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DENSITY-DEPENDENT LESLIE MATRIX MODELING FOR LOGISTIC POPULATIONS WITH STEADY-STATE DISTRIBUTION CONTROL

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Abstract

The Leslie matrix model allows for the discrete modeling of population age-groups whose total population grows exponentially. Many attempts have been made to adapt this model to a logistic model with a carrying capacity (see [1], [2], [4], [5], and [6]), with mixed results. In this paper we provide a new model for logistic populations that tracks age-group populations with repeated multiplication of a density-dependent matrix constructed from an original Leslie matrix, the chosen carrying capacity of the model, and the desired steady-state age-group distribution. The total populations from the model converge to a discrete logistic model with the same initial population and carrying capacity, and growth rate equal to the dominant eigenvalue of the Leslie matrix minus 1.

Keywords: Leslie matrices; discrete population models; exponential population model; logistic population model

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1. Introduction

Ecologists use population models to predict population sizes within a closed ecosystem. The most basic of these models are the exponential model and the logistic model,

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both of which can be constructed over a continuous or a discrete time domain. Continuous models are the solutions to differential equations, and the discrete models are recursively defined difference equations. Leslie matrices are used to track population age groups within a population in a discrete model where the age span of the age groups is equal to the time step, but has the same limitations for long-term modeling that are present in the exponential model. This paper develops a method for using Leslie matrices in such a way that the total populations adhere more closely to the logistic model, while providing the choice of the ending age distribution.

1.1. Exponential and logistic population models

Exponential models assume that the ecosystem in which the population lives has unlimited resources. The continuous exponential model follows from the differential equation

$$\frac{dP}{dt} = rP(t), \tag{1}$$

where $P(t)$ is the population size at time t, and r is the constant continuous growth rate over the unit of time used for t (annual if time is measured in years, for example). The exponential model,

$$P(t) = P(0)e^{rt}$$

is the solution to equation (1). The analogous discrete difference formula for the population size after n time-steps of length Δt, denoted P_n, is given by

$$P_n = P_{n-1} + \tilde{r}P_{n-1}, \quad n \in \mathbb{Z}^+, \tag{2}$$

where $\tilde{r}$ is the constant periodic growth rate over a period of time-length Δt, and P_0 is the initial population size at $t = 0$. This is a recursive definition, but it can be simplified to the closed-form solution

$$P_n = (1 + \tilde{r})^n P_0. \tag{3}$$

Either exponential model is useful for short-term or fixed-term modeling, but is not realistic for long-term modeling, since no real ecosystem has unlimited resources. An example of discrete and continuous exponential models is shown in Figure 1.

Unlike exponential models, logistic models account for limited resources in the ecosystem. The continuous logistic model follows from the differential equation

$$\frac{dP}{dt} = r\left(1 - \frac{P(t)}{C}\right)P(t), \tag{4}$$

where $P(t)$ is the population size at time t, r is the growth rate, and C is the carrying capacity of the ecosystem. The logistic model,

$$P(t) = \frac{CP(0)e^{rt}}{C + P(0)(e^{rt} - 1)}$$

is the solution to equation (4). The analogous difference formula for the population size after n time-steps of length Δt, denoted P_n is given by

$$P_n = P_{n-1} + \tilde{r}\left(1 - \frac{P_{n-1}}{C}\right)P_{n-1}, \tag{5}$$

where $\tilde{r}$ is the constant periodic growth rate over a period of time-length Δt, C is the carrying capacity of the population, and P_0 is the initial population size at $t = 0$, or equivalently,

$$P_n = (1 + \tilde{r})\left(1 - \frac{\tilde{r}}{(1 + \tilde{r})C}P_{n-1}\right)P_{n-1}, \quad n \in \mathbb{Z}^+ \tag{6}$$

The discrete logistic population model is intimately connected to the logistic map

$$x_n = r(1 - x_{n-1})x_{n-1}, \tag{7}$$

which maps the interval $[0, 1]$ to $\left[0, \frac{r}{4}\right]$. The stability of this map has been well-studied, with the following results known:

- for $0 < r \leq 1$, the sequence $\{x_n\}$ with $0 < x_0 < 1$ converges to 0 as $n \to \infty$, and
- for $1 < r \leq 3$, the sequence $\{x_n\}$ with $0 < x_0 < 1$ converges to $\frac{r-1}{r}$ as $n \to \infty$.

If we make the substitution $x_n = \frac{r-1}{rC}\tilde{x}_n$, for $1 < r \leq 3$ and $C > 0$, then equation (7) becomes

$$\tilde{x}_n = r\left(1 - \frac{r-1}{rC}\tilde{x}_{n-1}\right)\tilde{x}_{n-1},$$

which now maps the interval $\left[0, \frac{rC}{r-1}\right]$ to $\left[0, \frac{r^2C}{4(r-1)}\right]$ and has the same form as equation (6) with $r = 1 + \tilde{r}$. Thus, we can expect the discrete logistic population model (5) to converge to C for $0 < \tilde{r} \leq 2$.

