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Taylor's law for exponentially growing local populations linked by migration

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ABSTRACT

We consider the dynamics of a collection of $n > 1$ populations in which each population has its own rate of growth or decay, fixed in continuous time, and migrants may flow from one population to another over a fixed network, at a rate, fixed over time, times the size of the sending population. This model is represented by an ordinary linear differential equation of dimension n with constant coefficients arrayed in an essentially nonnegative matrix. This paper identifies conditions on the parameters of the model (specifically, conditions on the eigenvalues and eigenvectors) under which the variance of the n population sizes at a given time is asymptotically (as time increases) proportional to a power of the mean of the population sizes at that given time. A power-law variance function is known in ecology as Taylor's Law and in physics as fluctuation scaling. Among other results, we show that Taylor's Law holds asymptotically, with variance asymptotically proportional to the mean squared, on an open dense subset of the class of models considered here.

1. Introduction

We consider the dynamics of an ensemble of two or more local populations with two key features. First, each local population has a fixed rate of growth or decay specific to that population. This assumption, by itself, gives the exponential model in Cohen (2013). Second, migration can flow from one local population to another according to some graph (network) and some rates of migration. This model excludes immigration from external sources at a fixed or variable rate to any local population. However, the model takes account of deaths and emigration (exits from the collection of local populations) at fixed rates specific to each local population.

This model may be called a subdivided population model or a metapopulation model, although it does not represent extinction and recolonization of any local population.

The set of local populations of a metapopulation has, at any given time, a mean population size (or density) and a variance of population size (or density). Several ecologists observed that, in many situations, given a set of observations of sizes of local populations at different times, the variance (over the spatial locations) of the size of the local populations is approximately a power-law function of their mean size (over the spatial locations) at each given time (Taylor, 2019). This power-law variance function became known as a spatial Taylor's Law (TL) in ecology, named after the last ecologist who discovered it. A temporal Taylor's Law (TL) in ecology (which we do not consider further here) computes, separately for each local population, the mean and variance of population size over time and asserts that the pairs of mean and variance, one for each population, approximate a power law. The power-law dependence of the variance (or standard deviation) on the mean has also been observed in the physical sciences (where it is commonly called fluctuation scaling), demography, finance, computer engineering, and other fields (Eisler et al., 2008).

Here we give sufficient conditions for our model of exponentially changing local populations with internal migration to satisfy a spatial TL asymptotically, that is, with an increasingly close approximation to a power law, after a long time, for a fixed number n of local populations. We give sufficient conditions for the variance to be proportional asymptotically to the square of the mean. Equivalently, the coefficient of variation (defined as the standard deviation divided by the mean) is asymptotically constant. These conditions relate to the eigenvalues and eigenvectors of the model parameters (see Sections 3 and 4). Further, we show that almost all (in a sense we specify precisely) models of exponentially changing local populations with internal migration obey TL asymptotically with an asymptotically constant coefficient of variation (see Section 5).

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2. A model of local populations with exponential growth and internal migration

To describe the model of $n \geq 2$ local populations in detail, we let $N_i(t)$ be the population density of population $i = 1, \dots, n$ at time $t \geq 0$ where $N_i(0) > 0$, i.e. each population is assumed to be initially positive, and we let $\mathbf{N}(0) := [N_1(0)\ N_2(0)\ \dots\ N_n(0)]^T > \mathbf{0}$ be the vector of population densities at time $t = 0$. We define the matrices

$$R := \text{diag}[r_1, \dots, r_n] \in \mathbb{R}^{n\times n}, \quad -\infty < r_i < \infty, \ i = 1, \dots, n, \tag{1}$$

and $M = [m_{ij}] \in \mathbb{R}^{n\times n}$,

$$M := \begin{bmatrix} -\sum_{j\neq 1} m_{j1} & m_{12} & \dots & m_{1n} \\ m_{21} & -\sum_{j\neq 2} m_{j2} & \dots & m_{2n} \\ \vdots & & & \vdots \\ m_{n1} & m_{n2} & \dots & -\sum_{j\neq n} m_{jn} \end{bmatrix} \text{ with } m_{ij} \geq 0 \text{ if } i \neq j. \tag{2}$$

We refer to R in (1) and M in (2) as the *rate* matrix and *migration* matrix, respectively, and to their sum $A := R + M$ as the *coefficient* matrix. The rate r_i of R gives the instantaneous rate of change (growth or decline) of population i. For $i \neq j$, the entry m_{ij} of M describes the instantaneous rate at which individuals from population j migrate to population i, which is linear in the size of population j and independent of the size of population i. All of these rates (of change and migration) are *per individual of the source population*. We suppose the population densities satisfy the equation

$$\frac{d\mathbf{N}(t)}{dt} := A\mathbf{N}(t). \tag{3}$$

Then the population densities obey

$$\mathbf{N}(t) = e^{At}\mathbf{N}(0). \tag{4}$$

We refer to a set of populations $\mathbf{N}(t)$ that evolve according to Eq. (3) as the *exponential metapopulation model with internal migration*, or the EM model, with coefficient matrix A, and initial population densities $\mathbf{N}(0)$. The matrix M, which gives the migration rates in this model, can be represented by a weighted graph $G = G(M)$ (for example, Fig. 1(left)). This *graph of migrations* $G := (V, E, \omega)$ has *vertices* $V := \{1, \dots, n\}$ representing the model's populations and *edges* E where the edge e_{ij} from vertex j to vertex i is in E if the weight $\omega(e_{ij}) = m_{ij} \neq 0$, i.e. if there is migration from population j to population i (see Fig. 1).

Example 1. Consider the EM model with the graph of migrations given by the graph $G := (V, E, \omega)$ in Fig. 1(left) where $V := \{1, 2, \dots, 30\}$ consists of thirty distinct populations. We let each edge have unit weight so that the migration matrix $M = [m_{ij}]$ is given by

$$m_{ij} := \begin{cases} 1 & \text{if } e_{ij} = e_{ji} \in E, \\ 0 & \text{otherwise.} \end{cases}$$

We let the rate matrix $R = \text{diag}[r_1, \dots, r_n]$ be generated by choosing each rate uniformly from the interval $r_i \in [-20, 0]$ for $i = 1, 2, \dots, 30$. Choosing each initial population in the interval $N_i(0) \in (0, 10]$ results in the population dynamics shown in Fig. 1(center) for $\mathbf{N}(t)$.

An $n\times n$ real matrix with nonnegative off-diagonal elements is said to be *essentially nonnegative* (or equivalently, a Metzler matrix Mitkowski, 2008). Any real matrix $A = [a_{ij}] \in \mathbb{R}^{n\times n}$ can be decomposed into the sum of a rate matrix R and a migration matrix M if and only if A is essentially nonnegative: $a_{ij} \geq 0$ for all $i \neq j$. This decomposition is unique with

$$M = \begin{bmatrix} -\sum_{j\neq 1} a_{j1} & a_{12} & \dots & a_{1n} \\ a_{21} & -\sum_{j\neq 2} a_{j2} & \dots & a_{2n} \\ \vdots & & & \vdots \\ a_{n1} & a_{n2} & \dots & -\sum_{j\neq n} a_{jn} \end{bmatrix}$$

and $R = \text{diag}[\sum_{i=1}^n a_{i1}, \dots, \sum_{i=1}^n a_{in}]$. Instead of considering sums of rate and migration matrices, we can equivalently consider essentially nonnegative coefficient matrices $A \in \mathbb{R}^{n\times n}$. We denote the set of essentially nonnegative coefficient matrices by $\mathbb{A}$. An EM model can be described as a pair $(A, \mathbf{N}(0))$ for a coefficient matrix $A \in \mathbb{A}$ and an initial population vector $\mathbf{N}(0)$. Each EM model evolves according to (3) and (4). We have $e^{At} \geq 0$ for all $t \geq 0$ if and only if A is an essentially nonnegative matrix (Kaczorek, 1997). Hence, for $\mathbf{N}(0) > 0$, the metapopulation $\mathbf{N}(t) \geq 0$ for all $t \geq 0$, although this may not be true for $t < 0$ (cf. Fig. 1).

