3 Perron–Frobenius theorem

$\diamondsuit$ **3.1** (Mutation–selection equations)**.** Assume that we are considering a population that evolves in discrete times and is composed of N different types. Upon reproduction an individual of type i can produce offsprings of type j with probability p_{ij} (note the order of the indices). Let $P = [p_{ij}]$. Also assume that an individual of type i produces on average exactly w_i offsprings. Show that the dynamics of the sizes of different types is given by

$$n_i(t+1) = \sum_{j=1}^{N} w_j p_{ij} n_j(t),$$

or, in the matrix form, assuming $W = \operatorname{diag}(w_1, \ldots, w_N)$,

$$n(t+1) = PWn.$$

In theoretical genetics one is usually interested not in absolute sizes but in corresponding frequencies

$$p_i(t) = \frac{n_i(t)}{N(t)}\,, \quad N(t) = \sum_{i=1}^{N} n_i(t)\,.$$

1. Show that the equation for the frequencies is

$$p(t+1) = \frac{PWp}{\overline{w}(t)}\,, \quad \overline{w}(t) = \sum_{j=1}^{N} w_j p_j(t),$$

   which is a nonlinear difference equation.

2. Prove that if matrix PW is primitive, then the equation for the frequencies has a unique positive fixed point $\hat{p} > 0$, which is globally stable.

Now assume that the time is continuous and generations overlap. In this case the dynamics for the sizes is given by

$$\dot{n}_i = m_i n_i + \sum_{j=1}^{N} \mu_{ij} n_j, \quad i = 1, \ldots, N,$$

where now μ_{ij} are the rates (not probabilities!) of mutations of type j into i. In matrix form for $M = \operatorname{diag}(m_1, \ldots, m_N)$, $\mathcal{M} = [\mu_{ij}]$ we have

$$\dot{n} = (M + \mathcal{M})n.$$

Note that $\mu_{ii} = -\sum_{j\neq i} \mu_{ij}$, and hence $\mathcal{M}$ is not non-negative. It has, however, all off-diagonal entries non-negative, such matrices are called *quasi-positive*.

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1. Show that the equation for the corresponding frequencies takes the form

$$\dot{p} = (M + \mathcal{M})p - \overline{m}(t)p, \quad \overline{m}(t) = \sum_{j=1}^{N} m_j p_j(t),$$

   and is hence nonlinear.

2. Show that the simplex $S_n = \{x \in \mathbf{R}^n : x \geq 0, \sum_{i=1}^{n} x_i = 1\}$ is invariant with respect to this dynamical system.

3. Formulate a spectral theorem for the quasi-positive matrices.

4. Which conditions on $M + \mathcal{M}$ guarantee that the system for frequencies has a unique globally stable positive equilibrium $\hat{p}$?