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On a new perspective of the basic reproduction number in heterogeneous environments

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Abstract Although its usefulness and possibility of the well-known definition of the basic reproduction number R_0 for structured populations by Diekmann, Heesterbeek and Metz (J Math Biol 28:365–382, 1990) (the DHM definition) have been widely recognized mainly in the context of epidemic models, originally it deals with population dynamics in a constant environment, so it cannot be applied to formulate the threshold principle for population growth in time-heterogeneous environments. Since the mid-1990s, several authors proposed some ideas to extend the definition of R_0 to the case of a periodic environment. In particular, the definition of R_0 in a periodic environment by Bacaër and Guernaoui (J Math Biol 53:421–436, 2006) (the BG definition) is most important, because their definition of periodic R_0 can be interpreted as the asymptotic per generation growth rate, which is an essential feature of the DHM definition. In this paper, we introduce a new definition of R_0 based on the generation evolution operator (GEO), which has intuitively clear biological meaning and can be applied to structured populations in any heterogeneous environment. Using the generation evolution operator, we show that the DHM definition and the BG definition completely allow the generational interpretation and, in those two cases, the spectral radius of GEO equals the spectral radius of the next generation operator, so it gives the basic reproduction number. Hence the new definition is an extension of the DHM definition and the BG definition. Finally we prove a weak sign relation that if the average Malthusian parameter exists, it is nonnegative when $R_0 > 1$ and it is nonpositive when $R_0 < 1$.

Keywords Structured population · Basic reproduction number · Next generation operator · Generation evolution operator · Generation distribution

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1 Introduction

During the last two decades, the definition and computing methods of the basic reproduction number R_0 for structured populations have been widely developed mainly in the context of epidemic models, and it becomes a most important key idea in mathematical epidemiology. Historically speaking, as Heesterbeek (2002) pointed out, the concept of R_0 was already established at least in 1925 by Dublin and Lotka (1925) and Lotka (1998) in demography,[1] while it has taken more than 50 years for the concept to mature in epidemiology. However, the progress of mathematical population models in the context of epidemiology during the last two decades is remarkable, which modern developments were initiated by the epoch-making work of Diekmann et al. (1990). In this celebrated paper, the authors successfully established a principle that the basic reproduction number for heterogeneous populations is calculated as the spectral radius of a positive linear operator, called the *next generation operator* (NGO). In the following, I refer their definition as the DHM definition for short.

Although its usefulness and possibility of the DHM definition and its derivatives as the type-reproduction number have been widely recognized (Diekmann and Heesterbeek 2000; Inaba and Nishiura 2008a,b; Diekmann et al. 2010), originally it quantifies the threshold condition of population growth in a constant environment, so it cannot be applied to formulate the threshold principle for populations in time-heterogeneous environments, which are described by non-autonomous dynamical systems.[2]

Since the mid-1990s, several authors (Bacaër and Guernaoui 2006; Bacaër and Ouifki 2007; Bacaër 2007; Bacaër and Abdurahman 2008; Bacaër 2009; Bacaër and Ait Dads 2011a,b; Heesterbeek and Roberts 1995a,b; Thieme 2009; Wang and Zhao 2008) proposed some ideas to extend the definition of R_0 to the case of periodic environment. In particular, the definition of R_0 in periodic environments by Bacaër and Guernaoui (2006) (we call it the BG definition for short) is most important, because as is shown by Bacaër and Ait Dads (2011a,b), their definition of periodic R_0 can be interpreted as the asymptotic ratio of the size of successive generations of newborns (the *generational interpretation*), so it shares essential features with the DHM definition in a constant environment.

However, as is discussed in the next section, the biological interpretation of the next generation operator is not necessarily fully exhausted even in the classical definition for a constant environment. In fact, the next generation operator for periodic R_0 is acting on the space of periodic functions, which must be different from the function space of the next generation operator in a constant environment. In order to unify and go beyond those two definitions, we have to start our theory from the function space of

[1] In fact, the roots of demographic R_0 could be traced back to much earlier time, and epidemic R_0 has its roots in nineteenth century (Nishiura et al. 2006; Nishiura and Inaba 2007).

