NEST meeting on 8th April.

by Sejin Lim, Kyunghee University

Fixation and fluctuations in two-species cooperation

J.Phys.Complex. 3, 015011 (15pp) (2022)

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IOP Publishing J.Phys.Complex. 3 (2022) 015011 (15pp) https://doi.org/10.1088/2632-072X/ac52e7

Journal of Physics: Complexity

OPEN ACCESS

PAPER

Fixation and fluctuations in two-species cooperation

RECEIVED
19 September 2021

REVISED
1 February 2022

ACCEPTED FOR PUBLICATION
8 February 2022

PUBLISHED
28 February 2022

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Keywords: fixation, extinction, first passage, stochastic processes, cooperation

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1. Two-species cooperation model without migration

- Finite population of N particles, with n of species A and $N-n$ of species B.

- Repeated process
  1. Pick a random pair of paritcles
  2. If the pair is AB, one member of this pair reproduces (if the pair is AA or BB, nothing happens)
  3. The newly reproduced offspring, replaces one randomly selected particle in the remainder of the population.

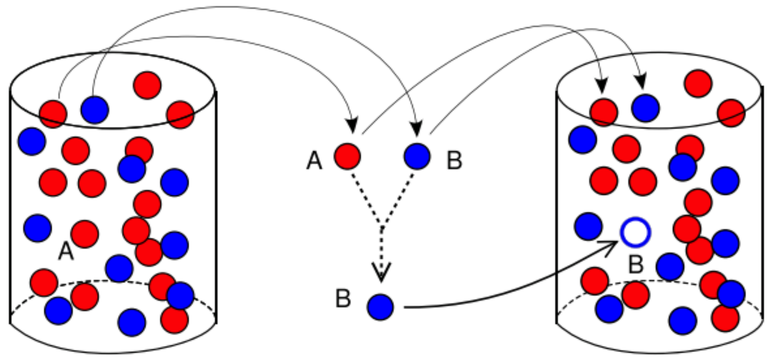


Figure 2. The reaction step in two-species cooperation. Two randomly selected particles happen to be from different species, namely A and B (red and blue). One of them reproduces (B, blue), an event that is aided by the presence of the other (A, red). The offspring replaces another randomly selected particle from the remainder of the population. In the example shown, the newly generated B replaces an A.

2. Rate equation

- $x \equiv \frac{n}{N}$, $x \in [0,1]$: *continuum approximation when* $N \to \infty$
- The probability a_n at which $n \to n+1$
  - $a_n = (picking\ \ AB\ \ pair) \times (replace\ \ randomly\ \ selected\ \ B) \times (offspring\ \ is\ \ A)$

  $= 2x(1-x) \times \frac{1}{2} \times (1-x) = x(1-x)^2$

- The probability b_n at which $n \to n-1$
  - $b_n = (picking\ \ AB\ \ pair) \times (replace\ \ randomly\ \ selected\ \ A) \times (offspring\ \ is\ \ B)$

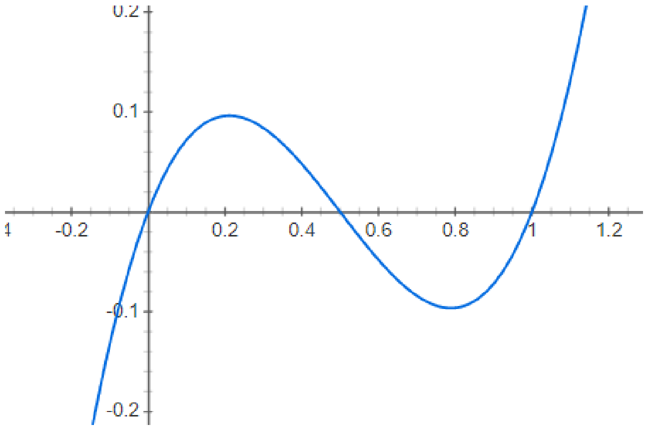
  $= 2x(1-x) \times \frac{1}{2} \times x = x^2(1-x)$

