Mathematical Biology

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Applications of Perron–Frobenius theory to population dynamics

Abstract. By the use of Perron–Frobenius theory, simple proofs are given of the Fundamental Theorem of Demography and of a theorem of Cushing and Yicang on the net reproductive rate occurring in matrix models of population dynamics. The latter result, which is closely related to the Stein–Rosenberg theorem in numerical linear algebra, is further refined with some additional nonnegative matrix theory. When the fertility matrix is scaled by the net reproductive rate, the growth rate of the model is 1. More generally, we show how to achieve a given growth rate for the model by scaling the fertility matrix. Demographic interpretations of the results are given.

1. Introduction

A *standard matrix model of population dynamics* is given by a sequence of non-negative vectors $x_0, x_1, \ldots$ of fixed length n defined by

$$x_k = P x_{k-1}, \quad k = 1, 2, \ldots, \tag{1}$$

for a given nonzero x_0 where P is an $n \times n$ matrix with nonnegative entries. As usual, we assume that

$$P = T + F \tag{2}$$

where T and F are nonnegative nonzero matrices such that all the column sums of T are not larger than one:

$$\Sigma_{i=1,\ldots,n} \, t_{ij} \leq 1, \quad j = 1, \ldots, n. \tag{3}$$

The mth entry of the vector x_k represents the population in the mth class at the time epoch k. The matrix $P = T + F$ is known as the *projection matrix*; the matrices T

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and F are known as the *transition matrix* and the *fertility matrix* resp., so that the (i, j) entry of T represents the fraction of the individuals in the jth class that will survive and move to the ith class in a unit interval of time, and the (i, j) entry of F represents the number of newborns in the ith class that descend from one individual in the jth class in a unit interval. Because of these demographic interpretations, one sees why the column sums of T are always less than or equal to 1. The special case of this matrix model for Leslie matrices, introduced by Bernardelli [Bern], Lewis [Lew] and Leslie [Les1], has a long history [1]. We concentrate on properties of the general case introduced above.

The following argument shows that a further assumption is warranted for our matrix model. The *spectral radius* $\rho(T)$ of a matrix T is the maximum of the moduli of its eigenvalues. Since we wish to exclude the possibility of an immortal population, we shall always assume in the rest of the paper that $\lim_{k \to \infty} T^k x_0 = 0$ for all initial populations (nonnegative vectors) x_0. By examining the effect of T^k on the standard basis of unit vectors, this condition may be shown to be equivalent to $\lim_{k \to \infty} T^k = 0$. In turn, it is known that this condition is equivalent to

$$\rho(T) < 1, \tag{4}$$

[W2, Theorem 3.5], [HJ, Theorem 5.612]. We shall thus always assume that our model satisfies (4) together with (1) and (2); the assumption (3) is not used in our proofs. We remark that (3) implies the weaker condition $\rho(T) \leq 1$, but that (4) does not imply (3) as is easily shown by examples.

Under the assumption (4) we have

$$(I - T)^{-1} = I + T + T^2 + \dots, \tag{5}$$

e.g. [W2, Theorem 6.1], [HJ, Corollary 5.6.16]. Let $Q = F(I - T)^{-1}$. Then we have

$$Qx_0 = Fx_0 + FTx_0 + FT^2x_0 + \dots,$$

which represents the distribution with respect to state-at-birth of all newborn descendants accumulated during the entire lifespan of the population x_0, see [Cush, p.8] and [DH, p.71], where the matrix Q is called the "next generation matrix". Following [Cas2, p. 126], we call the spectral radius $\rho(Q)$ of Q the *net reproductive rate* of the model, see [CY] and [Cush, p.8], for a definition in this generality. As usual it is denoted by R_0. Other names for R_0 are "net reproductive number" ([Cush]) and "basic reproduction ratio" ([DH]).

The purpose of this note is to explore some applications of the Perron–Frobenius theory to results in Population Dynamics; particularly we wish to study the role of the net reproductive rate. In Section 2 we state needed standard results from this theory which will be used throughout the paper. We first apply the theory to obtain the Fundamental Theorem of Demography for a model with a primitive projection matrix. This approach is well-known, see for example [Pol], [I], or [Cas2].