[2] Even when environmental parameters are changing as time evolves, if the time scale of population reproduction is much shorter than the time scale of environmental change, the assumption of constant environment is reasonable. Therefore when we discuss the case of heterogeneous environments, we implicitly assume that there is no such time scale separation.

biologically natural, generation distributions and corresponding generation evolution operator.

In this paper, we introduce a new definitions of R_0 in a heterogeneous environment based on a new integral operator, called the *generation evolution operator* (GEO), acting on the extended b-state state space to which generation distributions belong, which has a clear, realistic biological meaning. Then the next generation operators are naturally induced from the GEO by aggregating generation distributions with respect to time parameter.

Using the generation evolution operator, we show that the DHM definition and the BG definition completely allow the generational interpretation and the spectral radius of GEO coincides with the spectral radius of NGO, so it gives the basic reproduction number and the new definition is an extension of the DHM definition and the BG definition. Although our definition can be applied to linear population process in any general heterogeneous environment, the price is that it is no longer clear whether R_0 for general heterogeneous environments is always given by the spectral radius of the generation evolution operator. Finally, we establish a weak sign relation that the average Malthusian parameter, if it exists, is nonnegative if $R_0 > 1$ and it is nonpositive if $R_0 < 1$.

2 The DHM definition in a constant environment

Let us start our argument by reviewing the DHM definition. In the following, we state our theory based on terminologies of general structured population dynamics (demographic setting, see Diekmann et al. 1998), although original ideas have developed mainly in epidemic models. For example, the reader can easily interpret the basic model as an epidemic model, if we read childbearing as reproduction of new infection.

Suppose that the individuals are characterized by a variable $\zeta \in \Omega$, which is called the *h-state variable* (h for heterogeneous). The set $\Omega \subset \mathbf{R}^n$ is the h-state space.[3] Define $A(\tau, \zeta, \eta)$ to be the expected number of newborns with h-state ζ produced per unit time by an individual which was born τ units of time ago at h-state η.

Let $b(t, \zeta),\ \zeta \in \Omega_b$ denote the density of newborns at time t, where $\Omega_b \subset \Omega$ is the set of *states-at-birth*,[4] which are the h-states at which newborns can be produced. Then the real-time development of newborns (in the linear phase) is described by the renewal integral equation:

$$b(t, \zeta) = g(t, \zeta) + \int_0^t \int_{\Omega_b} A(\tau, \zeta, \eta) b(t - \tau, \eta) d\eta d\tau, \quad t > 0, \tag{2.1}$$

where $g(t, \zeta)$ is the density of newborns produced by an initial population.

Let $E_+ := L^1_+(\Omega_b)$ be the set of density distributions of newborns,[5] called the b-state space. Define a linear positive integral operator $\Psi(\tau)$ leaving the cone E_+ invariant by

[3] It is also called i-state space (i for individual).

[4] For detailed argument about the state-at-birth [infection], the reader may refer to Diekmann et al. (2010).

[5] If the h-state space is a finite set, then the b-state space is $E_+ = \mathbf{R}^n_+$ with norm $\|x\| := \sum_{k=1}^n |x_k|,\ x = (x_1, x_2, \ldots, x_n) \in \mathbf{R}^n$.

$$(\Psi(\tau)f)(\zeta) := \int_{\Omega_b} A(\tau,\zeta,\eta)f(\eta)d\eta, \quad f \in E_+.$$

Then $\Psi(\tau)$, which we call the *net reproduction operator*, is an operator that maps the density (distribution) of newborns to the density of their children produced at τ time later.

If we set $b(t) := b(t,\cdot) \in E_+$ and so $b(t)$ is interpreted as an E-valued function, (2.1) is written as an abstract renewal equation in E_+:

$$b(t) = g(t) + \int_0^t \Psi(\tau)b(t-\tau)d\tau, \quad t > 0. \tag{2.2}$$

It is well known that for any $t_0 > 0$, the renewal equation (2.2) has a unique solution $b \in L^1_+([0,t_0]; E)$.

