SPATIAL IMPACTS OF CHANGES IN THE POPULATION GROWTH MATRIX

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There are in fact two approaches to trace through the impacts of particular changes in the components of the population growth[1]:

a) Examination of model stable multiregional populations (simulation approach);

b) Mathematical analysis of the impacts (analytical approach).

Some mathematical impact analysis has already been performed in the paper on spatial population dynamics. It follows essentially Keyfitz's chain of derivations, but centers on the multiregional generalization of some principal formulas[2]. In order to pursue the impact analysis further, we need some additional findings of matrix algebra. Most of the relevant ideas are collected in a recent volume on sensitivity analysis and on methods for incorporating sensitivity considerations in engineering design procedures[3]. This paragraph deals with the analysis of

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[1] ROGERS, A. and WILLEKENS, F., 1975, Spatial population dynamics; Draft, p. 30.

[2] KEYFITZ, N., 1971, Linkages of intrinsic to age-specific rates, "Journal of the American Statistical Association," Vol. 66, No. 334 (June), pp. 275-281.

[3] CRUZ, J.B., Jr., 1973, System sensitivity analysis, Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

the impact of changes in the growth matrix on:

a) growth rate of the stable population,

b) coefficients of the characteristic equation,

c) stable population distribution.

A. Sensitivity of Stable Growth Rate.

Population projection can be represented as a matrix multiplication.

$$\{\underset{\sim}{w}(t + 1)\} = \underset{\sim}{G}\{\underset{\sim}{w}(t)\} \quad (1)$$

where $\{\underset{\sim}{w}(t)\}$ is the population vector at time t. $\underset{\sim}{G}$ is the growth matrix. If t gets sufficiently large, we have

$$\underset{\sim}{G}\{\underset{\sim}{w}(t)\} = \lambda\{\underset{\sim}{w}(t)\} \quad (2)$$

where λ is the eigenvalue of $\underset{\sim}{G}$, and $\underset{\sim}{w}(t)$ is the eigenvector associated with λ.

B. Morgan shows that the formula for the change $d\lambda_i$ in any root λ_i for a change in $\underset{\sim}{G}$ is [1, 2]:

$$d\lambda_i = [\mathrm{tr}\ \underset{\sim}{R}(\lambda_i)]^{-1}\ [\underset{\sim}{R}(\lambda_i)] * d\underset{\sim}{G} \quad (3)$$

where

1) * denotes the inner product of two matrices,

$$\underset{\sim}{A} * \underset{\sim}{B} = \sum_i \sum_k a_{ik}\, b_{ki}$$

[1] It is assumed throughout this paragraph that the roots are distinct.

[2] MORGAN, B.S., Jr., 1973, Sensitivity analysis and synthesis of multivariable systems, in CRUZ, J.B., op. cit., p. 77.

2) $\underset{\sim}{R}(\lambda_i)$ is the adjoint matrix of the characteristic matrix $(\underset{\sim}{G} - \lambda_i \underset{\sim}{I})$. The element $r_{jk}(\lambda_i)$ is the algebraic complement of the element $g_{jk} - \lambda_i \delta_{jk}$ in the determinant $|\underset{\sim}{G} - \lambda_i \underset{\sim}{I}|$ (Appendix I.).

The impact on the intrinsic growth rate of the stable population (r) is straightforward:

$$\lambda = e^{hr}$$

where h is the time interval considered.

$$\frac{dr}{d\underset{\sim}{G}} = \frac{dr}{d\lambda_1} \frac{d\lambda_1}{d\underset{\sim}{G}}$$

$$dr = [h\ e^{hr}\ \mathrm{tr}\ \underset{\sim}{R}(\lambda_1)]^{-1}\ [\underset{\sim}{R}(\lambda_1)] * d\underset{\sim}{G} \qquad (4)$$

Numerical example:

$$\underset{\sim}{G} = \begin{bmatrix} \frac{1}{2} & \frac{1}{4} \\ \frac{1}{2} & \frac{3}{4} \end{bmatrix}$$

The eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = \frac{1}{4}$. The eigenvector associated with λ_1 is proportional to $\begin{bmatrix} 1 \\ 2 \end{bmatrix}$. Following Gantmacher's computation scheme (cf. Appendix I.):

$$\underset{\sim}{G}_1 = \begin{bmatrix} \frac{1}{2} & \frac{1}{4} \\ \frac{1}{2} & \frac{3}{4} \end{bmatrix} \qquad c_1 = \frac{5}{4} \qquad \underset{\sim}{R}_1 = \begin{bmatrix} -\frac{3}{4} & \frac{1}{4} \\ \frac{1}{2} & -\frac{1}{2} \end{bmatrix}$$

$$\underset{\sim}{G}_2 = \begin{bmatrix} -\frac{1}{4} & 0 \\ 0 & -\frac{1}{4} \end{bmatrix} \qquad c_2 = -\frac{1}{4} \qquad \underset{\sim}{R}_2 = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}$$

$$\underset{\sim}{R}(\lambda_1) = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} 1 + \begin{bmatrix} -\frac{3}{4} & \frac{1}{4} \\ \frac{1}{2} & -\frac{1}{2} \end{bmatrix} 1 = \begin{bmatrix} \frac{1}{4} & \frac{1}{4} \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix}$$

$$tr[\underset{\sim}{R}(\lambda_1)] = \frac{3}{4}$$

$$d\lambda_1 = \left[\frac{3}{4}\right]^{-1} \begin{bmatrix} \frac{1}{4} & \frac{1}{4} \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix} * d\underset{\sim}{G}$$

Let $d\underset{\sim}{G} = \begin{bmatrix} \frac{1}{10} & 0 \\ 0 & 0 \end{bmatrix}$ $\qquad \underset{\sim}{G} + d\underset{\sim}{G} = \begin{bmatrix} \frac{6}{10} & \frac{1}{4} \\ \frac{1}{2} & \frac{3}{4} \end{bmatrix}$

$$d\lambda_1 = \frac{4}{3} \begin{bmatrix} \frac{1}{4} & \frac{1}{4} \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix} * \begin{bmatrix} \frac{1}{10} & 0 \\ 0 & 0 \end{bmatrix} = \frac{4}{3} \cdot \frac{1}{40} = \frac{1}{30} = 0.0333$$

$$dr = \frac{1}{30\ h\ e^{hr}} \quad .$$

As a check, the dominant eigenvalue of $\underset{\sim}{G} + d\underset{\sim}{G}$ is computed, and is equal to 1.0365. The deviation between 1.0365 and 1.0333 is due to the fact that $d\underset{\sim}{G}$ in this example is not an infinitesimal small change, but a change of 20% of the first element.

It should be noted that in order to compare the impacts of various changes in a specified growth matrix, the value of $\underset{\sim}{Z}(\lambda_i) = [tr\ \underset{\sim}{R}(\lambda_i)]^{-1}\ [\underset{\sim}{R}(\lambda_i)]$ has to be computed only once. The impacts of various $d\underset{\sim}{G}$'s are:

$$d\lambda_i = \underset{\sim}{Z}(\lambda_i) * d\underset{\sim}{G} \quad . \tag{5}$$

B. <u>Sensitivity of the Coefficients of the Characteristic Equation</u>.

Equation (2) may be written as

$$(\underset{\sim}{G} - \lambda\underset{\sim}{I}) \{\underset{\sim}{w}(t)\} = 0 \quad . \tag{6}$$

There exists a nontrivial solution to this system of homogeneous equations if the determinant of the characteristic matrix is zero.

$$|\underset{\sim}{G} - \lambda\underset{\sim}{I}| = 0 \tag{7}$$

The characteristic equation (7) may be expanded to a polynomial in λ

$$g(\lambda) = |\underset{\sim}{G} - \lambda\underset{\sim}{I}| = (-1)^n [\lambda^n - c_1\lambda^{n-1} - c_2\lambda^{n-2} \ldots - c_n] \tag{8}$$

and

$$c_1 = g_{11} + g_{22} + \ldots + g_{nn}$$

$$c_n = (-1)^{n-1} |\underset{\sim}{G}| \quad .$$

B. Morgan shows that the differential change dc_p in the coefficients of the characteristic polynomial $g(\lambda)$ for a differential change in the matrix $\underset{\sim}{G}$ is given by the following formulas:

$$dc_1 = \underset{\sim}{I} * d\underset{\sim}{G}$$

$$dc_2 = \underset{\sim}{R}_1 * d\underset{\sim}{G} \tag{9}$$

$$\vdots$$

$$dc_p = \underset{\sim}{R}_{p-1} * d\underset{\sim}{G}$$

where * denotes the inner product, and $\underset{\sim}{R}_i$ is a coefficient of the polynomial of the adjoint matrix.

