv) For $E_4 = (\frac{ac(b-d)}{bc-ad}Mr, \frac{bd(c-a)}{bc-ad}Mr)$, the Jacobian matrix in this equilibrium is

$$J_{E_{4}} = \begin{bmatrix} r - \frac{2(b-d)c}{bc-ad}r - \frac{d(c-a)}{bc-ad}r & -\frac{ac(b-d)}{b(bc-ad)}r \\ -\frac{bd(c-a)}{c(bc-ad)}r & r - \frac{a(b-d)}{bc-ad}r - \frac{2b(c-a)}{bc-ad}r \end{bmatrix}$$

$$= r \begin{bmatrix} -\frac{c(b-d)}{bc-ad} & -\frac{ac(b-d)}{b(bc-ad)} \\ -\frac{bd(c-a)}{c(bc-ad)} & -\frac{b(c-a)}{bc-ad} \end{bmatrix}.$$
 (15)

Thus the eigenvalues λ can be obtained given

$$\left(\underbrace{-\frac{c(b-d)}{bc-ad}}_{A} - \lambda\right) \left(\underbrace{-\frac{b(c-a)}{bc-ad}}_{B} - \lambda\right) - \underbrace{\frac{ad(b-d)(c-a)}{(bc-ad)^2}}_{C} = 0.$$
 (16)

We can write Eq.(16) as $\lambda^2 - (A+B)\lambda + AB - C = 0$, thus $\lambda = \frac{A+B}{2} \pm \sqrt{\frac{(A-B)^2}{4} + C}$. This equilibrium exists only if the densities of both types are positive, i.e. $\frac{ac(b-d)}{bc-ad} > 0$ and $\frac{bd(c-a)}{bc-ad} > 0$. This yields two cases: b > d & c > a and b < d & c < a, which both result in C > 0 and A + B < 0.

Thus, the first eigenvalue $\lambda_1 = \frac{A+B}{2} - \sqrt{\frac{(A-B)^2}{4} + C}$, is always negative. The second eigenvalue $\lambda_2 = \frac{A+B}{2} + \sqrt{\frac{(A-B)^2}{4} + C}$ is negative if $\frac{(A+B)^2}{4} > \frac{(A-B)^2}{4} + C$, which can be simplified to AB - C > 0. From Eq. (16), we have

$$AB - C = \frac{c(b-d)}{bc-ad} \frac{b(c-a)}{bc-ad} - \frac{ad(b-d)(c-a)}{(bc-ad)^2}$$

= $\frac{(bc-ad)(b-d)(c-a)}{(bc-ad)^2}$
= $\frac{(b-d)(c-a)}{bc-ad}$. (17)

Thus, if b > d & c > a, then AB - C > 0 and the equilibrium is stable; if b < d & c < a, the equilibrium is unstable.

In general, although the equilibria in the deterministic limit are different from those in the replicator dynamics, their stability remains the same.

4 Ranking of equilibria in a coexistence game

In a coexistence game where a < c and b > d, two types stably coexist with each other in the deterministic system. Here, we list all possible rankings of the carrying capacities in two homogenous populations and the equilibrium densities in a heterogeneous population, see Tab. 1. One particularly interesting ranking is $K^x > K^y > K_{cox}^y > K_{cox}^x$: a homogenous population of type X reaches higher densities than type Y but in the mixed equilibrium type Xis maintained at lower densities than type Y. In stochastic processes this becomes particularly important because smaller carrying capacities result in a higher risk of extinction. For this particular ranking, a mutant Y has an increased chance to take over the entire population because in the mixed equilibrium X is outnumbered and hence is more likely to go extinct due to stochastic fluctuations. If this happens, the density of type Y individuals will increase until it reaches K^y . Over the course of this invasion, the total density of individuals changes from K^x to K_{cox} and ends at K^y .

In co-existence games where b < a holds, the ranking is $K^y < K^x < K_{cox}$ and the total population size first increases and then decreases. In co-existence games where b > a holds, the ranking is $K^y < K_{cox} < K^x$ and hence the total population size continuously declines to the carrying capacity of type Y in isolation. This implies that evolution is not a simple process of accumulating beneficial mutations, which have higher carrying capacities in isolation, but instead the adaptive process can favour invasion and fixation of mutations that are disadvantageous for the entire population [5]. Similar evolutionary patterns are apparent in the prisoner's dilemma.