Let $\hat{\Psi}(\lambda)$ be the Laplace transform of the operator Ψ:

$$\hat{\Psi}(\lambda) := \int_0^\infty e^{-\lambda\tau}\Psi(\tau)d\tau.$$

By using positivity arguments (Heijmans 1986; Inaba 1990), it is proved that under appropriate conditions for Ψ, there exists a real λ_0 such that $r(\hat{\Psi}(\lambda_0)) = 1$[6] and there exists a positive number $\alpha(g)$ depending on the initial data g such that

$$b(t) \sim \alpha(g)e^{\lambda_0 t}\psi_0, \quad t \to \infty, \tag{2.3}$$

where ψ_0 is a positive eigenvector of $\hat{\Psi}(\lambda_0)$ associated with eigenvalue unity. Moreover it holds that

$$\mathrm{sign}(\lambda_0) = \mathrm{sign}(r(\hat{\Psi}(0)) - 1). \tag{2.4}$$

In the DHM definition, the *next generation operator* (NGO for short) is defined by

$$K_E := \hat{\Psi}(0) = \int_0^\infty \Psi(\tau)d\tau, \tag{2.5}$$

and the basic reproduction number R_0 is defined by its spectral radius:

$$\lim_{m\to\infty} \sqrt[m]{\|K_E^m\|_{\mathcal{L}(E)}} = r(K_E) = R_0, \tag{2.6}$$

[6] $r(A)$ denotes the spectral radius of operator A.

where $\|\cdot\|_{\mathcal{L}(E)}$ denotes the operator norm of bounded linear operator from E into itself. Then (2.4) shows the well-known *sign relation* as

$$\operatorname{sign}(\lambda_0) = \operatorname{sign}(R_0 - 1), \tag{2.7}$$

so the definition (2.6) is reasonable from the real-time perspective.

On the other hand, from the generational perspective, the reason of the above choice for R_0 is originally explained as follows (Diekmann et al. 1990, p. 367):

"After m generations the magnitude of the infected population is (in the linear approximation) $K(S)^m\phi$ and consequently the per-generation growth factor is $\|K(S)^m\|^{1/m}$."

In the above statement, $K(S)$ denotes the next generation operator in their notations and ϕ is explained as a density of a "distributed" individual. However, it is not self-evident that the spectral radius of NGO gives the (asymptotic) per-generation growth factor, because "the per-generation growth factor" associated with initial data ϕ is given by $\sqrt[m]{\|K_E^m\phi\|_E}$ and in general it holds that

$$\lim_{m\to\infty} \sqrt[m]{\|K_E^m\phi\|_E} \le r(K_E).$$

However, for this constant environment case, we can apply the positive operator theory (Krein–Rutman theory and its extensions) to show that the equality holds in the above inequality. Now let us check this generational interpretation.

Returning to the renewal equation (2.1), we can define the successive generations of newborns by

$$b_0(t) = g(t), \quad b_m(t) = \int_0^t \Psi(\tau) b_{m-1}(t-\tau)d\tau, \quad m = 1, 2, \ldots, \tag{2.8}$$

Then the solution of the renewal equation (2.1) is given by the generation expansion:

$$b(t) = \sum_{m=0}^{\infty} b_m(t),$$

and $b_m(t) \in E_+$ gives the density of mth generation of newborns at time t, called the *generation distribution*.[7] That is, $b_0(t)$ denotes the density of newborns produced by the initial population, $b_1(t)$ is the density of grandchildren of the initial population, and so on.

[7] The generation distribution $b_m(t)$ was first investigated by Lotka (1928, 1929) in demographic context.

From the biological meaning, it is reasonable to assume that[8]

$$b_m \in Y_+ := L^1_+(\mathbf{R}_+; E) \simeq L^1_+(\mathbf{R}_+ \times \Omega_b),$$

where Y_+ is the positive cone of the Banach lattice Y with norm defined by

$$\|b_m\|_Y := \int_0^\infty \|b_m(t)\|_E dt = \int_0^\infty \int_{\Omega_b} |b_m(t,\zeta)| d\zeta dt,$$

where we do not have to write absolute value sign when b_m is positive.[9] If we see the time variable t as a kind of h-state variable, $\mathbf{R}_+ \times \Omega_b$ is the extended h-state space of newborns and Y_+ is the extended b-state space. In the following, we assume that the initial data is nontrivial, that is, $b_0 \in Y_+ \setminus \{0\}$.