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[1] [Les1] acknowledges the contribution of [Bern] and [Les2] mentions [Lew], but [Bern] and [Lew] do not refer to each other, which is extraordinary as both authors were at University College, Rangoon, Burma, in 1940 - 41 when their papers were submitted.

In Section 3, we consider the net reproductive rate. We state and give a short proof of a somewhat stronger form of an interesting comparison theorem on the net reproductive rate due to Cushing and Yicang, see [CY, Theorem 3] and [Cush, Theorem 1.1.3]. This theorem, which is closely related to the Stein–Rosenberg theorem in numerical linear algebra, is further refined in Section 4 using a result from graph theoretic Perron–Frobenius theory. For a model with an irreducible projection matrix, the net reproductive rate may be viewed as a factor producing a model with growth rate 1 when one scales only the fertility matrix by this constant factor. More generally, given a positive s subject to one restriction, we determine a $q(s)$ as a function of s such that the growth rate of the model is s when the fertility matrix is scaled by $q(s)$. In our last section, we give demographic interpretations of our results.

2. Perron–Frobenius theory and the Fundamental Theorem of Population Demography

In this section we give the sketch of a proof of the fundamental theorem of demography, see [Cush, Theorem 1.1.2] or [Cas2, p. 86] using the Perron–Frobenius theory of nonnegative matrices. This theory is also needed for applications in subsequent sections.

A nonnegative matrix is *irreducible* if it is not the 1×1 zero matrix and it is not permutationally similar to a matrix of the form

$$\begin{pmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{pmatrix}$$

for nontrivial square matrices A_{11} and A_{22}. The celebrated Perron–Frobenius theorem for irreducible matrices can be stated as follows.

Theorem 2.1. *Let P be an irreducible nonnegative matrix. Then*

(a) *The spectral radius $\rho(P)$ of P is positive and it is an algebraically simple eigenvalue of P with corresponding left and right positive eigenvector, which are unique up to scalar multiples.*
(b) *The spectral radius of P is the unique eigenvalue with a nonnegative eigenvector.*
(c) *The spectral radius of the matrix P increases (strictly), resp. decreases, if any entry of it increases, resp. decreases.* □

One may see [W2, Theorem 10.7], [HJ, Theorem 8.4.4, Problem 15, p. 515], [V, Theorem 2.1], [G, Theorem 2, p. 53] for proofs.

Following a common practice in matrix literature, we call the spectral radius $\rho(P)$ of a nonnegative matrix P the *Perron root* of P. In some fields of mathematics this term is defined as the reciprocal of the radius of convergence of the power series $\Sigma_0^\infty z^r P^r$ but by a classical result this is precisely $\rho(P)$ when P is a finite complex matrix, see [W2, Theorem 5.5], or see the more general theorem by Hensel [W2, Theorem 5.4]. We also call a nonnegative left or right eigenvector corresponding to the Perron root of a nonnegative matrix a *Perron vector*. We usually denote the

Perron root of a projection matrix P by r and left and right Perron vectors by v^t and u respectively.

Since the eigenvalues and eigenvectors (with proper normalization) are continuous in the elements of a matrix and every nonnegative matrix is a limit of a sequence of irreducible nonnegative matrices, one immediately deduces:

Corollary 2.2. *Let P be a nonnegative matrix. Then*

(a) *The spectral radius $\rho(P)$ of P is an eigenvalue of P with a corresponding nonnegative Perron vector.*
(b) *The spectral radius of the matrix P does not decrease, resp. increase, if any entry of it increases, resp. decreases.* ☐

An irreducible nonnegative matrix P is *primitive* if there is only one eigenvalue of P that attains the modulus $\rho(P)$. In this case, the Perron root is properly called the *dominant eigenvalue* of A, which is the usual term in the demographic literature (even under less restrictive conditions), e.g. [Cas2, p. 83]. A nonnegative matrix P is primitive if and only if P^k is positive for some positive integer k, [HJ, Theorem 8.5.2]. This shows that primitivity (like irreducibility) depends only on the *pattern* of a nonnegative matrix, i.e. if P is primitive (irreducible) then every matrix that has positive entries in exactly the same positions is also primitive (irreducible). Applying a standard result on the convergence of powers of matrices [W2, Theorem 3.5], one may derive from Theorem 2.1 the following well known result, for closely related results see for example [Cas2, p. 86], or in the special case of Leslie matrices, [Pol, Lemma 4.5.1] or [I], where proofs are given in the same spirit as ours.

