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On the biological interpretation of a definition for the parameter R_0 in periodic population models

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Abstract An adaptation of the definition of the basic reproduction number R_0 to time-periodic seasonal models was suggested a few years ago. However, its biological interpretation remained unclear. The present paper shows that in demography, this R_0 is the asymptotic ratio of total births in two successive generations of the family tree. In epidemiology, it is the asymptotic ratio of total infections in two successive generations of the infection tree. This result is compared with other recent work.

Keywords Demography · Epidemiology · Generations · Basic reproduction number · Seasonality

Mathematics Subject Classification (2000) 92D25 · 92D30

1 Introduction

Seasonality is an important aspect of animal or plant demography and of some parts of epidemiology, e.g., vector-borne diseases and air-borne diseases. Following the earlier attempt in Heesterbeek and Roberts (1995), we proposed a few years ago an adaptation of the definition of the basic reproduction number R_0 to continuous-time models that are periodic in time (Bacaër and Guernaoui 2006). The idea was to focus on the renewal equation satisfied by the birth rate $\beta(t)$ (or by the disease incidence in epidemiology):

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$$\beta(t) = \int_0^\infty K(t,x)\,\beta(t-x)\,dx. \tag{1}$$

The kernel $K(t,x)$, which may be a matrix function, is T-periodic with respect to t for models including seasonality. R_0 was defined as the spectral radius of the operator

$$L : u(t) \longmapsto \int_0^\infty K(t,x)\,u(t-x)\,dx \tag{2}$$

on the space of continuous T-periodic functions. It was shown that: this R_0 coincides with the familiar definition of R_0 as the spectral radius of the next-generation matrix for models with no seasonality (Diekmann et al. 1990); the position of R_0 with respect to 1 determines whether the population will be increasing or decreasing; for the simplest seasonal model $dp/dt = a(t)\,p(t) - b(t)\,p(t)$, where the birth rate per capita $a(t)$ and the death rate per capita $b(t)$ are T-periodic functions, $\beta(t) = a(t)\,p(t)$ satisfies (1) with the kernel $K(t,x) = a(t)\,\exp(-\int_{t-x}^t b(s)\,ds)$ and the spectral radius R_0 of (2) is equal to $(\int_0^T a(t)\,dt)/(\int_0^T b(t)\,dt)$.

Bacaër and Guernaoui (2006) applied these ideas to a coupled system of ordinary and partial differential equations. After that, a number of works have discussed R_0 in various classes of periodic population models: ordinary differential equations (Bacaër 2007; Wang and Zhao 2008; Bacaër and Gomes 2009) (particular applications can be found in Gedeon et al. 2010; Parham and Michael 2010; Wesley et al. 2010), delay differential equations (Bacaër and Ouifki 2007; Bacaër and Abdurahman 2008), other infinite-dimensional models (Thieme 2009), models with pulses (van den Berg et al. 2011). Numerous works also study persistence using this R_0: see Rebelo et al. (2012) and references therein. But none of these references says anything about the biological meaning of R_0 in a periodic setting.

In Bacaër (2009), the case of periodic discrete-time matrix models of the form $p(t+1) = (A(t) + B(t))p(t)$, $A(t)p(t)$ being the births and T being an integer period, was considered using the same renewal equation approach. R_0 was defined as the spectral radius of the operator

$$u(t) \longmapsto \sum_{x=1}^{\infty} K(t,x)\,u(t-x)$$

on the space of continuous T-periodic functions, where $K(t,x) = A(t)B(t-1)B(t-2)\cdots B(t-x+1)$. It was shown that R_0 is also the spectral radius of the matrix $\Omega = \mathcal{A}\mathcal{B}^{-1}$, where

$$\mathcal{A} = \begin{pmatrix} A(0) & 0 & \cdots & 0 \\ 0 & A(1) & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & A(T-1) \end{pmatrix}, \quad \mathcal{B} = \begin{pmatrix} -B(0) & I & 0 & \cdots & 0 \\ 0 & -B(1) & I & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & & & \ddots & I \\ I & 0 & \cdots & 0 & -B(T-1) \end{pmatrix},$$

with I standing for the identity matrix. Bacaër (2009, §3.4) suggested without giving details that the matrix Ω might be seen as a kind of next-generation matrix, where the season of birth is included in the state space.

The question of computing R_0 for seasonal models received some impetus when the 2009 H1N1 influenza "pandemic" broke out. According to standard mathematical epidemiology (in a constant environment), it should have been enough for governments to order a number of vaccine doses so as to vaccinate a fraction $1 - 1/R_0$ of the population. An overestimation of R_0 leads to millions of unused vaccine doses, while an underestimate might lead to unsuccessful epidemic control. However, estimates published at the beginning of the epidemic in late spring and early summer 2009 did not take seasonality into account even though these estimates were supposed to help predicting whether the epidemic would continue during the summer (when schools are closed) and predicting the size of a possible second wave in falls or winter. Strangely enough, many governments—e.g., those in the UK, in France, and in the Netherlands—finally did not base the size of their vaccine orders on R_0 estimates at all: they ordered much more vaccine doses than if they had applied a "$1 - 1/R_0$ rule", and much more than were finally needed (Assemblée Nationale 2010).

Nevertheless, in order to facilitate possible applications of the periodic R_0 theory described above to real public health problems, Bacaër and Ait Dads (2011) tried to clarify the biological interpretation of R_0 for seasonal models. Returning to the terminology of demography, let $\beta(n, t)$ be the birth rate due to generation n at time t. It satisfies the renewal equation

$$\beta(n+1, t) = \int_0^{t-t_0} K(t, x)\, \beta(n, t-x)\, dx, \quad (t \geq t_0), \tag{3}$$

where t_0 stands for the initial time. When $K(t, x)$ is a scalar function the total births due to generation n, i.e., the size of generation $n+1$ is given by $g(n) = \int_{t_0}^{\infty} \beta(n, t)\, dt$. Notice however that the functions $t \mapsto \beta(n, t)$ in (3) are not periodic. So the connection between $g(n)$ defined through (3) and the definition of R_0 as the spectral radius of the operator (2) is not obvious. Bacaër and Ait Dads (2011) showed that $\limsup \sqrt[n]{g(n)} = R_0$, suggesting that R_0 can be interpreted as an asymptotic per generation growth rate but in a somewhat weak sense. The stronger result $\lim \sqrt[n]{g(n)} = R_0$ could be obtained only for the simplest periodic model $dp/dt = a(t)p(t) - b(t)p(t)$, $a(t)p(t)$ being the birth rate.

Besides, it was recently brought to our attention that a different definition of "R_0" has been developed in the periodic case, with a different interpretation and with different properties. This approach may be traced back to Hunter and Caswell (2005, Appendix), Caswell (2009, pp. 1772–1773), and Ackleh and Chiquet (2009, §2.2). It has recently been generalized in Cushing and Ackleh (2011). See also Ackleh et al. (2011), Caswell (2011). Finally the usual definition of R_0 in autonomous models has also been recently criticized (Li et al. 2011).

In order to strengthen the interpretation of our definition of R_0 and to help the reader balance the advantages and disadvantages of the different approaches, we first improve the results of Bacaër (2009), Bacaër and Ait Dads (2011) by showing in the present paper that $g(n+1)/g(n) \to R_0$ as $n \to +\infty$ under quite general conditions. Thus R_0 is the asymptotic "ratio of total births in two successive generations", following the same terminology as in the original article that introduced the notation R_0 (Dublin and Lotka 1925). In epidemiology, "total births" should be replaced by "total infections". This is proved for discrete-time models in Sect. 2 and for continuous-time models in Sect. 3, the details being in the appendices A and B. A comparison between the proof in Appendix B and an alternative but essentially equivalent proof may be found in a recent article (Inaba 2012). Section 4 focuses on another interpretation of R_0, namely as the minimal control effort on the "reproduction coefficients" to bring the population to extinction, using the discrete-time framework. A remark considers the case of periodic continuous-time models with spatial diffusion. The interpretation of Sect. 4 is particularly useful for applications in epidemiology as it shows that our approach gives the critical threshold $1 - 1/R_0$ for vaccination coverage. Estimating this critical coverage is arguably one of the main real world applications of the concept of basic reproduction number. In Sect. 5, we compare our approach with the one adopted in Cushing and Ackleh (2011).