Then $\|b_m\|_Y$ gives the total size of mth generation (total number of newborns produced as the mth generation), and the asymptotic *per-generation growth factor* of the genealogy is given by $\lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}$.

Here we define a positive integral operator $K_Y : Y \to Y$ leaving the cone $Y_+ = L^1_+(\mathbf{R}_+; E_+)$ invariant by

$$(K_Y f)(t) := \int_0^t \Psi(\tau) f(t-\tau) d\tau, \quad f \in Y_+. \tag{2.9}$$

Then the generation evolution process (2.8) is expressed as the iteration process in Y_+:

$$b_0 = g, \quad b_m = K_Y b_{m-1}. \tag{2.10}$$

So we call K_Y the *generation evolution operator* (GEO).

It is remarked that as a function of the extended h-state variables, the solution b of (2.2) does not necessarily belong to the extended b-state space, while the iteration process (2.10) is performed in the extended b-state space.

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[8] If $f \in L^1(\mathbf{R}_+ \times \Omega_b)$, it follows from Fubini's theorem that $f(t) := f(t,\cdot) \in E = L^1(\Omega_b)$ and it is proved that $f(t)$ is Bochner integrable and

$$\int_0^\infty \|f(t)\|_E dt = \int_0^\infty \int_{\Omega_b} |f(t,\zeta)| d\zeta dt.$$

Conversely if $f \in L^1(\mathbf{R}_+; E)$, it is proved that there exists an integrable function $g \in L^1(\mathbf{R}_+ \times \Omega_b)$ such that $f(t) = g(t)$ for almost all $t \in \mathbf{R}_+$. In this sense, the set of Bochner integrable functions $L^1(\mathbf{R}_+; E)$ can be identified with $L^1(\mathbf{R}_+ \times \Omega_b)$. If we see $f \in L^1(\mathbf{R}_+ \times \Omega_b)$ as a vector-valued function of $t \in \mathbf{R}_+$, we write as $f(t)$.

[9] If we consider more general situation that $b_m \in (Y_+)^n$, we need the absolute sign, but it only indicates the sum of n positive entries, so it does not affect the following argument.

Lemma 1 *Suppose that*

$$\int_0^\infty \|\Psi(\tau)\|_{\mathcal{L}(E)} d\tau < \infty. \tag{2.11}$$

Then K_Y is a bounded linear operator from Y into itself leaving the cone Y_+ invariant and

$$\|K_Y\|_{\mathcal{L}(Y)} \le \int_0^\infty \|\Psi(\tau)\|_{\mathcal{L}(E)} d\tau. \tag{2.12}$$

Proof Observe that for $f = f(t, \zeta) \in Y$

$$\begin{aligned}
\|K_Y f\|_Y &= \int_0^\infty dt \int_{\Omega_b} d\zeta \left| \int_0^t d\tau \int_{\Omega_b} d\eta A(\tau, \zeta, \eta) f(t-\tau, \eta) \right| \\
&\le \int_0^\infty dt \int_{\Omega_b} d\zeta \int_0^t d\tau \int_{\Omega_b} d\eta A(\tau, \zeta, \eta) |f(t-\tau, \eta)| \\
&= \int_{\Omega_b} d\zeta \int_{\Omega_b} d\eta \int_0^\infty d\tau \int_\tau^\infty dt A(\tau, \zeta, \eta) |f(t-\tau, \eta)| \\
&= \int_0^\infty d\tau \int_0^\infty dt \int_{\Omega_b} d\zeta \int_{\Omega_b} d\eta A(\tau, \zeta, \eta) |f(t, \eta)|.
\end{aligned}$$