1.2. Leslie matrices and other definitions

Let $\mathbf{P}_0$ be an $k \times 1$ column vector, where the entry in the i^{th} row denotes the initial size of the population with ages in the range $[(i-1)\Delta t, i\Delta t)$ for $i = 1, \ldots, k$. Let b_i be the average offspring per occupant in the $[(i-1)\Delta t, i\Delta t)$ age group for $i = 1, \ldots, k$, not all 0, and let $s_i \in (0, 1]$ be the percentage in that age group that survive to the next age group for $i = 1, \ldots, k-1$. Then the **Leslie** matrix $\mathbf{L}$ for a population is defined by the $k \times k$ matrix

$$\mathbf{L} = \begin{bmatrix} b_1 & b_2 & \cdots & b_{k-1} & b_k \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{k-1} & 0 \end{bmatrix}.$$

Then the population distribution for each age group after n time-steps Δt, denoted $\mathbf{P}_n$, is given by

$$\mathbf{P}_n = \mathbf{L}\mathbf{P}_{n-1}, \tag{8}$$

or equivalently

$$\mathbf{P}_n = \mathbf{L}^n\mathbf{P}_0. \tag{9}$$

Note the similarity of equations (8) and (9) to the discrete exponential model in equations (2) and (3), respectively. A nonnegative square matrix $\mathbf{A}$ is said to be **primitive** if there is a positive integer n such that $\mathbf{A}^n$ has all positive entries. It is straightforward to show that if b_k is nonzero and any consecutive b_i and b_{i+1}, $i = 1, \ldots, k-1$, are nonzero, then the Leslie matrix is primitive.

Leslie matrices have several well-known properties. A Leslie matrix $\mathbf{L}$ will have k **eigenvalues** λ_i and associated **eigenvectors** $\mathbf{x}_i$, $i = 1, \ldots, k$ - that is, λ_i and $\mathbf{x}_i$ satisfying $\mathbf{L}\mathbf{x}_i = \lambda_i\mathbf{x}_i$ for $i = 1, \ldots, k$. Note that any scalar multiple of an eigenvector $\mathbf{x}$ associated with λ is also an eigenvector, since $\mathbf{L}(c\mathbf{x}) = c\mathbf{L}\mathbf{x} = c\lambda\mathbf{x} = \lambda(c\mathbf{x})$ for a constant c. If the eigenvalues of $\mathbf{L}$ are distinct, then the eigenvectors of $\mathbf{L}$ form a linearly independent set that spans $\mathbb{R}^k$. The Perron-Frobineus theorem guarantees that a primitive $\mathbf{L}$ will have a simple positive real eigenvalue λ, called the **dominant eigenvalue**, with other eigenvalues indexed λ_i for $i = 2, \ldots, k$, such that $\lambda > |\lambda_i|$ for $i = 2, \ldots, k$. An eigenvector $\mathbf{x}$ with positive entries that is associated with λ is called a **dominant eigenvector**. The sequence of vectors $\mathbf{P}_n$ described in (9) will approach a multiple of a dominant eigenvector of $\mathbf{L}$ as $n \to \infty$, although the total population size will grow without bound similar to the exponential model. In fact, if the initial population vector $\mathbf{P}_0$ is a dominant eigenvector of Leslie matrix $\mathbf{L}$ with eigenvector λ, the growth is completely analogous to exponential growth, since

$$\mathbf{P}_n = \mathbf{L}^n \mathbf{P}_0 = \mathbf{L}^{n-1}(\mathbf{L}\mathbf{P}_0) = \mathbf{L}^{n-1}(\lambda \mathbf{P}_0) = \cdots = \lambda^n \mathbf{P}_0.$$

Leslie realized the limitation of the model he proposed in [3], and attempted to modify it in [4] by scaling his matrix entries according to previous total populations. This model was analyzed for convergence and stability by Allen in [1], showing convergence of the steady-state to a scaled version of the dominant eigenvector of the original Leslie matrix with the desired total population. Lui and Cohen in [6] applied a matrix model to an approximate solution of the discrete logistic model,

$$P_n = P_{n-1} e^{r\left(1 - \frac{P_{n-1}}{C}\right)}.$$

Their model was inexact by nature of their choice of using an approximation, used many new parameters based on additional information, involved matrix exponentials, and, as such, was difficult to apply. Jensen in [2] reexamined the matrix model (8), with a suggestion (without mathematical justification) for a damping matrix that would reduce the growth rate so that the total population approached the carrying capacity C. The model worked in the short term, but behaved chaotically as $n \to \infty$.