2 R_0 and the next-generation matrix in a discrete-time framework

We shall note $\rho(\cdot)$ the spectral radius of a matrix. For a real vector w of any size, we set $||w|| = \sum_i |w_i|$. Let the period $T \geq 1$ be an integer, for example $T = 12$ for a seasonal model with a time step of 1 month. Let $A(t)$ and $B(t)$ be nonnegative T-periodic square matrix functions. $A(t)$ is a reproduction matrix and $B(t)$ a survival matrix. Set

$$M(t) = A(t) + B(t).$$

Assume that the population vector at time t satisfies the equation

$$p(t+1) = M(t)p(t) \quad \forall t \geq t_0$$

with the nonnegative column-vector initial condition $p(t_0)$ at time t_0. Without loss of generality, we can assume that $0 \leq t_0 \leq T-1$. Let us set $\tau_0 = t_0 - 1$ if $t_0 \neq 0$ and $\tau_0 = T-1$ if $t_0 = 0$, so that τ_0 is the season preceding time t_0: this notation will be used in the definition of $\widehat{p}$ below. Let us call "compartments" the different components of the population vector $p(t)$.

We shall assume that $\rho(B(T-1)\cdots B(1)B(0)) < 1$: the population dies out if there is no reproduction. For the survival matrix $B(t)$ to make sense biologically, we should also assume that $\max_j \sum_i B_{i,j}(t) \leq 1$ for all t. But the latter assumption will not be used anywhere below.

Assume that the initial population at time t_0 belongs to generation 0. Let $\pi(n,t)$ be the population belonging to generation n at time t, given for all $t \geq t_0$ and all $n \geq 0$ by

$$\pi(0,t_0) = p(t_0), \quad \pi(0,t+1) = B(t)\,\pi(0,t), \tag{4}$$

$$\pi(n+1,t_0) = 0, \quad \pi(n+1,t+1) = A(t)\,\pi(n,t) + B(t)\,\pi(n+1,t). \tag{5}$$

Thus $\sum_{n\geq 0} \pi(n,t) = p(t)$ for all $t \geq t_0$. Similarly, let $\beta(n,t)$ be the births due to generation n between time t and time $t+1$, given for all $t \geq t_0$ and all $n \geq 0$ by

$$\beta(n,t) = A(t)\,\pi(n,t). \tag{6}$$

Let us say that a newborn was born in season τ if it was born between time τ and time $\tau+1$ modulo T. Let

$$G(n,\tau) = \sum_{q\geq q_\tau} \beta(n,\tau+qT) \quad \text{with } q_\tau = \begin{cases} 0 & \text{if } t_0 \leq \tau \leq T-1 \\ 1 & \text{if } 0 \leq \tau \leq t_0-1 \end{cases} \tag{7}$$

be the total birth vector due to generation n in season τ. Define the "big" column vectors $\widehat{G}(n)$ and $\widehat{p}$ from the smaller column vectors $G(n,\tau)$ and $p(t_0)$ by

$$\widehat{G}(n) = \begin{pmatrix} G(n,0) \\ G(n,1) \\ \vdots \\ G(n,T-1) \end{pmatrix}, \quad \widehat{p} = \begin{pmatrix} 0 \\ \vdots \\ 0 \\ p(t_0) \\ 0 \\ \vdots \\ 0 \end{pmatrix},$$

where $p(t_0)$ is in "row" τ_0 and where the 0 are zero vectors (the "rows" of the different blocks are numbered from 0 to $T-1$). $\widehat{G}(n)$ is the total birth vector due to generation n structured by the seasons where the births occur. Let

$$g(n) = ||\widehat{G}(n)|| = \sum_{t\geq t_0} \|\beta(n,t)\|$$

be the total births due to generation n, i.e., the size of generation $n+1$.

Recall that the matrices $\mathcal{A}$, $\mathcal{B}$, and $\Omega = \mathcal{A}\mathcal{B}^{-1}$ were defined in Sect. 1 and that $R_0 = \rho(\Omega)$, as in Bacaër (2009). Given all this notation and preliminary remarks, we arrive at:

Proposition 1 *For all $n \geq 0$, we have $\widehat{G}(n) = \Omega^{n+1}\,\widehat{p}$. Thus Ω can be interpreted as a next-generation matrix, the season of birth serving as an additional structuring type.*

Proof See Appendix A.

Corollary 1 *If Ω is primitive, if U is a right eigenvector and V a left eigenvector of Ω associated with R_0, if $p(t_0) \neq 0$, then*

$$\widehat{G}(n) \underset{n\to+\infty}{\sim} (R_0)^{n+1}\frac{\langle V,\widehat{p}\rangle}{\langle V,U\rangle}\,U \quad \textit{and} \quad \frac{g(n+1)}{g(n)} \underset{n\to+\infty}{\longrightarrow} R_0,$$

where $\langle\cdot,\cdot\rangle$ stands for the usual scalar product of real vectors. Thus R_0 can be interpreted as the asymptotic ratio of total births in two successive generations. It is independent of the initial condition and of the initial starting time.

Remarks

- Recall that if $R > 0$ is a constant and if (u_n) is a sequence of positive real numbers, then $u_{n+1}/u_n \to R$ implies $\sqrt[n]{u_n} \to R$ (Hardy 2007, Chap. IX). So Corollary 1 implies that $\sqrt[n]{g(n)} \to R_0$. Recall that the converse of "$u_{n+1}/u_n \to R$ implies $\sqrt[n]{u_n} \to R$" is not true: take for example $u_n = 2^n(2+(-1)^n)$, for which $\sqrt[n]{u_n} \to 2$ while u_{n+1}/u_n oscillates between two values and therefore has no limit. For example, if the matrix Ω in Proposition 1 is irreducible but not primitive, the ratio $g(n+1)/g(n)$ may oscillate.
- Bacaër (2009) already showed that the matrix $\mathcal{B}$ is invertible and that $\mathcal{B}^{-1}$ and Ω are both nonnegative matrices, as should be. More precisely, for all τ and σ, set $Y(\tau,\sigma) = I$ if $\tau < \sigma$ and $Y(\tau,\sigma) = B(\tau)B(\tau-1)\cdots B(\sigma)$ if $\tau \geq \sigma$. Set $Z(\sigma) = Y(\sigma, \sigma - T + 1)$. Then Bacaër (2009) showed that Ω is the block matrix $(\Omega(\tau,\sigma))_{0\leq\tau,\sigma\leq T-1}$ with

  $$\Omega(\tau,\sigma) = \begin{cases} A(\tau)\,(I - Z(\tau-1))^{-1}\,Y(\tau-1,\sigma+1) & \text{if } 0 \leq \sigma \leq \tau - 1, \\ A(\tau)\,(I - Z(\tau-1))^{-1}\,Y(\tau-1,\sigma-T+1) & \text{if } \tau \leq \sigma \leq T-1. \end{cases}$$

  With this notation, Proposition 1 proves that $\Omega_{i,j}(\tau,\sigma)$ is the average number of children born in season τ in compartment i of an individual born in season σ in compartment j, as suggested in Bacaër (2009, §3.4).
- Proposition 1 can be generalized to the case where the $M(t)$ are linear operators in ordered Banach spaces (Thieme 2009).
- If the matrices $A(t)$ and $B(t)$ for all $0 \leq t \leq T-1$ do not depend on time t (call them A and B), then the spectral radius of the matrix Ω is equal to the spectral radius of $A(I-B)^{-1}$, as in the autonomous theory (Caswell 2001). For a proof, see the last paragraph of Appendix A.