Theorem 2.3. *Let P be a primitive nonnegative matrix with spectral radius $\rho(P)$ $= r$ and left and right Perron vectors v^t and u such that $v^t u = 1$. Then*

$$\lim_{k\to\infty} (P/r)^k = uv^t. \tag{6}$$

☐

The following application of Theorem 2.3 is called the *fundamental theorem of demography* in [Cush, Theorem 1.1.2], where a different proof is given.

Theorem 2.4. *Let P be the projection matrix of a standard population model x_k, $k = 0, 1, \ldots$, given by (1). Suppose that P is primitive with spectral radius $\rho(P) = r$ and has left and right Perron vectors v^t and u resp. normalized so that $v^t u = 1$. Then*

$$\lim_{k\to\infty} x_k/r^k = (v^t x_0)u.$$

Consequently, if $|w|$ denotes the sum of entries of the vector w, so that $|x_k|$ will denote the total population at time k in the population model, then

$$\lim_{k\to\infty} |x_k| = \begin{cases} 0 & \text{if } r < 1, \\ |(v^t x_0)u| & \text{if } r = 1, \\ \infty & \text{if } r > 1. \end{cases}$$

☐

Mathematically, a *population* is a vector that is nonnegative and nonzero. As is usual in the demographic literature, we call a population x *stable* (for a given matrix model), though this terminology is not consistent with definitions of stability in other parts of mathematics. If, for some positive r, $Px = rx$, and we call x a *stationary population* if $Px = x$. We call a population *eventually stable* if $\lim_{k \to \infty} x_k / r^k$ exists and is nonzero, and we call the population *eventually stationary* if $\lim_{k \to \infty} x_k$ exists and is nonzero. The spectral radius $\rho(P) = r$ is called the *growth rate* of the model, which for primitive P is justified by Theorem 2.4.

Suppose that P is primitive. It follows immediately from the fundamental theorem that, whatever the initial population x_0, the number of individuals in x_k grows to infinity if $r > 1$, shrinks to 0 if $r < 1$, and remains finite if $r = 1$. Furthermore, in all cases, there exists a unique stable population (except for a constant factor), which is a stationary population if $r = 1$. Furthermore, in this case, the fundamental theorem shows that every population is eventually stationary.

The assumption that P is primitive cannot be omitted from this last remark, for the conclusion (6) of Theorem 2.4 depends strongly on this assumption. If one merely assumes that P is irreducible one may show that $x_k / r^k, k = 1, 2 \ldots$ is bounded above. For reducible nonnegative P the description of the possible limiting behavior of $P^k x_0$ is quite complicated, see [FS] for applications of graph theoretic concepts to this problem. An example is given near the end of this article where $r = 1$, but all populations except for the stable populations grow to be infinitely large.

For primitive P, the reciprocal of the growth factor r of P may also be interpreted as a factor for stationarity for the model, viz. if both T and F are scaled by the same factor $1/r$ then the resultant model with matrix $P' = (T + F)/r$ has the property that every population is eventually stationary. We are however particularly interested in scaling the fertility matrix F without scaling the transition matrix T so that in the resultant model every population eventually has a preassigned growth rate s, and this leads naturally to the considerations in the rest of this paper.

3. The net reproductive rate

The main result of this section is a somewhat stronger form of a comparison theorem due to Cushing and Yicang, [CY, Theorem 3], see also [Cush, Theorem 1.1.3]. Using standard results of Perron–Frobenius theory reviewed in Section 2, we give a very short and simple proof of this theorem stated below as Theorem 3.1. In the next section we show that this theorem can be further refined and generalized using some more nonnegative matrix theory.