- The probability at which $n \to n$
  - $(for\ \ picking\ \ AA\ \ pair) + (for\ \ picking\ \ BB\ \ pair) + (for\ \ picking\ \ AB\ \ pair)$

  $= x^2 + (1-x)^2 + 2x(1-x)\left[\frac{1}{2}x + \frac{1}{2}(1-x)\right] = 1 - x(1-x) = 1 - a_n - b_n$

2. Rate equation

- $\dot{n} = N(a_n - b_n) = Nx(1-x)(1-2x)$
- $\dot{x} = x(1-x)(1-2x)$



- stable fixed point : $x = \frac{1}{2}$
- unstable fixed points : $x = 0$ and $x = 1$

- Solve rate equation : $t = -4\ln\frac{x(1-x)(1-2x)}{x_0(1-x_0)(1-2x_0)}$, $\qquad x(t) \cong \frac{1}{2} - 2x_0(1-x_0)(1-2x_0)e^{-\frac{t}{4}}$
  - the stable fixed point is approached exponentially quickly in time.

3. Master equation

- $P_n(t)$: the probability that the population consists of $\boldsymbol{n}$ A's at time $\boldsymbol{t}$. (and $N - \boldsymbol{n}$ B's)
- $\delta t = \frac{1}{N}$, time change each particle being updated once, on average, in a single time unit

- $P_n(t + \delta t) = a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) + (1 - a_n - b_n)P_n(t)$
- $P_n(t + \delta t) - P_n(t) = a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)$
- $\dot{P}_n(t) = N[a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)]$

- First moment of $\dot{x}$

$\langle \dot{x} \rangle = \frac{1}{N}\sum_{n=1}^{N} n\dot{P}_n$

$= \sum_{n=1}^{N} n[a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)]$

$= \sum_{n=1}^{N}(n + 1)a_nP_n(t) + (n - 1)b_nP_n(t) - n(a_n + b_n)P_n(t)$

$= \sum_{n=1}^{N}(a_n - b_n)P_n(t) = \langle x(1 - x)(1 - 2x) \rangle$

3. Master equation

- $P_n(t+\delta t) = a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) + (1 - a_n - b_n)P_n(t)$
- $P_n(t+\delta t) - P_n(t) = a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)$
- $\dot{P}_n(t) = N[a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)]$

- Second moment of $\dot{x}$

$\langle \dot{x}^2 \rangle = \frac{1}{N^2}\sum_{n=1}^{N} n^2 \dot{P}_n$

$= \frac{1}{N}\sum_{n=1}^{N} n^2[a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)]$

$= \frac{1}{N}\sum_{n=1}^{N}(n+1)^2 a_n P_n(t) + (n-1)^2 b_n P_n(t) - n^2(a_n + b_n)P_n(t)$

$= \frac{1}{N}\langle x(1-x)\rangle + 2\langle x^2(1-x)(1-2x)\rangle$

3. Master equation (low-order moments)

- First moment of $\dot{x}$

$$\langle \dot{x} \rangle = \langle x(1-x)(1-2x) \rangle$$

- Second moment of $\dot{x}$

$$\langle \dot{x}^2 \rangle = \frac{1}{N}\langle x(1-x) \rangle + 2\langle x^2(1-x)(1-2x) \rangle$$

- $z \equiv 2x - 1, \quad z \in [-1,1]$

- $\langle \dot{z} \rangle = -\frac{1}{2}\langle z(1-z^2) \rangle$
- $\langle \dot{z}^2 \rangle = \left\langle (1-z^2)\left(\frac{1}{N} - z^2\right) \right\rangle$

3. Master equation (low-order moments)

- $z \equiv 2x - 1, \quad z \in [-1,1]$

- $\langle \dot{z} \rangle = -\frac{1}{2}\langle z(1 - z^2)\rangle$
- $\langle \dot{z}^2 \rangle = \left\langle (1 - z^2)\left(\frac{1}{N} - z^2\right)\right\rangle$

- the assumption of no correlations : $\left\langle z^k \right\rangle = \langle z \rangle^k$