3. Taylor's law

An asymptotic spatial Taylor's Law states that the variance of population densities in a collection of local populations is asymptotic to a power function of the average (or mean) of population densities in the limit of large time. A natural way to define the mean and the variance for the EM model is to give population i the weight $w_i = 1/n$ so that each population has the same weight regardless of its density. With such weights, the *average population density* at time t is given by

$$\mathbb{E}(\mathbf{N}(t)) := \frac{1}{n}\sum_{i=1}^{n} N_i(t) = \frac{1}{n}\sum_{i=1}^{n}[e^{At}\mathbf{N}(0)]_i. \tag{5}$$

Using the same weights, the *variance* of the population density at time t is defined to be

$$\mathbb{V}(\mathbf{N}(t)) := \mathbb{E}\big(\mathbf{N}(t) - \mathbb{E}(\mathbf{N}(t))\big)^2 = \frac{1}{n}\sum_{i=1}^{n}[e^{At}\mathbf{N}(0)]_i^2 - \left(\frac{1}{n}\sum_{i=1}^{n}[e^{At}\mathbf{N}(0)]_i\right)^2. \tag{6}$$

Taylor's Law is said to hold asymptotically for the EM model $(A, \mathbf{N}(0))$ if there exist real constants $a > 0$ and b such that

$$\lim_{t\to\infty}\big(\log \mathbb{V}(\mathbf{N}(t)) - b \log \mathbb{E}(\mathbf{N}(t))\big) = \log a. \tag{7}$$

In this paper, we investigate the class of EM models $(A, \mathbf{N}(0))$ for which TL equation (7) holds.

3.1. Visualizing dynamics

To visualize the dynamics of an EM model, define a finite-time approximation $b(t)$ to b, following Cohen (2013):

$$b(t) := \frac{\frac{d\mathbb{V}(\mathbf{N}(t))}{dt}\mathbb{E}(\mathbf{N}(t))}{\frac{d\mathbb{E}(\mathbf{N}(t))}{dt}\mathbb{V}(\mathbf{N}(t))} = \frac{d\log[\mathbb{V}(\mathbf{N}(t))]}{d\log[\mathbb{E}(\mathbf{N}(t))]}, \tag{8}$$

which is well defined when $\mathbb{V}(\mathbf{N}(t)) \neq 0$, $\mathbb{E}(\mathbf{N}(t)) \neq 0$, and $d\mathbb{E}(\mathbf{N}(t))/dt \neq 0$. Using Eqs. (5) and (6) in Eq. (8) gives

$$b(t) = \frac{d\log[\frac{1}{n^2}\sum_{i<j}(N_i(t) - N_j(t))^2]}{d\log[\frac{1}{n}\sum_{i=1}^{n} N_i(t)]} \tag{9}$$

$$= 2\frac{\big(\sum_{i<j}(N_i(t) - N_j(t))(N_i'(t) - N_j'(t))\big)\big(\sum_{i=1}^{n} N_i(t)\big)}{(\sum_{i<j}(N_i(t) - N_j(t))^2)(\sum_{i=1}^{n} N_i'(t))}. \tag{10}$$

For instance, using the EM model with coefficient matrix $A = R+M$ and the initial population $\mathbf{N}(0)$ from Example 1, Fig. 1(right) suggests that $\lim_{t\to\infty} b(t) = 2$. We confirm that suggestion mathematically to show that TL equation (7) holds asymptotically with $b = 2$ for this EM.

A helpful referee, Lee Altenberg, gave an example of functions $\mathbb{V}(\mathbf{N}(t))$ and $\mathbb{E}(\mathbf{N}(t))$ for which $\lim_{t\to\infty} b(t) = 2$ but Taylor's law cannot be satisfied. These functions were not derived from any EM model but were created to show that, in general, $\lim_{t\to\infty} b(t) = 2$ does not imply Taylor's Law equation (7). Hence we prove Taylor's Law directly from Eq. (7) and use $b(t)$ for illustration only.

Altenberg's example deserves to be stated. Let $\mathbb{V}(\mathbf{N}(t)) := V(t) = \exp(2t^2)v_0$, $v_0 > 0$ and $\mathbb{E}(\mathbf{N}(t)) := E(t) = \exp[t(t+1)]m_0$, $m_0 > 0$. Then $\log V(t) = 2t^2 + \log v_0$, $\log E(t) = t(t+1) + \log m_0$, and $d\log V(t)/dt = 4t$, $d\log E(t)/dt = 2t + 1$. Hence $b(t) := d\log V(t)/d\log E(t) = 4t/(2t+1)$. So $\lim_{t\to\infty} b(t) = 2$. However, $\log V(t) - 2\log E(t) = 2t^2 + \log v_0 - 2(t(t +$

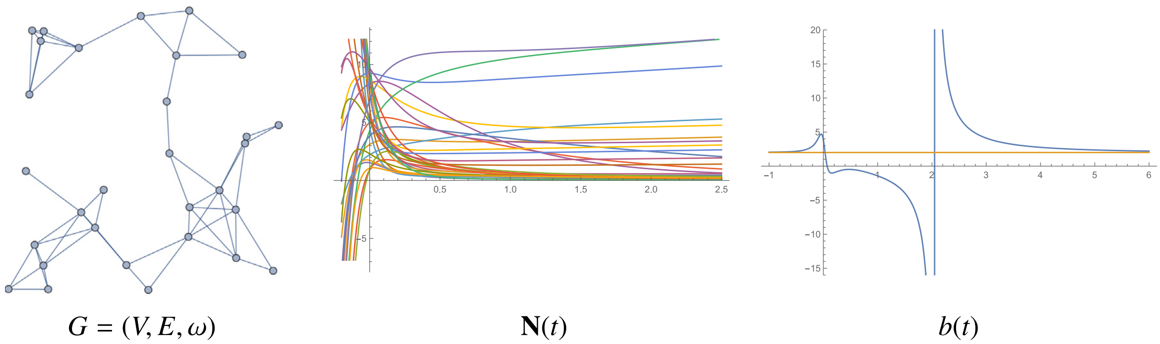


Fig. 1. Left: The graph of interactions $G := (V, E, \omega)$ of the EM model in Example 1. Here $V := \{1, 2, \ldots, 30\}$ and each undirected edge $e_{ij} \in E$ is given unit weight $\omega(e_{ij}) := 1$. Center: The population dynamics of $\mathbf{N}(t)$ when each initial population $N_i(0)$ is chosen uniformly in $(0, 10]$. Right: The finite-time approximation $b(t)$ of b converges to 2. For this EM model, TL holds asymptotically with asymptotic exponent $b = 2$.

$1) + \log m_0) = \log v_0 - 2 \log m_0 - 2t$, which is not constant in t and does not converge to a constant. So Taylor's Law does not hold in this construction.

3.2. Spectral analysis of asymptotic convergence to Taylor's law

Cohen (2013) showed that TL holds asymptotically if there is no migration, i.e. $M = 0$, and $r_1 > r_2 > \cdots > r_n$ for arbitrary population weights w_i. Here we take a spectral approach to prove an asymptotic spatial TL for a much broader class of systems described by EM models with uniform population weights $w_i = 1/n$. Instead of writing the solution of Eq. (3) as a matrix exponential, as in Eq. (4), we write the solution as a linear combination of the eigenvectors or generalized eigenvectors of the coefficient matrix A. Following the standard linear algebraic solution to systems of ordinary linear differential equations, we let

$$\sigma(A) := \{\lambda_j = \alpha_j + i\beta_j \in \mathbb{C} : j = 1, \ldots, n\}$$

be the eigenvalues of $A = [a_{ij}]$. For the eigenvalue $\lambda \in \sigma(A)$, the time-dependent vector

$$\mathbf{X}(t) := e^{\lambda t} \left(\frac{t^{k-1}}{(k-1)!}\mathbf{x}_k + \cdots + \frac{t}{1!}\mathbf{x}_2 + \mathbf{x}_1 \right) \tag{11}$$

corresponding to a Jordan block $J(\lambda) \in \mathbb{C}^{k \times k}$ of A is a solution to Eq. (3). Here the vectors $\{\mathbf{x}_j\}_{j=1}^k$ are linearly independent where $\mathbf{x}_k$ is an eigenvector and the others are generalized eigenvectors of A.