Consider the numerical example presented in the preceding section. The characteristic polynomial of $\underset{\sim}{G}$ is

$$g(\lambda) = \lambda^2 - \frac{5}{4}\lambda + \frac{1}{4} = 0 \quad .$$

A change in $\underset{\sim}{G}$ by $d\underset{\sim}{G}$ has the following impact on the coefficients of $g(\lambda)$:

$$dc_1 = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} * \begin{bmatrix} \frac{1}{10} & 0 \\ 0 & 0 \end{bmatrix} = \frac{1}{10}$$

$$dc_2 = \begin{bmatrix} -\frac{3}{4} & \frac{1}{4} \\ \frac{1}{2} & -\frac{1}{2} \end{bmatrix} * \begin{bmatrix} \frac{1}{10} & 0 \\ 0 & 0 \end{bmatrix} = -\frac{3}{40}$$

Hence $g(\lambda)$ of $\underset{\sim}{G} + d\underset{\sim}{G}$ becomes

$$g^2(\lambda) = \lambda^2 - \left[\frac{5}{4} + \frac{1}{10}\right]\lambda - \left[-\frac{1}{4} - \frac{3}{40}\right]$$

$$g(\lambda) = \lambda^2 - \frac{27}{20}\lambda + \frac{13}{40} = 0 \quad .$$

As a check, we compute the characteristic polynomial of $\underset{\sim}{G} + d\underset{\sim}{G}$

$$\underset{\sim}{G} + d\underset{\sim}{G} = \begin{bmatrix} \frac{6}{10} & \frac{1}{4} \\ \frac{1}{2} & \frac{3}{4} \end{bmatrix}$$

$$g(\lambda) = \left(\frac{6}{10} - \lambda\right)\left(\frac{3}{4} - \lambda\right) - \frac{1}{2} \cdot \frac{1}{4} = 0$$

$$g(\lambda) = \lambda^2 - \frac{27}{20}\lambda + \frac{13}{40} = 0 \quad .$$

C. Sensitivity of the Stable Population Distribution.

The stable population distribution, which results of a certain growth regime, is the eigenvector, associated with the dominant eigenvalue of the growth matrix. The eigenvector is proportional to the columns of the adjoint matrix $\underset{\sim}{R}(\lambda_1)$. The change in $\underset{\sim}{R}(\lambda_1)$ caused by $d\underset{\sim}{G}$ is:

$$d\underset{\sim}{R}(\lambda_1) = \underset{\sim}{I}d\lambda^{n-1} + [d\underset{\sim}{R}_1]\ \lambda^{n-2} + \underset{\sim}{R}_1 d\lambda^{n-2} + \ldots$$

$$+ [d\underset{\sim}{R}_i]\ \lambda^{n-i-1} + \underset{\sim}{R}_i[d\lambda^{n-i-1}] \qquad (10)$$

where $d\lambda^{n-i} = (n - i)\ \lambda^{n-i-1}\ d\lambda$

$$d\underset{\sim}{R}_1 = d\underset{\sim}{G} - dc_1 \underset{\sim}{I} \quad \text{and } dc_1 = \underset{\sim}{I} * d\underset{\sim}{G}$$

$$d\underset{\sim}{R}_2 = d\underset{\sim}{G}_2 - dc_2 \underset{\sim}{I} \quad \text{and } \begin{cases} d\underset{\sim}{G}_2 = [d\underset{\sim}{G}]\ \underset{\sim}{R}_1 + \underset{\sim}{G}[d\underset{\sim}{R}_1] \\ dc_2 = \underset{\sim}{R}_1 * d\underset{\sim}{G} \end{cases} \qquad (11)$$

$$\vdots$$

$$d\underset{\sim}{R}_i = d\underset{\sim}{G}_i - dc_i \underset{\sim}{I} \quad \text{and } d\underset{\sim}{G}_i = [d\underset{\sim}{G}]\ \underset{\sim}{R}_{i-1} + \underset{\sim}{G}[d\underset{\sim}{R}_{i-1}] \quad .$$

The impact of a small change in the growth matrix of the numerical example on the stable population distribution is:

$$dR(\lambda_1) = \underset{\sim}{I}\lambda^o\, d\lambda + \lambda^o [d\underset{\sim}{G} - dc_1\, \underset{\sim}{I}]$$

$$dR(\lambda_1) = \frac{1}{30}\, \underset{\sim}{I} + \left\{ \begin{bmatrix} \frac{1}{10} & 0 \\ 0 & 0 \end{bmatrix} - \frac{1}{10} \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \right\}$$

$$dR(\lambda_1) = \begin{bmatrix} \frac{1}{30} & 0 \\ 0 & \frac{1}{30} \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ 0 & -\frac{1}{10} \end{bmatrix} = \begin{bmatrix} \frac{1}{30} & 0 \\ 0 & -\frac{2}{30} \end{bmatrix}$$

$$\underset{\sim}{R}(\lambda_1) + d\underset{\sim}{R}(\lambda_1) = \begin{bmatrix} \frac{1}{4} & \frac{1}{4} \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix} + \begin{bmatrix} \frac{1}{30} & 0 \\ 0 & -\frac{2}{30} \end{bmatrix} = \begin{bmatrix} \frac{17}{60} & \frac{1}{4} \\ \frac{1}{2} & \frac{13}{30} \end{bmatrix} .$$

