Exercise 4

(a) invader dynamics:

$$\frac{\dot{m}}{m} = r(y)\left(1 - \frac{\sum_j n_j}{K}\right) - \frac{\beta(y)\,\theta}{1+\sum_j \beta(x_j)T(x_j)n_j}$$

(b)

$$s_E(y) = \lim_{t\to\infty} \frac{1}{t}\int_0^t \frac{\dot{m}(\tau)}{m(\tau)}\,d\tau$$

$$= \lim_{t\to\infty} \frac{1}{t}\left[r(y)\underbrace{\int_0^t d\tau}_{t} - \frac{r(y)}{K}\int_0^t \sum_j n_j(\tau)\,d\tau - \beta(y)\int_0^t \frac{\theta(\tau)\,d\tau}{1+\sum_j \beta(x_j)T(x_j)n_j(\tau)}\right]$$

$$= r(y)\Bigg(1 - \frac{1}{K}\underbrace{\lim_{t\to\infty}\frac{1}{t}\int_0^t \sum_j n_j(\tau)\,d\tau}_{E_1 :=}\Bigg) - \beta(y)\underbrace{\lim_{t\to\infty}\frac{1}{t}\int_0^t \frac{\theta(\tau)\,d\tau}{1+\sum_j \beta(x_j)T(x_j)n_j(\tau)}}_{E_2 :=}$$

$$= r(y)\left(1 - \frac{E_1}{K}\right) - \beta(y)E_2$$

(c) If x_1 and x_2 coexist, then $s_E(x_1) = s_E(x_2) = 0$.

$$\begin{cases} s_E(x_1) = r(x_1)\left(1 - \frac{E_1}{K}\right) - \beta(x_1)E_2 = 0 & (*) \\ s_E(x_2) = r(x_2)\left(1 - \frac{E_1}{K}\right) - \beta(x_2)E_2 = 0 & (**) \end{cases}$$

$(*)$: $E_2 = \dfrac{r(x_1)}{\beta(x_1)}\left(1 - \dfrac{E_1}{K}\right)$

$(*)\to(**)$: $r(x_2)\left(1 - \dfrac{E_1}{K}\right) - \beta(x_2)\dfrac{r(x_1)}{\beta(x_1)}\left(1 - \dfrac{E_1}{K}\right) = 0$

$$\Rightarrow \left(r(x_2) - \frac{\beta(x_2)\,r(x_1)}{\beta(x_1)}\right)\left(1 - \frac{E_1}{K}\right) = 0$$

$$\Rightarrow \frac{r(x_2)}{\beta(x_2)} = \frac{r(x_1)}{\beta(x_1)} \quad \text{or} \quad E_1 = K$$

We have not explicitly specified the functions $r(x)$ and $\beta(x)$.

The condition $\frac{r(x_1)}{\beta(x_1)} = \frac{r(x_2)}{\beta(x_2)}$ is not generically true.$^{(*)}$

If $E_2 > 0$, then $E_1 = K$ implies that $s_E(x_i) \neq 0$; so no coexistence. However, if $E_2 = 0$ (e.g., if there are no predators) then we can have coexistence (even for infinitely many different types).

(*) If we set $H(x) = \frac{r(x)}{\beta(x)}$, then our condition becomes $H(x_1) = H(x_2)$. If, for example, $H(x)$ is monotonous, the condition does not hold for any $x_1 \neq x_2$.

So, the condition is generically not true, but it may be true for some $x_1 \neq x_2$, if we can choose $r(x)$ and $\beta(x)$ appropriately (, which we in general cannot do!)

(d) 1° $s_x(x) = r(x)\left(1 - \frac{E_1}{K}\right) - \beta(x) E_2 = 0$

$$\Rightarrow E_2 = \frac{r(x)}{\beta(x)}\left(1 - \frac{E_1}{K}\right)$$

2° $s_x(y) = r(y)\left(1 - \frac{E_1}{K}\right) - \beta(y) E_2 = r(y)\left(1 - \frac{E_1}{K}\right) - \beta(y)\frac{r(x)}{\beta(x)}\left(1 - \frac{E_1}{K}\right)$

$$= \left(r(y) - \beta(y)\frac{r(x)}{\beta(x)}\right)\left(1 - \frac{E_1}{K}\right) > 0$$

I assume $E_1 < K$, so $1 - \frac{E_1}{K} > 0$

$$\Rightarrow \frac{\beta(y)}{r(y)} < \frac{\beta(x)}{r(x)}$$

(e) For these calculations, we have not needed the dynamics of θ.