- $\langle \dot{z} \rangle = -\frac{1}{2}\langle z \rangle(1 - \langle z \rangle^2)$
- $\langle \dot{z}^2 \rangle = (1 - \langle z \rangle^2)\left(\frac{1}{N} - \langle z \rangle^2\right)$

3. Master equation (low-order moments)

- $\langle \dot{z} \rangle = -\frac{1}{2}\langle z \rangle (1 - \langle z \rangle^2)$
  - $z = 0$: stable fixed point

- $\langle \dot{z}^2 \rangle = (1 - \langle z \rangle^2)\left(\frac{1}{N} - \langle z \rangle^2\right)$
  - The width of the distribution initially grows and eventually 'sticks' at the value $\sqrt{N}$.

  - There is slow leakage of the probability distribution : $t \rightarrow \infty$, the true stochastic fixed points at $z = \pm 1$.
  - It can be captured by the full stochastic dynamics. (not captured by low-order moments)

  - the true stochastic fixed points $z = \pm 1$ is same with $n = 0$ or $n = N$.

4. Full stochastic dynamics

- Fixation probability E_n

  : the probability that a population of size N that initially contains n particles of type A reaches the static fixation state of all A's.

- Fixation time T_n

  : the average time for the population of N particles to first reach either of the two fixation states $n = 0$ or $n = N$, when the population initially contains n A's.

4. Full stochastic dynamics (fixation probabaility)

- Fixation probability E_n

  : the probability that a population of size N that initially contains $\boldsymbol{n}$ particles of type A reaches the static fixation state of all A's.

- $E_n = a_n E_{n+1} + b_n E_{n-1} + (1 - a_n - b_n) E_n$
  - by using similar method with master equation (backward Kolmogorov equation)
  - hopping probabilities to these respective states : a_n, b_n, $(1 - a_n - b_n)$
  - boundary conditions : $E_0 = 0$ and $E_N = 1$

- $E_n = \frac{\sum_{m=0}^{n-1}\left[\binom{N-1}{m}\right]^{-1}}{\sum_{m=0}^{N-1}\left[\binom{N-1}{m}\right]^{-1}}$, $\quad E(x) = \frac{1}{2}\left[1 + \frac{\mathrm{erfi}\left(\sqrt{2N}\left(x - \frac{1}{2}\right)\right)}{\mathrm{erfi}\left(\sqrt{\frac{N}{2}}\right)}\right]$, $\quad \mathrm{erfi}(z) \equiv -i\,\mathrm{erf}(iz)$
  - Appendix A.

4. Full stochastic dynamics (fixation probabaility)

$$E(x) = \frac{1}{2}\left[1 + \frac{\operatorname{erfi}\left(\sqrt{2N}\left(x-\frac{1}{2}\right)\right)}{\operatorname{erfi}\left(\sqrt{\frac{N}{2}}\right)}\right], \quad \operatorname{erfi}(z) \equiv -i\operatorname{erf}(iz)$$