2. New model

We propose a model that includes a Leslie matrix, but also a damping matrix that is density-dependent. This model will

- have a total population that approaches a chosen carrying capacity,
- reach a steady distribution of our choosing that meets certain basic criteria consistent with Leslie matrices, and
- will implement repeated matrix multiplication, interrupted only by a calculation (sum) of the total population represented by the previous step.

The convergence of the model is stable for primitive Leslie matrices with distinct eigenvalues and dominant eigenvalue λ satisfying $1 < \lambda \leq 3$, and a nonnegative initial population distribution. The model is effectively a logistic population model for population vectors.

We begin with some necessary definitions and notation. Since repeated multiplication by a Leslie matrix converges to a multiple of its dominant eigenvalue, and since the presence of population in all but the youngest age group is a result of survival from the previous age group, dominant eigenvectors of Leslie matrices have to meet certain criteria.

Definition 1. (*Valid Leslie matrix steady state vectors.*) We say that a vector $\mathbf{x} = \begin{bmatrix} x_1 \cdots x_k \end{bmatrix}^T$ is a **valid Leslie matrix steady state vector** if the entries satisfy the inequalities $x_i \geq x_{i+1} > 0$ for $i = 1, \ldots, k-1$.

Note that any dominant eigenvector of a Leslie matrix will be a valid Leslie matrix steady state vector.

Definition 2. (*Total population operator.*) For a population vector $\mathbf{x} = \begin{bmatrix} x_1 \cdots x_k \end{bmatrix}^T$, we define the **total population operator** $T(\mathbf{x})$ as

$$T(\mathbf{x}) = \begin{bmatrix} 1 \cdots 1 \end{bmatrix}_{k \times 1} \begin{bmatrix} x_1 \cdots x_k \end{bmatrix}^T = x_1 + \ldots + x_k.$$

Lemma 1. *Let λ be the dominant eigenvalue of the primitive $k \times k$ Leslie matrix $\mathbf{L}$, $1 < \lambda \leq 3$, with dominant eigenvector $\mathbf{u}$, and let $\mathbf{v}$ be a valid Leslie matrix steady state vector. Let the $k \times k$ matrix $\mathbf{A}$ satisfy the following conditions:*

1. *$\mathbf{v}$ is an eigenvector of the matrix $\mathbf{LA}$ associated with the eigenvalue 1, and*

2. *$\mathbf{LAu} = \lambda \mathbf{v} + \mathbf{u} - \mathbf{Lv}$.*

Then $\tau(p) = (1-p)\lambda + p$ is an eigenvalue of the $k \times k$ matrix $\mathbf{M}(p) = \mathbf{L}((1-p)\mathbf{I}_{k \times k} + p\mathbf{A})$, with associated eigenvector $\mathbf{w}(p) = (1-p)\mathbf{u} + p\mathbf{v}$ for $0 \leq p \leq \omega(\lambda)$, where

$$\omega(\lambda) = \begin{cases} 1 & \text{for } 1 < \lambda \leq 2 \\ \frac{\lambda^2}{4(\lambda - 1)} & \text{for } 2 < \lambda \leq 3. \end{cases} \tag{10}$$

Proof. Note that

$$
\begin{aligned}
&\mathbf{L}((1-p)\mathbf{I}_{k\times k}+p\mathbf{A})((1-p)\mathbf{u}+p\mathbf{v})\\
&\quad=(1-p)^2\mathbf{L}\mathbf{u}+p(1-p)\mathbf{L}\mathbf{v}+p(1-p)\mathbf{L}\mathbf{A}\mathbf{u}+p^2\mathbf{L}\mathbf{A}\mathbf{v}\\
&\quad=(1-p)^2\lambda\mathbf{u}+p(1-p)\mathbf{L}\mathbf{v}+p(1-p)(\lambda\mathbf{v}+\mathbf{u}-\mathbf{L}\mathbf{v})+p^2\mathbf{v}\\
&\quad=(1-p)^2\lambda\mathbf{u}+p(1-p)\mathbf{L}\mathbf{v}+p(1-p)\lambda\mathbf{v}+p(1-p)\mathbf{u}-p(1-p)\mathbf{L}\mathbf{v}+p^2\mathbf{v}\\
&\quad=(1-p)\lambda((1-p)\mathbf{u}+p\mathbf{v})+p((1-p)\mathbf{u}+p\mathbf{v})\\
&\quad=((1-p)\lambda+p)((1-p)\mathbf{u}+p\mathbf{v})=\tau(p)\mathbf{w}(p).
\end{aligned}
$$

Thus, $\tau(p)$ is an eigenvalue of $\mathbf{M}(p)$ with associated eigenvector $\mathbf{w}(p)$ over the interval $0 \le p \le \omega(\lambda)$. □

We actually want $\tau(p)$ to be a dominant eigenvalue of $\mathbf{M}(p)$ as defined in Lemma 1. In the following theorem, we demonstrate that we can always construct a matrix $\mathbf{A}$ so that this is the case.