Complex eigenvalues occur in conjugate pairs: if $\lambda_+ = \alpha + i\beta$ where $\beta \neq 0$, then its conjugate $\lambda_- = \alpha - i\beta$ is also an eigenvalue of A. In this case, the eigenvectors $\mathbf{x}_j := \mathbf{u}_j + i\mathbf{w}_j$ in Eq. (11) for $j = 1, \ldots, k$ are also complex. Taking their real and imaginary parts, we have the two real solutions

$$\begin{aligned}\mathbf{X}_+(t) :=& e^{\alpha t} \left[\sin(\beta t) \left(\frac{t^{k-1}}{(k-1)!}\mathbf{u}_k + \cdots + \frac{t}{1!}\mathbf{u}_2 + \mathbf{u}_1 \right) \right. \\ &\left. + \cos(\beta t) \left(\frac{t^{k-1}}{(k-1)!}\mathbf{w}_k + \cdots + \frac{t}{1!}\mathbf{w}_2 + \mathbf{w}_1 \right) \right], \end{aligned} \tag{12}$$

$$\begin{aligned}\mathbf{X}_-(t) :=& e^{\alpha t} \left[\cos(\beta t) \left(\frac{t^{k-1}}{(k-1)!}\mathbf{u}_k + \cdots + \frac{t}{1!}\mathbf{u}_2 + \mathbf{u}_1 \right) \right. \\ &\left. - \sin(\beta t) \left(\frac{t^{k-1}}{(k-1)!}\mathbf{w}_k + \cdots + \frac{t}{1!}\mathbf{w}_2 + \mathbf{w}_1 \right) \right] \end{aligned} \tag{13}$$

to Eq. (3) corresponding to the conjugate eigenvalues $\lambda_\pm$. Using Eqs. (11)–(13), the collective set of solutions corresponding to each Jordan block gives a fundamental set of real solutions to Eq. (3), which we write as $\mathbf{X}(t) := \{\mathbf{X}_1(t), \ldots, \mathbf{X}_n(t)\}$. Thus, any solution to Eq. (3) can be written as

$$\mathbf{N}(t) = c_1\mathbf{X}_1(t) + \cdots + c_n\mathbf{X}_n(t)$$

where the constants $c_1, \ldots, c_n$ can be determined using the initial populations $\mathbf{N}(0)$ (cf. Proposition 2.22 in Chicone, 2008).

To determine whether TL holds asymptotically for an EM model, we use the notion of a leading eigenvalue and leading eigenvector. These are often referred to as the *Perron root* and *Perron vector*, respectively, for nonnegative irreducible matrices.

Definition 3.1 (*Leading Eigenvalues and Eigenvectors*)**.** A coefficient matrix $A = [a_{ij}]$ with eigenvalues $\sigma(A) = \{\alpha_j + i\beta_j\}_{j=1}^n$ has a *leading eigenvalue* $\lambda_1 = \alpha_1 + i\beta_1$ if λ_1 is real, i.e., $\beta_1 = 0$, and $\lambda_1 > \alpha_j$ for $j = 2, \ldots, n$. In this case, λ_1 is simple and the corresponding eigenspace is spanned by a single nonzero vector $\mathbf{x}_1$. We call $\mathbf{x}_1$ the *leading eigenvector* of A if all of its components are nonnegative.

Assuming the coefficient matrix A has a leading eigenvalue λ_1 with leading eigenvector $\mathbf{x}_1$, then the solution to Eq. (4) can be written as

$$\mathbf{N}(t) = c_1 e^{\lambda_1 t}\mathbf{x}_1 + \sum_{j=2}^{n} c_j t^{p_j} e^{\alpha_j t} f_j(\beta_j t)\mathbf{x}_j, \tag{14}$$

where each p_j is a nonnegative integer, each $\mathbf{x}_j \in \mathbb{R}^n$ is a nonzero vector, and the function f_j is either $f_j(t) = 1$, $f_j(t) = \cos(t)$, or $f_j(t) = \sin(t)$ using the principle of superposition. In Eq. (14), the initial term $c_1 e^{\lambda_1 t}\mathbf{x}_1$ has the *leading coefficient* c_1 and contains the leading eigenvalue λ_1 and leading eigenvector $\mathbf{x}_1$. The leading coefficient c_1 must be real because the leading eigenvalue, leading eigenvector, and solution Eq. (14) are all real.

Not every coefficient matrix has a leading eigenvalue and leading eigenvector. But if A has a leading eigenvalue λ_1, then it has a leading eigenvector $\mathbf{x}_1$.

Lemma 3.2 (*Leading Eigenvalues and Vectors for Coefficient Matrices*)**.** *If a coefficient matrix $A = [a_{ij}]$ has a leading eigenvalue λ_1, then it has a leading eigenvector $\mathbf{x}_1$.*

Proof. Suppose $A = [a_{ij}]$ is a coefficient matrix. Let $m := \min_{1 \le i \le n} a_{ii}$ and $A := B + \mathrm{diag}[m, \ldots, m] = B + mI$. Define the *spectral radius* $\rho(B)$ of a matrix $B \in \mathbb{R}^{n \times n}$ as

$$\rho(B) := \max\{|\lambda| : \lambda \in \sigma(B)\}.$$

Then B is a nonnegative matrix with spectral radius $\rho(B) \in \sigma(B)$, and there is a nonnegative nonzero vector $\mathbf{x}_1$ such that $B\mathbf{x}_1 = \rho(B)\mathbf{x}_1$ (see Theorem 8.3.1 in Horn and Johnson, 1990). We claim that

$$\sigma(A) = \{\lambda + m : \lambda \in \sigma(B)\}, \tag{15}$$

meaning that the spectrum $\sigma(A)$ is a translation of the spectrum $\sigma(B)$ by m. To see this, note that if $\lambda \in \sigma(B)$ then there is a nonzero vector $\mathbf{v} \in \mathbb{R}^n$ such that $B\mathbf{v} = \lambda\mathbf{v}$. Hence,

$$A\mathbf{v} = (B + mI)\mathbf{v} = \lambda\mathbf{v} + m\mathbf{v} = (\lambda + m)\mathbf{v} \tag{16}$$

implying $\lambda + m \in \sigma(A)$, which verifies Eq. (15).

Since A has a leading eigenvalue λ_1, $\lambda_1 = \rho(B) + m$ as $\rho(B)$ is the eigenvalue of B with largest real part. Using Eq. (16) it also follows that $A\mathbf{x}_1 = (\rho(B) + m)\mathbf{x}_1$ so that $\mathbf{x}_1$ is an eigenvector associated with $\lambda_1 = \rho(B) + m$. Then $\lambda_1 \neq \lambda_j$ for $j \neq 1$ since its real part is strictly larger than all other eigenvalues and is therefore simple. Thus $\mathbf{x}_1$ is a leading eigenvector of A as its entries are nonnegative. □

The following theorem gives our most general account of when TL holds for a given EM model. We say a vector $\mathbf{x} \in \mathbb{R}^n$ is *constant* if all its elements are equal, i.e., if it is a scalar multiple of the vector $\mathbf{1} := [1 \ \dots \ 1]^T$ with all components equal to 1.

Theorem 3.3 (*Taylor's Law for the EM Model*). *Let $A = [a_{ij}]$ be a coefficient matrix for the EM model with initial population $\mathbf{N}(0)$. If*

(a) the real leading coefficient $c_1 \neq 0$;

(b) the matrix A has a leading eigenvalue λ_1; and

(c) the leading eigenvector $\mathbf{x}_1$ is not constant, then the EM model satisfies Taylor's Law asymptotically with $b = 2$.

