OLM 4.2. How do we calculate eigenvalues and eigenvectors?

Eigenvaules and eigenvectors were introduced in TBox 4.3. These concepts were instrumental in understanding the behaviour of structured populations. Here we learn, how to determine them analytically and apply the formulas for the two-patch model of TBox 4.2 for insight.

We say that $\boldsymbol{w}$ is a (right) eigenvector of $\boldsymbol{A}$ with eigenvalue λ, if

$$\boldsymbol{Aw} = \lambda\boldsymbol{w} \qquad\qquad (4.2.1)$$

holds (Eq. 4.10). Rearranging leads to

$$(\boldsymbol{A} - \lambda\boldsymbol{I})\boldsymbol{w} = \boldsymbol{0}, \qquad\qquad (4.2.2)$$

where $\boldsymbol{I}$ is the identity matrix (a matrix with 1s in the diagonal and 0s elsewhere) and $\boldsymbol{0}$ is the null vector (a vector with 0 elements). Were the matrix $(\boldsymbol{A} - \lambda\boldsymbol{I})$ invertible, Eq. (4.2.2) would be solvable by left-multiplying it with the inverse matrix, yielding the trivial solution $\boldsymbol{w}=\boldsymbol{0}$. Therefore, a biologically sensible solution with $\boldsymbol{w} \neq \boldsymbol{0}$ requires $(\boldsymbol{A} - \lambda\boldsymbol{I})$ to be non-invertible. It happens when the determinant of the matrix vanishes:

$$\det(\boldsymbol{A} - \lambda\boldsymbol{I}) = \boldsymbol{0}. \qquad\qquad (4.2.3)$$

Therefore eigenvalues λ of matrix $\boldsymbol{A}$ are the roots of Eq. (4.2.3), which is often referred as the characteristic equation of matrix $\boldsymbol{A}$ (Otto and Day 2007, p.237). For each λ the corresponding eigenvector can be determined easily from Eq. (4.2.1).

The determinant of a k x k matrix is a polynomial of order k, which has k roots in general. Therefore, such matrix has k eigenvalues with the corresponding k eigenvectors. Often they are complex numbers. As explained in Ch4.3, the eigenvalue of largest absolute value is the leading eigenvalue of the matrix, and that is the relevant one, determining the asymptotic growth rate (TBox 4.3). The Perron– Frobenius theorem guarantees that the leading eigenvalue is a positive real number, as it should be, for the kinds of matrices we usually encounter in context of structured populations (Caswell 2001, p.83). OLM 4.3 provides an example for exceptional behaviour.

Principal importance of the characteristic equation notwithstanding, it is not necessarily the best way to actually calculate the eigenvalues. For $k > 2$ one probably would determine the roots of the polynomial numerically. However, there are more direct and more efficient numerical methods to calculate the eigenvalues and eigenvectors. These algorithms are readily available in scientific software packages, like R, or Mathematica.

The luxury of the two-state model is that the quadratic characteristic equation for $k = 2$ is easily solvable and provides an intuitively comprehensible result. For the two-patch example of TBox 4.2 the characteristic equation reads, as

$$\begin{vmatrix} (1-\mu)m_1 - \lambda & \mu m_2 \\ \mu m_1 & (1-\mu)m_2 - \lambda \end{vmatrix} = 0, \qquad (4.2.4)$$

expanding to the quadratic equation

$$\lambda^2 - \lambda(1-\mu)(m_1 + m_2) + (1-2\mu)m_1 m_2 = 0. \qquad (4.2.5)$$

The quadratic formula yields the two eigenvalues:

$$\lambda_{1,2} = (1-\mu)\frac{m_1+m_2}{2} \pm \sqrt{(1-\mu)^2\left(\frac{m_1+m_2}{2}\right)^2 - (1-2\mu)m_1 m_2}, \quad (4.2.6)$$

using

$$\left(\frac{m_1+m_2}{2}\right)^2 = \left(\frac{m_1}{2}\right)^2 + \left(\frac{m_2}{2}\right)^2 + \frac{m_1 m_2}{2} = \left(\frac{m_1-m_2}{2}\right)^2 - m_1 m_2, \qquad (4.2.7)$$

it can also be written into the form

$$\lambda_{1,2} = (1-\mu)\frac{m_1+m_2}{2} \pm \sqrt{(1-\mu)^2\left(\frac{m_1-m_2}{2}\right)^2 + \mu^2 m_1 m_2}. \qquad (4.2.8)$$

The larger eigenvalue obtains using the positive sign. Some more rearrangement and approximations lead to

$$\lambda_1 = \begin{cases} (1-\mu)\max(m_1, m_2), & \text{if } \mu \approx 0 \\ \frac{m_1+m_2}{2}, & \text{if } \mu = \frac{1}{2} \\ \sqrt{m_1 m_2}, & \text{if } \mu = 1 \end{cases} \qquad (4.2.9)$$

The second approximation comes from Eq. (4.2.6), the first and the third one from Eq. (4.2.8). This result is easy to interpret intuitively: If the dispersal between the two patches is weak, then the population will soon become more abundant on the better one, because the ratio of the numbers in the two patches increases exponentially, and the subpopulation of the less favourable patch becomes negligible. The overall growth rate of the population approaches the larger one of the two rates in the different habitats, minus the small loss due to seed dispersal. If dispersal is ½, then the two habitats receive the same number of seeds in every time step, so that the long-term overall growth rate of the population approaches the arithmetic mean of the two local rates. Finally, in the biologically unrealistic case of the complete swap of habitat type for all descendants in every time step (μ=1.0) the overall rate of population increase is the geometric mean of the local rates.

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.