Theorem 3.1. *Suppose a standard matrix model of population dynamics satisfies* (1) *and* (2), *and assume that the projection matrix* $P = T + F$ *is irreducible where* T *is nonzero and satisfies* (4). *Denote the growth factor* $\rho(P)$ *by* r *and the net reproductive rate* $\rho(Q)$, *where* $Q = F(I - T)^{-1}$, *by* R_0. *Suppose that* $R_0 > 0$. *Then*

$$\rho(T + F/R_0) = 1, \tag{7}$$

and one of the following holds:

$$r = R_0 = 1, \quad \text{or} \quad 1 < r < R_0, \quad \text{or} \quad 0 < R_0 < r < 1. \quad (8)$$

Proof. Since $\rho(T) < 1$, by (5) the matrix $(I - T)^{-1}$ is nonnegative and hence so is $Q = F(I - T)^{-1}$. Clearly $F \neq 0$ since $\rho(Q) > 0$. $\qquad\square$

To prove the equality (7), note that by Corollary 2.2., there exists a nonnegative left eigenvector y^t of $F(I - T)^{-1}$ corresponding to the eigenvalue R_0, i.e. $y^t F(I - T)^{-1} = R_0 y^t$. Then $y^t F = R_0 y^t(I - T)$ and hence $y^t(T + F/R_0) = y^t$. Since $R_0 > 0$, the matrix $T + F/R_0$ is irreducible and hence it follows by Theorem 2.1.(b) that $\rho(T + F/R_0) = 1$.

To prove that one of the conditions in (8) holds we consider three cases.

(i) If $R_0 = 1$, then $1 = \rho(T + F) = r$.

(ii) If $R_0 > 1$, then

$$T + F/R_0 \leq T + F \leq R_0 T + F$$

with equalities excluded since F is nonzero. Hence by Theorem 2.1.(c)

$$1 = \rho(T + F/R_0) < \rho(T + F) = r < \rho(R_0 T + F) = R_0.$$

(iii) If $0 < R_0 < 1$, then again by Theorem 2.1.(c),

$$1 = \rho(T + F/R_0) > \rho(T + F) = r > \rho(R_0 T + F) = R_0. \qquad\square$$

The special case of Theorem 3.1 when T is strictly lower triangular and F is upper triangular is known in numerical linear algebra as the Stein-Rosenberg Theorem, see [V, pp.68-70] for a proof to which our proof of the more general result is somewhat similar. See [RV] for a result close to Theorem 3.1.

Corollary 3.2. *Under the hypotheses of Theorem* 3.1, *consider the modified model given by* $\tilde{P} = T + F/R_0$ *with left and right Perron vectors* $\tilde{v}^t$ *and* $\tilde{u}$ *such that* $\tilde{v}^t \tilde{u} = 1$. *If P is primitive, then for every initial population* x_0 *we have*

$$\lim_{k \to \infty} (T + F/R_0)^k x_0 = (\tilde{v}^t x_0)\tilde{u}.$$

Proof. This follows immediately by Theorem 3.1.(a) and Theorem 2.3, since $\tilde{P}$ is also primitive. $\qquad\square$

There is a corresponding theorem for general nonnegative matrices.

Theorem 3.3. *Suppose a standard matrix model of population dynamics satisfies* (1) *and* (2), *and the transition matrix T satisfies* (4). *Denote the growth factor* $\rho(P)$ *by r and the net reproductive rate* $\rho(Q)$, *where* $Q = F(I - T)^{-1}$, *by* R_0. *Then one of the following holds:*

$$r = R_0 = 1, \quad \text{or} \quad 1 < r \leq R_0, \quad \text{or} \quad 0 \leq R_0 \leq r < 1. \quad (9)$$

If $R_0 > 0$, *then*

$$\rho(T + F/R_0) = 1. \quad (10)$$

$\qquad\square$

Most of the derivation of this theorem by continuity from Theorem 3.1 is straightforward and therefore omitted. However, we shall show why $r = 1$ implies that $R_0 = 1$. For positive ε, let $F(\varepsilon) = F + \varepsilon E$, where E is a matrix of the appropriate size all of whose entries are 1. Let $P(\varepsilon) = T + F(\varepsilon)$. Since $P(\varepsilon)$ is irreducible, we have $\rho(P(\varepsilon)) > \rho(P) = 1$, and hence by Theorem 3.1, $\rho(F(\varepsilon)(I - T)^{-1})$ > 1. If $r = 1$, letting ε tend to 0 we obtain $R_0 \geq 1$. Now consider $P'(\varepsilon) = P(\varepsilon)/\rho(P(2\varepsilon))$. Since $\rho(P(2\varepsilon)) > \rho(P(\varepsilon))$ we have $\rho(P'(\varepsilon)) < 1$ and hence $\rho(F/\rho(P(2\varepsilon))(I - T/\rho(P(2\varepsilon)^{-1}))) < 1$, again by Theorem 3.1. Letting ε tend to 0 we now obtain $R_0 \leq r = 1$. It follows that $R_0 = 1$. We observe that Theorem 3.3. may also be deduced by means of [Sch, Theorem 4.5].

