



1 Modeling Population Dynamics:

Let's consider a simple population model involving many organisms all living in a single large petri-dish. We'll assume that each of these organisms belongs to one of $N = 19$ different species. In addition to assuming that these species are all living in a single large petri dish, we'll also assume the population is 'well-mixed'. This means that the interactions between the organisms are randomly determined, and that each pair of organisms is equally likely to interact over any given time-window.

In addition to the above, we'll assume that each time any two organisms interact, they 'battle'. These battles end up with one organism winning, and the other losing. The winner is then allowed to multiply (i.e, create another organism of the same species), whereas the loser dies (this world is harsh!!). The winner/loser of each battle is determined randomly, but the chance of any one organism winning depends on their species, as well as the species of their opponent.

More specifically, we'll assume that each species n has a 'battle-score' $A_{nn'}$ representing how effective that species is at fighting species n' . Thus, $A_{nn'}$ will be high if species n is strong against species n' , and low if species n is weak against species n' . This 'battle-score' $A_{nn'}$ is coded in an $N \times N$ matrix A . The matrix entries $A_{nn'}$ take on values of 0, 1/2, 1 or 2 (see figure – blanks correspond to values of 1). For the purposes of our model, let's assume that a battle between species n and n' is randomly determined as follows:

$$\begin{aligned} \text{Probability that } n \text{ wins} &= B_{nn'} = \frac{A_{nn'}}{A_{nn'} + A_{n'n}}, \\ \text{Probability that } n' \text{ wins} &= B_{n'n} = \frac{A_{n'n}}{A_{nn'} + A_{n'n}}, \end{aligned}$$

with terms of 0/0 replaced with 1/2.

2 Markov Model:

To start with, we'll model this population with a discrete-time markov process. We'll assume that our population has $M \gg 1$ organisms (say, e.g., $M = 8192$). Each organism will be one of the $N = 19$ different species. As time marches on, the species of each organism could change (representing that organism dying and being replaced by a new organism of a different species). Note that – as stated so far – the 'state-space' for our Markov model is quite large! At each time any one of the M organisms could be any one of N possible species. Thus, at each time our system could be in any one of N^M possible states¹.

¹Of course, we don't really care which organisms are which; we only really care how many there are of each species. So instead of tracking each organism's species separately, we could record the number M_n of organisms that are species n . The sum $\sum_{n=1}^{19} M_n$ must equal M , which is the number of organisms in our system. The number of configurations possible isn't quite as big as N^M , but it is still very large (i.e., $\sim M^{N-1}$).

Rather than defining the state-transition probabilities on this very large set of states, we'll directly describe how our system changes state from one time-step to the next:

1. Each time-step is a 'round', in which each organism is randomly paired with another organism. Organisms that cannot be paired get a 'bye' for this round.
2. Paired organisms fight, with the victor determined randomly: if the first organism is species n and the second n' , then the victor is determined via $B_{nn'}$ and $B_{n'n}$.
3. The loser dies, and the winner multiplies: In effect, the loser is replaced by a new organism of the same species as the winner.

Can you simulate this markov-model? See (pokemon_markov_ver1.m) as a hint. See if you can answer the following questions:

1. Run multiple trials of this markov-model with different initial-conditions (I.e., change the initial fractions of each species in the population). Also run multiple trials for different values of M .
2. Do the results of the simulation depend on the initial conditions?
3. Do the results of the simulation depend on the total number of organisms (i.e., on M). What if M is small (e.g., $M = 128$); do the results of the simulation vary from trial to trial? What about if M is large (e.g., $M = 8192$); now do the results of the simulation vary significantly across trials?
4. Can you measure roughly how well each species does in each simulation (averaged across trials) as a function of M ? Which species typically dominate over a long period of time when M is small? What about when M is large?
5. Which species are typically driven to extinction when M is small? What about when M is large?
6. Do your observations in any way correlate with the most popular pokemon used in 'pokemon go'? See, e.g., :

(a) <https://www.primagames.com/games/pokemon-go/>

(b) <https://www.pastemagazine.com/articles/2016/07/the-50-best-pokemon-to-use-in-pokemon-go.html>

Now let's change the rules of the markov-model a little bit. Let's introduce a small 'quit-chance' q (typically $q \sim 0.01$ or smaller) which represents the probability that, after any given round, any particular organism 'quits' and picks a new species. This time our system changes like this (steps 1-3 are the same as before):

1. Each time-step is a 'round', in which each organism is randomly paired with another organism. Organisms that cannot be paired get a 'bye' for this round.
2. Paired organisms fight, with the victor determined randomly: if the first organism is species n and the second n' , then the victor is determined via $B_{nn'}$ and $B_{n'n}$.
3. The loser dies, and the winner multiplies: In effect, the loser is replaced by a new organism of the same species as the winner.
4. Before the next round starts each organism has a chance q of quitting, and randomly drawing its new species from the $N = 19$ possibilities.

Now can you simulate this new modified-markov-model?

1. How do the dynamics differ from the original model?
2. What if the quit-chance is small (e.g., $q \lesssim 0.001$); do you see any differences?
3. What if the quit-chance is high (e.g., $q \sim 0.1$ or higher); now are there any differences?
4. Can you explain these differences? (Hint: see below).

