METAPOPULATION CAPACITY

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1. Perron–Frobenius

1.1. **Theorem** (Perron–Frobenius theorem [1]). *Let $M_{n\times n} \geq 0$ be a non-negative irreducible matrix. Then*

- *There exists a positive eigenvalue $\lambda(M) > 0$ dominating all other eigenvalues in absolute value in the sense that $\lambda(M) \geq |\lambda|$ for all eigenvalues λ for M.*
- *$\lambda(M)$ has multiplicity one as a root in the characteristic polynomial.*
- *There exists a positive eigenvector $x > 0$ so that $Mx = \lambda(M)x$. Any other non-negative eigenvector for M is a positive scalar multiplum of x.*
- *Collatz–Wielandt formula*
$$\lambda(M) = \sup\{\min\{\frac{(Mx)_i}{x_i} \mid 1 \leq i \leq n, x_i > 0\} \mid x \geq 0, x \neq 0\}$$

The unique positive eigenvalue $\lambda(M) > 0$ is called *the Perron root* and the (essentially) unique positive eigenvector x is called *the Perron vector* of M

2. The star operation

2.1. **Definition.** *The star product of two n-vectors is their coordinatewise product:*
$$\begin{pmatrix} u_1 \\ \vdots \\ u_n \end{pmatrix} \star \begin{pmatrix} v_1 \\ \vdots \\ v_n \end{pmatrix} = \begin{pmatrix} u_1 v_1 \\ \vdots \\ u_n v_n \end{pmatrix}$$

The operation $\star$ obviously satisfies these rules:

- $u \star \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} = u$
- $u \star v = v \star u$
- $(u_1 + u_2) \star v = u_1 \star v + u_2 \star v$

2.2. **Theorem.** [2, Theorem 2.1] *Let $M_{n\times n} \geq 0$ be irreducible. There is a nonzero vector p in $[0,1]^n$ such that*
$$Mp \star p = Mp - p$$
if and only if $\lambda(M) > 1$.

Proof. First observe that for any matrix $M \geq 0$ and vector $p \geq 0$ we have that
$$Mp \star p = Mp - p \iff \forall i\colon (Mp)_i p_i = (Mp)_i - p_i \iff p_i(1 + (Mp)_i) = (Mp)_i$$
$$\iff \forall i\colon p_i = \frac{(Mp)_i}{1 + (Mp)_i}$$

Let $p \geq 0$ be a nonzero vector (in $[0,1]^n$ or not) so that $Mp \star p = Mp - p$ or $p_i = \frac{(Mp)_i}{1+(Mp)_i}$, $1 \leq i \leq n$. If $p_i > 0$, then $(Mp)_i > 0$, and $\frac{(Mp)_i}{p_i} = 1 + (Mp)_i > 1$. Hence the Perron root satisfies
$$\lambda(M) = \sup\{\min\{\frac{(Mx)_i}{x_i} \mid 1 \leq i \leq n, x_i > 0\} \mid x \geq 0, x \neq 0\} \geq \min\{\frac{(Mp)_i}{p_i} \mid 1 \leq i \leq n, p_i > 0\} > 1$$
by the Collatz–Wielandt formula.

Conversely, assume that $\lambda(M) > 1$. Choose $x \geq 0$, $x \neq 0$, so that
$$\frac{(Mx)_i}{x_i} > 1 \text{ for all } i \text{ with } x_i > 0$$

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Since the fraction on the left is unchanged when we replace x by sx, $s > 0$, we may assume that

$$\frac{(Mx)_i}{x_i} > 1 + (Mx)_i \text{ for all } i \text{ with } x_i > 0$$

or, equivalently,

$$x_i < \frac{(Mx)_i}{1 + (Mx)_i} \text{ for all } i \text{ with } x_i > 0$$

Then

$$x_i \leq \frac{(Mx)_i}{1 + (Mx)_i}, \qquad 1 \leq i \leq n$$

The function $F\colon \mathbf{R}^n \to \mathbf{R}^n$ given by $F_i(v) = \frac{(Mv)_i}{1+(Mv)_i}$ maps all non-negative vectors to $[0,1]^n$ and F is increasing in the sense that $u \leq v \Longrightarrow F(u) \leq F(v)$. The vector x satisfies $0 \lneqq x \leq F(x)$ so that

$$0 \lneqq x \leq F(x) \leq F \circ F(x) \leq \cdots \leq F \circ \cdots \circ F(x) \leq \cdots$$