Theorem 1. *Let λ be the dominant eigenvalue of the primitive $k \times k$ Leslie matrix $\mathbf{L}$ with distinct eigenvalues and $1 < \lambda \le 3$, with dominant eigenvector $\mathbf{u}$, and let $\mathbf{v}$ be a valid Leslie matrix steady state vector. Then there exists a $k \times k$ matrix $\mathbf{A}$ such that $\tau(p) = (1-p)\lambda + p$ is the dominant eigenvalue of $\mathbf{M}(p) = \mathbf{L}((1-p)\mathbf{I}_{k\times k} + p\mathbf{A})$ with associated eigenvector $\mathbf{w}(p) = (1-p)\mathbf{u} + p\mathbf{v}$ over the interval $0 \le p \le \omega(\lambda)$, with $\omega(\lambda)$ as defined in (10).*

Proof. Let λ_i, $i = 2, \ldots, k$ be the other non-dominant eigenvalues of $\mathbf{L}$, so that $\lambda > |\lambda_i|$ for $i = 2, \ldots, k$, and let $\mathbf{x}_i$ be an associated eigenvector of λ_i, $i = 2, \ldots, k$. There are two cases to consider.

Case 1. Let $\mathbf{u} = \mathbf{v}$. Note that condition 2 in Lemma 1 is now identical to condition 1. We may let $\mathbf{A} = \frac{1}{\lambda}\mathbf{I}_{k\times k}$. Note that

$$\mathbf{L}\mathbf{A}\mathbf{u} = \mathbf{L}\left(\frac{1}{\lambda}\mathbf{I}_{k\times k}\right)\mathbf{u} = \frac{1}{\lambda}\mathbf{L}\mathbf{u} = \frac{1}{\lambda}(\lambda\mathbf{u}) = \mathbf{u}.$$

Thus, matrix $\mathbf{A}$ satisfies condition 1 of Lemma 1, and $\tau(p)$ is an eigenvalue of $\mathbf{M}(p)$ with associated eigenvector $\mathbf{w}(p) = (1-p)\mathbf{u} + p\mathbf{u} = \mathbf{u}$ for $0 \le p \le \omega(\lambda)$. Also, since

$$\mathbf{M}(p) = \mathbf{L}\left((1-p)\mathbf{I}_{k\times k} + \frac{p}{\lambda}\mathbf{I}_{k\times k}\right) = \left(1 - p + \frac{p}{\lambda}\right)\mathbf{L},$$

then the other eigenvalues of $\mathbf{M}(p)$ are $\left(1 - p + \dfrac{p}{\lambda}\right)\lambda_i$ for $i = 2, \ldots, k$. Note that

$$\left|\left(1 - p + \frac{p}{\lambda}\right)\lambda_i\right| < \left(1 - p + \frac{p}{\lambda}\right)\lambda = \tau(p) \text{ for } 0 \le p \le \omega(\lambda),\ i = 2, \ldots, k.$$

Thus, $\tau(p)$ is the dominant eigenvalue with associated eigenvector $\mathbf{u}$ for $0 \le p \le \omega(\lambda)$ in this case with the given choice of matrix $\mathbf{A}$. Note that this case is effectively the model preposed by Leslie in [5] and analyzed by Allen in [1].

Case 2. Suppose that $\mathbf{u} \ne \mathbf{v}$. Due to the invariance of eigenvectors to scaling, we may, without loss of generality, select a scaling of $\mathbf{v}$ so that for constants c, c_2, ..., c_k satisfying $\mathbf{u} = c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i$, the constant c satisfies the condition

$$\max_{i=2,\ldots,k}\left|1 + \frac{\lambda_i}{c} - \frac{\lambda}{c}\right| < 1.$$

Notice that $c \ne 0$, since both $\mathbf{u}$ and $\mathbf{v}$ are valid Leslie matrix steady state vectors, and that the condition can always be met, since $|\lambda_i| < \lambda$ for $i = 2, \ldots, k$, and since $1 < \lambda \le 3$.