Example The simplest example is that where the population vector $p(t)$ and the matrices $A(t)$ and $B(t)$ are scalars and where $T = 2$. Then

$$\Omega = \begin{pmatrix} A(0) & 0 \\ 0 & A(1) \end{pmatrix} \begin{pmatrix} -B(0) & 1 \\ 1 & -B(1) \end{pmatrix}^{-1} = \begin{pmatrix} \frac{A(0)B(1)}{1-B(0)B(1)} & \frac{A(0)}{1-B(0)B(1)} \\ \frac{A(1)}{1-B(0)B(1)} & \frac{A(1)B(0)}{1-B(0)B(1)} \end{pmatrix}. \tag{8}$$

One individual born in season 0 will have on average $A(1)$ children in the first time step, $A(0)B(1)$ children in the next time step as $B(1)$ is the probability of surviving season 1, then $A(1)B(0)B(1)$ children, then $A(0)B(1)B(0)B(1)$ children, etc. So he has $A(0)B(1) + A(0)B(1)B(0)B(1) + \cdots = \frac{A(0)B(1)}{1-B(0)B(1)}$ children born in season 0 and $A(1) + A(1)B(0)B(1) + \cdots = \frac{A(1)}{1-B(0)B(1)}$ children born in season 1. This is the first column of Ω. Similarly, we can check that one individual born in season 1 will have $\frac{A(0)}{1-B(0)B(1)}$ children born in season 0 and $\frac{A(1)B(0)}{1-B(0)B(1)}$ children born in season 1, as in the second column of Ω.

The matrix Ω^2 gives the average number of grandchildren born in season 0 and in season 1 (first and second line respectively) of an individual born in season 0 or in season 1 (first and second column respectively). The matrix Ω^3 gives the number of great-grandchildren in the same way, etc.

As for the interpretation of R_0, imagine for example that we start with one individual—the "ancestor"—born in season 0 (so $t_0 = 1$ and $p(t_0) = 1$). The number of his children $g(0)$ is the sum of the first column of Ω, i.e., $g(0) = \frac{A(0)B(1)+A(1)}{1-B(0)B(1)}$. The number of grandchildren $g(1)$ is the sum of the first column of Ω^2. The number of great-grandchildren $g(2)$ is the sum of the first column of Ω^3, etc. Proposition 1 shows that $g(n+1)/g(n)$ converges to R_0, the spectral radius of Ω: the family tree grows asymptotically like $(R_0)^n$. If the ancestor had been born in season 1, $g(n+1)/g(n)$ would have converged to the same R_0.

3 R_0 and the next-generation operator in continuous-time models

Linear systems of ordinary or delay differential equations in population dynamics and the linear age-structured systems of partial differential equations of McKendrick and von Foerster can usually be rewritten in the form of integral renewal equations for the birth rate.

In this section, the period T is a positive real number. Assume that the birth rate $\beta(n,t)$ due to generation n at time t satisfies for $n \geq 0$ and $t \geq t_0$ the renewal equation

$$\beta(n+1,t) = \int_0^{t-t_0} K(t,x)\,\beta(n,t-x)\,dx, \tag{9}$$

where $K(t,x)$ is a continuous nonnegative square matrix kernel, T-periodic with respect to t, and such that there exists $c > 0$ and $\gamma > 0$ with $K_{i,j}(t,x) \leq c\,e^{-\gamma x}$ for all i, j. Let

$$G(n,\tau) = \sum_{q \geq q_\tau} \beta(n,\tau+qT) \quad \text{with } q_\tau = \begin{cases} 0 & \text{if } t_0 \leq \tau < T \\ 1 & \text{if } 0 \leq \tau < t_0 \end{cases} \tag{10}$$

be the total birth rate due to generation n at time τ modulo T, i.e., in season τ. Extend the function $G(n,\tau)$ by periodicity to all real values of τ. The total births $g(n)$ due to generation n is given by

$$g(n) = \int_0^T \|G(n,\tau)\|\,d\tau = \int_{t_0}^{\infty} \|\beta(n,t)\|\,dt. \tag{11}$$

The following proposition is analogous to Proposition 1 and Corollary 1.

Proposition 2 *For all $n \geq 0$ and all τ, we have*

$$G(n+1,\tau) = \int_0^{\infty} K(\tau,x)\,G(n,\tau-x)\,dx.$$

If the integral operator L given by (2)—defined on the space of continuous T-periodic functions—is strongly positive, if R_0 is its spectral radius, and if $\beta(0,t)$ is not identically zero, then

$$\frac{g(n+1)}{g(n)} \underset{n\to+\infty}{\longrightarrow} R_0.$$

So R_0 can once again be interpreted as the asymptotic ratio of total births in two successive generations.

Proof See Appendix B.

Remarks

- Recall that a linear mapping is strongly positive if it maps nonnegative functions into positive functions. The space of continuous T-periodic functions is equipped with the norm $||f||_\infty = \max_i \max\{|f_i(\tau)|;\ 0 \le \tau \le T\}$.
- If $K(t,x)$ does not depend on time—call it $K(x)$—then R_0 is also the spectral radius of the next-generation matrix $\int_0^\infty K(x)\,dx$ (Bacaër and Guernaoui 2006). If this matrix is primitive, then R_0 is the asymptotic ratio of total births in two successive generations. Notice that considering the asymptotic ratio is not specific to time-periodic models: it already appears in autonomous structured models (a similar remark could have been made in the discrete-time case). However, if $K(x)$ is a scalar, then $R_0 = \int_0^\infty K(x)\,dx$ and $g(n+1) = R_0\, g(n)$: R_0 is not just the asymptotic ratio but the exact ratio of total births in two successive generations. In this case the common definition of R_0 in epidemiology, namely as the "average number of secondary cases infected by an index case", is appropriate.
- Proposition 2 can be generalized to the case where the kernel $K(t,x)$ is a linear operator in an ordered Banach space, as in the case of epidemic models with a continuous age or space structure (Thieme 2009, §6).

Example 1 Let $A(t)$ and $B(t)$ be T-periodic continuous matrix functions. Assume that $A(t)$ is nonnegative for all t and that the off-diagonal elements of $B(t)$ are nonpositive. Assume, as e.g. in Wang and Zhao (2008), that the population satisfies in the linear approximation the ODE system $\frac{dp}{dt} = (A(t) - B(t))p(t)$, $A(t)p(t)$ being the birth rate, with the nonnegative initial condition $p(t_0)$ at time t_0 ($0 \le t_0 < T$). We shall assume that the periodic matrix system $\frac{dz}{dt} = -B(t)z(t)$ with the initial condition $z(0) = I$ (the identity matrix) is such that $\rho(z(T)) < 1$. In other words, the dominant Floquet multiplier is less than 1; the population dies out if there is no reproduction. Assume that the initial population at time t_0 belongs to generation 0. Let $\pi(n,t)$ be the population belonging to generation n at time t, given for all $t > t_0$ and all $n \ge 0$ by

$$\pi(0,t_0) = p(t_0), \quad \frac{d\pi}{dt}(0,t) = -B(t)\,\pi(0,t), \tag{12}$$

$$\pi(n+1,t_0) = 0, \quad \frac{d\pi}{dt}(n+1,t) = A(t)\,\pi(n,t) - B(t)\,\pi(n+1,t). \tag{13}$$

