ETH zürich | D BSSE | Computational Biology Group

# Evolutionary Dynamics

## Exercises 9

Prof. Dr. Niko Beerenwinkel
Johannes Gawron
Michael Schneider
Norio Zimmermann

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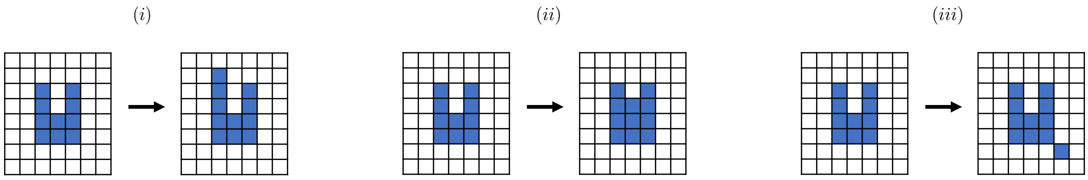
**Problem 1: Eden model dynamics**

Consider a two-dimensional Eden growth model with von Neumann neighborhood.

(a) **(tutorial exercise)**

Consider the three state changes depicted below. $S_1$ sites are coloured blue (occupied), $S_0$ sites are white (unoccupied).




Calculate the probabilities of each change under the following update rules:

(A) *Available site-focussed:* randomly choose an $S_0$ site that adjoins at least one $S_1$ site, and switch it from $S_0$ to $S_1$.

(B) *Bond-focussed:* randomly choose an $S_1$ site with probability proportional to the number of adjoining $S_0$ sites, then uniformly sample an $S_0$ neighbour and switch it to $S_1$.

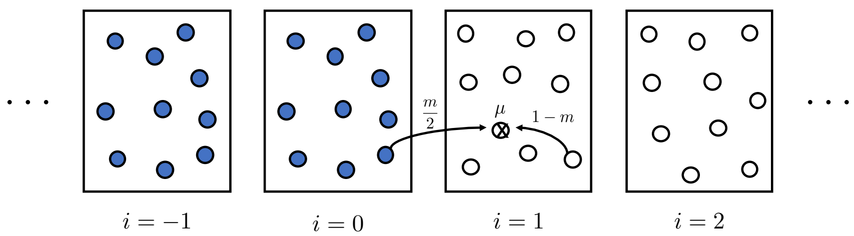
(C) *Cell-focussed:* randomly choose an $S_1$ site that adjoins at least one $S_0$ site, then sample uniformly an $S_0$ neighbour and switch it to $S_1$.

Under which update rule is each change the most/least likely to be observed?

(b) Consider the R code at https://git.io/vF0KH. What is the update rule implemented in the code? Modify the code to simulate the other two update rules from question (a) and then explain the difference between the spatial boundaries of the population obtained for the different evolutionary dynamics. 💻 **(2 points)**

**Problem 2: Diffusion approximation of a spatial Moran model**

Consider the spatial Moran model for a mutation spreading through an infinite row of demes. Let $\mu$ denote the death rate, $s$ the fitness advantage of the mutant, $m$ the dispersion probability, and $N$ the number of individuals per deme. Assume initially that $n_i = N\ \forall i \leq 0$ and $n_i = 0$ otherwise, where $n_i$ is the number of mutants in deme $i$.



The rate at which mutants in a deme die is $\mu n_i$. Once an individual has died, it is replaced by the offspring of a wild type individual of its own deme with probability $\frac{N-n_i}{(1+s)n_i+(N-n_i)} \approx \frac{N-n_i}{N}$, and it is replaced by the offspring of a wild type individual from any of the neighbouring demes with probability

$$\frac{m(N-n_{i-1})}{2N} + \frac{m(N-n_{i+1})}{2N} \approx \frac{m(2N-(n_{i-1}+n_{i+1}))}{2N}$$

(a) Using these results, show that the rate for the number of mutants in deme $i$ decreasing by one individual is

$$W_i^-(\mathbf{n}) = \frac{\mu}{N} n_i \left((N-n_i) - \frac{m}{2} n_i''\right), \tag{1}$$

where $n_i'' = n_{i-1} + n_{i+1} - 2n_i$.

**(1 points)**

(b) In general,

$$\frac{d\mathbb{E}[n_i]}{dt} = \mathbb{E}\left[W_i^+(\mathbf{n}) - W_i^-(\mathbf{n})\right], \tag{2}$$

where $\mathbb{E}[X]$ denotes the expected value of a random variable $X$. Using the expression for $W_i^+(\mathbf{n})$ given in the lecture, and applying the approximation $\mathbb{E}[n_i n_k] \approx \mathbb{E}[n_i]\,\mathbb{E}[n_k]$ (called the mean-field approximation), show that

$$\frac{d\mathbb{E}[n_i]}{dt} = \frac{\mu m}{2}\mathbb{E}\left[n_i''\right] + \frac{s\mu}{N}(N - \mathbb{E}[n_i])\left(\mathbb{E}[n_i] + \frac{m}{2}\mathbb{E}\left[n_i''\right]\right). \tag{3}$$

**(2 points)**

(c) We can approximate distance along the row of demes using the continuous variable $x = li$, where $l$ is the deme width. Setting $u(x) = \mathbb{E}[n_i]/N$, use the previous approximation to show that process (3) can be approximated by the diffusion equation

$$\frac{\partial u}{\partial t} = D[1+s(1-u)]\frac{\partial^2 u}{\partial x^2} + \mu s u(1-u) \tag{4}$$

where diffusion coefficient $D = \mu m l^2/2$. Note: We assume that $\frac{\partial u(x)}{\partial i}$ is the expected difference in $u$ between the $i$th and $i+1$th deme and that $\frac{\partial^2 u(x)}{\partial i^2}$ is the expected difference in $\frac{\partial u(x)}{\partial i}$ between the $i$th and $i+1$th deme. Compute $\frac{\partial u(x)}{\partial i^2}$ and perform a change of variables.

**(2 points)**

(d) Simulate the the system change over time under the diffusion equation (4) and starting with the configuration depicted above. Describe how the system evolves over time if $s = 0$ compared to $s > 0$. Note: Initialize the starting conditions for a finite number of points in some spacial interval $[-a, a]$ and incrementally update the state at each position for a small time step using a difference equation approximation of (4). Choose appropriate values for $s$, $\mu$ and $m$ to plot the states of $u$ at different time points. 💻

**(2 points)**

(e) Briefly explain the roles of $s$, $\mu$ and $m$ in the diffusion equation.

**(1 point)**