Let $\mathbf{A}$ be the solution to the linear system

$$\begin{cases} \mathbf{LAv} = \mathbf{v} \\ \mathbf{LAx}_2 = \left(1 + \frac{\lambda_2}{c} - \frac{\lambda}{c}\right)\mathbf{x}_2 \\ \qquad\vdots \\ \mathbf{LAx}_k = \left(1 + \frac{\lambda_k}{c} - \frac{\lambda}{c}\right)\mathbf{x}_k. \end{cases} \tag{11}$$

Thus, $\mathbf{A}$ satisfies condition 1 of Lemma 1. As the vectors $\mathbf{v}$, $\mathbf{x}_2$, ..., $\mathbf{x}_k$ form a basis for $\mathbb{R}^k$, we may alternatively form the matrices

$$\mathbf{E} = \begin{bmatrix} \mathbf{v} & \mathbf{x}_2 & \cdots & \mathbf{x}_k \end{bmatrix} \text{ and } \mathbf{D} = \begin{bmatrix} 1 & 0 & \cdots & 0 \\ 0 & 1 + \frac{\lambda_2}{c} - \frac{\lambda}{c} & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & 1 + \frac{\lambda_k}{c} - \frac{\lambda}{c} \end{bmatrix}$$

and restate (11) as $\mathbf{LAE} = \mathbf{ED}$, where $\mathbf{LA} = \mathbf{EDE}^{-1}$, or in the case of an invertible Leslie matrix, $\mathbf{A} = \mathbf{L}^{-1}\mathbf{EDE}^{-1}$.

There exist constants $c_2, \ldots, c_k$ such that $\mathbf{u} = c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i$. Then

$$\mathbf{Lu} = \mathbf{L}\left(c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i\right) = c\mathbf{Lv} + \sum_{i=2}^{k} c_i \lambda_i \mathbf{x}_i$$

and

$$\lambda \mathbf{u} = \lambda \left(c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i \right) = c\lambda \mathbf{v} + \lambda \sum_{i=2}^{k} c_i \mathbf{x}_i.$$

Since $\mathbf{Lu} = \lambda \mathbf{u}$, then we have

$$\mathbf{Lv} = \lambda \mathbf{v} + \frac{1}{c} \sum_{i=2}^{k} c_i (\lambda - \lambda_i) \mathbf{x}_i.$$

Then

$$\begin{aligned}
\mathbf{LAu} = \mathbf{LA} \left(c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i \right) &= c\mathbf{v} + \sum_{i=2}^{k} c_i \left(1 + \frac{\lambda_i}{c} - \frac{\lambda}{c} \right) \mathbf{x}_i \\
&= \left(c\mathbf{v} + \sum_{i=2}^{k} c_i \mathbf{x}_i \right) - \frac{1}{c} \sum_{i=2}^{k} c_i (\lambda - \lambda_i) \mathbf{x}_i + \lambda \mathbf{v} - \lambda \mathbf{v} \\
&= \lambda \mathbf{v} + \mathbf{u} - \left(\lambda \mathbf{v} + \frac{1}{c} \sum_{i=2}^{k} c_i (\lambda - \lambda_i) \mathbf{x}_i \right) \\
&= \lambda \mathbf{v} + \mathbf{u} - \mathbf{Lv}.
\end{aligned}$$

Thus, the matrix $\mathbf{A}$ satisfies condition 2 of Lemma 1, and so $\tau(p)$ is an eigenvalue of $\mathbf{M}(p)$ with associated eigenvector $\mathbf{w}(p) = (1-p)\mathbf{u} + p\mathbf{v}$ for $0 \leq p \leq \omega(\lambda)$.

The vectors $\mathbf{x}_i$, $i = 2, \ldots, k$, are also eigenvectors of $\mathbf{M}(p)$, since

$$\mathbf{M}(p)\mathbf{x}_i = \mathbf{L} \left((1-p)\mathbf{I}_{k \times k} + p\mathbf{A} \right) \mathbf{x}_i = \left((1-p)\lambda_i + p \left(1 + \frac{\lambda_i}{c} - \frac{\lambda}{c} \right) \right) \mathbf{x}_i$$

for $i = 2, \ldots, k$. Note that

$$\left| (1-p)\lambda_i + p \left(1 + \frac{\lambda_i}{c} - \frac{\lambda}{c} \right) \right| \leq (1-p)|\lambda_i| + p \left| 1 + \frac{\lambda_i}{c} - \frac{\lambda}{c} \right| < (1-p)\lambda + p = \tau(p),$$

so $\tau(p)$ is the dominant eigenvalue for this choice of $\mathbf{A}$. □

It is important to note that there may be many possible choices for the matrix $\mathbf{A}$ in Theorem 1, and we are not restricted to the matrices constructed in the theorem. We are now ready to state our main theorem.