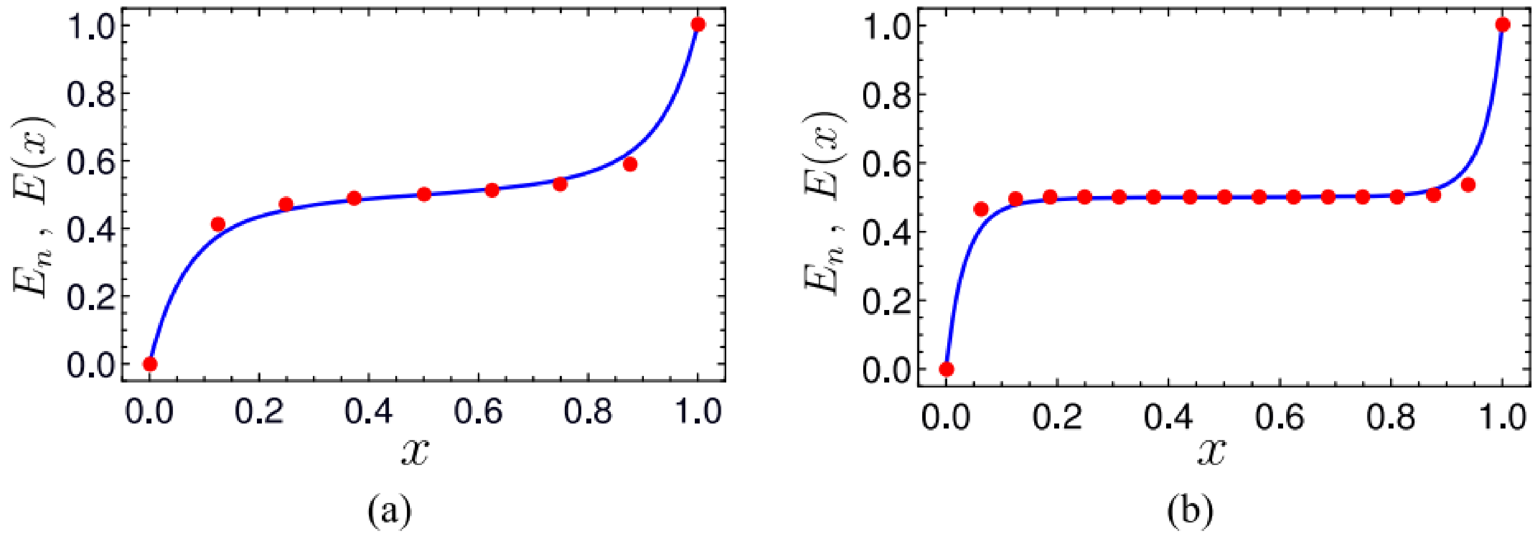


Figure 3. Dependence of the discrete and continuum fixation probabilities, E_n and $E(x)$, versus x for the cases $N = 8$ and 16. The smooth curves represent $E(x)$ from equation (A.5) and the dots represent simulation results.

4. Full stochastic dynamics (fixation time)

- Fixation time T_n

  : the average time for the population of N particles to first reach either of the two fixation states $n = 0$ or $n = N$, when the population initially contains n A's.

- $T_n = a_n T_{n+1} + b_n T_{n-1} + (1 - a_n - b_n) T_n + \delta t$
  - backward Kolmogorov equation
  - hopping probabilities to these respective states : a_n, b_n, $(1 - a_n - b_n)$
  - for a single hopping event (δt)
  - boundary conditions : $T_0 = T_N = 0$

- $T_n = E_n \sum_{m=1}^{N-1} Q_m - \sum_{m=1}^{n-1} Q_m$
  - $Q_n \equiv \alpha_n + r_n \alpha_{n-1} + r_n r_{n-1} \alpha_{n-2} + \cdots + r_n r_{n-1} \ldots r_2 \alpha_1$
  - $Q_0 = 0,\ r_n = b_n / a_n,\ \alpha_n = \delta t / a_n$
  - Appendix B.

4. Full stochastic dynamics (slow leakage rate)

- Slow leakage rate $\Gamma(N)$: slow leakage rate from the quasi-steady state to the fixation state.

- $\Gamma(N)\delta t = (Proba[n \to 0]) + (Proba[n \to N]) = b_1\tilde{P}_1 + a_{N-1}\tilde{P}_{N-1} = 2b_1\tilde{P}_1$
  - same method with the getting master equation.
  - $\tilde{P}_n$: the steady-state distribution of n.
  - by using symmetry nature about $n \leftrightarrow N-n$: $a_{N-n}\tilde{P}_{N-n} = b_n\tilde{P}_n$

- The continuum probability distribution $\tilde{P}(x)$: $\frac{n}{N} \to x, \quad \frac{1}{N} \to \delta x$

- $a(x-\delta x)\tilde{P}(x-\delta x) + b(x+\delta x)\tilde{P}(x+\delta x) = [a(x)+b(x)]\tilde{P}(x)$
  - from the master equation when $\frac{\partial \tilde{P}(x)}{\partial t} \to 0$.