We have $\sum_{n\geq 0}\pi(n,t) = p(t)$ for all $t \geq t_0$. Let $\beta(n,t)$ be the birth rate due to generation n at time t, given for all $t \geq t_0$ and all $n \geq 0$ by $\beta(n,t) = A(t)\,\pi(n,t)$. Consider the matrix function $\Phi(\tau,\sigma)$ such that for all $\tau > \sigma$, $\frac{\partial \Phi}{\partial \tau}(\tau,\sigma) = -B(\tau)\,\Phi(\tau,\sigma)$ and $\Phi(\sigma,\sigma) = I$. Then (13) implies that $\beta(n,t)$ satisfies a renewal equation (9) with the kernel $K(t,x) = A(t)\,\Phi(t,t-x)$ satisfying the preliminary assumptions of Proposition 2. To emphasize the similarity with Proposition 1 in this case, Proposition 2 can also be written as $G(n+1,\cdot) = L\,G(n,\cdot)$, where $L = \mathcal{A}\mathcal{B}^{-1}$ and the operators $\mathcal{A}$ and $\mathcal{B}$ are as in Thieme (2009, §5): $(\mathcal{A}u)(\tau) = A(\tau)u(\tau)$ and $(\mathcal{B}u)(\tau) = \frac{du}{d\tau} + B(\tau)\,u(\tau)$. The proof given in Appendix A for discrete-time models can be adapted to get a proof of Proposition 2 for ODE models that is simpler than the general proof given in Appendix B.

Example 2 Let $a(t)$ and $b(t)$ be positive T-periodic scalar functions. Consider the model $dp/dt = (a(t) - b(t))p(t)$, $a(t)p(t)$ being again the birth rate, with the initial condition $p(t_0)$. This is just a special case of Example 1. Here, $K(t,x) = a(t)\,\exp(-\int_{t-x}^{t} b(s)\,ds)$. Bacaër and Guernaoui (2006, Sect. 5) showed that $R_0 = \int_0^T a(t)\,dt / \int_0^T b(t)\,dt$ and that $U(t) = a(t)\,e^{\int_0^t [a(s)/R_0 - b(s)]ds}$ is an eigenfunction of the operator L associated with R_0. Considering the scalar product $\langle u, v\rangle = \int_0^T u(t)\,v(t)\,dt$ for any T-periodic continuous functions $u(t)$ and $v(t)$, the adjoint of the operator L is given by $(L^*v)(t) = \int_0^\infty K'(t+x,x)\,v(t+x)\,dx$, where $K'(t,x)$ is (in the general case) the transpose of $K(t,x)$. The positive eigenfunctions of L^* associated with the eigenvalue R_0 satisfy $(L^*V)(t) = R_0\,V(t)$. Taking the derivative of this integral equation as in Bacaër and Guernaoui (2006, Sect. 5), we get $-dV/dt = (a(t)/R_0 - b(t))V(t)$. So these eigenfunctions are proportional to $V(t) = e^{-\int_0^t [a(s)/R_0 - b(s)]ds}$. As in Inaba (2012), it then follows from the theory of positive operators and from Proposition 2 that

$$G(n,\tau) \underset{n\to+\infty}{\sim} (R_0)^n \, \frac{\int_0^T V(t)\,G(0,t)\,dt}{\int_0^T V(t)\,U(t)\,dt}\, U(\tau). \tag{14}$$

But since $\pi(0,t) = e^{-\int_{t_0}^t b(s)\,ds}\,p(t_0)$, one can easily check that $G(0,t) = (L\widehat{\delta}_{t_0})(t)\,p(t_0)$, where $\widehat{\delta}_{t_0}$ is the T-periodic extension of Dirac's measure at $t = t_0$. So $\int_0^T V(t)\,G(0,t)\,dt = \int_0^T (L^*V)(t)\,\widehat{\delta}_{t_0}(t)\,dt\;p(t_0) = R_0\,V(t_0)\,p(t_0)$. In summary, (14) shows that

$$G(n,\tau) \underset{n\to+\infty}{\sim} (R_0)^{n+1}\, \frac{a(\tau)\,e^{\int_{t_0}^{\tau}[a(t)/R_0 - b(t)]\,dt}}{\int_0^T a(t)\,dt}\, p(t_0),$$

which implies that

$$g(n) \underset{n\to+\infty}{\sim} (R_0)^{n+1}\, \frac{\int_0^T a(\tau)\,e^{\int_{t_0}^{\tau}[a(t)/R_0 - b(t)]\,dt}\,d\tau}{\int_0^T a(\tau)\,d\tau}\, p(t_0). \tag{15}$$

This last asymptotic result can be checked on specific numerical examples: first compute $\pi(n,t)$ either by solving the system (12)–(13) or directly by using the formula

$$\pi(n,t) = e^{-\int_{t_0}^{t} b(s)\,ds}\ \frac{1}{n!}\left(\int\limits_{t_0}^{t} a(s)\,ds\right)^{n}\ p(t_0)$$

proved in Bacaër and Ait Dads (2011, Lemma 4); then recall that $g(n) = \int_{t_0}^{\infty} a(t)\,\pi(n,t)\,dt$. Formula(15) is more precise than the inequalities $c_1(R_0)^n \le g(n) \le c_2(R_0)^n$ obtained in Bacaër and Ait Dads (2011, p. 749). Example 2 is related to the linearization of many SIS- or SIR-type epidemic models near the disease-free state, with $p(t)$ standing for $I(t)$.

Example 3 Consider the system of McKendrick and von Foerster

$$\frac{\partial p}{\partial t} + \frac{\partial p}{\partial x} = -b(t,x)\,p(t,x), \quad p(t,0) = \int\limits_{0}^{\infty} a(t,x)\,p(t,x)\,dx\ ,$$

where $a(t,x)$ and $b(t,x)$ are positive scalar functions that are T-periodic with respect to t. Then the birth rate $p(t,0)$ satisfies a renewal equation with the kernel $K(t,x) = a(t,x)\ \exp(-\int_0^x b(t-x+y,y)\,dy)$. So the basic reproduction number R_0 is the spectral radius of the integral operator (2) with kernel $K(t,x)$ and it is the asymptotic ratio of total births in two successive generations. Notice that there is one major difference between Examples 1 and 3. In the former, R_0 was the spectral radius of the operator $L = \mathcal{A}\mathcal{B}^{-1}$, which is also the spectral radius of the operator $\mathcal{B}^{-1}\mathcal{A}$ (the latter approach being the one emphasized in Wang and Zhao 2008). In contrast, there is no such decomposition for the operator L in Example 3.

4 Another interpretation of R_0

Let us return to the discrete-time framework of Sect. 2. It is important to notice that the next-generation matrix Ω and its spectral radius R_0 depend linearly upon the set of matrices $A(t)$: if we call $\Omega(\mu)$ and $\mathcal{R}_0(\mu)$ the next-generation matrix and the basic reproduction number of the model where all the matrices $A(t)$ have been divided by μ, then $\Omega(\mu) = \Omega/\mu$ and $\mathcal{R}_0(\mu) = R_0/\mu$ (a similar remark for a particular continuous-time periodic model appears in Bacaër (2007, pp. 1073,1079)). Thus $\mathcal{R}_0(\mu) < 1$ if and only if $\mu > R_0$. The basic reproduction number R_0 can be interpreted as the minimal control effort on the "reproduction terms" to bring the population to extinction. It is precisely because of this property that R_0 is so often used in epidemiology. In this context the model $p(t+1) = (A(t) + B(t))p(t)$, $A(t)p(t)$ being the disease incidence, is the linearization near the disease-free state of a nonlinear epidemic model (Allen and van den Driessche 2008). The matrices $A(t)$ are transmission matrices while the matrices $B(t)$ include all other terms (death, recovery, migration...). In particular, since the matrices $A(t)$ are usually proportional to the susceptible populations in the disease-free state as a result of the "mass action" assumption for the incidence, we see that disease eradication occurs when the susceptible populations are reduced by a factor greater than R_0. So the minimal vaccination coverage is $1 - 1/R_0$ in a periodic environment as in a constant environment.