Proof. Suppose the EM model $(A, \mathbf{N}(0))$ with coefficient matrix $A = [a_{ij}]$ has leading eigenvalue λ_1 and leading eigenvector $\mathbf{x}_1$ and conditions (a)–(c) hold. Then the solution to the differential equation $d\mathbf{N}(t)/dt = A\mathbf{N}(t)$ in Eq. (14) can be written as the function $\mathbf{N}(t) = e^{\lambda_1 t}(c_1\mathbf{x}_1 + \mathbf{F}(t))$ where

$$\mathbf{F}(t) := \sum_{j=2}^{n} c_j t^{p_j} e^{(\alpha_j - \lambda_1)t} f_j(\beta_j t)\mathbf{x}_j. \tag{17}$$

As $\lambda_1 - \alpha_j > 0$ for all $j = 2, \dots, n$, we have

$$\lim_{t\to\infty} \mathbf{F}(t) = \lim_{t\to\infty} \sum_{j=2}^{n} \frac{c_j t^{p_j} f_j(\beta_j t)}{e^{(\lambda_1 - \alpha_j)t}} \mathbf{x}_j = \mathbf{0}, \tag{18}$$

because the polynomial and trigonometric terms in the numerator are dominated by the exponential growth of the denominator in each term.

Using Eq. (14), the ith component of $\mathbf{N}(t)$ can be written as $N_i(t) = e^{\lambda_1 t}(c_1 x_{1i} + F_i(t))$ where x_{ji} is the ith component of the vector $\mathbf{x}_j$. This, together with Eqs. (5) and (6), yields

$$\mathbb{E}(\mathbf{N}(t)) := \frac{1}{n}\sum_{i=1}^{n} N_i(t) = \frac{e^{\lambda_1 t}}{n}\sum_{i=1}^{n}(c_1 x_{1i} + F_i(t))$$

and

$$\mathbb{V}(\mathbf{N}(t)) := \frac{1}{n^2}\sum_{i<j}(N_i(t) - N_j(t))^2 = \frac{e^{2\lambda_1 t}}{n^2}\sum_{i<j}((c_1 x_{1i} + F_i(t)) - (c_1 x_{1j} + F_j(t)))^2.$$

Substituting $\mathbb{E}(\mathbf{N}(t))$ and $\mathbb{V}(\mathbf{N}(t))$ into Eq. (7), it follows that TL holds asymptotically if $\lim_{t\to\infty} W_b(t) = 0$, where

$$\begin{aligned} W_b(t) &:= \log\left[\frac{e^{2\lambda_1 t}}{n^2}\sum_{i<j}((c_1 x_{1i} + F_i(t)) - (c_1 x_{1j} + F_j(t)))^2\right] \\ &\quad - b\log\left[\frac{e^{\lambda_1 t}}{n}\sum_{i=1}^{n}(c_1 x_{1i} + F_i(t))\right] - \log a \\ &= (2-b)(\lambda_1 t - \log n) + \log\left[\sum_{i<j}((c_1 x_{1i} + F_i(t)) - (c_1 x_{1j} + F_j(t)))^2\right] \\ &\quad - b\log\left[\sum_{i=1}^{n}(c_1 x_{1i} + F_i(t))\right] - \log a. \end{aligned}$$

By (18), $\lim_{t\to\infty} F_i(t) = 0$ for all $i = 1, \dots, n$. For $b = 2$, as $c_1 \neq 0$ by condition (a), we have, in the limit,

$$\begin{aligned} \lim_{t\to\infty} W_2(t) &= \log\left[\sum_{i<j}((c_1 x_{1i}) - (c_1 x_{1j}))^2\right] - 2\log\left[\sum_{i=1}^{n}(c_1 x_{1i})\right] - \log a \\ &= \log\left[c_1^2\sum_{i<j}(x_{1i} - x_{1j})^2\right] - 2\log\left[c_1\sum_{i=1}^{n} x_{1i}\right] - \log a \\ &= \log\left[\frac{\sum_{i<j}(x_{1i} - x_{1j})^2}{\left(\sum_{i=1}^{n} x_{1i}\right)^2}\right] - \log a. \end{aligned}$$

We let

$$a := \left(\sum_{i<j}(x_{1i} - x_{1j})^2\right) \Big/ \left(\sum_{i=1}^{n} x_{1i}\right)^2. \tag{19}$$

Then $a > 0$ since, by assumption Theorem 3.3(c), the leading eigenvector $\mathbf{x}_1$ is not constant, so $\sum_{i<j}(x_{1i} - x_{1j})^2 \neq 0$. Also, as $\mathbf{x}_1$ is an eigenvector, it follows that $\mathbf{x}_1 \neq \mathbf{0}$, and as a leading eigenvector its entries all have the same sign and may, without loss of generality, be made nonnegative. Hence, $a > 0$ is well defined and

$$\lim_{t\to\infty} W_2(t) = \log\left[\frac{\sum_{i<j}(x_{1i} - x_{1j})^2}{\left(\sum_{i=1}^{n} x_{1i}\right)^2}\right] - \log\left[\frac{\sum_{i<j}(x_{1i} - x_{1j})^2}{\left(\sum_{i=1}^{n} x_{1i}\right)^2}\right] = 0.$$

Thus TL holds asymptotically with $b = 2$. □

In the EM model in Example 1, the coefficient matrix A has a nonzero leading eigenvalue $\lambda_1 \approx 0.0735651$ with a non-constant leading eigenvector $\mathbf{x}_1 \neq \mathbf{1}$. For the initial condition $\mathbf{N}(0)$ shown in Fig. 1(center), $c_1 \neq 0$. Hence, TL holds asymptotically for this model with $b = 2$, as suggested by Fig. 1(right).

If the leading eigenvalue $\lambda_1 = 0$ but the other assumptions of Theorem 3.3 are satisfied, as in Example 2, then TL may hold for a range of values of b. This range always includes $b = 2$, by Theorem 3.3, and each value of b has its corresponding value of a.

Example 2 (*Zero Leading Eigenvalue*). Consider the EM model $(A, \mathbf{N}(0))$ with coefficient matrix given by

$$A := \begin{bmatrix} -2 & 3 & 1 \\ 1 & -5 & 4 \\ 1 & 2 & -5 \end{bmatrix}.$$

This matrix has the leading eigenvalue $\lambda_1 = 0$ and non-constant leading eigenvector $\mathbf{x}_1 = [17\ 9\ 7]^T$. For the arbitrary initial condition $\mathbf{N}(0) = [N_1(0),\ N_2(0),\ N_3(0)]^T > 0$, the leading coefficient is

$$c_1 = (N_1(0) + N_2(0) + N_3(0))/33 \neq 0,$$

which can be found by solving for c_1 in the linear system of equations $c_1\mathbf{x}_1 + c_2\mathbf{x}_2 + c_3\mathbf{x}_3 = \mathbf{N}(0)$ where $\mathbf{x}_2, \mathbf{x}_3$ are the other eigenvectors of A (cf. Eq. (14)). By Theorem 3.3, TL holds asymptotically for this EM model with $a = 56/363$, $b = 2$, and any nonzero initial population $\mathbf{N}(0)$. That $a = 56/363$ follows from Eq. (19) in the proof of Theorem 3.3 and that $\mathbf{x}_1 = [17\ 9\ 7]^T$. As $\lambda_1 = 0$, a slight modification of the proof of Theorem 3.3 shows that TL holds asymptotically for any $b \in \mathbb{R}$ with

$$a = n^{2-b}\frac{\sum_{i<j}(x_{1i} - x_{1j})^2}{(\sum_{i=1}^{n} x_{1i})^2} = n^{2-b}\frac{56}{363}.$$

However, the expectation

$$\mathbb{E}(\mathbf{N}(t)) = (N_1(0) + N_2(0) + N_3(0))/3$$

is constant so that $d\mathbb{E}(\mathbf{N}(t))/dt = 0$ for all t. This results in a division by zero in Eq. (8). Consequently, $b(t)$ does not exist at any time t. That is, it is not always the case that we can write $b = \lim_{t\to\infty} b(t)$ for some finite constant b for which TL holds asymptotically.

If an EM model has an essentially nonnegative matrix with leading eigenvalue $\lambda_1 = 0$, then Eq. (14) can be used to show that $\lim_{t\to\infty}\mathbf{N}(t) = c_1\mathbf{x}_1$. In this case $\lim_{t\to\infty} d\mathbb{E}(\mathbf{N}(t))/dt = 0$, which suggests why $\lim_{t\to\infty} b(t)$ may not exist even if the constant $b \in \mathbb{R}$ does (see Eq. (8)). If Part (c) of Theorem 3.3 does not hold, then the situation is more complicated. This is discussed in more detail in the following section.