Conditions	Ranking
a > d and $ad(c-d) < bc(a-d)$	$K^x > K^x_{\text{cox}} > K^y > K^y_{\text{cox}}$
a > d and $ad(c-d) > bc(a-d)$ and b > c or $ad(c-b) < bc(a-d)$	$K^x > K^y > K^x_{\rm cox} > K^y_{\rm cox}$
a > d and $ad(c-b) > bc(a-d)$	$K^x > K^y > K^y_{\rm cox} > K^x_{\rm cox}$
a < d and $ad(b-a) < bc(d-a)$	$K^y > K^y_{\rm cox} > K^x > K^x_{\rm cox}$
a < d and $ad(b-a) > bc(d-a)$ and	$K^y > K^x > K^y_{\rm cox} > K^x_{\rm cox}$
b < c or $ad(c-b) > bc(a-d)$	
a < d and $ad(c-b) < bc(a-d))$	$K^y > K^x > K^x_{\rm cox} > K^y_{\rm cox}$

Table 1: In a coexistence game (a < c and d < b), different conditions on the payoffs lead to certain rankings between the carrying capacities at homogenous and heterogenous equilibria. Here we list all possible rankings assuming identical intrinsic growth rates $r_x = r_y$.

5 Cyclic dynamics

In our stochastic model, cyclic oscillation can be observed in a population with three types. Here, we show an example where the cycles spiral into an internal equilibrium according to the deterministic equations, but periodic oscillations persist under the corresponding stochastic process, see Fig. 1.

According to the payoff matrix (see inset in Fig. 1) in the deterministic dynamics, X can invade a homogenous Y population, Y can invade a homogenous Z population, and Z can invade a homogenous X population. The three types cycle into an internal equilibrium (see Fig. 1). However, demographic stochasticity drives the population away from the deterministic equilibrium and thus maintain the fluctuations over time. Note for small M, the population size is so small that demographic stochasticity will quickly lead to the extinction of the whole population.



Figure 1: Cyclic dynamics of three types under competitive Lotka-Volterra dynamics. The interactions are given by the payoff matrix in the inset. Saturated lines represent the deterministic dynamics, pale lines show one stochastic realisation (parameters $\lambda_{x \to xx} = \lambda_{y \to yy} = \lambda_{z \to zz} = 0.6$, $\lambda_{x \to 0} = \lambda_{y \to 0} = \lambda_{z \to 0} = 0.1$, M = 10000, $x_0 = 90$, $y_0 = z_0 = 10$).

6 Fixed population size

Stochastic evolutionary dynamics under frequency dependent selection in populations of constant size, N, has recently attracted considerable interest, see e.g. [6, 7]. The most popular examples are based on birth-death models in discrete time. This results in a reduced set of microscopic interactions for two types, $X+Y \rightarrow X+X, X+Y \rightarrow Y+Y$. The deterministic rate equations are $\dot{x} = (\lambda_{xy \to xx} - \lambda_{xx \to xy}) x y$ and $\dot{y} = -\dot{x}$. In this case, x and y can be rescaled to indicate the frequencies due to constant population size. Constant reaction rates just lead to logistic growth of both types. Instead, to accommodate frequency dependent interactions, frequency dependent reaction rates are needed, e.g. $\lambda_{xy \to xx} = f_x/N$ and $\lambda_{xy \to yy} = f_y/N$, where f_x and f_y represent the frequency dependent fitness. This yields $\dot{x} = x(1-x)(f_x - f_y)$, which is just the replicator dynamics [8]. Alternatively, setting $\lambda_{xy\to xx} = f_x/(\bar{f}N)$ and $\lambda_{xy\to yy} = f_y/(\bar{f}N)$ where $ar{f}=xf_x+yf_y$ denotes the average fitness of the population, leads to $\dot{x}=x(1-x)(f_x-f_y)/ar{f}$ and recovers the adjusted replicator equation [9], which describes the deterministic limit of the frequency-dependent Moran process in discrete time [7]. Interpreting frequency dependent interactions under fixed population size based on individual reactions is somewhat problematic. First, it is unintuitive to define frequency dependent reaction rates on the microscopic level because each reaction should occur independently. Second, for an evolving population we expect changes in the population size resulting by the changes of population composition rather than merely due to stochastic effects, which questions the basic tenet of models with constant population size.

References

- [1] Nowak, MA (2006) Evolutionary Dynamics (Harvard University Press, Cambridge MA).
- [2] Mallet, J (2012) The struggle for existence: how the notion of carrying capacity, *K*, obscures the links between demography, Darwinian evolution, and speciation. *Evolutionary Ecology Research* 14:627–665.
- [3] van Kampen, NG (1997) *Stochastic Processes in Physics and Chemistry* (Elsevier, Amsterdam), 2 edition.
- [4] Gardiner, CW (2004) Handbook of Stochastic Methods (Springer, NY), third edition.

- [5] Huang, W, Haubold, B, Hauert, C, Traulsen, A (2012) Emergence of stable polymorphism driven by evolutionary games between mutants. *Nature Communications* 3:919.
- [6] Nowak, MA, Sasaki, A, Taylor, C, Fudenberg, D (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428:646–650.
- [7] Traulsen, A, Claussen, JC, Hauert, C (2005) Coevolutionary dynamics: From finite to infinite populations. *Physical Review Letters* 95:238701.
- [8] Hofbauer, J, Sigmund, K (1998) *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, UK).
- [9] Maynard Smith, J (1982) *Evolution and the Theory of Games* (Cambridge University Press, Cambridge).