A somewhat different way of expressing this interpretation of R_0 is given in Proposition 3 below, which is similar to the case of ordinary differential equations in Wang and Zhao (2008), but which we prove using a log-convexity argument. The discrete-time autonomous case (corresponding to $T = 1$) was considered in Li and Schneider (2002). Bacaër (2009, §3.3) showed under an unnecessary assumption of irreducibility that $\rho(N_{R_0}) = 1$ (see notation below). Related work on nonlinear population models may be found in a recent manuscript (Cao H, Zhou Y, The basic reproduction number of discrete SIR and SEIS models with periodic parameters).

Proposition 3 *Same notation and assumptions as for Proposition 1. For all $\mu > 0$, set $N_\mu = (\frac{A(T-1)}{\mu} + B(T-1))(\frac{A(T-2)}{\mu} + B(T-2)) \cdots (\frac{A(0)}{\mu} + B(0))$. Then either the mapping $\mu \mapsto \rho(N_\mu)$ is positive, nonincreasing and log-convex, or it is identically zero. If $R_0 > 0$, then there exists a unique $\mu^* > 0$ such that $\rho(N_{\mu^*}) = 1$. Moreover, $\mu^* = R_0$.*

Corollary 2 *Let $\lambda = \rho(N_1)^{1/T}$ be the Malthusian parameter. Then $R_0 > 1 \Leftrightarrow \lambda > 1$, $R_0 = 1 \Leftrightarrow \lambda = 1$, $R_0 < 1 \Leftrightarrow \lambda < 1$.*

Proofs of Proposition 3 and Corollary 2 are given in Appendix C.

Remark As mentioned above, there exist analogues of Proposition 3 for ODE models (Bacaër 2007, §3.4; Wang and Zhao 2008) and PDE models (see Bacaër 2012, §5.2 for age-structured PDE models). As another example extending the autonomous model in Allen et al. (2008), consider a linearized time-periodic epidemic model with spatial diffusion such as

$$\frac{\partial I}{\partial t}(t, y) = a(t, y)I(t, y) - b(t, y)I(t, y) + c(t, y) \cdot \nabla_y I(t, y) + D\Delta_y I(t, y) \quad (16)$$

on a bounded domain Ω with homogeneous Dirichlet, Neumann or Robin boundary conditions and with an initial condition $I(t_0, y)$. The coefficient $a(t, y)$ (resp. $b(t, y)$) is an effective contact rate (resp. a recovery rate) that is positive (resp. nonnegative) and T-periodic with respect to t, $c(t, y)$ is a T-periodic vector field for convection, and D is a positive diffusion coefficient. We assume that the principal eigenvalue Λ associated with the parabolic equation (16) with $a(t, y) \equiv 0$ is positive: the epidemic dies out without new infections like $e^{-\Lambda t}$. For precise assumptions concerning the function spaces, we refer to Hess (1991). Let us look for the renewal equation satisfied by the incidence $i(t, y) = a(t, y)\, I(t, y)$. The problem can be rewritten as

$$\frac{\partial I}{\partial t}(t, y) - D\Delta_y I(t, y) - c(t, y) \cdot \nabla_y I(t, y) + b(t, y)I(t, y) = i(t, y).$$

Its solution can be put in the form

$$I(t,y) = \int_{t_0}^{t} \int_{\Omega} \widehat{k}(t,x,y,y')\, i(t-x,y')\, dy'\, dx + \int_{\Omega} \widehat{k}(t,t-t_0,y,y')\, I(t_0,y')\, dy'$$

with some nonnegative Green function $\widehat{k}(t,x,y,y')$ (Alimov and Il'in 2011). So $i(t,y) = a(t,y)\, I(t,y)$ satisfies a renewal equation with the kernel $k(t,x,y,y') = a(t,y)\, \widehat{k}(t,x,y,y')$ and R_0 can be defined as the spectral radius of the integral operator

$$u(t,y) \longmapsto \int_0^{\infty}\int_{\Omega} k(t,x,y,y')\, u(t-x,y')\, dy'\, dx.$$

on the space of continuous functions that are T-periodic with respect to t. The incidence grows (resp. decays) exponentially in time if $R_0 > 1$ (resp. $R_0 < 1$). This R_0 is the asymptotic ratio of total infections in two successive generations. Besides, there exists a unique positive number $\mu = \mu^*$ such that the operator

$$\frac{\partial I}{\partial t}(t,y) - D\Delta_y I(t,y) - c(t,y)\cdot\nabla_y I(t,y) + b(t,y) I(t,y) - \frac{a(t,y)}{\mu} I(t,y)$$

with the boundary condition has a principal eigenvalue λ_μ equal to zero; indeed, it follows from Hess (1991, Lemmas 15.4 and 15.5) that this eigenvalue is an increasing continuous function of μ that tends to $-\infty$ as $\mu \to 0^+$ and to a positive limit as $\mu \to +\infty$. Moreover, $I(t,y)$ grows or decays exponentially in time if and only if $i(t,y)$ does the same. So with the same notations as in the beginning of Sect. 4, we have $\mathcal{R}_0(\mu^*) = 1$. But $\mathcal{R}_0(\mu^*) = R_0/\mu^*$. So $\mu^* = R_0$. Knowing how to compute numerically the principal eigenvalue of a parabolic operator, it is thus possible to compute R_0 by a dichotomy method similar to that introduced in Bacaër (2007, §3.4). If the coefficients do not depend on time, then this way of defining R_0 coincides with that in Allen et al. (2008, §2.3), Thieme (2009, §6), and Krkošek and Lewis (2010), but not with that in Smith and Thieme (2011, §11.5.1).[1] R_0 for time-periodic integrodifferential equations as in Jin and Lewis (2012) may be defined in a similar way.

5 Comparison with another approach

Following Ackleh and Chiquet (2009), Caswell (2009) and Hunter and Caswell (2005), it was recently suggested (Cushing and Ackleh 2011) that the spectral radius of the matrix

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[1] This reference notes that there exists y_1 such that $\lambda_1 = \Lambda - a(y_1)$ and defines "R_0" as $a(y_1)/\Lambda$. Notice that if $a(y)$ is divided by a constant, the corresponding "R_0" is not necessarily divided by the same constant since y_1 may not be the same. This contrasts with our approach.

$$(M^*(\tau) - B^*(\tau))(I - B^*(\tau))^{-1} \tag{17}$$

where $M(t) = A(t) + B(t)$, $M^*(\tau) = M(\tau + T - 1) \cdots M(\tau + 1)M(\tau)$ and $B^*(\tau) = B(\tau + T - 1) \cdots B(\tau + 1)B(\tau)$, was also a kind of "net reproductive number" for discrete-time models. It was shown that its position with respect to 1 determined population growth or decay. Here we just want to emphasize the properties, which distinguish it from our approach:

- Our R_0 does not depend on the season τ, unlike (17) which usually yields T different spectral radii for $\tau = 0, 1, \ldots, T - 1$. The notation $R_0^{(\tau)}$ used in Caswell (2009) might be more appropriate than the notation "R_0" used in Cushing and Ackleh (2011). In the simple scalar example with period 2 of Sect. 2,

$$\begin{aligned} R_0^{(0)} &= \frac{A(1)A(0) + B(1)A(0) + A(1)B(0)}{1 - B(1)B(0)} \\ &= \sum_{m=0}^{\infty} (A(1)A(0) + B(1)A(0) + A(1)B(0))(B(1)B(0))^m \end{aligned}$$

  and $R_0^{(1)} = R_0^{(0)}$. Notice that the second and third term in the numerator of $R_0^{(0)}$ appear on the diagonal of the matrix Ω given by (8), unlike the first term.
- Inspired by the definition of the type reproduction numbers for autonomous models (Roberts and Heesterbeek 2003; Heesterbeek and Roberts 2007), it is possible to define "seasonal type reproduction numbers" as follows. Take for example the general discrete-time matrix model of Sect. 2. Define the next-generation matrix Ω as in the introduction. For $0 \le \tau \le T - 1$, let $\Pi(\tau)$ be the block-diagonal projection matrix $\mathrm{diag}(0, \ldots, 0, I, 0, \ldots, 0)$ of the same size as Ω, with the identity matrix I in the "row" (and "column") τ and the 0 standing for zero matrices (see Sect. 2). Consider a nonempty subset of all the seasons $\mathcal{E} = \{\tau_1, \ldots, \tau_k\} \subset \{0, 1, \ldots, T - 1\}$, the idea being that we would like to measure the effort needed to bring the population to extinction by decreasing the births during the seasons in $\mathcal{E}$. Set $\Pi = \Pi(\tau_1) + \cdots + \Pi(\tau_k)$. Define the seasonal type reproduction number associated with $\mathcal{E}$ by

$$\mathcal{T}(\mathcal{E}) = \rho(\Pi\Omega\,(I - (I - \Pi)\Omega)^{-1}) = \rho\left(\Pi\Omega \sum_{m=0}^{\infty} ((I - \Pi)\Omega)^m\right),$$

  provided $\rho((I - \Pi)\Omega) < 1$. This assumption means the following: in some cases, if $\mathcal{E}$ is a too small subset, it may be impossible to bring the population to extinction. Under this assumption, $R_0 = \rho(\Omega) > 1$ (resp. $= 1$ and < 1) is equivalent to $\mathcal{T}(\mathcal{E}) > 1$ (resp. $= 1$ and < 1), as shown in Roberts and Heesterbeek (2003). Notice that $\mathcal{T}(\{0, 1, \ldots, T - 1\}) = R_0$. For the 2-periodic example of Sect. 2, $\Omega = (\Omega(\tau, \sigma))_{0 \le \tau, \sigma \le 1}$ is given by (8) and we have the expressions

$$\begin{aligned}\mathcal{T}(\{0\}) &= \Omega(0,0) + \frac{\Omega(0,1)\Omega(1,0)}{1-\Omega(1,1)}\\ &= \Omega(0,0) + \sum_{m=0}^{\infty} \Omega(0,1)\Omega(1,1)^m\Omega(1,0)\\ &= \frac{A(0)(A(1)+B(1))}{1-(A(1)+B(1))B(0)}\\ &= \sum_{m=0}^{\infty} A(0)[(A(1)+B(1))B(0)]^m(A(1)+B(1)) \qquad (18)\end{aligned}$$

provided $\Omega(1,1) < 1$, i.e., $(A(1)+B(1))B(0) < 1$. There are similar expressions for $\mathcal{T}(\{1\})$ permuting the indices 0 and 1. Following the interpretation in Roberts and Heesterbeek (2003), and as can be seen from the second expression for $\mathcal{T}(\{0\})$ above, $\mathcal{T}(\{0\})$ is the expected number of offspring (children, grandchildren…) born in season 0 of a parent born in season 0, under the condition that no individual in the family tree between the parent and the offspring be born in season 0 (in other words, the branches of the family tree are cut just after any new birth in season 0). This number would be infinite if $\Omega(1,1) \geq 1$. Such an interpretation holds not just for the example of Sect. 2 but in general. As with Proposition 3, one can also prove—when $\mathcal{T}(\mathcal{E})$ is well defined—that

$$\rho\left(\left(\frac{A(T-1)}{w(T-1)} + B(T-1)\right)\cdots\left(\frac{A(0)}{w(0)} + B(0)\right)\right) = 1 \qquad (19)$$

where $w(\tau) = 1$ if $\tau \notin \mathcal{E}$ and $w(\tau) = \mathcal{T}(\mathcal{E})$ if $\tau \in \mathcal{E}$. Indeed, for $\mu > 0$, define $\mathcal{A}(\mathcal{E};\mu)$, $\Omega(\mathcal{E};\mu)$ and $\mathcal{T}(\mathcal{E};\mu)$ in the same way as $\mathcal{A}$, Ω and $\mathcal{T}(\mathcal{E})$ except that all the matrices $A(\tau)$ with $\tau \in \mathcal{E}$ are divided by the scalar μ. Since $\Omega(\mathcal{E};\mu) = \mathcal{A}(\mathcal{E};\mu)\,\mathcal{B}^{-1}$, we see that $\Pi\Omega(\mathcal{E};\mu) = (\Pi\Omega)/\mu$ while $(I-\Pi)\Omega(\mathcal{E};\mu) = (I-\Pi)\Omega$. So $\mathcal{T}(\mathcal{E};\mu) = \mathcal{T}(\mathcal{E})/\mu$. In particular, $\mathcal{T}(\mathcal{E};\mathcal{T}(\mathcal{E})) = 1$, which is equivalent to (19). QED. One can also show as for Proposition 3 that (19) characterizes $\mathcal{T}(\mathcal{E})$. For the 2-periodic scalar example, solving (19) easily leads to (18). In summary, this seasonal type reproduction number focuses on generations as for our R_0 but may depend on the season as for $R_0^{(\tau)}$.

- When $A(t)$ and $B(t)$ do not depend on t (call them A and B and set $M = A + B$), we see that $R_0^{(\tau)}$ is the spectral radius of $(M^T - B^T)(I - B^T)^{-1}$, for all τ. This is different from the spectral radius of $A(I-B)^{-1}$, which is the standard definition of R_0 for autonomous models (Caswell 2001). It is only by specifying that $T = 1$ that the two formulas coincide. This contrasts with the last remark of Sect. 2.
- $R_0^{(\tau)}$ does not have a simple connection to the minimal vaccination coverage necessary to eradicate an infectious disease, unlike our R_0 which gives $1 - 1/R_0$ as the threshold coverage. As far as we understand, the estimation of this coverage is important for public health agencies. However, $R_0^{(\tau)}$ may be more useful in ecology.

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Appendix A: Proofs for Sect. 2

Proof of Proposition 1 For all $n \geq 0$ and $0 \leq \tau \leq T-1$, set

$$F(n,\tau) = \sum_{q \geq q_\tau} \pi(n, \tau + qT)$$

where q_τ is defined in (7). Assume first that $0 \leq \tau \leq t_0 - 2$ or $t_0 \leq \tau \leq T-2$. In both cases, $q_{\tau+1} = q_\tau$. We get from (5) that

$$\begin{aligned} F(n+1,\tau+1) &= \sum_{q \geq q_{\tau+1}} \pi(n+1, \tau+1+qT) \\ &= \sum_{q \geq q_\tau} A(\tau+qT)\,\pi(n,\tau+qT) + B(\tau+qT)\,\pi(n+1,\tau+qT). \end{aligned}$$

Since $A(\tau+qT) = A(\tau)$ and $B(\tau+qT) = B(\tau)$, we get

$$F(n+1,\tau+1) = A(\tau)\,F(n,\tau) + B(\tau)\,F(n+1,\tau).$$

Using $\pi(n+1,t_0) = 0$, we get in the same way

$$\begin{aligned} F(n+1,t_0) &= A(t_0-1)F(n,t_0-1) + B(t_0-1)F(n+1,t_0-1) \quad \text{if } t_0 \neq 0, \\ F(n+1,0) &= A(T-1)\,F(n,T-1) + B(T-1)\,F(n+1,T-1). \end{aligned}$$