Part (a) of Theorem 3.3 requires that the leading coefficient c_1 be nonzero and it is currently an open question as to whether or not there is an EM model for which $c_1 = 0$. In the present state of our understanding, to guarantee that $c_1 \neq 0$ requires additional assumptions. The additional assumption in Corollary 1 of Theorem 3.3 is that the coefficient matrix A is a normal matrix. A matrix $A = [a_{ij}] \in$

$\mathbb{R}^{n\times n}$ is *normal* if it commutes with its transpose, that is, if $AA^T = A^TA$. If the coefficient matrix in an EM model is normal, then $c_1 \neq 0$.

Corollary 1 (*Normal Matrices and Taylor's Law*). *Let $A = [a_{ij}]$ be a normal coefficient matrix for the EM model with initial population $\mathbf{N}(0)$. If*

(a) the matrix A has a leading eigenvalue λ_1; and

(b) the leading eigenvector $\mathbf{x}_1$ is not constant; then the EM model satisfies Taylor's Law asymptotically with $b = 2$.

Proof. If $A \in \mathbb{R}^{n\times n}$ is normal, then it has an orthogonal eigenbasis $\mathbf{x}_1, \dots, \mathbf{x}_n$ and the solution to Eq. (3) is

$$\mathbf{N}(t) = c_1 e^{\lambda_1 t}\mathbf{x}_1 + \cdots + c_n e^{\lambda_n t}\mathbf{x}_n,$$

where $\mathbf{x}_j$ is an eigenvector associated with the eigenvalue $\lambda_j \in \mathbb{C}$ of A (see Eq. (11)). Hence the initial population vector is $\mathbf{N}(0) = c_1\mathbf{x}_1 + \cdots + c_n\mathbf{x}_n$. Since A is assumed to have a leading eigenvalue λ_1, Lemma 3.2 implies that A has the leading eigenvector $\mathbf{x}_1$. Because $\mathbf{N}(0)$ is assumed to be strictly positive, $\mathbf{x}_1$ is nonnegative. Because the vectors $\mathbf{x}_1, \dots, \mathbf{x}_n$ are an orthogonal eigenbasis, we have $0 < \mathbf{x}_1^T\mathbf{N}(0) = c_1\|\mathbf{x}_1\|_2^2$. Given that $\mathbf{x}_1$ is a nonzero eigenvector, c_1 must also be real and nonzero and it follows from Theorem 3.3 that TL holds asymptotically with $b = 2$ in the associated EM model. □

Example 3 (*Exponential Model*). In the original exponential model (Cohen, 2013), the coefficient matrix is the diagonal rate matrix $A = \text{diag}[r_1, \dots, r_n] \in \mathbb{R}^{n\times n}$ without internal migration, and it is assumed that $r_1 > r_2 > \cdots > r_n$. In this case, the matrix A is normal with leading eigenvalue $\lambda_1 = r_1$ with non-constant leading eigenvector $\mathbf{x}_1 = [1\ 0\ \dots\ 0]^T$. The main result in Cohen (2013), that TL holds for the exponential model with $\lim_{t\to\infty} b(t) = 2$, is therefore a special case of Corollary 1 if the population weights are $w_i = 1/n$.

In Section 5, we show that the conditions of Theorem 3.3, which insure that TL holds asymptotically with $b = 2$, specify an open dense subset of EM models, i.e., are satisfied for nearly every EM model we consider.

In an EM model, the *total population* $P(t) = \sum_{i=1}^n N_i(t)$ may grow or decrease over time through migration. However, if the migration matrix M has columns that sum to zero, as in Example 2, then

$$P'(t) = \sum_{i=1}^n N_i'(t) = \sum_{i=1}^n r_i N_i(t)$$

and the total population does not increase or decrease due to migration as $P'(t)$ depends only on the rate matrix $R = \text{diag}[r_1, \dots, r_n]$. A special case of this is discussed in Altenberg (2010) where $M = P - I$ for a column-stochastic matrix P. The EM models that have migration matrices with zero column sums are special cases of the models considered in Theorem 3.3 and, as such, satisfy Taylor's Law with $b = 2$ if (a)–(c) hold.

4. Perron Frobenius and Taylor's law

In the previous section, our primary assumption regarding the coefficient matrix $A := R + M$ was only that it was essentially nonnegative, with no restrictions on the structure of migrations in M. In this section, we assume also that A and M are irreducible. By definition, the migration matrix M is *irreducible* if and only if it is possible to migrate from any population to any other population directly or via some sequence of intermediate populations. Equivalently, the associated graph of migrations is *strongly connected*: there is a path from any vertex to any other vertex in the graph.

Irreducibility of the coefficient matrix affects the spectrum, as shown by the Perron Frobenius theorem. Although the Perron Frobenius theorem contains more results than parts (a)–(b) below, we use only the results stated here to prove the next theorem, which extends Theorem 3.3 to irreducible coefficient matrices.

Theorem 4.1 (*Perron Frobenius Theorem, in Part*). *Let $B \in \mathbb{R}^{n\times n}$ be a nonnegative irreducible matrix. Then*

(a) the spectral radius $\rho(B)$ is a simple eigenvalue of B; and

(b) any eigenvector $\mathbf{x}_1$ corresponding to the eigenvalue $\rho(B)$ has all strictly positive elements, i.e. $\mathbf{x}_1 > 0$.

The eigenvalue $\rho(B)$ of a nonnegative irreducible matrix B is sometimes called its *Perron root* and the corresponding eigenvector its *Perron vector*.

Theorem 4.2 (*Irreducible Matrices and Taylor's Law*). *Let $A := [a_{ij}]$ be an irreducible essentially nonnegative coefficient matrix for the EM model with initial population $\mathbf{N}(0)$. Then A has a positive leading eigenvalue λ_1 and positive leading eigenvector $\mathbf{x}_1$. Additionally, if*

(a) the real leading coefficient $c_1 \neq 0$; and

(b) the leading eigenvector $\mathbf{x}_1$ is not constant,
then the EM model satisfies Taylor's Law asymptotically with $b = 2$.

Proof. Suppose A is an irreducible essentially nonnegative coefficient matrix and let $m := \min_{1\le i\le n} a_{ii}$. Then the matrix

$$B := A - \text{diag}[m, \dots, m] = A - mI$$

is nonnegative and irreducible. Also, as $A = B + mI$, then $\sigma(A) = \{\lambda + m : \lambda \in \sigma(B)\}$ and $A\mathbf{x} = (\lambda + m)\mathbf{x}$ if $B\mathbf{x} = \lambda\mathbf{x}$ (see Eq. (16)).

By the Perron Frobenius theorem, there exists a simple eigenvalue $\lambda_1 = \rho(B) + m \in \sigma(A)$. If $\lambda_* \in \sigma(B)$ is not λ_1, then $\lambda_* = pe^{i\theta}$ where $p \le \rho(B)$ and $\theta \in [0, 2\pi)$. In particular, if $p = \rho(B)$, then $\theta \in (0, 2\pi)$ since $\lambda_* \neq \lambda_1$. The real part of $\lambda_* + m$ is then

$$Re(\lambda_* + m) = Re(pe^{i\theta} + m) = p\cos(\theta) + m < \rho(B) + m = \lambda_1,$$

so λ_1 is a leading eigenvalue of A.

If $\mathbf{x}_1$ is any eigenvector associated with the spectral radius $\rho(B)$, then $\mathbf{x}_1 > 0$ and by the Perron Frobenius theorem, $B\mathbf{x}_1 = \rho(B)\mathbf{x}_1$. From Eq. (16) it follows that

$$A\mathbf{x}_1 = (\rho(B) + m)\mathbf{x}_1 = \lambda_1\mathbf{x}_1,$$

so $\mathbf{x}_1$ is a leading eigenvector of A as it has positive and therefore nonnegative components.

Since A has leading eigenvalue λ_1 and leading eigenvector $\mathbf{x}_1$, if $c_1 \neq 0$ and $\mathbf{x}_1$ is not constant, we have by Theorem 3.3 that TL holds asymptotically with $b = 2$. □

The difference between Theorems 4.2 and 3.3 is that an EM model with an irreducible coefficient matrix A is guaranteed to have a leading eigenvector and leading eigenvector, but not if A is reducible. For instance, in Example 1 the coefficient matrix A is irreducible as the associated graph of migrations G is strongly connected. Hence A has both a leading eigenvalue and leading eigenvector.

