

Recall that we are looking at the (P.1)  
population growth model governed by

$$\frac{dP_n}{dt} = \beta \cdot (n-1) \cdot P_{n-1} - (\beta + \delta) \cdot n \cdot P_n + \delta \cdot (n+1) \cdot P_{n+1}$$

$$P_n(0) = \begin{cases} 1 & n = N_0 \\ 0 & n \neq N_0 \end{cases}$$

where  $P_n(t) = \Pr[N(t) = n]$ .

We found, among other things, that the probability of being extinct at time  $t$  was given by

$$P_0(t) = \begin{cases} \left[ \frac{\beta + \delta}{1 + \beta t} \right]^{N_0} & \text{if } \beta = \delta, \\ \left[ \frac{\delta e^{\beta t} - \delta}{\beta e^{\delta t} - \delta} \right]^{N_0} & \text{if } \beta \neq \delta. \end{cases}$$

If we let  $P_{\text{EXT}}$  denote the probability that the population goes extinct eventually, then

$$P_{\text{EXT}} = \lim_{t \rightarrow \infty} P_0(t).$$

If  $\beta = \delta$ , then

LP.2

$$\lim_{t \rightarrow \infty} P_0(t) = \lim_{t \rightarrow \infty} \left[ \frac{\beta + \delta}{1 + \beta + \delta} \right]^{N_0} = 1^{N_0} = 1,$$

so the population almost certainly goes extinct.

If  $\beta < \delta$ , then  $r = \beta - \delta < 0$  and we have

$$P_{\text{Ext}} = \lim_{t \rightarrow \infty} P_0(t) = \lim_{t \rightarrow \infty} \left[ \frac{\delta e^{rt} - \delta}{\beta e^{rt} - \delta} \right]^{N_0} = \left[ \frac{-\delta}{-\delta} \right]^{N_0} = 1,$$

so the population still almost certainly dies out.

If  $\beta > \delta$ , then  $r = \beta - \delta > 0$  and we have

$$P_{\text{Ext}} = \lim_{t \rightarrow \infty} P_0(t) = \lim_{t \rightarrow \infty} \left[ \frac{\delta e^{rt} - \delta}{\beta e^{rt} - \delta} \right]^{N_0} = \left( \frac{\delta}{\beta} \right)^{N_0} \neq 1,$$

so there is a nonzero chance that the population lasts forever.

This should be somewhat surprising - it's exactly the same as the result from our first toy model. All the added complexity (continuous time,  $n$  independent individuals, chance of no birth or death in a time step) had no effect on  $P_{\text{Ext}}$ !

These changes certainly had other effects: (P.3)

All of the  $P_i(t)$  are different, and so are the expected value and standard deviation. However, the long term behavior is essentially unchanged.

This is because there are really two separate processes going on here:

- 1) Time between birth/death events
- 2) Probability of birth vs death when we have an event.

The toy model drastically simplified 1 - we always waited exactly one time step between events - while <sup>this</sup> model let the time between events be random and depend on  $N$ . However, both models treated 2 in exactly the same way. Once you have an event, the chance of a birth is  $\frac{\beta}{\delta}$  times bigger than the chance of a death. This is why we use toy models - they capture one piece of a more complicated phenomenon.

We can also look at the "time process" in (P.4) more detail. For this class, we will look at one particular question: How long does it take to go extinct? Actually, even that is more complicated than we want to get into, so we will assume that the population starts at  $N_0 = 1$ . (Nothing really changes when  $N_0 > 1$ , but the integrals get harder). Furthermore, we only expect extinction if  $\beta < \delta$ , so we will assume  $\beta < \delta$ .

Let  $T$  be the (random) time at which the last individual dies. We want the cdf for  $T$ , or

$$F_T(t) = P_r[T \leq t].$$

If  $T \leq t$ , that means that the population is already extinct by time  $t$ , so  $N(t) = 0$ . If  $T > t$ , then the population is not extinct yet, so  $N(t) \neq 0$ . This means that

$$F_T(t) = P_r[T \leq t] = P_r[N(t) = 0] = P_0(t).$$

We therefore have

(P.5)

$$F_T(t) = \begin{cases} \frac{\beta t}{1 + \beta t} & \text{if } \beta = \delta \\ \frac{\delta e^{rt} - \delta}{\beta e^{rt} - \delta} & \text{if } \beta \neq \delta. \end{cases}$$

We would like to find the expected value of  $T$ ;  $\langle T \rangle$ . Here is a useful computational trick.