In summary, we have

$$\begin{aligned} -B(\tau)\,F(n+1,\tau) + F(n+1,\tau+1) &= A(\tau)\,F(n,\tau)\,, \quad 0 \leq \tau \leq T-2, \\ -B(T-1)\,F(n+1,T-1) + F(n+1,0) &= A(T-1)\,F(n,T-1). \end{aligned}$$

So if we set $\widehat{F}(n) = (F(n,0)'\;F(n,1)' \cdots F(n,T-1)')'$, then $\mathcal{B}\,\widehat{F}(n+1) = \mathcal{A}\,\widehat{F}(n)$. But

$$G(n,\tau) = \sum_{q \geq q_\tau} A(\tau+qT)\,\pi(n,\tau+qT) = A(\tau)\,F(n,\tau).$$

So $\widehat{G}(n) = \mathcal{A}\,\widehat{F}(n) = \mathcal{B}\,\widehat{F}(n+1)$. It follows that $\widehat{G}(n+1) = \mathcal{A}\,\widehat{F}(n+1) = \mathcal{A}\mathcal{B}^{-1}\,\widehat{G}(n)$ for all $n \geq 0$.

Assume now that $0 \le \tau \le T-2$. Using (4), we see that

$$\begin{aligned}
-B(\tau)\,F(0,\tau)+F(0,\tau+1) &= -\sum_{q\ge q_\tau} B(\tau+qT)\,\pi(0,\tau+qT)+F(0,\tau+1)\\
&= -\sum_{q\ge q_\tau}\pi(0,\tau+qT+1)+\sum_{q\ge q_{\tau+1}}\pi(0,\tau+qT+1)\\
&= \begin{cases} 0 & \text{if } \tau\ne t_0-1,\\ p(t_0) & \text{if } \tau=t_0-1.\end{cases}
\end{aligned}$$

Similarly, we get

$$-B(T-1)\,F(0,T-1)+F(0,0)=\begin{cases} 0 & \text{if } t_0\ne 0,\\ p(0) & \text{if } t_0=0.\end{cases}$$

So $\mathcal{B}\widehat{F}(0)=\widehat{p}$ and $\widehat{G}(0)=\mathcal{A}\,\widehat{F}(0)=\mathcal{A}\mathcal{B}^{-1}\widehat{p}$. Corollary 11 follows from the theorem of Perron and Frobenius (Seneta 2006, Theorem 1.2). □

Proof of the remark at the end of Sect. 2 We have $\Omega=\mathcal{A}\mathcal{B}^{-1}$, where $\mathcal{A}$ is the block diagonal matrix $\operatorname{diag}(A,\ldots,A)$ and where

$$\mathcal{B}^{-1}=\operatorname{diag}((I-B^T)^{-1},\ldots,(I-B^T)^{-1})\begin{pmatrix} B^{T-1} & B^{T-2} & \cdots & I\\ I & B^{T-1} & \ddots & \vdots\\ \vdots & \ddots & \ddots & B^{T-2}\\ B^{T-2} & \cdots & I & B^{T-1}\end{pmatrix}.$$

Now let r_0 be the spectral radius of $A(I-B)^{-1}$. Assume first that A and B are positive matrices (all entries are positive). Let v be a positive right eigenvector of the positive matrix $A(I-B)^{-1}=A+AB+AB^2+\cdots$ associated with r_0 (Berman and Plemmons 1994, Theorem 2.1.3). Set $V=(v'\ldots v')'$, the vector v being repeated T times and $'$ standing for transposition. Then $\Omega\,V=(w'\ldots w')'$ with $w=A(I-B^T)^{-1}(I+B+\cdots+B^{T-1})v=A(I-B)^{-1}v=r_0\,v$. So $\Omega\,V=r_0\,V$ and $r_0=R_0$ since R_0 is the only eigenvalue of the positive matrix Ω with a positive eigenvector (Berman and Plemmons 1994, Theorem 2.1.4). If the matrix A or the matrix B is not positive, consider the matrix E of the same size but full of 1 and the matrices $A^{(\varepsilon)}=A+\varepsilon\,E$ and $B^{(\varepsilon)}=B+\varepsilon\,E$ for $\varepsilon>0$ small enough. Define $R_0^{(\varepsilon)}$ and $r_0^{(\varepsilon)}$ in the same way as R_0 and r_0 except that A and B are replaced by $A^{(\varepsilon)}$ and $B^{(\varepsilon)}$. Then $r_0^{(\varepsilon)}=R_0^{(\varepsilon)}$ as shown above. By continuity of the spectral radius as $\varepsilon\to 0$, we get $r_0=R_0$. □

Appendix B: Proof of Proposition 2

Assume first that $t_0 \le \tau < T$. It follows from (9) and (10) that

$$G(n+1,\tau) = \sum_{q\ge 0} \int_0^{\tau+qT-t_0} K(\tau,x)\,\beta(n,\tau+qT-x)\,dx.$$

Reorganizing the double summation, we get

$$\begin{aligned} G(n+1,\tau) = &\sum_{s\ge 0} \int_{sT}^{\tau-t_0+sT} \sum_{q\ge s} K(\tau,x)\,\beta(n,\tau+qT-x)\,dx \\ &+ \sum_{s\ge 0} \int_{\tau-t_0+sT}^{T+sT} \sum_{q\ge s+1} K(\tau,x)\,\beta(n,\tau+qT-x)\,dx. \end{aligned}$$

With the change of variable $y = x - sT$ and $r = q - s$, we arrive at

$$G(n+1,\tau) = \sum_{s\ge 0} \int_0^{\tau-t_0} \sum_{r\ge 0} K(\tau,y+sT)\,\beta(n,\tau+rT-y)\,dy \tag{20}$$

$$+ \sum_{s\ge 0} \int_{\tau-t_0}^{T} \sum_{r\ge 1} K(\tau,y+sT)\,\beta(n,\tau+rT-y)\,dy. \tag{21}$$

In the first set of integrals (20), we have $0 \le y \le \tau - t_0$, so $t_0 \le \tau - y \le \tau < T$. In the second set (21), we distinguish the case $\tau - t_0 \le y \le \tau$ (for which $0 \le \tau - y \le t_0$) from the case $\tau \le y \le T$ (for which $t_0 \le \tau \le T + \tau - y \le T$). With the definition (10) of $G(n,\tau)$, we arrive at

$$\begin{aligned} G(n+1,\tau) = &\sum_{s\ge 0} \int_0^{\tau-t_0} K(\tau,y+sT)\,G(n,\tau-y)\,dy \\ &+ \sum_{s\ge 0} \int_{\tau-t_0}^{\tau} K(\tau,y+sT)\,G(n,\tau-y)\,dy \\ &+ \sum_{s\ge 0} \int_{\tau}^{T} K(\tau,y+sT)\,G(n,T+\tau-y)\,dy. \end{aligned}$$

With the change of variable $\sigma = \tau - y$, we get

$$G(n+1,\tau) = \int_0^T \Omega(\tau,\sigma)\, G(n,\sigma)\, d\sigma\ . \tag{22}$$

with $\Omega(\tau,\sigma)$ defined by

$$\Omega(\tau,\sigma) = \begin{cases} \sum_{s\geq 0} K(\tau, \tau-\sigma+sT) & \text{if } 0 \leq \sigma < \tau, \\ \sum_{s\geq 1} K(\tau, \tau-\sigma+sT) & \text{if } \tau \leq \sigma < T. \end{cases} \tag{23}$$