To describe when TL holds asymptotically for an EM model with $b \neq 2$, we define the notion of a second leading eigenvalue.

Definition 4.3 (*Second Leading Eigenvalue*). A coefficient matrix $A := [a_{ij}]$ with eigenvalues $\sigma(A) := \{\alpha_j + i\beta_j\}_{j=1}^n$ and leading eigenvalue $\lambda_1 = \alpha_1$ has a *second leading eigenvalue* $\lambda_2 := \alpha_2 + i\beta_2$ if λ_2 is real, i.e. $\beta_2 = 0$, and $\lambda_2 > \alpha_j$ for all $j = 3, \dots, n$.

Alternatively, a coefficient matrix A has a second leading eigenvector if it has a strictly positive *spectral gap* $\lambda_1 - \lambda_2 > 0$, where $\lambda_1, \lambda_2 \in \mathbb{R}$. If A has a constant leading eigenvector, then TL may still hold but we may get a constant $b \neq 2$, different from $b = 2$ in Theorem 3.3 and Corollary 1.

Proposition 1 (*Constant Eigenvectors and Taylor's Law*). *Let* $A := [a_{ij}]$ *be an irreducible coefficient matrix for the EM model with initial population* $\mathbf{N}(0)$. *If* A *has a second leading eigenvalue* λ_2 *where*

(a) the coefficients $c_1, c_2 \neq 0$;

(b) the leading eigenvalue $\lambda_1 \neq 0$; *and*

(c) the leading eigenvector $\mathbf{x}_1$ *is constant,*
then the EM model satisfies Taylor's Law asymptotically with $b = 2\lambda_2/\lambda_1 \neq 2$.

We cannot claim that $2\lambda_2/\lambda_1 < 2$ because λ_1 could be negative. For example, if $\lambda_1 = -1/2,\ \lambda_2 = -1$, then $2\lambda_2/\lambda_1 = 4$.

Proof. From the proof of Theorem 3.3, we can write $W_b(t) := (2 - b)(\lambda_1 t - \log n) + \nu(t) - b\mu(t) - \log a$ where

$$\nu(t) := \log\left[\sum_{i<j}((c_1 x_{1i} + F_i(t)) - (c_1 x_{1j} + F_j(t)))^2\right],$$

$$\mu(t) := \log\left[\sum_{i=1}^{n}(c_1 x_{1i} + F_i(t))\right].$$

For $\mu(t)$,

$$\lim_{t\to\infty}\mu(t) = \log\left[\sum_{i=1}^{n}(c_1 x_{1i})\right].$$

For $\nu(t)$, Eq. (17) implies

$$F_i(t) - F_j(t) = \sum_{\ell=2}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell - \lambda_1)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j}),$$

so that

$$\begin{aligned}
\nu(t) &= \log\left[\sum_{i<j}(c_1(x_{1i} - x_{1j}) + (F_i(t) - F_j(t)))^2\right] \\
&= \log\left[\sum_{i<j}\left(\sum_{\ell=2}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell-\lambda_1)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j})\right)^2\right] \\
&= \log\left[\sum_{i<j}\left(\sum_{\ell=2}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell-\lambda_1)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j})\right)^2\right] \\
&\quad + \log(e^{2(\lambda_2-\lambda_1)t}) - \log(e^{2(\lambda_2-\lambda_1)t}) \\
&= \log\left[\sum_{i<j}\left(\sum_{\ell=2}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell-\lambda_2)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j})\right)^2\right] + 2(\lambda_2 - \lambda_1)t.
\end{aligned}$$

The second equality follows from assumption (c) that $\mathbf{x}_1$ is a constant vector, i.e. $x_{1i} = x_{1j}$ for all i, j.

Recall that λ_2 is the second leading eigenvalue of A and is therefore a simple real eigenvalue of A where the corresponding eigenspace is spanned by a single nonzero eigenvector $\mathbf{x}_2 \in \mathbb{R}^n$. As such $X_2(t) := c_2 e^{\lambda_2 t}\mathbf{x}_2$ is a solution to Eq. (3) so that $p_2 = 0$, $f_2(t) = 1$, and $G_2(t) = (\lambda_2 - \lambda_1)$. Thus

$$\begin{aligned}
\xi(t) &:= \sum_{i<j}\left(\sum_{\ell=2}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell-\lambda_2)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j})\right)^2 \\
&= \sum_{i<j}\left(c_2(x_{2i} - x_{2j}) + \sum_{\ell=3}^{n} c_\ell t^{p_\ell} e^{(\alpha_\ell-\lambda_2)t} f_j(\beta_\ell t)(x_{\ell i} - x_{\ell j})\right)^2.
\end{aligned}$$

Assuming that A has a second leading eigenvalue, $\lambda_2 = \alpha_2$ and $\lambda_2 > \alpha_j$ for $j = 3, \dots, n$, we have

$$\lim_{t\to\infty}\xi(t) = c_2^2\sum_{i<j}(x_{2i} - x_{2j})^2.$$

Setting $b = 2\lambda_2/\lambda_1$, then combining our results for $\nu(t)$ and $\mu(t)$, we have

$$\begin{aligned}
\lim_{t\to\infty} W_b(t) &= \lim_{t\to\infty}\big[(2-b)(\lambda_1 t - \log n) + \log[\xi(t)] \\
&\quad + 2(\lambda_2 - \lambda_1)t - b\mu(t) - \log a\big] \\
&= \left(2 - \frac{2\lambda_2}{\lambda_1}\right)\log n + \log\left[c_2^2\sum_{i<j}(x_{2i} - x_{2j})^2\right] \\
&\quad - \frac{2\lambda_2}{\lambda_1}\log\left[c_1\sum_{i=1}^{n} x_{1i}\right] - \log a.
\end{aligned}$$

If we choose a to be

$$a := \frac{n^{\left(2-\frac{2\lambda_2}{\lambda_1}\right)} c_2^2 \sum_{i<j}(x_{2i} - x_{2j})^2}{\left(c_1\sum_{i=1}^{n} x_{1i}\right)^{\frac{2\lambda_2}{\lambda_1}}},$$

then we claim that $a > 0$. This follows from the fact that $\mathbf{x}_1$ is a constant eigenvector and $c_1 \neq 0$, implying $c_1\sum_{i=1}^{n} x_{1i} \neq 0$, so the denominator of a is nonzero and a is defined. The numerator is also nonzero as $n > 0$, $c_1 \neq 0$, and $\mathbf{x}_2$ is not constant. Because all quantities are squared, we have $a > 0$.

Using this value of a and $b := 2\lambda_2/\lambda_1$, we have $\lim_{t\to\infty} W_b(t) = 0$. Since $\lambda_2 \neq \lambda_1 \neq 0$, TL holds asymptotically with $b = 2\lambda_2/\lambda_1 \neq 2$. □

The main difference between Theorem 3.3 and Proposition 1 is that in the latter we assume the leading eigenvector $\mathbf{x}_1$ is constant. An example follows.

Example 4 (*Constant Leading Eigenvector*). Consider the EM model $(A, \mathbf{N}(0))$ with coefficient matrix

$$A := \begin{bmatrix} 1 & 1 & 1 \\ 1 & 2 & 0 \\ 2 & 1 & 0 \end{bmatrix}.$$

This matrix is irreducible, has leading eigenvalue $\lambda_1 = 3$, second leading eigenvalue $\lambda_2 = 1$, third eigenvalue $\lambda_3 = -1$. The matrix also has the constant leading eigenvector $\mathbf{x}_1 = \mathbf{1}$. For the initial population vector $\mathbf{N}(0)^\delta := [1,\ 2,\ 3+\delta]^T$ the coefficients $c_1, c_2 \neq 0$ for small positive $\delta > 0$. Proposition 1 implies that TL holds asymptotically in this case with $\lim_{t\to\infty} b(t) = 2/3$ as shown in Fig. 2(right). However, for the initial condition $\mathbf{N}(0)^0 = [1,\ 2,\ 3]^T$, the scalar $c_2 = 0$ and $\lim_{t\to\infty} b(t) = 2\lambda_3/\lambda_1 = -2/3$ (Fig. 2(right)).

