On dispersal and population growth for multistate matrix models

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Here we want to study the change of the overall growth rate if dispersions take place in the m age classes governed by the $n \times n$ column substochastic matrices $S_1, \ldots, S_m$.

[The (p, q) entry of S_j represents the fraction of the individuals in the jth age class moving from patch q to patch p.]

The system is now described by $\mathbf{SD}$, where

$$\mathbf{S} = S_1 \oplus \cdots \oplus S_m \quad \text{and} \quad \mathbf{D} = (D_{ij})_{1\le i,j\le m}$$

such that each $D_{ij} \in M_n$ is a diagonal matrix and

$$\mathbf{D}[1, n+1, \ldots, (m-1)n+1; 1, n+1, \ldots, (m-1)n+1] = A_1,$$

$$\mathbf{D}[2, n+2, \ldots, (m-1)n+2; 2, n+2, \ldots, (m-1)n+2] = A_2, \ldots,$$

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Example Suppose $S_1, S_2 \in M_3$, and $A_1, A_2, A_3 \in M_2$. Then

$$\mathbf{D} = \left(\begin{array}{ccc|ccc} (A_1)_{11} & 0 & 0 & (A_1)_{12} & 0 & 0 \\ 0 & (A_2)_{11} & 0 & 0 & (A_2)_{12} & 0 \\ 0 & 0 & (A_3)_{11} & 0 & 0 & (A_3)_{12} \\ \hline (A_1)_{21} & 0 & 0 & (A_1)_{22} & 0 & 0 \\ 0 & (A_2)_{21} & 0 & 0 & (A_2)_{22} & 0 \\ 0 & 0 & (A_3)_{21} & 0 & 0 & (A_3)_{22} \end{array}\right).$$

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here $\|\cdot\|$ is the column sum norm.

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Question How about the general case?

An Example

Consider a population of juveniles and mature adults living in two spatial locations (e.g., small salmon develop in fresh water and mature salmon move to ocean to reproduce). Suppose

$$A_1 = \begin{pmatrix} 0 & 0 \\ 1 & 0 \end{pmatrix} \text{ and } A_2 = \begin{pmatrix} 0 & 100 \\ 0 & 0 \end{pmatrix}.$$

That is, each small salmon grows to a mature salmon in fresh water, and each salmon reproduces 100 salmon in the ocean. If no dispersion is allowed, i.e., $\mathbf{S} = I_2 \oplus I_2$, then the growth rate of the whole system equals

$$\rho(\mathbf{D}) = \rho \left(\begin{array}{cc|cc} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 100 \\ \hline 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{array} \right) = 0.$$

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In fact, the population goes extinct in two time steps as $\mathbf{D}^2 = 0$.

Alternatively, if all juveniles move to patch 1 and all adults move to patch 2, then

$$S_1 = \begin{pmatrix} 1 & 1 \\ 0 & 0 \end{pmatrix} \quad \text{and} \quad S_2 = \begin{pmatrix} 0 & 0 \\ 1 & 1 \end{pmatrix}.$$

In which case,

$$\rho(\mathbf{SD}) = \rho \begin{pmatrix} 0 & 0 & 0 & 100 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix} = 10,$$

and the population grows asymptotically at a geometric rate.

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Question Determine $\mathbf{S}$ so that $\rho(\mathbf{SD}) \leq \rho(\mathbf{D})$ for all $\mathbf{D}$.

Result

Definition Suppose $\mathbf{S} = S_1 \oplus \cdots \oplus S_m$ is given. For $i = 1, \ldots, m$, let G_i be the directed graph of S_i with vertices $1, \ldots, n$. Here we ignore the diagonal entries of S_i, and assume that the edges of G_i has color i.

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We say that $S_1, \ldots, S_m$ admits a polychromatic cycle if there are nonzero entries of $S_1 + \cdots + S_m$ at the $(i_1, i_2), (i_2, i_3) \ldots, (i_{k-1}, i_k), (i_k, i_1)$ positions for some distinct $i_1, \ldots, i_k \in \{1, \ldots, n\}$, and these nonzero entries do not come from a single matrix S_j.

Theorem [Li & Schreiber,2006] Suppose $\mathbf{S} = S_1 \oplus \cdots \oplus S_m$ so that $S_1, \ldots, S_m$ are $n \times n$ column substochastic matrices. The following conditions are equivalent.

(a) For any nonnegative block matrix $\mathbf{D} = (D_{ij})_{1 \le i,j \le m}$ such that $D_{ij} \in M_n$ is a diagonal matrix, we have

$$\rho(\mathbf{SD}) \le \rho(\mathbf{D}).$$

(b) $S_1, \ldots, S_m$ does not admit a polychromatic cycle.

Idea of Proof

Note that $\rho(\mathbf{SD}) = \rho(\mathbf{PSP}^t\mathbf{PDP}^t) = \rho(\mathbf{RA})$, where

$$\mathbf{A} = A_1 \oplus \cdots \oplus A_n \quad \text{and} \quad \mathbf{R} = (R_{ij})_{1 \le i,j \le n}$$

such that R_{ij} is a diagonal matrix and

$\mathbf{R}[1, m+1, \ldots, (n-1)m+1; 1, m+1, \ldots, (n-1)m+1] = S_1, \ \ldots,$

$\mathbf{R}[2, m+2, \ldots, (n-1)m+2; 2, m+2, \ldots, (n-1)m+2] = S_2,$

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(b) $\Rightarrow$ (a): Assume that $S_1, \ldots, S_m$ admit a polychromatic cycle. We cook up $\mathbf{D}$ strategically so that $\mathbf{D}$ is similar to $\mathbf{A} = \mathbf{A}_1 \oplus \cdots \oplus \mathbf{A}_n$, where for each $j = 1, \ldots, n$, $\rho(\mathbf{A}_j) = 1$ and (some) $\mathbf{A}_j$ has large off-diagonal entries positioned in such a way that $\rho(\mathbf{SD}) > 1$.