Theorem 2. *Let λ be the dominant eigenvalue of the primitive $k \times k$ Leslie matrix $\mathbf{L}$ with distinct eigenvalues and $1 < \lambda \leq 3$, with dominant eigenvector $\mathbf{u}$, let $\mathbf{v}$ be the desired final distribution of age-groups that is a valid Leslie matrix steady state vector, and let $\mathbf{P}_0$ be an initial population vector where $T(\mathbf{P}_0) < C$, the desired carrying capacity. Let the $k \times k$ matrix $\mathbf{A}$ be chosen so that $\tau(p) = (1-p)\lambda + p$ is the dominant* *eigenvalue of* $\mathbf{M}(p) = \mathbf{L}((1-p)\mathbf{I}_{k\times k} + p\mathbf{A})$ *with associated eigenvector* $\mathbf{w}(p) = (1-p)\mathbf{u} + p\mathbf{v}$ *over the interval* $0 \le p \le \omega(\lambda)$*, with* $\omega(\lambda)$ *as defined in (10). Then the sequence of vectors* $\{\mathbf{P}_n\}_{n=1}^{\infty}$ *generated by*

$$\mathbf{P}_n = \mathbf{M}\left(\frac{T(\mathbf{P}_{n-1})}{C}\right)\mathbf{P}_{n-1} \tag{12}$$

satisfy the property that $\lim_{n\to\infty} \mathbf{P}_n = c\mathbf{v}$ *where* c *is a constant such that* $T(c\mathbf{v}) = C$*.*

Proof. Let $\mathbf{P}_0$ be an initial population vector with nonnegative entries where $T(\mathbf{P}_0) < C$. We know from Lemma 1 and Theorem 1 that we may find a matrix $\mathbf{A}$ satisfying the conditions of the theorem. Consider the sequence of vectors $\{\mathbf{P}_n\}_{n=0}^{\infty}$ generated by the repeated application of equation (12). Let $p_n = \dfrac{T(\mathbf{P}_n)}{C}$ be the percentage of the carrying capacity of the total population of $\mathbf{P}_n$ for integer $n \ge 0$.

For integer $n \ge 0$, we have $\mathbf{w}(p_n)$ as the dominant eigenvector of $\mathbf{M}(p_n)$ with dominant eigenvalue $\tau(p_n)$ as guaranteed by Lemma 1 and Theorem 1, and we let $\{\mathbf{w}_{n,2}, \ldots, \mathbf{w}_{n,k}\}$ be the remaining eigenvectors of $\mathbf{M}(p_n)$ with associated eigenvalues $\{\gamma_{n,2}, \ldots, \gamma_{n,k}\}$, respectively. Then, for each integer $n \ge 0$, there exist constants $c_{n,i}$, $i = 1, \ldots, k$, such that

$$\mathbf{P}_n = c_{n,1}\mathbf{w}(p_n) + c_{n,2}\mathbf{w}_{n,2} + \cdots + c_{n,k}\mathbf{w}_{n,k}, \text{ with } c_{n,1} \ne 0. \tag{13}$$

Then for integer $n > 0$,

$$\begin{aligned}
\mathbf{P}_n &= \mathbf{M}(p_{n-1})\mathbf{P}_{n-1} \\
&= c_{n-1,1}\mathbf{M}(p_{n-1})\mathbf{w}(p_{n-1}) + c_{n-1,2}\mathbf{M}(p_{n-1})\mathbf{w}_{n-1,2} + \cdots + c_{n-1,k}\mathbf{M}(p_{n-1})\mathbf{w}_{n-1,k} \\
&= c_{n-1,1}\tau(p_{n-1})\mathbf{w}(p_{n-1}) + c_{n-1,2}\gamma_{n-1,2}\mathbf{w}_{n-1,2} + \cdots + c_{n-1,k}\gamma_{n-1,k}\mathbf{w}_{n-1,k} \\
&= \tau(p_{n-1})\Bigg[c_{n-1,1}\mathbf{w}(p_{n-1}) + c_{n-1,2}\left(\frac{\gamma_{n-1,2}}{\tau(p_{n-1})}\right)\mathbf{w}_{n-1,2} + \cdots \\
&\qquad\qquad + c_{n-1,k}\left(\frac{\gamma_{n-1,k}}{\tau(p_{n-1})}\right)\mathbf{w}_{n-1,k}\Bigg].
\end{aligned}$$

Note that, due to the dominance of $\tau(p_n)$ for all integer $n > 0$, $\left|\dfrac{\gamma_{n,i}}{\tau(p_n)}\right| < 1$ for $i = 2, \ldots, k$, and that the sequence $\{\mathbf{P}_n\}_{n=0}^{\infty}$ converges to the sequence $\{\tilde{\mathbf{P}}_n\}_{n=1}^{\infty}$ where

$$\tilde{\mathbf{P}}_n = c_{n-1,1}\tau(p_{n-1})\mathbf{w}(p_{n-1}). \tag{14}$$

Then, from equations (13) and (14),

$$\begin{aligned}\lim_{n\to\infty} T(\mathbf{P}_n) &= \lim_{n\to\infty} T(\tilde{\mathbf{P}}_n) = \lim_{n\to\infty} \tau(p_{n-1})T(\mathbf{P}_{n-1}) \\ &= \lim_{n\to\infty} \left(\lambda T(\mathbf{P}_{n-1}) - \frac{\lambda}{C}T(\mathbf{P}_{n-1})^2 + \frac{1}{C}T(\mathbf{P}_{n-1})^2\right) \\ &= \lim_{n\to\infty} \lambda \left(1 - \frac{\lambda-1}{\lambda C}T(\mathbf{P}_{n-1})\right) T(\mathbf{P}_{n-1}) \qquad (15)\end{aligned}$$