If we add $\epsilon > 0$ to any entry of A, the resulting perturbed matrix A_ϵ does not have a constant leading eigenvector. In particular, if we add ϵ to both $a_{1,2}$ and $a_{1,3}$, then in the perturbed EM model $(A_\epsilon, \mathbf{N}(0)^0)$, both the leading coefficient c_1 and the leading eigenvalue λ_1 are not zero (cf. Example 5). Hence, by Theorem 4.2, $b = 2$ for arbitrarily small $\epsilon > 0$ (Fig. 2 (right)).

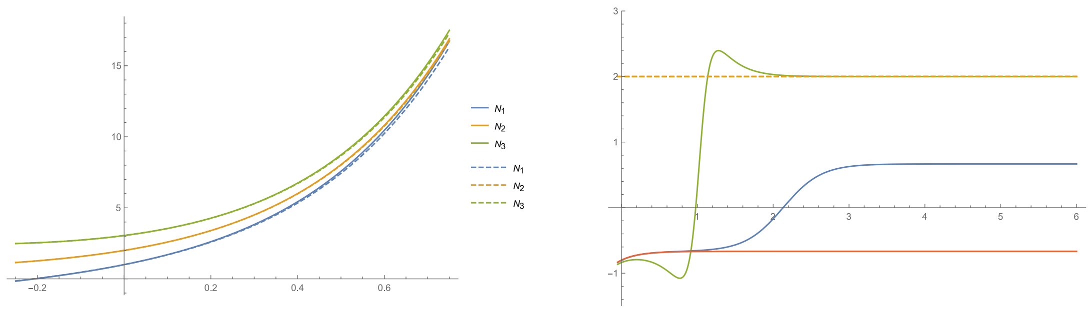
Example 4 suggests that the behavior of an EM model $(A, \mathbf{N}(0))$ with irreducible A and constant leading eigenvector depends on which coefficients c_i are zero or nonzero.

In Theorems 3.3, 4.2, Proposition 1, and Example 4, the constant b can be written entirely in terms of the eigenvalues of A. However, which combination of eigenvalues depends on both the leading eigenvector and the initial population vector $\mathbf{N}(0)$.

5. The prevalence of Taylor's law for the EM model

Taylor's Law with $b = 2$ does not hold for every EM model. Here we show that Taylor's Law with $b = 2$ is the typical behavior of an EM model with a typical coefficient matrix $A := [a_{ij}]$ and initial vector of population densities $\mathbf{N}(0)$.

Let $\mathbb{A}$ be the set of essentially nonnegative $n \times n$ matrices. Define $\mathbb{A}_{TL}$ as the set of matrices $A \in \mathbb{A}$ that have a leading eigenvalue and a leading eigenvector that satisfy the assumptions of Theorem 3.3(a)–(c). Let $\mathbb{M}$ be the set of all EM models, that is $(A, \mathbf{N}(0)) \in \mathbb{M}$ if $A \in \mathbb{A}$ and $\mathbf{N}(0) > 0$. Let $\mathbb{M}_{TL} \subset \mathbb{M}$ be the set of EM models where the coefficient matrix $A \in \mathbb{A}_{TL}$. By Theorem 3.3, $\mathbb{M}_{TL}$ is a subset of $\mathbb{M}$ on which TL holds with $b = 2$.



$\mathbf{N}(t)$ $b(t)$

Fig. 2. Left: The population dynamics $\mathbf{N}(t)$ for the EM model in Example 4 with a constant leading eigenvector. Solid lines correspond to the unperturbed initial population vector $\mathbf{N}(0)^0 := [1, 2, 3]^T$ and dashed lines correspond to the perturbed initial population vector $\mathbf{N}(0)^\delta := [1, 2, 3 + \delta]$ where $\delta := 0.01$. Right: The functions $b(t)$ are plotted in red for the unperturbed initial population vector where $\lim_{t\to\infty} b(t) = -2/3$ and in blue for the perturbed initial population vector for which $\lim_{t\to\infty} b(t) = 2/3$. The green curve plots $b(t)$ for the perturbed EM model in Example 5 with coefficient matrix A_ϵ with $\epsilon := 0.01$, which has a non-constant leading eigenvector and $\lim_{t\to\infty} b(t) = 2$.

For two EM models $(A_1, \mathbf{N}(0)^1)$ and $(A_2, \mathbf{N}(0)^2) \in \mathbb{M}$, define addition and scalar multiplication by

$$(A_1, \mathbf{N}(0)^1) + (A_2, \mathbf{N}(0)^2) := (A_1 + A_2, \mathbf{N}(0)^1 + \mathbf{N}(0)^2); \text{ and}$$
$$c(A_1, \mathbf{N}(0)^1) := (cA_1, c\mathbf{N}(0)^1) \text{ for } c \in \mathbb{R}.$$

Not every linear combination $\alpha(A_1, \mathbf{N}(0)^1) + \beta(A_2, \mathbf{N}(0)^2)$ is an EM model, but this combination is an EM model under certain conditions, e.g. $\alpha, \beta \geq 0$. For an EM model $(A, \mathbf{N}(0))$, define the metric

$$\|(A, \mathbf{N}(0))\|_{EM} := \max\{|||A|||, \|\mathbf{N}(0)\|\},$$

where $|||\cdot|||$ is a matrix norm and $\|\cdot\|$ a vector norm. This norm induces a topology on the set $\mathbb{M}$ of EM models. Under this norm, the set $\mathbb{M}_{TL}$ is an open dense subset of $\mathbb{M}$.

Theorem 5.1 (*Prevalence of Taylor's Law for the EM Model*). *The set $\mathbb{M}_{TL}$ is an open dense set of $\mathbb{M}$. Thus, on an open dense set of EM models, TL holds asymptotically with $b = 2$.*

Proof. We show first that the coefficient matrices that have a leading eigenvalue and leading eigenvector form an open dense set in the set of all coefficient matrices. We then prove a similar result for the initial population vectors that result in a nonzero leading coefficient c_1. Combining the two results will prove the theorem.

Let $A \in \mathbb{A}$ be an essentially nonnegative matrix and let $J_\epsilon \in \mathbb{R}^{n\times n}$ be a matrix in which all entries are $\epsilon > 0$ except that a single entry of J_ϵ is zero. Define $A_\epsilon := A + J_\epsilon$. Because A has nonnegative off-diagonal entries and $J_\epsilon \geq 0$, A_ϵ also has nonnegative off-diagonal entries, implying that $A_\epsilon \in \mathbb{A}$. Second, as J_ϵ is irreducible, A_ϵ is also irreducible and Theorem 4.2 states that A_ϵ has a leading eigenvalue λ_ϵ and leading eigenvector $\mathbf{x}_\epsilon$.

Suppose that A has no constant eigenvectors. As the eigenvectors of a matrix depend continuously on the entries of the matrix, A_ϵ has constant no eigenvectors for small enough $\epsilon > 0$ and therefore no constant leading eigenvector. If A has a constant eigenvector, then $A\mathbf{1} = \lambda\mathbf{1}$ and A has constant row sums λ for some $\lambda \in \mathbb{R}$. Then for any $\epsilon > 0$, A_ϵ does not have constant row sums because one row of J_ϵ is ϵ less than the others. Consequently, A_ϵ cannot have constant eigenvectors and therefore does not have a constant leading eigenvector. Thus, for small enough ϵ, the matrix A_ϵ has a leading eigenvalue with a non-constant leading eigenvector implying $A \in \mathbb{A}_{TL}$. Additionally, $|||A_\epsilon - A||| = |||J_\epsilon|||$ can be made arbitrarily small by letting $\epsilon \to 0^+$. Thus, arbitrarily close to the matrix $A \in \mathbb{A}$ is a matrix $A_\epsilon \in \mathbb{A}_{TL}$ implying $\mathbb{A}_{TL}$ is dense in $\mathbb{A}$.