4. The refined stability and comparison theorem

In this section we show that the hypothesis $R_0 = \rho(Q) > 0$ in Theorem 3.1 actually follows from the remaining assumptions thus allowing us to state a refined version of this theorem. Our proof depends on the following proposition, which is a restatement of [Sch, Lemma 3.4], see also [Sz] and [Z].

Proposition 4.1. *Let T and F be nonnegative matrices with $\rho(T) < 1$ and $F \neq 0$. Suppose $T + F$ is irreducible and $Q = F(I - T)^{-1}$. Then, after a permutation similarity,*

$$Q = \begin{pmatrix} Q_{11} & Q_{12} \\ 0 & 0 \end{pmatrix}, \tag{11}$$

where Q_{11} is a nontrivial irreducible nonnegative matrix, Q_{12} is a nonnegative matrix every column of which has a positive entry, and the 0 rows of Q correspond to the 0 rows of F, if any. □

Our stability and comparison theorem may now be stated as:

Theorem 4.2. *Suppose a standard matrix model of population dynamics satisfies (1) and (2), and assume that the projection matrix $P = T + F$ is irreducible with T satisfying (4) and $F \neq 0$. Denote the growth rate $\rho(P)$ by r and the net reproductive rate $\rho(Q)$, where $Q = F(I - T)^{-1}$, by R_0. Then equation (7) holds and so does one of the conditions in (8). Furthermore, the matrix Q is irreducible if and only if every row of F contains a positive element.*

Proof. We have $\rho(Q) = \rho(Q_{11})$ and since Q_{11} is irreducible, $\rho(Q_{11}) > 0$ by Theorem 2.1. The first conclusion follows from Theorem 3.1 and the second from Proposition 4.1 (which was also observed in [Z]). □

Seneta [Sen, p. 42] gives a proof of the Stein–Rosenberg theorem which may be adapted to show $R_0 > 0$ under the hypotheses of Theorem 4.2. The key ingredient is the observation that $(I - T)^{-1}$ and $(I - T/r)^{-1}$ have the same zero–nonzero pattern.

In contrast to the situation for irreducible P, one may construct examples of a reducible projection matrix P with a nonzero fertility matrix F such that the corresponding net reproductive rate $R_0 = 0$. In this connection, we shall prove the following theorem.

Theorem 4.3. *Let P, T and F satisfy the hypotheses of Theorem 3.3. Then the net reproductive rate $R_0 > 0$ if and only if for some $a > 0$, $\rho(T + aF) > \rho(T)$.*

Proof. First suppose that $R_0 > 0$. Then, for sufficiently large positive a, we have $aR_0 > 1$. But this is the net reproductive rate of the projection matrix $T + aF$ and hence, by Theorem 3.3, $\rho(T + aF) > 1 > \rho(T)$.

Conversely, suppose $\rho(T + aF) > \rho(T)$ for some positive number a. Let $\det(\lambda I - (T + aF)) = \sum_{k=1}^{n} \lambda^k f_k(a)$. Using the usual determinantal expansions, we see that the $f_k(a)$, $k = 1, \ldots, n$, are polynomials in a. But they are also signed sums of the k-th elementary symmetric functions of the eigenvalues of the matrix $T + aF$. Since $\rho(T + aF) > \rho(T)$, there exists k such that $f_k(a)$ is not a constant polynomial, and hence, for this k, $|f_k(a)|$ is unbounded as a goes to infinity. Hence at least one eigenvalue cannot be bounded in a, and it follows that $\rho(T + aF)$ is unbounded, and thus there exists a such that $\rho(T + aF) > 1$. Again applying Theorem 3.3 to $T + aF$, we obtain $aR_0 > 1$ and hence $R_0 > 0$. $\square$

Our proof of Theorem 4.3 also shows that if R_0 is positive, then F may be scaled to achieve an arbitrarily large growth rate in the general nonnegative case. Returning to an irreducible projection matrix $P = T + F$ with $F \neq 0$ we observe that Theorem 4.3 provides a second proof that $R_0 > 0$, since in this case $\rho(T + aF) > \rho(T)$ for all $a > 0$.