- Assume that $\tilde{P}(x) \sim \exp\left(\frac{S(x)}{\delta x}\right) = \exp(NS_0(x) + S_1(x) + \cdots)$

4. Full stochastic dynamics (slow leakage rate)

- Assume that $\tilde{P}(x) \sim \exp\left(\frac{S(x)}{\delta x}\right) = \exp(NS_0(x) + S_1(x) + \cdots)$: WKB approximation (Appendix C.) for large deviation
  - $S_0(x) = \int^x dz \log\left[\frac{a(z)}{b(z)}\right]$, $S_1(x) = -\frac{1}{2}\log[a(x)b(x)]$, from $a(x-\delta x)\tilde{P}(x-\delta x) + b(x+\delta x)\tilde{P}(x+\delta x) = [a(x)+b(x)]\tilde{P}(x)$
  - $S_0(x) = \int^x dz \log\left[\frac{a(z)}{b(z)}\right] = -x\ln x - (1-x)\ln(1-x)$
- $\tilde{P}(x) \cong A\frac{e^{NS_0(x)}}{x^{1.5}(1-x)^{1.5}}$, A : Normalization factor

- Normalize $\tilde{P}(x)$: $A\int_0^1 \frac{e^{NS_0(x)}}{x^{1.5}(1-x)^{1.5}}dx = 1$
- $P(N) = \int_0^1 \tilde{P}(x)dx$ → by using Laplace transform table.. (Laplace transform : $\tilde{P}(x) = \lim_{N\to\infty}\int_0^N P(N)\, e^{-xN}dN$)
- $P(N) \approx \sqrt{\frac{32\pi}{N}}e^{N\ln 2} = \frac{1}{A}$
- $\tilde{P}(x) \cong \frac{N}{\sqrt{32\pi}}\frac{e^{NS_0(x) - N\ln 2}}{x^{1.5}(1-x)^{1.5}}$

4. Full stochastic dynamics (slow leakage rate)

- by using $\Gamma(N)\delta t = 2b_1\tilde{P}_1$ and $\tilde{P}(x) \cong \frac{N}{\sqrt{32\pi}}\frac{e^{NS_0(x)-N\ln 2}}{x^{1.5}(1-x)^{1.5}}$,

- $\tilde{P}\left(\frac{1}{N}\right) \cong \frac{N^3}{\sqrt{32\pi}}e^{1-N\ln 2}$ and $b\left(\frac{1}{N}\right) \approx \frac{1}{N^2}$
- $\Gamma(N) = \frac{N}{\sqrt{8\pi}}e^{1-N\ln 2} = \frac{Ne}{\sqrt{8\pi}}e^{-N\ln 2}$

