Appendix B. An extension of the discrete model with two populations

An extension of the analysis for two populations of the discrete system from Ch. 2, section 2.6.2 is presented in this appendix. Consider a system of *n* populations with values λ_1, λ_2, ..., λ_n with $\lambda_1 < \lambda_2 < ... < \lambda_n$ and evenly spaced with λ-step Δλ. Suppose these populations are affecting each other through competition and no other population are affecting them. The system is

$$\begin{cases} \dfrac{dF_i}{d\tau} = \dfrac{\lambda_i S_i(\tau)}{1+(\Delta\lambda)\sum_{j=1}^{n} S_j(\tau)} - F_i(\tau) = g_i \\ \dfrac{dS_i}{d\tau} = P_i F_i(\tau) - C\lambda_i S_i(\tau) = h_i \end{cases}$$

where g_i is a function of F_1, ..., F_n, S_1, ..., S_n.

Let f_1, s_1, f_2, s_2, ..., f_n and s_n be the steady state solutions. Then, the possible steady states for this system are the trivial steady state $\{f_1, s_1, f_2, s_2, ..., f_n, s_n\} = \{0, ..., 0\}$ and

$$\{f_1, s_1, f_2, s_2, ..., f_n, s_n\} = \begin{cases} f_i \neq 0, s_i \neq 0, \text{ for } i = i_1, i_2, ..., i_k \text{ with } 1 \le k \le n, \\ f_j = 0, s_j = 0 \ \ \forall \ \ j \neq i. \end{cases}$$

In the non-zero steady state

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_1}}{C}$$

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_2}}{C}$$

$$\vdots$$

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_k}}{C}$$

This is only possible if $P_{i_1} = P_{i_2} = \ldots = P_{i_k}$. Say $P_0 = P_{i_1} = P_{i_2} = \ldots = P_{i_k}$. In that case the populations can coexist, and their values are determined by the initial conditions and by the relationship

$$1 + (\Delta\lambda)(s_{i_1} + s_{i_2} + \ldots + s_{i_k}) = \frac{P_0}{C} \qquad \text{(B.1)}$$

and therefore

$s_{i_1} + s_{i_2} + \ldots + s_{i_k} = \frac{1}{(\Delta\lambda)}\left(\frac{P_0}{C} - 1\right)$. This is the only constraint, and having picked the values of s_i, f_i can be found by

$$f_i = \frac{C\lambda_i s_i}{P_0}.$$

For the linear stability analysis, first consider the case when $P_0 = P_1 = P_2 = \ldots = P_n$, *i.e.* all peaks have the same value of P_0, and they all survive. A short description of the linear stability analysis is presented in Appendix A, section A.0.

The Jacobian matrix is defined by

$$M = \begin{bmatrix} \frac{\partial g_1}{\partial f_1} & \frac{\partial g_1}{\partial f_2} & \cdots & \frac{\partial g_1}{\partial f_n} & \frac{\partial g_1}{\partial s_1} & \cdots & \frac{\partial g_1}{\partial s_n} \\ \vdots & \ddots & & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial g_n}{\partial f_1} & \frac{\partial g_n}{\partial f_2} & \cdots & \frac{\partial g_n}{\partial f_n} & \frac{\partial g_n}{\partial s_1} & \cdots & \frac{\partial g_n}{\partial s_n} \\ \frac{\partial h_1}{\partial f_1} & \cdots & & \frac{\partial h_1}{\partial f_n} & \frac{\partial h_1}{\partial s_1} & \cdots & \frac{\partial h_1}{\partial s_n} \\ \vdots & \ddots & & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial h_n}{\partial f_1} & \cdots & & \frac{\partial h_n}{\partial f_n} & \frac{\partial h_n}{\partial s_1} & \cdots & \frac{\partial h_n}{\partial s_n} \end{bmatrix}$$

where

$\frac{\partial h_i}{\partial f_i} = P_0$, $\frac{\partial h_i}{\partial f_j} = 0$ when $i \neq j$, $\frac{\partial h_i}{\partial s_i} = -C\lambda_i$, $\frac{\partial h_i}{\partial s_j} = 0$, when $i \neq j$,

$\frac{\partial g_i}{\partial f_i} = -1$, $\frac{\partial g_i}{\partial f_j} = 0$ when $i \neq j$.