When $0 \leq \tau < t_0$, a completely analogous computation also leads to (22). Finally, a simple computation (see, e.g., Bacaër 2007, §2) using the fact that $G(n,\tau)$ has been extended by periodicity to all τ shows that

$$\int_0^T \Omega(\tau,\sigma)\, G(n,\sigma)\, d\sigma = \int_0^\infty K(\tau,x)\, G(n,\tau-x)\, dx.$$

It remains to use the theorem of Krein and Rutman (Dautray and Lions 1984, Chap. VIII). The spectral radius of the strongly positive compact operator (22)—for the compactness, see Bacaër and Ait Dads (2011, Appendix 1)—is a simple eigenvalue with a positive vector eigenfunction $\widetilde{G}(\tau)$ and this eigenvalue dominates all other eigenvalues. So there exists a constant $c > 0$ such that $||G(n,\cdot)/R_0^n - c\,\widetilde{G}(\cdot)||_\infty \to 0$ as $n \to \infty$. It follows that

$$\frac{g(n)}{R_0^n} = \frac{\int_0^T \|G(n,\tau)\|\, d\tau}{R_0^n} \underset{n\to\infty}{\longrightarrow} c \int_0^T \|\widetilde{G}(\tau)\|\, d\tau$$

and that $g(n+1)/g(n) \to R_0$. □

Appendix C: Proofs for Sect. 4

Proof of Proposition 3 For all $\mu > 0$, let C_μ be the matrix

$$\begin{pmatrix} 0 & 0 & \cdots & 0 & \frac{A(T-1)}{\mu} + B(T-1) \\ \frac{A(0)}{\mu} + B(0) & 0 & \cdots & 0 & 0 \\ 0 & \frac{A(1)}{\mu} + B(1) & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & \frac{A(T-2)}{\mu} + B(T-2) & 0 \end{pmatrix}.$$

One can check that $(C_\mu)^T$ is the block diagonal matrix with the matrix product N_μ and its circular permutations on the diagonal. So $\rho(N_\mu) = \rho((C_\mu)^T) = (\rho(C_\mu))^T$. The mapping $\mu \mapsto C_\mu$ is nonincreasing, i.e., all matrix elements are nonincreasing functions of μ. So Berman and Plemmons (1994, Corollary 2.1.5) shows that the mapping $\mu \mapsto \rho(C_\mu)$ is nonincreasing. This mapping is also continuous. Following Kingman (1961), call $\mathfrak{S}$ the set of real functions on $(0, +\infty)$ that are either identically zero or positive and log-convex. For any $a \geq 0$ and $b \geq 0$, the function $\mu \mapsto a/\mu + b$ belongs to $\mathfrak{S}$ since the second derivative of $\log(a/\mu + b)$ with respect to μ is positive. So each element of the matrix C_μ belongs to $\mathfrak{S}$. It follows from Kingman (1961) that the mapping $\mu \mapsto \rho(C_\mu)$ belongs to $\mathfrak{S}$. A product of log-convex functions being also log-convex, it follows that the mapping $\mu \mapsto \rho(N_\mu)$ also belongs to $\mathfrak{S}$.

Assume that $R_0 > 0$. If the matrix C_1 is irreducible, then Bacaër (2009, §3.3) showed that $\rho(C_{R_0}) = 1$; so $\rho(N_{R_0}) = 1$. If C_1 is not irreducible, let E be the matrix of the same size as the matrices $A(t)$ but full of 1. Set $A^{(\varepsilon)}(t) = A(t) + \varepsilon E$ for all $\varepsilon \geq 0$. Define $\mathcal{A}^{(\varepsilon)}$, $R_0^{(\varepsilon)}$, $N_\mu^{(\varepsilon)}$ and $C_\mu^{(\varepsilon)}$ in the same way as $\mathcal{A}$, R_0, N_μ and C_μ except that $A(t)$ is replaced by $A^{(\varepsilon)}(t)$. Since $R_0 > 0$ and by continuity of the spectral radius, we see that $R_0^{(\varepsilon)} > 0$ for all $\varepsilon \geq 0$ small enough. The matrix $C_1^{(\varepsilon)}$ is irreducible for all $\varepsilon > 0$. So applying the result above, we get $\rho(N^{(\varepsilon)}_{R_0^{(\varepsilon)}}) = 1$ for all $\varepsilon > 0$ small enough. By continuity as $\varepsilon \to 0^+$, we get $\rho(N_{R_0}) = 1$.

Imagine that there exists $0 < \mu_1 < \mu_2$ such that $\rho(N_{\mu_1}) = \rho(N_{\mu_2}) = 1$. Since $\rho(C_\mu) = (\rho(N_\mu))^{1/T}$ for all $\mu > 0$, we have $\rho(C_{\mu_1}) = \rho(C_{\mu_2}) = 1$. As $\mu \mapsto \rho(C_\mu)$ is nonincreasing, we have $\rho(C_\mu) = 1$ for all $\mu \in [\mu_1, \mu_2]$. In the present case, the mapping $\mu \mapsto \rho(C_\mu)$ is not identically zero so it is positive and log-convex (and thus convex). The mapping $\mu \mapsto \rho(C_\mu)$ being nonincreasing but convex, it is impossible to find $\mu_3 > \mu_2$ such that $\rho(C_{\mu_3}) < 1$. Thus $\rho(C_\mu) = 1$ for all $\mu \geq \mu_1$ and we get a contradiction with the fact that $\rho(C_\mu) \to (\rho(B(T-1)\cdots B(1)B(0)))^{1/T} < 1$ as $\mu \to +\infty$. So there is at most one μ such that $\rho(N_\mu) = 1$. From the discussion above on the case $R_0 > 0$, we see in that case there is a unique such μ and that $\mu = R_0$. □

Remark If $R_0 = 0$ (or equivalently if the matrix Ω is nilpotent so that the population goes extinct in a finite number of generations), then the equation $\rho(N_\mu) = 1$ has no solution $\mu > 0$. Indeed, imagine that the equation $\rho(N_\mu) = 1$ has a solution $\mu > 0$. Then $\rho(C_\mu) = 1$ and Berman and Plemmons (1994, Theorem 2.1.1) shows that there exists a nonnegative vector $v \neq 0$ such that $C_\mu v = v$. Let us write $v = (v(0)' \ldots v(T-1)')'$. Then $(A(t)/\mu + B(t))v(t) = v(t+1)$ for all $t = 0, \ldots, T-1$, where for convenience we set $v(T) = v(0)$. So $A(t)v(t) = \mu\, v(t+1) - \mu\, B(t)v(t)$ for all $t = 0, \ldots, T-1$. This shows that $\mathcal{A}v = \mu\,\mathcal{B}v$ and hence $\mathcal{B}^{-1}\mathcal{A}v = \mu\, v$. So $R_0 = \rho(\mathcal{A}\mathcal{B}^{-1}) = \rho(\mathcal{B}^{-1}\mathcal{A}) \geq \mu > 0$. Contradiction.

Proof of Corollary 2 Set $\lambda = \rho(N_1)^{1/T}$. Assume for example that $R_0 > 1$. As the mapping $\mu \mapsto \rho(N_\mu)$ is nonincreasing, it follows that $1 = \rho(N_{R_0}) \leq \rho(N_1) = \lambda^T$. But $\rho(N_1) \neq 1$ since $R_0 \neq 1$ and since R_0 is the unique μ such that $\rho(N_\mu) = 1$. Thus $1 < \lambda^T$ and $1 < \lambda$. Similarly, reversing all inequalities, we can show that

$R_0 < 1$ implies $\lambda < 1$. Finally, since $\rho(N_{R_0}) = 1$, we see that $R_0 = 1$ implies $\lambda = \rho(N_1)^{1/T} = 1$. So all the equivalences in Corollary 2 are in fact proved. □

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