- $T_{n=N/2}\Gamma(N) = 1$

  because the quasi-steady state is at $x = \frac{1}{2}$

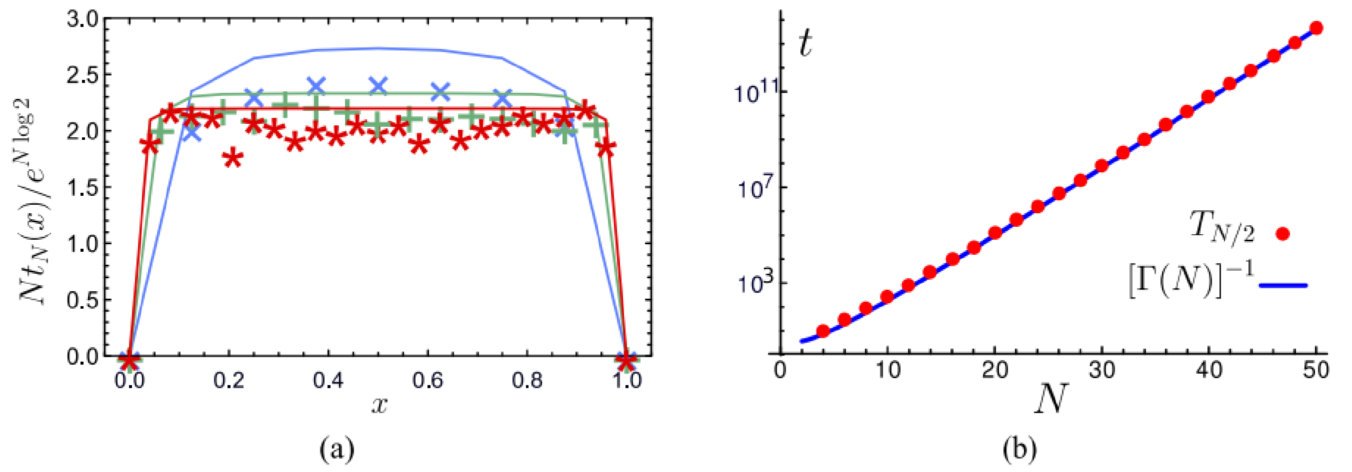


Figure 4. (a) Dependence of the fixation time T_n versus $x = \frac{n}{N}$ using a data-collapse scheme by resetting the scale $T_n \to N e^{-N\log 2} T_n$ for each N value. This scaling factor corresponds to the prediction made in equation (16). The solid lines follow the predictions obtained from equation (10). The plot marks $\{\times, +$ and $*\}$ correspond to simulated average fixation times for $N = 8, 16$ and 24 in blue, green and red colors, respectively. Each data point is obtained by averaging 10^3 simulated fixation processes at corresponding values of n and N. (b) Dependence of the fixation time from the symmetric initial state, $T_{N/2}$ (red dots) computed by (10) and the WKB prediction for the inverse leakage rate from the quasi-steady state (blue line), following (16).

4. Two-species cooperation with migration and its model definition

- Finite population of N particles, with n of species A and $N-n$ of species B.

- Repeated process
  - With probability $(1-\lambda)$
    1. Pick a random pair of paritcles
    2. If the pair is AB, one member of this pair reproduces (if the pair is AA or BB, nothing happens)
    3. The newly reproduced offspring, replaces one randomly selected particle in the remainder of the population.
  - With probability λ
    1. With probability $\frac{1}{2}(1-x)$, A migrant replaces a B.
    2. With probability $\frac{1}{2}x$, B migrant replaces an A.

λ : migration probability

4. Two-species cooperation with migration and its full stochastic dynamics

- Rate equation

$$\langle \dot{n} \rangle = N(1-\lambda)[x(1-x)(1-2x)] + \frac{1}{2}N\lambda[(1-x)-x] = N(1-\lambda)[x(1-x)(1-2x)] + \frac{1}{2}N\lambda(1-2x)$$

- Master equation

$$\dot{P}_n = N(1-\lambda)[a_{n-1}P_{n-1}(t) + b_{n+1}P_{n+1}(t) - (a_n + b_n)P_n(t)] + N\lambda[c_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - (c_n + d_n)P_n(t)]$$

$$c_n = \frac{1}{2}\left(1 - \frac{n}{N}\right), \quad d_n = \frac{1}{2}\frac{n}{N}$$

- The continuum probability distributioin in the Fokker-Planck approximation, $x = \frac{n}{N}$, $dx = \frac{1}{N}$, $P_n \to P(x)$.
- $P_t = -\left\{(1-2x)\left[(1-\lambda)x(1-x) + \frac{\lambda}{2}\right]P(x,t)\right\}_x + \frac{1}{2N}\left\{\left[(1-\lambda)x(1-x) + \frac{\lambda}{2}\right]P(x,t)\right\}_{xx}$

$$= -\{v(x)P(x,t)\}_x + \{D(x)P(x,t)\}_{xx}$$

4. Two-species cooperation with migration and its full stochastic dynamics

- $P_t = -\left\{(1-2x)\left[(1-\lambda)x(1-x)+\frac{\lambda}{2}\right]P(x,t)\right\}_x + \frac{1}{2N}\left\{\left[(1-\lambda)x(1-x)+\frac{\lambda}{2}\right]P(x,t)\right\}_{xx}$

$= -\{v(x)P(x,t)\}_x + \{D(x)P(x,t)\}_{xx}, \qquad \{f(x)\}_{xx} \equiv \frac{\partial^2}{\partial x^2}f(x)$

$(DP)_x - vP = B$, at $x = \frac{1}{2}$, $v(x) = 0$ and $\left(D(x)\right)_x = 0$, thus $B = 0$.