We now generalize Theorem 4.2. If $F + T$ is irreducible with Perron root r and positive left Perron vector z^t then it easily follows that $z^t F(I - T/r)^{-1} = rz^t$ and since $z^t > 0$ we deduce that $\rho(F(I - T/r)^{-1}) = r$, see e.g. [HJ, Cor. 8.1.30]. Thus Theorem 4.2 is the special case $s = r$, $q(s) = 1$ of the result which now follows.

Theorem 4.4. *Let P, T and F satisfy the conditions of Theorem 4.2. For $s > \rho(T)$ define*

$$q(s) = \rho(F(I - T/s)^{-1})/s. \tag{12}$$

Then $q(s) > 0$. Let $P(s) = T + F/q(s)$. Then its growth rate, $\rho(P(s))$, is s, and its net reproductive rate is

$$R_0(s) = R_0/q(s).$$

Further, one of the following holds:

$$1 = s = R_0(s), \quad \text{or} \quad 1 < s < R_0(s), \quad \text{or} \quad 0 < R_0(s) < s < 1. \tag{13}$$

Proof. We observe that $Q(s) = F(I - T/s)^{-1}$ is nonnegative since $\rho(T/s) < 1$ and hence $q(s) > 0$ by Theorem 4.2, as $F + T/s$ is irreducible. Let z^t be the left Perron vector of $Q(s)$. Thus $z^t Q(s) = z^t F(I - T/s)^{-1} = sq(s)z^t$. An easy computation now yields

$$z^t(T + F/q(s)) = sz^t$$

and hence s is the Perron root of $T + F/q(s)$ as asserted in the theorem. The corresponding net reproductive rate is $R_0(s) = \rho((F/q(s))(I - T)^{-1}) = R_0/q(s)$. Then (13) follows by Theorem 4.2. $\square$

We note that the inequalities (13) are strict and are equivalent to $\rho(F(I - T)^{-1}) < \rho(F(I - T/s)^{-1})$ if $\rho(T) < s < 1$ and $\rho(F(I - T)^{-1}) > \rho(F(I - T/s)^{-1})$ if $s > 1$. Further, since $\rho(F(I - T/s)^{-1})$ is a decreasing function of s, it follows that $q(s)$ is a strictly decreasing function of s and that $\lim_{s \to \infty} q(s) = 0$.

5. Demographic interpretations

We now discuss the demographic interpretations of our theorems. As we shall impose various assumptions on the projection matrix P, we begin each paragraph with an assumption which holds throughout the paragraph.

Assume that P is a primitive nonnegative matrix. As previously observed, the reciprocal of $r = \rho(P)$ may be viewed as a factor for the scaling of the fertility and transition matrices in order to obtain a model with every initial population eventually stationary population, viz. $\rho(P/r) = 1$. Similarly, since $R_0 = \rho(Q) > 0$, (Theorem 4.2.) we may leave the transition matrix fixed and scale the fertility matrix by the reciprocal of R_0 and in the resultant model every initial population will tend to a stationary population which is unique except for a multiplicative constant (Corollary 3.2). Intuitively, scaling the fertility matrix only should be more radical than scaling both the fertility and the transition matrix to achieve the same objective, and that is exactly the content of Theorems 3.1 and 3.3.

Suppose now that P is irreducible. It is possible to adapt the previous paragraph to this case by considering scalings to achieve a growth rate of 1, but we shall immediately turn to interpeting the more general Theorem 4.4. Given any $s > \rho(T)$, it is possible to obtain a growth rate of s without changing the transition matrix T by scaling the fertility matrix F to $F/q(s)$, where $q(s)$ is given by (12). Since $q(s)$ is a strictly decreasing function of s for $s > \rho(T)$, to achieve a higher growth rate we require greater fertility, which again is intuitively clear. We shall discuss these points further when we turn to the Leslie model.

Suppose that P is irreducible. By Proposition 4.1 every column of the submatrix (Q_{11}, Q_{12}) has a positive entry, and this implies that every class in the initial population has descendants during its lifetime. By the last assertion of Theorem 4.2 the matrix Q is irreducible if and only if there are newborns in every population class in the case of a population that has members in each class.