The eigenvector, after the small change in $\underset{\sim}{G}$ has taken place, is proportional to the columns of $\underset{\sim}{R}(\lambda_1) + d\underset{\sim}{R}(\lambda_1)$. The ratio $\left[\frac{17}{60} / \frac{1}{2}\right] = \frac{17}{30}$ is not exactly equal to $\left[\frac{1}{4} / \frac{13}{30}\right] = \frac{15}{26}$ since the change in $\underset{\sim}{G}$ is not infinitesimally small. As a check, we compute the eigenvector associated with λ_1 of $\underset{\sim}{G} + d\underset{\sim}{G}$

$$\begin{bmatrix} \frac{6}{10} - \frac{31}{30} & \frac{1}{4} \\ \frac{1}{2} & \frac{3}{4} - \frac{31}{30} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} .$$

Let $x_2 = 1$. If we omit the second equation, x_1 becomes $\frac{15}{26}$. Omitting the first equation, x_1 becomes $\frac{17}{30}$.

APPENDIX I.

Let $\underset{\sim}{R}(\lambda_i)$ be the adjoint matrix of the characteristic matrix $(\underset{\sim}{G} - \lambda_i \underset{\sim}{I})$[1]. The definition of $\underset{\sim}{R}(\lambda_i)$ implies that

$$(\underset{\sim}{G} - \lambda_i \underset{\sim}{I})\ \underset{\sim}{R}(\lambda_i) = |\underset{\sim}{G} - \lambda_i \underset{\sim}{I}|\ \underset{\sim}{I}$$

$$\underset{\sim}{R}(\lambda_i)(\underset{\sim}{G} - \lambda_i \underset{\sim}{I}) = |\underset{\sim}{G} - \lambda_i \underset{\sim}{I}|\ \underset{\sim}{I} \quad .$$

Since $|\underset{\sim}{G} - \lambda_i \underset{\sim}{I}| = g(\lambda) = \lambda^n - c_1\lambda^{n-1} - c_2\lambda^{n-2} \ldots - c_n$, we may write

$$\begin{aligned} (\underset{\sim}{G} - \lambda_i \underset{\sim}{I})\ \underset{\sim}{R}(\lambda_i) &= g(\lambda_i)\ \underset{\sim}{I} \\ \underset{\sim}{R}(\lambda_i) &= (\underset{\sim}{G} - \lambda_i \underset{\sim}{I})^{-1}\ g(\lambda_i) \end{aligned} \qquad \text{(a)}$$

$\underset{\sim}{R}(\lambda_i)$ is a polynomial matrix. It can be represented in the form of a polynomial arranged with respect to the powers of λ_i.

$$\underset{\sim}{R}(\lambda_i) = \underset{\sim}{R}_o\ \lambda_i^{n-1} + \underset{\sim}{R}_1\ \lambda_i^{n-2} + \ldots + \underset{\sim}{R}_{n-1} \qquad \text{(b)}$$

$$g(\lambda_i) = \lambda_i^{n} - c_1\ \lambda_i^{n-1} - \ldots\ldots\ldots - c_n \quad . \qquad \text{(c)}$$

Equating the coefficients gives[2]:

$$\begin{aligned} \underset{\sim}{R}_o &= \underset{\sim}{I} \\ \underset{\sim}{R}_1 &= \underset{\sim}{G} - c_1\ \underset{\sim}{I} \\ \underset{\sim}{R}_2 &= \underset{\sim}{G}\ \underset{\sim}{R}_1 - c_2\ \underset{\sim}{I} = \underset{\sim}{G}^2 - c_1\ \underset{\sim}{G} - c_2\ \underset{\sim}{I} \\ &\vdots \\ \underset{\sim}{R}_k &= \underset{\sim}{G}\ \underset{\sim}{R}_{k-1} - c_k\ \underset{\sim}{I} = \underset{\sim}{G}^k - c_1\ \underset{\sim}{G}^{k-1} - c_2\ \underset{\sim}{G}^{k-2} \ldots - c_k\ \underset{\sim}{I} \end{aligned} \qquad \text{(d)}$$

$$k = 1 \ldots n-1$$

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[1] GANTMACHER, F.R., 1959, The theory of matrices. Vol. I., Chelsea Publishing Co., New York, p. 82.

[2] GANTMACHER, F.R., 1959, op. cit., p. 85.