Note that the expression in (15) is the same as the logistic equation (6), with $\lambda = 1+\tilde{r}$. Thus, $\lim_{n\to\infty} T(\mathbf{P}_n) = C$ for $1 < \lambda \leq 3$. Also note that

$$\lim_{n\to\infty} \mathbf{P}_n = \lim_{n\to\infty} \tilde{\mathbf{P}}_n = \left(\lim_{n\to\infty} c_{n,1}\right)\left(\lim_{n\to\infty} \tau(p_{n-1})\right)\left(\lim_{n\to\infty} \mathbf{w}(p_{n-1})\right) = c\mathbf{v},$$

where $c = \lim_{n\to\infty} c_{n,1}$ is the constant so that $T(c\mathbf{v}) = C$. □

3. Examples

For each of our examples, we will use the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} \frac{1}{5} & \frac{1}{2} & \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \\ \frac{24}{25} & 0 & 0 & 0 & 0 \\ 0 & \frac{9}{10} & 0 & 0 & 0 \\ 0 & 0 & \frac{4}{5} & 0 & 0 \\ 0 & 0 & 0 & \frac{3}{5} & 0 \end{bmatrix},$$

with dominant eigenvalue $\lambda = \dfrac{6}{5}$ and dominant eigenvector $\mathbf{u} = \begin{bmatrix} \frac{1}{3} & \frac{4}{15} & \frac{1}{5} & \frac{2}{15} & \frac{1}{15} \end{bmatrix}^T$, and the initial population vector $\mathbf{P}_0 = \begin{bmatrix} 30 & 0 & 0 & 0 & 0 \end{bmatrix}^T$. The standard application of the Leslie matrix, as described in (8) and (9), yields the population distributions with exponential growth shown in Figure 1, with the youngest age-group shown in the bottom section of the graph, and the oldest at the top. Notice that after only 15 iterations, the distribution is already quite close to a multiple of $\mathbf{u}$.

3.1. Example 1

In this first example, we will set the carrying capacity $C = 300$, and let the ending distribution $\mathbf{v} = \mathbf{u}$. Let $p_k = \dfrac{T(\mathbf{P}_k)}{C}$, and let $\mathbf{A} = \dfrac{1}{\lambda}\mathbf{I}_{5\times5} = \dfrac{5}{6}\mathbf{I}_{5\times5}$, as in the first case of the proof of Theorem 1. Then let

$$\mathbf{M}(p_k) = \mathbf{L}\left((1-p_k)\mathbf{I}_{5\times5} + p_k\mathbf{A}\right) = \left(1 - \frac{1}{6}p_k\right)\mathbf{L},$$

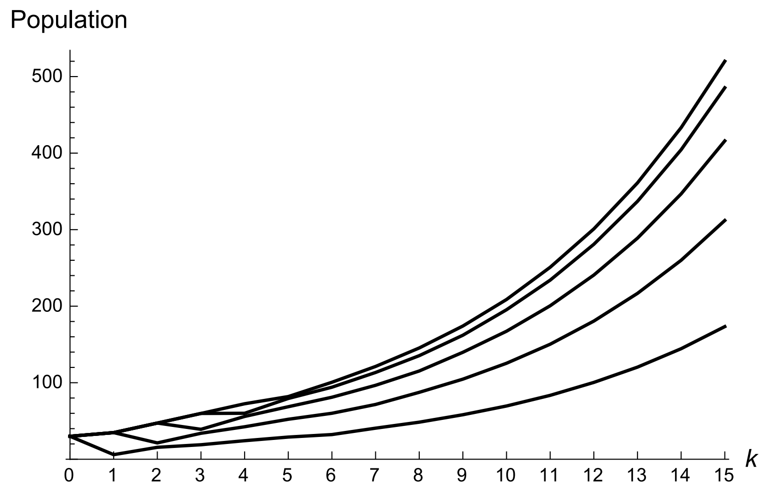

FIGURE 1: Exponential growth from repeated application of the Leslie matrix $\mathbf{L}$.

and let $\mathbf{P}_k = \mathbf{M}(p_{k-1})\mathbf{P}_{k-1}$ for integer $k > 0$. The results for $k = 0, \ldots, 40$ are shown in Figure 2. Note that, by $k = 40$, the distribution is already quite close to $C\mathbf{v} = \begin{bmatrix} 100 & 80 & 60 & 40 & 20 \end{bmatrix}^T$.