$= \frac{C}{D(x)}\exp\left\{\int^x dy 2N(1-2y)\right\}$

$= C'\left[\frac{1}{(1-\lambda)x(1-x)+\frac{\lambda}{2}}\right]e^{2Nx(1-x)}$, C' is determined by normalization

$P'(x) \propto (1-2x)e^{2Nx(1-x)}\left[2N - \frac{\lambda-1}{D(x)^2}\right]$, for fixed N

$2N = \frac{1-\lambda}{(\lambda/2)^2}$, from $\left[2N - \frac{\lambda-1}{D(x)^2}\right] = 0$ at $x = 0$ or $x = 1$

$D(x) = \frac{1}{2N}\left[(1-\lambda)x(1-x)+\frac{\lambda}{2}\right]$

4. Two-species cooperation with migration and its full stochastic dynamics

$2N = \frac{1-\lambda}{(\lambda/2)^2}$, from $\left[2N - \frac{\lambda-1}{D(x)^2}\right] = 0$ at $x = 0$ or $x = 1$

$\lambda \ll 1,\ \lambda_c = \sqrt{\frac{2}{N}}$

$2N \cong \frac{1}{\left(2\epsilon+\frac{\lambda}{2}\right)^2}$, $\epsilon \cong \frac{1}{4}(\lambda_c - \lambda)$ for $\lambda < \lambda_c$.

For $\lambda < \lambda_c$, the distribution $P(x)$ is trimodal function.

For $\lambda \to \lambda_c$, the distribution $P(x)$ is unimodal function.

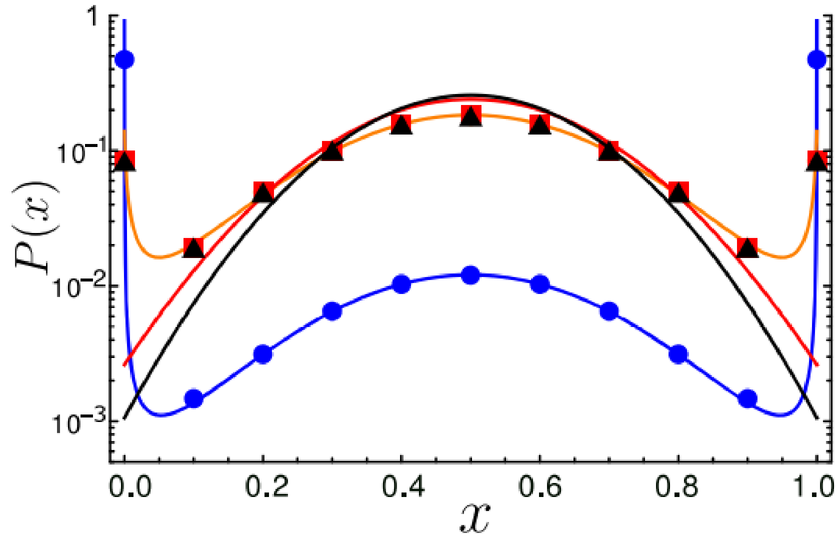


Figure 5. Steady-state probability distributions for $N = 10$ on a semi-logarithmic scale for values of $\lambda/\lambda_c = 10^{-4}, 10^{-2}, 10^{0}$ and 10^{1} in blue, orange, red and black, respectively. The respective data points correspond to simulation results.