Now assume again that P is irreducible. We turn to characterizations of R_0 which may be obtained from Theorem 4.2 and from the following characterization of the Perron root of an irreducible nonnegative matrix A which is a reformulation of a well-known characterization due to Wielandt [W1], see also [G, p.65]:

$$\rho(A) = \max\{s : Ax \geq sx, \text{ for some } x \geq 0, \ x \neq 0\}$$
$$= \min\{s : Ax \leq sx, \text{ for some } x \geq 0, \ x \neq 0\},$$

and the equality is attained in either inequality if and only if x is the Perron vector of A. For this formulation and references to it, see the commentary following [W1] in Wielandt's Mathematical Works. Let z denote a nonnegative vector with the same number of entries as there are columns in Q_{11}, and let z_i be its ith entry. Then there exist indices i and j such that $(Q_{11}z)_i \geq R_0 z_i$ and $(Q_{11}z)_j \leq R_0 z_j$. We may put the case $r = R_0 = 1$ into words thus: For *every* initial population, there must be one class of newborns that over its lifetime produces at least as many descendants in the same class and there must be one class of newborns that over its lifetime produces at most as many descendants in the same class. Furthermore, *there exists a population of newborns* (i.e. corresponding to the nonzero rows of F) which over

the course of its lifetime reproduces itself exactly if and only if there exists a stationary population (but note that this population of newborns is in general not part of a stationary population).

Still under the assumption that P is irreducible, it is easily proved using an additional part of the Perron–Frobenius theorem, [BP, Theorem 2.20], [HJ, Corollary 8.4.6 and Remark 8.4.9], [V, Theorem 2.3], [G, Theorem 2, p.53], that for some positive integer d, P^d is the direct sum of primitive matrices, and hence that there is a population that is stable in a periodic sense for this model, that is for some positive integer d and every initial population x_0 there exist populations $w_0, \dots, w_{d-1}$ (depending on x_0) such that $(\lim_{k\to\infty} x_{kd+i})/r^k = w_i$, $i = 0, \dots, d-1$. To obtain the previous primitive case, we put $d = 1$. Another equivalent condition for $\rho(P) = 1$ in the irreducible case is that there should exist an initial population x_0 such that $\lim_{k\to\infty} x_k$ exists and is nonzero. This may be proved by means of Theorem 2.1(c).

We now turn to the case of the Leslie model, where T is a matrix with nonzero elements on the first subdiagonal and 0's elsewhere, and F is a matrix all of whose nonzero elements are in its first row, see [Les1], [Pol, p.38] or [Cush, p.4]:

$$T = \begin{pmatrix} 0 & \cdots & 0 & 0 \\ t_1 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & t_{n-1} & 0 \end{pmatrix} \quad \text{and} \quad F = \begin{pmatrix} f_1 & \cdots & f_{n-1} & f_n \\ 0 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \end{pmatrix}.$$

Whether P is irreducible or not, the situation is simpler as there is only one class of newborns, see [Par] for a discussion of reducible Leslie models. In this case, the net reproductive rate R_0 is the $(1, 1)$ entry of Q and is given by the well-known formula (e.g. [Cas2, p.126])

$$R_0 = \sum_{i=1}^{n} (f_i \prod_{j=1}^{i-1} t_j),$$

which may be interpreted as the expected number of offspring per newborn over the course of its lifetime, see [Cush, p.9, l.7] for this observation. Thus in this case R_0 equals the net reproductive rate as defined in the early papers [Bern, p.16] and [Lew, p.96], where formulas equivalent to the above expression for R_0 may be found, see also [Les1, p.190]. In turn, this definition, is an adaptation of a concept previously used in continuous population models, see Samuelson's instructive account [Sam] of a controversy concerning priority for this concept. By Theorem 3.3 we have $R_0 = 1$ if and only if $r = 1$, and if P is a primitive projection matrix for a Leslie model then this has the interpretation that every population is eventually stationary if and only if the expected number of offspring over the course of a newborn's lifetime is 1, viz. the $(1, 1)$ entry of Q is 1.