3 Mean-field (ODE) Model:

Now we'll write down what's called a 'mean-field' model for the system above. This 'mean-field' model will assume that the changes to the population of each species can be well approximated by the 'average' change one would expect over each time-step. As you'll see, this 'mean-field' approximation will result in a mean-field model which is not random any longer! While the loss of randomness might seem somewhat strange, this kind of assumption is common in many other mathematical models used in the physical sciences (e.g., recall the models of chemical kinetics you studied at the beginning of the course). Generically, one expects/hopes that the mean-field approximation will be accurate when the population is large (i.e., when $M \gg 1$).

With this in mind, we'll assume that M is very large. Instead of modeling individual organisms, we'll just record – at each time – the fraction of each species within the population. That is, we'll assume that the population is given by \vec{y} , with y_n representing the fraction of the population associated with species n . In addition, instead of modeling discrete times, we'll assume that time is a continuous variable. Leveraging our assumption that the population is 'well-mixed', we'll assume that over each small time Δt , every pair of organisms has an equal probability of interacting (and battling), with this probability of interaction depending linearly on Δt .

1. With these assumptions, can you explain why the growth rate of population n is proportional to:

$$y_n \sum_{n'} B_{nn'} y_{n'}?$$

2. Can you explain why the death rate of population n is proportional to:

$$y_n \sum_{n'} B_{n'n} y_{n'}?$$

3. Now putting all these assumptions together, can you explain why the rate at which the population y_n changes is given by:

$$\begin{aligned} \frac{d}{dt} y_n(t) &= [F(\vec{y})]_n \\ &= +y_n \sum_{n'} B_{nn'} y_{n'} - y_n \sum_{n'} B_{n'n} y_{n'} \\ &= y_n \cdot (B - B^T) \vec{y}. \end{aligned}$$

Can you simulate this mean-field model? See `pokemon_ode_ver1.m` as a hint. See if you can answer the following questions:

1. Run multiple trials of this mean-field-model with different initial-conditions (I.e., change the initial fractions of each species in the population).
2. Do the results of the simulation depend on the initial conditions?
3. Which species typically dominate? Which are driven to extinction? Can you measure roughly how well each species does for this mean-field model (averaged across trials)?
4. Can you find any equilibrium for this ODE? Are these equilibria stable?
5. How large does M need to be before the results of the markov-model match the results of the mean-field-model?

Now let's allow organisms to quit: as before, we'll introduce a quitting probability q ; during time Δt , we expect $q\Delta t$ of the population to quit and then randomly pick a new species (from the N possible choices).

1. Can you explain why the rate at which population y_n decreases due to organisms quitting is given by:

$$-qy_n?$$

2. Can you explain why the rate at which population y_n increases due to organisms picking a new species (after quitting) is given by:

$$+\frac{1}{N} \sum_{n'=1}^N qy_{n'}$$

3. Can you explain why the rate at which the population y_n changes is now given by:

$$\begin{aligned} \frac{d}{dt} y_n(t) &= [F(\vec{y})]_n + qZ \cdot \vec{y}, \text{ where} \\ [F(\vec{y})]_n &= y_n \cdot (B - B^T) \vec{y}, \text{ and} \end{aligned} \tag{1}$$

$$Z = \frac{1}{N} \mathbf{1}\mathbf{1}^T - I_{N \times N} = \frac{1}{19} \begin{bmatrix} 1-19 & 1 & \cdots & 1 \\ 1 & 1-19 & \cdots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 & \cdots & 1-19 \end{bmatrix}.$$

Can you simulate this modified mean-field model?

1. For which values of q, M do the results of the modified-markov-model match the results of this modified mean-field model?
Note that the q you pick for the modified-markov-model might not necessarily have the same value as the q you pick for the modified-mean-field model.
2. What happens when $q \sim 0.1$ or larger for the modified-mean-field-model? How is this dynamics different than when $q \sim 0.001$ or smaller?
3. Can you find any equilibrium for this ODE when $q > 0$? Are these equilibria stable?
4. Can you linearize this ODE about an equilibrium?

(a) Note that:

$$\begin{aligned}\partial_{y_j} [F(\vec{y})]_n &= y_n (B_{nj} - B_{jn}) \text{ when } j \neq n, \text{ and} \\ \partial_{y_j} [F(\vec{y})]_n &= (B - B^\top) \vec{y} \text{ when } j = n \text{ (because } B_{nj} - B_{jn} = 0\text{)}.\end{aligned}$$

(b) This means that, for an equilibrium point \bar{y} , the derivative $DF(\bar{y})$ will look something like:

$$DF(\bar{y}) = \text{diag}(\bar{y}) \cdot (B - B^\top) + \text{diag}((B - B^\top) \bar{y}).$$

(c) Note also that

$$\partial_{y_j} [qZ \cdot \vec{y}]_n = qZ_{nj}.$$

(d) This implies that the derivative $D(qZ \cdot \bar{y})$ will look like:

$$D[qZ \cdot \bar{y}] = qZ.$$

(e) Note also that the eigenvalues of Z are particularly simple (what are they)?

(f) Can you try out a few arbitrary vectors \vec{y} (even if they aren't equilibria) just to see what the eigenvalues of $DF(\bar{y})$ might look like?

(g) What about the eigenvalues of $DF(\bar{y}) + D[qZ \cdot \bar{y}]$?

(h) Can you argue that, for sufficiently large q , the addition of $qZ \cdot \vec{y}$ to F (to form the right-hand-side of Eq. 1) stabilizes the equilibria by ensuring that all eigenvalues of $DF(\bar{y}) + D[qZ \cdot \bar{y}]$ have negative real-part?

(i) Can you use this line of reasoning to explain why the modified markov-model (with large quitting rate q) behaved differently from the original markov-model (with quitting-rate $q \sim 0$)?