$$\begin{aligned} \langle T \rangle &= \int_0^\infty t \frac{dF_T}{dt} dt = - \int_0^\infty \underbrace{t}_{u} \cdot \underbrace{\frac{d}{dt}[1 - F_T]}_{dv} dt \\ &= - \left[ \cancel{t \cdot (1 - F_T)} \Big|_0^\infty - \int_0^\infty 1 - F_T(t) dt \right] \\ &= \int_0^\infty 1 - F_T(t) dt. \end{aligned}$$

We therefore have (for  $\beta < \delta$ )

$$\begin{aligned} \langle T \rangle &= \int_0^\infty 1 - \frac{\delta e^{rt} - \delta}{\beta e^{rt} - \delta} dt \\ &= \int_0^\infty \frac{(\beta - \delta)e^{rt}}{\beta e^{rt} - \delta} dt \quad \begin{array}{l} u = e^{rt} \\ du = (\beta - \delta)e^{rt} dt \end{array} \\ &= \int_1^0 \frac{1}{\beta u - \delta} du = \frac{1}{\beta} \ln|\beta u - \delta| \Big|_1^0 = \frac{1}{\beta} \ln|\delta| - \frac{1}{\beta} \ln|\beta - \delta| \end{aligned}$$

$$\text{So } \langle T \rangle = \frac{1}{\beta} \ln \left( \frac{\delta}{\delta - \beta} \right).$$

Similarly, if  $\beta = \delta$ , then

$$\langle T \rangle = \int_0^{\infty} \left( 1 - \frac{\beta t}{1 + \beta t} \right) dt$$

$$= \int_0^{\infty} \frac{1}{1 + \beta t} dt$$

$$= \frac{1}{\beta} \ln |1 + \beta t| \Big|_0^{\infty} = \infty$$

This means that

$$\langle T \rangle = \begin{cases} \frac{1}{\beta} \ln \left( \frac{\delta}{\delta - \beta} \right) & \text{if } \beta < \delta \\ \infty & \text{if } \beta = \delta. \end{cases}$$

So the closer  $r$  is to zero, the longer it takes for the population to go extinct and (somewhat strangely) if  $\beta = \delta$  we know the population will die out with probability 1, but it will take (on average) infinite time. It's also worth noting that this information can't possibly come from

$\langle N(t) \rangle$  alone, because  $\langle N(t) \rangle$  only depends on the net growth rate  $\beta - \delta = r$ , but  $\langle T \rangle$  depends on  $\beta$  and  $\delta$  individually. (P.7)

We've been searching for a good notion of 'equilibria and stability for stochastic processes.' So far, none of them have been particularly satisfactory. In particular, extinction is a state we would like to call an equilibrium, and we would like to be able to distinguish between cases where  $\beta < \delta$  (so you expect to go extinct in finite time) and  $\beta > \delta$  (so you expect to grow without bound).

One method is to look at differential equations for  $\langle N(t) \rangle$ . These are deterministic, so all our old definitions apply.

Since we found

(P.2)

$$\frac{d\langle N(t) \rangle}{dt} = r \cdot \langle N(t) \rangle,$$

this would mean that  $\langle N(t) \rangle = 0$  is the only equilibrium (unless  $\beta = d$ ) and that it is stable if  $\beta < d$  and unstable if  $\beta > d$ . This meshes well with our conclusion that the time to extinction is only finite for  $\beta < d$ .

There is another version of equilibrium that is harder to visualize but often more useful.

Imagine that we had a thousand independent populations with some initial distribution of starting populations. That is, there are  $a_0$  of them with no bacteria,  $a_1$  of them w/ 1 bacterium,  $a_2$  of them w/ 2, etc.



Suppose we wait for a long time, then (P.9) come back and count all the populations.

In general, we don't expect to get the same  $a_i$ 's, but there are some distributions that will stay the same. (For instance, if  $a_0 = 1000$  and all other  $a_i = 0$ .) If the total number of populations, say  $N_{\text{pop}}$ , is very large, then

$$\frac{a_i(t)}{N_{\text{pop}}} \approx P_i(t).$$

This means that finding a distribution of  $a_i$ 's that doesn't change is equivalent to finding a distribution of  $P_i$ 's that doesn't change. We will call such a set of  $P_i$ 's a "stationary distribution".

The stationary distribution is usually denoted by  $\pi = [\pi_0, \pi_1, \pi_2, \dots]$

Now imagine that you start with some (P.10)  
other set of  $a_i$ 's. For instance, maybe all

the populations start w/  $N_0$  individuals, so  
 $a_{N_0} = N_{pop}$  and all other  $a_i = 0$ . We will call

the stationary distribution stable if

$\frac{a_n(t)}{N_{pop}} \rightarrow \pi_n$  as time goes to infinity,  
and unstable otherwise.