4. Two-species cooperation with migration and fluctuations in the steady state

return time RT : the time interval between successive points where $x = \frac{1}{2}$

RT will be short for $\lambda \gg \lambda_c$, and RT will be long for $\lambda \ll \lambda_c$ ($\lambda \gg \lambda_c$: unimodal distribution, $\lambda \ll \lambda_c$: trimodal distribution)

τ_n : the average time to reach the balanced state of equal numbers of A's and B's when starting from a state where the number of A's equals $n > \frac{N}{2}$.

$$RT = \delta t + \tau_{1+N/2} = \frac{1}{N} + \tau_{1+N/2}$$

$$\tau_n = (1-\lambda)[a_n \tau_{n+1} + b_n \tau_{n-1} + (1 - a_n - b_n)\tau_n] + \lambda[c_n \tau_{n+1} + d_n \tau_{n-1} + (1 - c_n - d_n)\tau_n] + \delta t$$

(Appendix D.)

4. Two-species cooperation with migration and fluctuations in the steady state

return time RT : the time interval between successive points where $x = \frac{1}{2}$

RT will be short for $\lambda \gg \lambda_c$, and RT will be long for $\lambda \ll \lambda_c$

($\lambda \gg \lambda_c$: unimodal distribution, $\lambda \ll \lambda_c$: trimodal distribution)

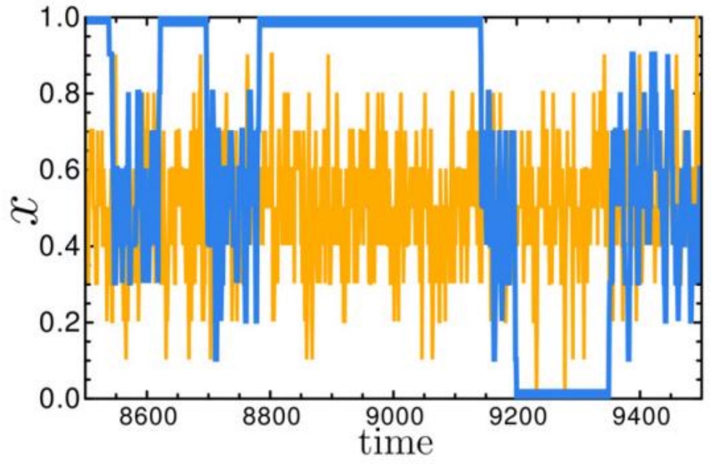


Figure 6. Typical population trajectories in composition space for $\lambda/\lambda_c = 2 \times 10^{-3}$ (blue) and $\lambda/\lambda_c = 2$ (orange) for the case $N = 10$.

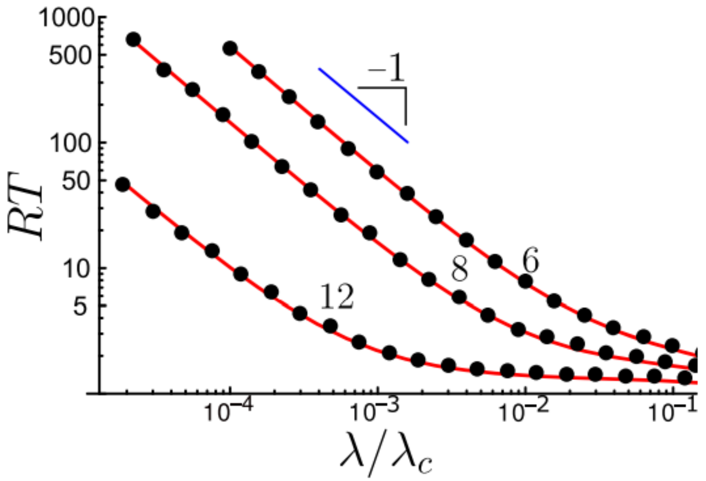


Figure 7. Dependence of the return time RT on λ/λ_c for various values of N.

5. Summary

- Two species cooperation with migration model.

- From the rate equation, we can know the stable fixed point of the population of A ($x = \frac{n}{N}$).
  - the stable fixed point of x : $x = \frac{1}{2}$

- From the master equation, we can know the fixed points of the stochastic dynamics of the population of A

  for very small migration probailtiy $\lambda \ll \lambda_c$

  the stochastic fixed points of x : $x = 0$ or $x = 1$ ($n = 0$ or $n = N$)

- Despite of cooperative interaction, if there is very small migration and $t \to \infty$, the only A or B survives.