OLM 8.2. Fitness in age structured populations

It is of central importance that any kind of reproductive unit has a well-defined fitness, i.e. asymptotic growth rate, at fixed values of the regulating and modifying variables. We introduced briefly a description of age-structured populations in TBox 8.2 (p.154). For this case fitness is defined by the Euler-Lotka equation (Eq. (8.15), p.155), which we derive here.

The transition matrix of an age structured population, also called Leslie matrix, reads as

$$\boldsymbol{A} = \begin{pmatrix} m_1 & m_2 & m_3 & \cdots & m_L \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}, \qquad (8.2.1)$$

where m_i and p_i are the effective fecundity and the survival probability to the next age group of an individual of age *i*, respectively; *L* is the last age group.

To be precise, we assume that reproduction in the population is synchronised, e.g., yearly. Census is made at the beginning of each breading season, when the youngest individuals are one year old. Effective fecundity m_i is the expected number of offspring of an individual of age *i* that survives to the next census, i.e. until becoming one year old. Note that a different notation exists also in the literature, in which 0 is the youngest age. It corresponds to census time at the end of the breeding seasons, when newborns are also counted. Fecundity replaces effective fecundity in this case.

Denote the size of the *i*th age group in a given generation by N_i ($i = 1,2, \dots, L$). The iteration of the *p*-states (Eq. (4.6), p.56) is

$$\begin{pmatrix} N_1' \\ N_2' \\ N_3' \\ \vdots \\ N_L' \end{pmatrix} = \begin{pmatrix} m_1 & m_2 & m_3 & \cdots & m_L \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_L \end{pmatrix}, \qquad (8.2.2)$$

where the next generation is denoted by prime. As most of the matrix elements are zero (so called *sparse matrix*), it is very easy to rewrite the multiplication with the matrix in simpler terms. The one-year olds are simply the surviving individuals born in the previous breeding season:

$$N_1' = \sum_{i=1}^{L} N_i m_i, \qquad (8.2.3)$$

while the older individuals are the ones surviving from the previous year:

$$N'_{i+1} = p_i N_i \qquad \text{for } i = 1, 2, \dots, L-1. \tag{8.2.4}$$

Assume, that age structure has already stabilized and the population is growing exponentially with rate λ, which is the leading eigenvalue of the Leslie matrix. Then,

$$N'_i = \lambda_i N_i \qquad \text{for } i = 1, 2, \dots, L. \tag{8.2.5}$$

Combining it with Eq. (8.2.4) leads to

$$N_{i+1} = \frac{p_i}{\lambda} N_i. \tag{8.2.6}$$

It follows, that

$$N_i = \frac{l_i}{\lambda^{i-1}} N_1 \tag{8.2.7}$$

where

$$l_i = p_{i-1} p_{i-2} \dots p_1 \tag{8.2.8}$$

is the probability of surviving from age 1 to age *i*. Then a similar argument for the first age group leads to the relation

$$\lambda N_1 = \sum_{i=1}^{L} N_i m_i, = \sum_{i=1}^{L} \frac{l_i}{\lambda^{i-1}} N_1 m_i,, \tag{8.2.9}$$

which implies the Euler-Lotka equation

$$f(\lambda) = \sum_{i=1}^{L} \frac{l_i}{\lambda^i} N_1 m_i, = 1. \tag{8.2.10}$$

That is, we calculate the discounted number of offspring expected at the birth of an individual. (Offspring are discounted according to the age of the parent at the birth of the offspring. See TBox 4.4 (p. 59) for the notion of discounting.) Discounted offspring number must be 1 in a population with stable age structure.

Eq. (8.2.10) always has a unique real solution for λ, which is a positive number (Figure 8.18, p.156). Therefore, the *L*-1 other eigenvalues of the matrix must be complex numbers. Biological common sense, as well as Perron-Frobenius theorem (Caswell 2001, p. 83), requires the real solution being the leading eigenvalue. This conclusion establishes the general notion of fitness for age-structured populations.

Note, however, the possibility for exceptional cases: OLM 4.3 provides an example and Caswell's book discuss the topic in depth. See also Otto and Day (2007, p. 403) for a didactic introduction to age-structured population growth

References

Caswell, H. (2001). Matrix population models: construction, analysis, and interpretation. Sunderland, Masssachusetts, Sinauer Associates.

Otto, S.P. and Day, T. (2007). A Biologist's Guide to Mathematical Modeling in Ecology and Evolution. Princeton and Oxford, Princeton University Press.