On the other hand $\frac{\partial g_i}{\partial s_i}$ and $\frac{\partial g_i}{\partial s_j}$ (when $i \neq j$) are more complicated, so leave them as they are for now.

$$M = \begin{bmatrix} \overbrace{\begin{matrix} -1 & & 0 \\ & \ddots & \\ 0 & & -1 \end{matrix}}^{n\times n} & \begin{matrix} \frac{\partial g_1}{\partial s_1} & \cdots & \frac{\partial g_1}{\partial s_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial g_n}{\partial s_1} & \cdots & \frac{\partial g_n}{\partial s_n} \end{matrix} \\ \begin{matrix} P_0 & & 0 \\ & \ddots & \\ 0 & & P_0 \end{matrix} & \underbrace{\begin{matrix} -C\lambda_1 & & 0 \\ & \ddots & \\ 0 & & -C\lambda_n \end{matrix}}_{n\times n} \end{bmatrix}$$

This can be transformed into

$$M^* = \begin{bmatrix} \begin{matrix} -1 & & 0 \\ & \ddots & \\ 0 & & -1 \end{matrix} & \begin{matrix} \frac{\partial g_1}{\partial s_1} & \cdots & & \frac{\partial g_1}{\partial s_1} \\ \vdots & \ddots & & \vdots \\ \frac{\partial g_n}{\partial s_1} & \cdots & & \frac{\partial g_n}{\partial s_n} \end{matrix} \\ \begin{matrix} 0 & \cdots & \cdots & 0 \\ \vdots & \ddots & & \vdots \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & 0 \end{matrix} & \begin{matrix} -C\lambda_1 + P_0\frac{\partial g_1}{\partial s_1} & P_0\frac{\partial g_1}{\partial s_2} & \cdots & P_0\frac{\partial g_1}{\partial s_n} \\ P_0\frac{\partial g_2}{\partial s_1} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & P_0\frac{\partial g_{n-1}}{\partial s_n} \\ P_0\frac{\partial g_n}{\partial s_1} & \cdots & P_0\frac{\partial g_n}{\partial s_{n-1}} & P_0\frac{\partial g_n}{\partial s_n} \end{matrix} \end{bmatrix}$$

This can be achieved by multiplying the first row of M by P_0, and subtract from row (n+1), then multiply the second row by P_0 and subtract from row (n+2), etc.

Now, $\det M = \det M^* = (\det B)(\det C)$ (B.2)

where

$$B = \begin{bmatrix} \underbrace{\begin{matrix} -1 & & 0 \\ & \ddots & \\ 0 & & -1 \end{matrix}}_{n \times n} \end{bmatrix} \text{ and } \det B = (-1)^n$$

and

$$C = \begin{bmatrix} -C\lambda_1 + P_0 \frac{\partial g_1}{\partial s_1} & P_0 \frac{\partial g_1}{\partial s_2} & \cdots & P_0 \frac{\partial g_1}{\partial s_n} \\ P_0 \frac{\partial g_2}{\partial s_1} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & P_0 \frac{\partial g_{n-1}}{\partial s_n} \\ P_0 \frac{\partial g_n}{\partial s_1} & \cdots & P_0 \frac{\partial g_n}{\partial s_{n-1}} & -C\lambda_n + P_0 \frac{\partial g_n}{\partial s_n} \end{bmatrix}$$

Consider the expressions in the matrix C

$$\frac{\partial g_i}{\partial s_i} = \frac{\left(1 + (\Delta\lambda)\sum_{i=1}^{n} s_i\right)\lambda_i - s_i \lambda_i (\Delta\lambda)}{\left(1 + (\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} = \lambda_i \frac{1 + (\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)}{\left(1 + (\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} \qquad \text{(B.3)}$$

For $i \neq j$

$$\frac{\partial g_i}{\partial s_j} = -\lambda_i \frac{(\Delta\lambda) s_i}{\left(1 + (\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} \qquad \text{(B.4)}$$

Using (B.1)

$$1 + (\Delta\lambda)(\sum_{m=1}^{n} s_m) = \frac{P_0}{C} \qquad \text{(B.5)}$$

(B.3) and (B.4) can be rewritten as

$$\frac{\partial g_i}{\partial s_i} = \lambda_i \frac{C^2}{P_0^2}\left(1 + (\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)\right) \text{ and}$$

$$\frac{\partial g_i}{\partial s_j} = -\lambda_i \frac{C^2}{P_0^2} (\Delta\lambda) s_i .$$

From each term $C\lambda_i$ can be factored out.

