OLM 4.3. Two age classes and a non-generic exception

As explained in TBox 4.3, the leading eigenvalue of the transition matrix provides the long-term growth rate of a structured population; the corresponding eigenvector determines the equilibrated population structure. This simple picture is not without exceptions. Here we consider a simple situation, where the two eigenvalues are of equal absolute value and the resulting behaviour is a population structure, which oscillates forever.

Instead of the two patches of TBox 4.2, consider here an age-structured population with two age classes as the *i*-states. (General age class models are discussed in TBox 8.2 and OLM 8.2.) Assume that the individuals of the population reproduce once in a year in synchrony, at their age 1 and age 2; they die afterwards. Censuses are made at the beginning of each breeding season, when we have two kinds of individuals: one year old and two years old. Then the *p*-state of the population is specified by the vector

$$\boldsymbol{N}(t) = \begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix}, \tag{4.3.1}$$

in which $N_1(t)$ and $N_2(t)$ are the numbers of one-year old and two-years old individuals at time t, respectively. The transition matrix (or, the Leslie matrix, as it is called for age structure) is

$$\boldsymbol{A} = \begin{pmatrix} m_1 & m_2 \\ p & 0 \end{pmatrix} \tag{4.3.2}$$

where m_1 and m_2 are the effective fecundities (the numbers of offspring alive at the next census time) of the two age groups. The probability of survival in the first age group is p, in the second one it is zero. The characteristic equation (Eq. 4.2.3) for this particular Leslie-matrix is

$$\begin{vmatrix} m_1 - \lambda & m_2 \\ p & -\lambda \end{vmatrix} = 0, \tag{4.3.3}$$

which expands to

$$\lambda^2 - \lambda m_1 - p m_2 = 0 \tag{4.3.4}$$

Its solution is

$$\lambda_{1,2} = \frac{m_1}{2} \pm \sqrt{\left(\frac{m_1}{2}\right)^2 + p m_2} \tag{4.3.5}$$

If $m_1 = 0$, i.e., if only the second age class reproduces, then

$$\lambda_{1,2} = \pm\sqrt{pm_2}. \qquad (4.3.6)$$

In this case the absolute values of the two eigenvalues are equal. Therefore, we do not have a unique leading eigenvalue and the mechanism illustrated on Figure 4.10 does not work.

Observe, that one of the eigenvalues is negative. (Recall, that positivity of the leading eigenvalue, when exists, is guaranteed by the Perron-Frobenius theorem.) Multiplication with a negative eigenvalue turns the component of the state vector parallel to the corresponding eigenvector to the opposite direction in each time step. This leads to the *p*-state oscillating with period 2 even in the long term. It is not an ergodic behaviour: the population “remembers” the age of the first individual that founded the population, whether it happened in an even or an odd year, forever. Which is not very surprising biologically, of course.

This exceptional, non-ergodic dynamics may show up in real populations only if some biological mechanism stabilizes m_1 at zero (e.g. oscillation in the periodical Magicicadas). Infinite oscillation disappears immediately as m_1 becomes different from 0 by an arbitrarily small value, even though the relaxation time (the time to approach the stable *p*-state distribution) may be very long. (We have seen in TBox 4.6 that it is the ratio of the first two eigenvalues that determines relaxation time. Relaxation time is infinite when the two absolute values are equal.)

This OLM serves to demonstrate that exceptional, non-ergodic behaviour is also possible for structured populations. Actually, we demonstrated this in a much simpler example by setting the migration rate zero in the two-patch example of TBox 4.2 in TBox 4.6. Population distribution between the patches will not relax to an equilibrium distribution without the possibility of migration. However, one can argue against considering the two separated populations, as a single, structured one. The oscillation example presented here is the simplest non-trivial one. The common feature of these, and all other non-ergodic cases, that an exceptional parameter value results in infinite relaxation time.

The Reader with serious interest in structured populations should invest to learn the exact conditions of the Perron-Frobenus theorem, which guaranties ergodicity when the conditions are met. A very good place to look it up for an ecologist is Caswell (2001, p. 79).

References

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