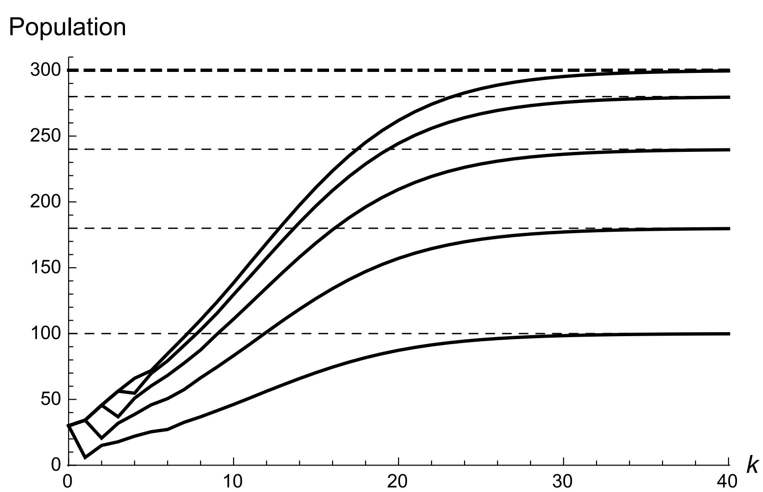

FIGURE 2: Logistic population growth with carrying capacity $C = 300$ and ending distribution a multiple of the dominant eigenvector of the original Leslie matrix $\mathbf{L}$.

3.2. Example 2

In this second example, we keep the carrying capacity $C = 300$, but choose the ending distribution $\mathbf{v} = \begin{bmatrix} \frac{7}{15} & \frac{7}{30} & \frac{1}{6} & \frac{1}{10} & \frac{1}{30} \end{bmatrix}^T$, a valid Leslie matrix steady state vector that is not a scalar multiple of $\mathbf{u}$. We choose matrix $\mathbf{A}$ satisfying (11) as in Case 2 of the proof of Theorem 1, with

$$\mathbf{A} = \begin{bmatrix} \frac{27}{32} & -\frac{713}{1536} & -\frac{21}{128} & -\frac{63}{512} & -\frac{21}{256} \\ -\frac{1}{80} & \frac{1973}{1920} & -\frac{413}{1440} & -\frac{1}{128} & -\frac{1}{192} \\ -\frac{3}{160} & -\frac{5}{256} & \frac{41}{40} & -\frac{413}{1280} & -\frac{1}{128} \\ -\frac{3}{80} & -\frac{5}{128} & -\frac{1}{32} & \frac{651}{640} & -\frac{413}{960} \\ \frac{1}{10} & \frac{697}{960} & \frac{223}{288} & \frac{219}{320} & \frac{409}{240} \end{bmatrix}$$

Then let

$$\mathbf{M}(p_k) = \mathbf{L}\left((1 - p_k)\mathbf{I}_{5\times 5} + p_k\mathbf{A}\right),$$

and let $\mathbf{P}_k = \mathbf{M}(p_{k-1})\mathbf{P}_{k-1}$ for integer $k > 0$. The results for $k = 0, \ldots, 40$ are shown in Figure 3. Note that, by $k = 40$, the distribution is already quite close to $C\mathbf{v} = \begin{bmatrix} 140 & 70 & 50 & 30 & 10 \end{bmatrix}^T$.

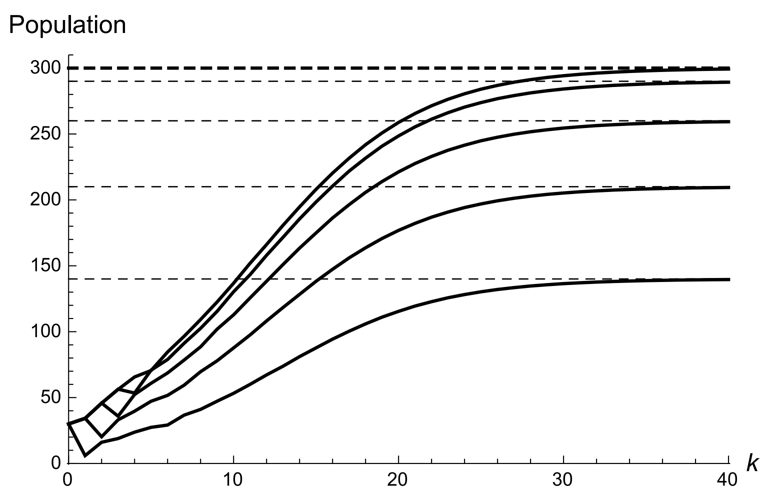

FIGURE 3: Logistic population growth with carrying capacity $C = 300$ and ending distribution chosen so as not to be a dominant eigenvector of the original Leslie matrix $\mathbf{L}$.

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