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(a) $\Rightarrow$ (b): Assume that $S_1, \ldots, S_m$ do not admit a polychromatic cycle. We show that there exists a nonnegative diagonal matrix $\mathbf{V}$ such that

* $\mathbf{VSV}^{-1}$ is column substochastic, and

* $\mathbf{VDV}^{-1}/\rho(\mathbf{D})$ is column stochastic.

Thus,

$$\rho(\mathbf{SD}) = \rho(\mathbf{VSDV}^{-1}) \leq \|\mathbf{VSDV}^{-1}\| \leq \|\mathbf{VSV}^{-1}\|\|\mathbf{VDV}^{-1}\| \leq \rho(\mathbf{D}).$$

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The construction of $\mathbf{V}$ was done by an intricate labelling scheme of the vertices of $S_1, \ldots, S_m$ using the information of the Perron vectors of $A_1, \ldots, A_m$.

Applications

Example 1 (**Patch development models**) Many species live in environments where the patches change state stochastically in time. In such cases,

$$\mathbf{S} = I_m \otimes S \quad \text{and} \quad \mathbf{D} = \sum_{j=1}^{n} A_j \otimes E_{jj}$$

then the population dynamics are given by $x(t+1) = \mathbf{S}\,\mathbf{D}\,x(t)$. Since $\mathbf{S}$ admits a polychromatic cycle if and only if S has a cycle, our theorem implies that $\rho(\mathbf{S}\,\mathbf{D}) \leq \rho(\mathbf{D})$ for all $\mathbf{D}$ if and only if S admits no cycle.

Example 2 (Planktonic dynamics) Caswell describes a stage structured and spatially structured model of Davis for planktonic species (e.g. copepods, water fleas, etc.) dispersing in ocean currents during their larval stage.

The model for the planktonic dynamics is given by

$$x(t+1) = \mathbf{A}\, x(t) \qquad \text{where} \qquad \mathbf{A} = T \otimes I_n + (S \oplus (I_{m-1} \otimes I_n))(F \otimes I_n),$$

where S is column substochastic, T, F are nonnegative so that only the first row of F is nonzero.

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Claim $\quad \rho(\mathbf{A}) \leq \rho((T+F) \otimes I_n) = \rho(T+F)$

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In other words, dispersal of the larva reduces the asymptotic growth rate of the population.

To prove this claim using our theorem, we need to introduce an extra variable $\widetilde{x}_j^0$ that keeps track of the newly born larval stage. Let $\widetilde{x}_j^i$ for $i = 0, 1, \ldots, m$ and $j = 1, \ldots, n$ correspond to the abundance of life stage i in location j, $\widetilde{x}^i = \begin{bmatrix} \widetilde{x}_1^i \\ \vdots \\ \widetilde{x}_n^i \end{bmatrix}$, and $\widetilde{x} = \begin{bmatrix} \widetilde{x}^0 \\ \vdots \\ \widetilde{x}^m \end{bmatrix}$. Moreover, define

$$\mathbf{D} = \begin{pmatrix} f_{11} & f_{11} & f_{12} & \cdots & f_{1m} \\ t_{11} & t_{11} & t_{12} & \cdots & t_{1m} \\ t_{21} & t_{21} & t_{22} & \cdots & t_{2m} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ t_{m1} & t_{m1} & t_{m2} & \cdots & t_{mm} \end{pmatrix} \otimes I_n \quad \text{and} \quad \mathbf{S} = S \oplus (I_m \otimes I_n)$$

With the inclusion of this additional variable, the planktonic model becomes

$$\widetilde{x}(t+1) = \mathbf{S}\,\mathbf{D}\,\widetilde{x}(t)$$

Since

$$\begin{pmatrix} I_n & I_n & 0_{n,n(m-1)} \\ 0_{n(m-1),n} & 0_{n(m-1),n} & I_{m-1} \otimes I_n \end{pmatrix} \mathbf{SD}$$

$$= \mathbf{A} \begin{pmatrix} I_n & I_n & 0_{n,n(m-1)} \\ 0_{n(m-1),n} & 0_{n(m-1),n} & I_{m-1} \otimes I_n \end{pmatrix},$$

we have $\rho(\mathbf{SD}) = \rho(\mathbf{A})$. Evidently, $\mathbf{S} = S \oplus I_n \oplus \cdots \oplus I_n$ does not admit a polychromatic cycle. By our theorem, we have

$$\rho(\mathbf{A}) = \rho(\mathbf{SD}) \leq \rho(\mathbf{D}) = \rho(T + F).$$

Thus, the desired inequality holds for any column substochastic matrix S.

Further research

- Study $\mathbf{S}$ and/or $\mathbf{D}$ with special structures.

- Determine conditions on $\mathbf{S}$ and $\mathbf{D}$ so that $\rho(\mathbf{SD}) \leq \rho(\mathbf{D})$.

- For a pair of $(\mathbf{S}, \mathbf{D})$, study the monotonicity behavior of $\rho(\mathbf{S}(t)\mathbf{D})$, where $\mathbf{S}(t) = (1-t)I + t\mathbf{S}$.

- Study the continuous models.

Thank you for your attention!!!