Let $P = T + F$ again be a Leslie matrix. Then $q(s)$ is the leading entry of $F(I - T/s)^{-1}/s$ which is

$$q(s) = f_1 s^{-1} + f_2 t_1 s^{-2} + \cdots + f_n (t_{n-1} \cdots t_1) s^{-n}, \tag{14}$$

a polynomial in s^{-1} with coefficients involving all nonzero entries in F and T. It is classical that the nonzero eigenvalues λ of P satisfy the equation $q(\lambda) = 1$, e.g. [Pol, p.42], and this is consistent with our more general results since by Theorem 4.4 the growth rate r of P satisfies $q(r) = 1$. We note that the operation of scaling the fertility matrix by a constant factor was previously considered by Leslie in [Les2, Sec. 5(b)]. His results in this area have a somewhat complicated appearance since he wished to determine s as a function of $q(s)$, which requires the solution of a polynomial equation. This gives rise to the following observation: To determine the growth rate for a Leslie matrix one needs to find a positive root of a polynomial equation, but to scale the fertility matrix to achieve an assigned growth rate s it suffices to divide the fertility matrix by $q(s)$ in (14).

Care needs to be taken to interpret the various terms used in this article when the matrix P is reducible. It is instructive to consider a simple example. Let

$$P = \begin{pmatrix} 1 & 0 \\ 1 & 1 \end{pmatrix}.$$

For the projection matrix P, an initial population is stable (in fact, stationary) if and only if its first element is 0, otherwise it will tend to infinity. The growth rate $r = \rho(P) = 1$, and the net reproductive rate $R_0 = 1$ whatever may be the transition matrix T and fertility matrix F chosen subject to conditions (1), (2) and (4).

We conclude by giving a numerical example which is based on a plant lifecycle involving vegetative as well as seed reproduction, [Cas1, Example 1.c]. Let

$$T = (1/2) \begin{pmatrix} 0&0&0&0&0 \\ 1&0&0&0&0 \\ 1&0&0&0&0 \\ 0&1&1&0&0 \\ 0&0&0&1&0 \end{pmatrix} \quad \text{and} \quad F = (1/2) \begin{pmatrix} 0&0&0&0&1 \\ 0&0&0&0&0 \\ 0&0&0&1&0 \\ 0&0&0&0&0 \\ 0&0&0&0&0 \end{pmatrix}.$$

Let $P = F + T$. This matrix is irreducible, but imprimitive. Then the growth rate $r = \sqrt{2}/2$ and the stable populations for P are $u = (\sqrt{2}, 1, 3, 2\sqrt{2}, 2)^t$ and its positive multiples. Further the next generation matrix is

$$Q = (1/8) \begin{pmatrix} 1&1&1&2&4 \\ 0&0&0&0&0 \\ 2&2&2&4&0 \\ 0&0&0&0&0 \\ 0&0&0&0&0 \end{pmatrix},$$

indicating that the population of newborns that reproduces itself with the same distribution of newborns in the next generation is $w = (1, 0, 2, 0, 0)^t$, the Perron vector of the next generation matrix Q. Note that the submatrix in rows and columns 1 and 3 of Q is irreducible and that $R_0 = \rho(Q) = 3/8$. We also note that $(P/\rho(P))^{2k} w$, $k = 0, 1, 2, \ldots$, tends to $(1, 1, 3, 2, 2)^t/3$ while $(P/\rho(P))^{2k+1} w$, $k = 0, 1, 2, \ldots$, tends to $(2, 1, 3, 4, 2)^t/\sqrt{2}$. Thus $(P/\rho(P))^k w$, $k = 0, 1, 2, \ldots$, does not tend to a limit, which indicates that generational

stability is compatible with permanent oscillation of the normalized population distribution over time.

If P is replaced by $P_1 = T + 8F/3$, then correspondingly $Q_1 = (8F/3)$ $(I - T)^{-1} = 8Q/3$ and we have both $\rho(P_1) = \rho(Q_1) = 1$. Since $\rho(T) = 0$, given any $s > 0$, we can use (12) to compute $q(s)$ such that $P(s) = T + F/q(s)$ has growth rate s. We obtain $q(s) = (1 + 2s^2)/8s^4$, and hence the corresponding net reproductive rate is $R_0(s) = 3s^4/(1 + 2s^2)$. The corresponding stable population is $(4s^3, 2s^2, 2s^2 + 8s^4, 2s + 4s^3, 1 + 2s^2)^t$.

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