If $\underset{\sim}{G}$ is non-singular

$$c_n = (-1)^{n-1} |\underset{\sim}{G}| \neq 0 \quad .$$

This leads to an alternative method to compute the inverse of $\underset{\sim}{G}$.

Since $\underset{\sim}{G} \underset{\sim}{R}_{n-1} - c_n \underset{\sim}{I} = 0$

we have $\underset{\sim}{G}^{-1} = \frac{1}{c_n} \underset{\sim}{R}_{n-1} \quad .$ (e)

If λ_i is a characteristic root of $\underset{\sim}{G}$,

$$|\underset{\sim}{G} - \lambda_i \underset{\sim}{I}| = 0$$

and (f)

$$(\underset{\sim}{G} - \lambda_i \underset{\sim}{I}) \underset{\sim}{R}(\lambda_i) = 0 \quad .$$

Assume $\underset{\sim}{R}(\lambda_i) \neq 0$ and denote by $\{\underset{\sim}{r}\}$ an arbitrary nonzero column of $\underset{\sim}{R}(\lambda_i)$. Then by (f):

$$(\underset{\sim}{G} - \lambda_i \underset{\sim}{I}) \{\underset{\sim}{r}\} = 0$$

or (g)

$$\underset{\sim}{G}\{\underset{\sim}{r}\} = \lambda_i \{\underset{\sim}{r}\} \quad .$$

Each nonzero column of $\underset{\sim}{R}(\lambda_i)$ is a characteristic vector corresponding to the characteristic root λ_i.

The set of formulas (e) to (g) gives a method to determine $\underset{\sim}{R}(\lambda_i)$, $\underset{\sim}{G}^{-1}$ and the characteristic vector associated with λ_i, if the coefficients of the characteristic polynomial are known. D. Faddeev proposes a method to determine simultaneously the coefficients of the characteristic polynomial and the adjoint matrix $\underset{\sim}{R}(\lambda_i)$ (improved Leverrier algorithm)[1]. Instead of computing $\underset{\sim}{G}$, $\underset{\sim}{G}^2$, $\underset{\sim}{G}^k$ required by the system (d), a sequence $\underset{\sim}{G}_1$, $\underset{\sim}{G}_2, \ldots, \underset{\sim}{G}_k$ is computed in the following way:

$$\begin{array}{lll} \underset{\sim}{G}_1 = \underset{\sim}{G} & c_1 = \mathrm{tr}\, \underset{\sim}{G}_1 & \underset{\sim}{R}_1 = \underset{\sim}{G}_1 - c_1 \underset{\sim}{I} \\ \underset{\sim}{G}_2 = \underset{\sim}{G}\, \underset{\sim}{R}_1 & c_2 = \frac{1}{2}\, \mathrm{tr}\, \underset{\sim}{G}_2 & \underset{\sim}{R}_2 = \underset{\sim}{G}_2 - c_2 \underset{\sim}{I} \\ \vdots & \vdots & \vdots \\ \underset{\sim}{G}_k = \underset{\sim}{G}\, \underset{\sim}{R}_{k-1} & c_k = \frac{1}{k}\, \mathrm{tr}\, \underset{\sim}{G}_k & \underset{\sim}{R}_k = \underset{\sim}{G}_k - c_k \underset{\sim}{I} \\ \vdots & \vdots & \vdots \\ \underset{\sim}{G}_n = \underset{\sim}{G}\, \underset{\sim}{R}_{n-1} & c_n = \frac{1}{n}\, \mathrm{tr}\, \underset{\sim}{G}_n & \underset{\sim}{R}_n = \underset{\sim}{G}_n - c_n \underset{\sim}{I} = 0 \end{array}$$

It has been proven that

a) c_i is a coefficient of the characteristic polynomial $g(\lambda_i) = \lambda_i^{\,n} - c_1 \lambda_i^{\,n-1} - c_2 \lambda_i^{\,n-2} \ldots - c_n$

b) $\underset{\sim}{R}_n$ is a null matrix. This may be used to check the computations.

c) if $\underset{\sim}{G}$ is non-singular, then

$$\underset{\sim}{G}^{-1} = \frac{1}{c_n} \underset{\sim}{R}_{n-1} \quad .$$

If $\underset{\sim}{G}$ is singular, then $(-1)^{n-1} \underset{\sim}{R}_{n-1}$ will be the matrix adjoint to $\underset{\sim}{G}$.

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[1] GANTMACHER, F.R., 1959, op. cit., pp. 87-89. FADDEEV, D.K. and FADDEEVA, V.N., 1963, Computational methods of linear algebra, W.H. Freeman and Co., San Francisco, pp. 260-265.