Exercise 5

(a) $$\frac{\dot m}{m} = \frac{\gamma(y)\,\beta(y)\,\theta}{1+\beta(y)T(y)\theta} - \delta(y)$$

(b) $$S_E(y) = \gamma(y)\beta(y)\underbrace{\left[\lim_{t\to\infty}\frac{1}{t}\int_0^t \frac{\theta(\tau)\,d\tau}{1+\beta(y)T(y)\theta(\tau)}\right]}_{E_1(y):=} - \delta(y)$$

$$= \gamma(y)\beta(y)E_1(y) - \delta(y)$$

(c) Notice that in the invasion fitness $E_1(y)$ is NOT a constant, but a function of y. Therefore we have an infinite-dimensional environment and we cannot give an upper bound to the number of coexisting residents. However, if we assume that the resident population is at an equilibrium, then $\theta(\tau) = \theta$ is a constant. Then

$$S_E(y) = \frac{\gamma(y)\beta(y)\theta}{1+\beta(y)T(y)\theta} - \delta(y).$$

For coexistence we need $S_E(x_i) = 0 \quad \forall i \qquad (\star)$

$$\Rightarrow \quad \gamma(x_i)\beta(x_i)\theta = \delta(x_i) + \delta(x_i)\beta(x_i)T(x_i)\theta \quad \forall i$$

$$\Rightarrow \quad \theta = \frac{\delta(x_i)}{[\gamma(x_i) - \delta(x_i)T(x_i)]\beta(x_i)} \quad \forall i$$

$(\star)$ is a system of i equations with one unknown variable θ. Generically no solutions exist, if the number of equations is greater than one.

(d) $$S_x(y) = \frac{\gamma(y)\beta(y)\theta}{1+\beta(y)T(y)\theta} - \delta(y) > 0 \Rightarrow \theta > \frac{\delta(y)}{[\gamma(y)-\delta(y)T(y)]\beta(y)}$$

On the left hand side we have the monomorphic equilibrium population density of x and on the right hand side the monomorphic eq. pop. dens. of an invading strategy y.

Exercise 6

(a) $\frac{\dot{m}}{m} = \beta(y)H - (\delta + y)$

(b) $s_E(y) = \beta(y)E_1 - (\delta + y)$, where

$$E_1 = \langle H \rangle = \lim_{t\to\infty} \frac{1}{t}\int_0^t H(\tau)\,d\tau$$

(c) $s_E(x_i) = \beta(x_i)E_1 - (\delta + x_i) = 0 \quad \forall i \quad (*)$

$$\Rightarrow \quad E_1 = \frac{\delta + x_i}{\beta(x_i)} \quad \forall i$$

(*) Since this is a system with one unknown variable, E_1, generically there exists no solution, if the number of equations is greater than one. So, generically, no coexistence.

(d) $s_x(y) > 0 \Rightarrow E_1 > \frac{\delta + y}{\beta(y)}$

Left hand side is the monomorphic eq. pop. dens. of resident x and the right hand side is the monomorphic eq. pop. dens. of an invading strategy y.

Exercise 7

(a) here there is density-dependance in the death rate, whereas in Ex. 6 there was density dependance in the birth rate

(b) $\frac{\dot{m}}{m} = \beta(y)H - (\sigma(N) + y)$

(c) $S_E(y) = \beta(y)E_1 - E_2 - y$, where

$$E_1 = \lim_{t\to\infty} \frac{1}{t}\int_0^t H(\tau)d\tau = \langle H \rangle$$

$$E_2 = \langle \sigma(N) \rangle = \lim_{t\to\infty} \frac{1}{t}\int_0^t \sigma(N(\tau))\,d\tau$$

(d) Coexistance is generically possible for at most <u>two</u> types (we have two unknown variables E_1 and E_2 and two equations):

$$\begin{cases} S_{\underline{x}}(x_1) = \beta(x_1)E_1 - E_2 - x_1 = 0 & (*) \\ S_{\underline{x}}(x_2) = \beta(x_2)E_1 - E_2 - x_2 = 0 & (**) \end{cases}$$

$(*)$: $E_2 = \beta(x_1)E_1 - x_1$

$(*) \to (**)$: $S_{\underline{x}}(x_2) = \beta(x_2)E_1 - (\beta(x_1)E_1 - x_1) - x_2 = 0$

$$\Rightarrow E_1 = \frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)}$$

$$\Rightarrow E_2 = \beta(x_1)\frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)} - x_1$$

(e)

$$S_{x_1,x_2}(y) = \beta(y)E_1 - E_2 - y$$

$$= \beta(y)\frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)} - \left(\beta(x_1)\frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)} - x_1\right) - y$$

Remark:

Note that in exercise 7 any two types x_1 and x_2, which give reasonable values for E_1 and E_2, can coexist. In exercise 6, for example, only types x_1 and x_2, which have the exact same value of $(\delta+x_i)/\beta(x_i)$ can coexist. Hence, generically, no coexistence.