Then $\det C = \left(\prod_{i=1}^{n} \lambda_i\right) \det C'$

where

$$C'_{ii} = -1 + \frac{C}{P_0}\left(1 + (\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)\right)$$

and

$$C'_{ij} = -\frac{C}{P_0}(\Delta\lambda)s_i$$

where *i*≠*j*.

For convenience, let $C^* = \frac{C}{P_0}$ and $s_i^* = (\Delta\lambda)s_i$. (B.6)

Then

$$C'_{ii} = -1 + C^*\left(1 + \left(\sum_{m=1}^{n} s^*_m - s_i\right)\right)$$

and

$$C'_{ij} = -C^* s^*_i$$

For clarity of notation omit the subscripts *, and call the new matrix *E*.

$$E = \begin{bmatrix} -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_1\right)\right) & -Cs_1 & \cdots & -Cs_1 \\ -Cs_2 & -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_2\right)\right) & \ddots & \vdots \\ \vdots & \ddots & \ddots & -Cs_{n-1} \\ -Cs_n & \cdots & -Cs_n & -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

Subtract column 2 from column 1

$$\begin{bmatrix} -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_1\right)\right)+Cs_1 & -Cs_1 & \cdots & -Cs_1 \\ 1-C\left(1+\left(\sum_{m=1}^{n}s_m - s_2\right)\right)-Cs_2 & -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_2\right)\right) & & \vdots \\ 0 & & \ddots & \\ \vdots & \vdots & \ddots & -Cs_{n-1} \\ 0 & -Cs_n & \cdots \quad -Cs_n & -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_n\right)\right) \end{bmatrix}$$

or

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n}s_m\right) & -Cs_1 & \cdots & -Cs_1 \\ 1-C\left(1+\sum_{m=1}^{n}s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_2\right)\right) & & \vdots \\ 0 & & \ddots & \\ \vdots & \vdots & \ddots & -Cs_{n-1} \\ 0 & -Cs_n & \cdots \quad -Cs_n & -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_n\right)\right) \end{bmatrix}$$

Subtract column 3 from column 2, column 4 from column 3, …, column *n* from column *n*-1.

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n}s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 1-C\left(1+\sum_{m=1}^{n}s_m\right) & -1+C\left(1+\sum_{m=1}^{n}s_m\right) & & \vdots & \vdots \\ 0 & 1-C\left(1+\sum_{m=1}^{n}s_m\right) & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n}s_m\right) & -Cs_{n-1} \\ 0 & 0 & 0 & 1-C\left(1+\sum_{m=1}^{n}s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n}s_m - s_n\right)\right) \end{bmatrix}$$

Diagonalise this matrix by adding row 1 to row 2,

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -Cs_{n-1} \\ 0 & 0 & 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

then add row 2 to row 3, row 3 to row 4, etc.

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 0 & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -C\sum_{m=1}^{n-1} s_m \\ 0 & 0 & 0 & 0 & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - \sum_{m=1}^{n} s_m\right)\right) \end{bmatrix}$$

and therefore,

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 0 & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -C\sum_{m=1}^{n-1} s_m \\ 0 & 0 & 0 & 0 & -1+C \end{bmatrix}$$

Call the resulting matrix E'. Now,

$$\det E = \det E' = \left(-1+C\left(1+\sum_{m=1}^{n} s_m\right)\right)^{n-1} (1-C)\,. \qquad \text{(B.7)}$$

Note that since (B.6), C in (B.7) actually stands for $\frac{C}{P_0}$, and s_m stands for $(\Delta\lambda)\, s_m$.

Therefore,

$$\det E = \det E' = \left(-1 + \frac{C}{P_0}\left(1 + (\Delta\lambda)\sum_{m=1}^{n} s_m\right)\right)^{n-1} (1 - \frac{C}{P_0})$$

But from (B.5)

$$1 + (\Delta\lambda)(\sum_{m=1}^{n} s_m) = \frac{P_0}{C}$$

and therefore,

$$\det E = \det E' = \left(-1 + \frac{C}{P_0}\frac{P_0}{C}\right)^{n-1} (1 - \frac{C}{P_0}) = 0\,.$$

Therefore, coming back to (B.2)

$\det M = 0$.

This means that the stability cannot be determined for steady state where populations for all λ_i are non-zero.