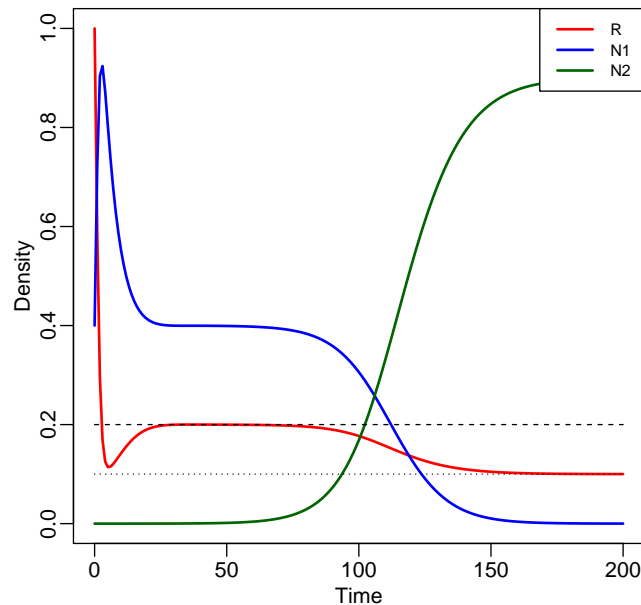


**Question 1. Competition (6 points)**

Consider a general model with two consumers competing for one (non-replicating) resource:

$$\frac{dR}{dt} = s - dR - a_1 N_1 R - a_2 N_2 R, \quad \frac{dN_1}{dt} = N_1(c_1 a_1 R - d_1) \quad \text{and} \quad \frac{dN_2}{dt} = N_2(c_2 a_2 R - d_2),$$

and a simulation of the model starting at the carrying capacity of the resource, an intermediate amount of  $N_1$  and very little of  $N_2$ :



- a. After a while  $N_1$  (blue) settles at a seemingly stable level, with  $R$  (red) approaching the dashed line. Explain this in biological terms and give the mathematical expression for the  $R$  density at this dashed line.

3 points: Because  $N_2$  is virtually absent,  $N_1$  depletes  $R$  to its critical level  $R^* = \frac{d_1}{c_1 a_1}$ .

- b. Later  $N_2$  (green) expands and takes over, while  $R$  approaches the dotted line. Explain this in biological terms and give the mathematical expression for the  $R$  density at this dotted line.

1 points: Now  $N_2$  outcompetes  $N_1$  and depletes the resource to  $R = \frac{d_2}{c_2 a_2}$ .

- c. Explain this behavior of the model in terms of  $r$ -selected and  $K$ -selected species.

2 points:  $N_1$  is  $r$ -selected and  $N_2$  is  $K$ -selected.

**Question 2. Killing rate (4 points)**

Consider an exponentially growing tumor,  $T$ , that is controlled by an immune response,  $E$ ,

$$\frac{dT}{dt} = rT - kTE \quad \text{and} \quad \frac{dE}{dt} = \frac{pET}{h + T} - dE,$$

where  $k$  is a killing rate,  $p$  a maximum division rate and  $d$  a death rate.

- a. What is the biological definition of the parameter  $h$ ?

1 point: The tumor density where the  $E$  cells divide at a rate  $p/2$ .

- b. What do you expect for the total killing rate,  $k\bar{E}$ , at steady state? Do patients with a better immune response (e.g., with a lower  $h$  or faster  $p$ ), kill tumor cells at steady state,  $\bar{T}$ , faster?

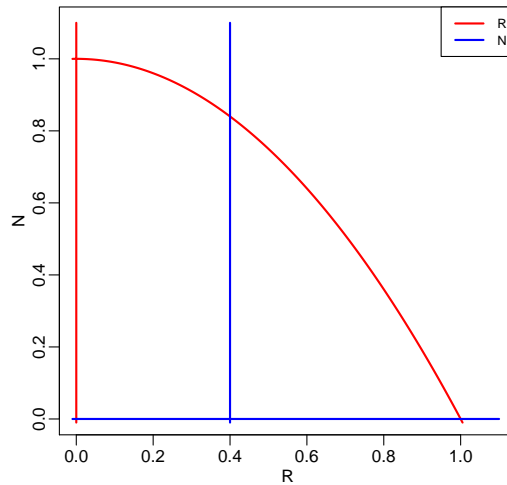
2 points:  $k\bar{E} = r$ : No the killing rate is always  $r$ .

- c. What is the size of the tumor at steady state? Does this depend on the killing rate  $k$ ?

1 point:  $\bar{T} = \frac{h}{p/d-1}$ : No,  $k$  is absent.

**Question 3. Parabolic nullclines (4 points)**

We have seen several models with a concave nullcline of the resource and a vertical nullcline of the consumers, e.g.,



Explain for each of the four models below if they can have a concave resource nullcline (not necessarily identical to the one shown above, just concave ('bol'), and a vertical consumer nullcline. Note that none, several, or all models could be valid.

1.  $dR/dt = rR(1 - R/K) - \frac{aNR}{h+R}$  and  $dN/dt = caNR - dN$
2.  $dR/dt = rR(1 - R/K) - aNR$  and  $dN/dt = \frac{caNR}{h+R} - dN$
3.  $dR/dt = rR(1 - [R/K]^2) - aNR$  and  $dN/dt = caNR - dN$
4.  $dR/dt = rR(1 - R/K) - \frac{aNR^2}{h+R^2}$  and  $dN/dt = \frac{caNR^2}{h+R^2} - dN$

Only 1 and 3 are concave and straight: every correct answer one point.

**Question 4. Make a model (6 points)**

Write a natural model for a population of butterflies that emerge from caterpillars which in turn emerge from eggs that are laid by the butterflies. The caterpillars are predated upon by birds. Assume for simplicity that this bird species only feeds on caterpillars of this population of butterflies, and ignore seasonality. Write a natural model.

$dB/dt = cC - dB$  ,  $dC/dt = eE - dC - aCN$  ,  $dE/dt = bE - dE$  ,  $dN/dt = aCN - dN$ , for butterflies, caterpillars, eggs and birds