This increasing bounded sequence converges to a limit vector $p \in [0,1]^n$, $p \neq 0$. The limit vector is a fixed point, $F(p) = p$, for F, which means that $Mp \star p = (M - E)p$. □

The proof shows that the solution to $Mp \star p = Mp - p$ can be approximated by an increasing sequence of vectors.

3. The spatially realistic Levins model

Suppose that we have a grid of n pathes. Let $A_i > 0$ be the carrying capacity of patch i and let $d_{ij} \geq 0$ denote the distance between patch i and j. The *landscape matrix* is the symmetric matrix M with entries

$$M_{ij} = \begin{cases} A_i A_j a^{-d_{ij}} & i \neq j \\ 0 & i = j \end{cases}$$

Write $p_i(t)A_i$ with $0 \leq p_i(t) \leq 1$ for the population density at patch i at time t. The *metapopulation vector* at time t is $p(t) = (p_1(t), \ldots, p_n(t)) \in [0,1]^n$.

The (discrete form of the) spatially realistic Levins model is

$$p_i(t+1) - p_i(t) = \frac{c}{A_i}\Big(\sum_{j \neq i} A_i A_j a^{-d_{ij}} p_j(t)(1 - p_i(t) - \delta p_i(t)\Big), \qquad 1 \leq i \leq n, \tag{3.1}$$

where a, c and δ are positive constants [2, Section 3]. (The factor $a^{-d_{ij}}$ can be replaced by another measure for the resistance to migration between patch i and j. The constant c has no relevance for our discussion.)

3.1. **Lemma.** *The metapopulation vector $p \in [0,1]^n$ is an equilibrium for the Levins model (3.1) if and only if $\delta^{-1}Mp \star p = \delta^{-1}Mp - p$.*

Proof. The equilibria are the solutions to the n equations

$$\sum_{j \neq i} A_i A_j a^{-d_{ij}} p_j(t)(1 - p_i(t)) - \delta p_i(t) = 0, \qquad 1 \leq i \leq n$$

These equations can also be written

$$M \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix} \star \begin{pmatrix} 1 - p_1 \\ \vdots \\ 1 - p_n \end{pmatrix} = \delta \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix}$$

and

$$M \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix} \star \begin{pmatrix} 1 - p_1 \\ \vdots \\ 1 - p_n \end{pmatrix} = \delta \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix} \iff \delta^{-1} M \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix} \star \begin{pmatrix} 1 - p_1 \\ \vdots \\ 1 - p_n \end{pmatrix} = \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix}$$

$$\iff \delta^{-1}Mp - \delta^{-1}Mp \star p = p \iff \delta^{-1}Mp \star p = \delta^{-1}Mp - p$$

□

3.2. **Corollary.** *The Levins model (3.1) has a nonzero equilibrium $p \in [0,1]^n$ if and only if $\delta < \lambda(M)$.*

Proof. By Lemma 3.1 and Theorem 2.2, the Levins model has a nontrivial equilibrium if and only if $1 < \lambda(\delta^{-1}M) = \delta^{-1}\lambda(M)$. □

Because of Corollary 3.2, the Perron root $\lambda(M)$ of the landscape matrix M is called the *metapopulation capacity* in this context [2, Definition 2.1].

References

[1] Carl Meyer, *Matrix analysis and applied linear algebra*, Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 2000, With 1 CD-ROM (Windows, Macintosh and UNIX) and a solutions manual (iv+171 pp.). MR MR1777382

[2] Otsao Ovaskainen and Ilkka Hanski, *Spatially structured metapopulation models: Global and local assessment of metapopulation capacity*, Theoret. Population Biol. **60** (2001), 281–302.

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