To show that $\mathbb{A}_{TL}$ is an open subset of $\mathbb{A}$, we observe, as above, that the eigenvectors of a matrix are continuous functions of the entries of the matrix. Thus, if $A \in \mathbb{A}_{TL}$ and $\tilde{A} \in \mathbb{A}$, then for small enough $\delta > 0$, if $|||A - \tilde{A}||| < \delta$, then $\tilde{A}$ has a non-constant leading eigenvector as A has a non-constant leading eigenvector implying $\tilde{A} \in \mathbb{A}_{TL}$. Thus $\mathbb{A}_{TL}$ is an open set of matrices in $\mathbb{A}$.

We now consider how a perturbation of the initial population vector $\mathbf{N}(0)$ affects the leading coefficient c_1. Using Eqs. (11)–(13) at $t = 0$, the initial population vector $\mathbf{N}(0)$ is

$$\mathbf{N}(0) = c_1\mathbf{x}_1 + c_2\mathbf{x}_2 + \cdots + c_n\mathbf{x}_n,$$

where $\mathbf{x}_1, \ldots, \mathbf{x}_n$ is a (generalized) eigenbasis of A forming a basis of $\mathbb{R}^n$. For $\mathbf{c} := [c_1\ c_2\ \cdots\ c_n]^T$ and $\boldsymbol{\Phi} := [\mathbf{x}_1\ \cdots\ \mathbf{x}_n]$, the initial population vector $\mathbf{N}(0) = \boldsymbol{\Phi}\mathbf{c}$. Because the columns of $\boldsymbol{\Phi}$ form a basis of $\mathbb{R}^n$, $\boldsymbol{\Phi}$ is invertible and $\mathbf{c} = \boldsymbol{\Phi}^{-1}\mathbf{N}(0)$ so that $c_1 = (\boldsymbol{\Phi}^{-1})_1\mathbf{N}(0)$ where $(\boldsymbol{\Phi}^{-1})_1$ is the first row of $\boldsymbol{\Phi}^{-1}$.

Suppose that $c_1 = 0$. Because $\boldsymbol{\Phi}^{-1}$ is nonsingular, at least one entry $(\boldsymbol{\Phi}^{-1})_{1i}$ of $(\boldsymbol{\Phi}^{-1})_1$ is nonzero. Let $\mathbf{z}_\epsilon \in \mathbb{R}^n$ be the vector with ith component $\epsilon > 0$ and all other components zero. Then the perturbed initial population vector $\mathbf{N}(0)^\epsilon := \mathbf{N}(0) + \mathbf{z}_\epsilon$ is strictly positive as $\mathbf{N}(0)$ is strictly positive and

$$\tilde{c}_1 := (\boldsymbol{\Phi}^{-1})_1\mathbf{N}(0)^\epsilon = (\boldsymbol{\Phi}^{-1})_{1i}\epsilon \neq 0.$$

Hence, for the perturbed initial population vector $\mathbf{N}(0)^\epsilon$, the leading coefficient $\tilde{c}_1$ is nonzero. Now $\|\mathbf{N}_0^\epsilon - \mathbf{N}(0)\| = \|\mathbf{z}_\epsilon\|$ can be made arbitrarily small by letting $\epsilon \to 0^+$ and the size $\|\mathbf{z}_\epsilon\|$ of $\mathbf{z}_\epsilon$ is continuous in ϵ. Therefore the set of initial population vectors for which $c_1 \neq 0$ is an open dense subset of the set of all initial population vectors.

Thus, for $(A, \mathbf{N}(0)) \in \mathbb{M}$, the EM model $(A_\epsilon, \mathbf{N}(0)^\epsilon) \in \mathbb{M}_{TL}$ for small enough $\epsilon > 0$. Additionally,

$$\|(A, \mathbf{N}(0)) - (A_\epsilon, \mathbf{N}(0)^\epsilon)\|_{EM} = \|(J_\epsilon, \mathbf{z}_\epsilon)\|_{EM} = \max\{|||J_\epsilon|||, \|\mathbf{z}_\epsilon\|\}.$$

As $\lim_{\epsilon\to 0^+} \max\{|||J_\epsilon|||, \|\mathbf{z}_\epsilon\|\} = 0$ and this maximum is a continuous function of $\epsilon \geq 0$, $\mathbb{M}_{TL}$ forms a dense subset of $\mathbb{M}$. The set $\mathbb{M}_{TL}$ is also an open subset of $\mathbb{M}$ using the same argument and the fact that $\mathbb{A}_{TL}$ is an open set of $\mathbb{A}$ and the set of initial populations vectors $\mathbf{N}(0) > 0$ for which $c_1 \neq 0$ is an open subset of the set of positive initial population vectors. □

Roughly speaking, TL with $b = 2$ holds for the vast majority of EM models. More precisely, for any EM model, either TL holds with $b = 2$ or TL holds with $b = 2$ for an arbitrarily small, non-zero perturbation of the model. The following example illustrates the latter alternative.

Example 5. In Example 4, the EM model $(A, \mathbf{N}(0))$ has $b = 2\lambda_3/\lambda_1 = -2/3$ for the initial population vector $\mathbf{N}0 := [1\ 2\ 3]^T$. The unperturbed model has a constant leading eigenvector but the perturbed version of the model $(A_\epsilon, \mathbf{N}(0))$ with

$$A_\epsilon := \begin{bmatrix} 1 & 1+\epsilon & 1+\epsilon \\ 1 & 2 & 0 \\ 2 & 1 & 0 \end{bmatrix}$$

for $\epsilon > 0$ has the nonzero leading eigenvalue $\lambda_\epsilon = 1 + \sqrt{4+3\epsilon}$ with non-constant leading eigenvector

$$\mathbf{x}_\epsilon = [3(1+\epsilon), 1+\sqrt{4+3\epsilon}, -1+2\sqrt{4+3\epsilon}]^T.$$

For any initial population vector $\mathbf{N}(0) > 0$, the leading coefficient $c_1 \neq 0$. Thus, by Theorem 3.3, for any $\epsilon > 0$, the perturbed model $(A_\epsilon, \mathbf{N}(0))$ obeys Taylor's Law asymptotically with $b = 2$. Fig. 2(right) shows in green that $\lim_{t\to\infty} b(t) = 2$.

6. Conclusion

This paper identifies the conditions under which the dynamics of a linear metapopulation model or subdivided population model, which we call the EM model, converge asymptotically to Taylor's Law. The EM model's key features are that (i) each population experiences a fixed rate of growth or decay and (ii) there is a network of fixed migration rates between local populations in the metapopulation. Theorems 3.3 and 4.2, Proposition 1, and Corollary 1 relate the eigenvalues and eigenvectors of an EM model to when TL holds asymptotically and to the value of the slope b in Eq. (7). Theorem 5.1 shows that, on an open dense set of EM models, TL holds asymptotically with $b = 2$. Our results raise several open questions.

First, can these results be extended to nonlinear metapopulation models? In such models, the dynamics near attracting hyperbolic fixed points are topologically conjugate to the dynamics of a linear system via the Hartman–Grobman theorem (Chicone, 2008; Perko, 2001). If this linear system satisfies the conditions given in our results, does TL hold asymptotically for the original nonlinear system near such points? The condition Eq. (7) for Taylor's Law will probably have to be replaced by the requirement that there exist a finite b and finite a such that $\mathbb{V}(\mathbf{N}(t))/\mathbb{E}(\mathbf{N}(t))^b \to a$ as $t \to \infty$, as in studies of Taylor's Law for heavy-tailed probability distributions.

Second, when TL holds asymptotically with $b = 2$ for a given model, what is the speed of convergence of $\log V(t) - b \log E(t)$ to $\log a$ or of $(\log V(t) - \log a)/\log E(t)$ to b? We conjecture that convergence is exponentially fast. If true, this would suggest that TL, in the systems where it holds asymptotically, would be quickly observed in many cases and that TL with $b = 2$ could be compared to real-world data.

Third, do all or some of our results hold when uniform weights $w_i = 1/n$ are replaced by arbitrary positive constant or changing weights? For example, weights might be proportional to the area, current magnitude, economic product, or political influence of a population, or to the reciprocal of these quantities.

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Data availability

No data was used for the research described in the article.

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