For $f \in Y$, we define its positive part $f_+ := \max\{f, 0\}$ and the negative part $f_- := \max\{-f, 0\}$. Then $f = f_+ - f_-$ and $|f| = f_+ + f_-$. Hence we can see

$$\begin{aligned}
&\int_{\Omega_b} d\zeta \int_{\Omega_b} d\eta A(\tau, \zeta, \eta) |f(t, \eta)| \\
&\quad = \int_{\Omega_b} d\zeta \int_{\Omega_b} d\eta A(\tau, \zeta, \eta) (f_+(t, \eta) + f_-(t, \zeta)) \\
&\quad = \|\Psi(\tau) f_+(t, \cdot)\|_E + \|\Psi(\tau) f_-(t, \cdot)\|_E \\
&\quad \le \|\Psi(\tau)\|_{\mathcal{L}(E)} (\|f_+(t, \cdot)\|_E + \|f_-(t, \cdot)\|_E) = \|\Psi(\tau)\|_{\mathcal{L}(E)} \|f(t, \cdot)\|_E.
\end{aligned}$$

Therefore we obtain that

$$\|K_Y f\|_Y \le \int_0^\infty d\tau \int_0^\infty dt \|\Psi(\tau)\|_{\mathcal{L}(E)} \|f(t, \cdot)\|_E = \int_0^\infty \|\Psi(\tau)\|_{\mathcal{L}(E)} d\tau \|f\|_Y,$$

which shows that (2.12) holds and so K_Y is a bounded linear operator from Y into itself. □

For $f = f(t, \zeta) \in Y, \ (t, \zeta) \in \mathbf{R}_+ \times \Omega_b$, we introduce an aggregation operator $T : Y \to E_+$ by

$$(Tf)(\zeta) := \int_0^\infty |f(t, \zeta)| dt. \tag{2.13}$$

Then it is easy to see that T is a bounded operator:

Lemma 2 *It holds that*

$$\|f\|_Y = \|Tf\|_E, \tag{2.14}$$

then the operator norm of T is unity. Moreover, for $f \in Y_+$, it follows that

$$TK_Y f = K_E Tf. \tag{2.15}$$

Proof Observe that

$$\|f\|_Y = \int_0^\infty dt \int_{\Omega_b} d\zeta |f(t, \zeta)| = \int_{\Omega_b} d\zeta (Tf)(\zeta) = \|Tf\|_E.$$

Next for $f \in Y_+$, we can observe that

$$TK_Y f = \int_0^\infty dt \int_0^t \Psi(s) f(t-s) ds = \int_0^\infty \Psi(s) ds \int_0^\infty f(t) dt = K_E Tf.$$

□

Although newborns are originally identified by time at birth t and h-state variable ζ, in a constant environment, newborns with the same h-state are identical with respect to their life cycle, even though they are produced in different time. Therefore, aggregating the generation distribution with respect to time parameter, we can define the aggregated (timeless) mth generation distribution as

$$Tb_m = \int_0^\infty b_m(t) dt \in E_+.$$

It follows from (2.15) that the generation evolution process (2.10) in Y_+ is reduced to the iterative process on the b-state space E_+ as

$$Tb_m = TK_Y b_{m-1} = K_E T b_{m-1}. \tag{2.16}$$

That is, the next generation operator K_E is a generation evolution operator in the space of aggregated generation distributions.[10]

Thanks to the positivity[11] of K_E, under suitable conditions like as compactness and primitivity (or nonsupporting property) of K_E, $r(K_E)$ is the dominant eigenvalue of K_E associated with a positive eigenvector $f_E \in E_+$ and there exists a positive eigenfunctional $F_E \in E_+^*$ such that

$$Tb_m = K_E^m T b_0 \sim \langle F_E, Tb_0 \rangle r(K_E)^m f_E, \quad m \to \infty, \tag{2.17}$$

where E^* denotes the dual space and $\langle F_E, \phi \rangle$ denotes the value of F_E at $\phi \in E$.

From (2.14), we have $\|Tb_m\|_E = \|b_m\|_Y$, it follows from (2.17) that

$$\lim_{m \to \infty} \sqrt[m]{\|b_m\|_Y} = \lim_{m \to \infty} \sqrt[m]{\|Tb_m\|_E} = r(K_E) = R_0. \tag{2.18}$$

Then we can state that:

Proposition 1 *The basic reproduction number R_0 by the DHM definition allows the generational interpretation as*

$$R_0 = r(K_E) = \lim_{m \to \infty} \sqrt[m]{\|b_m\|_Y}. \tag{2.19}$$

Note that the above statement implies that the asymptotic per-generation growth factor $\lim_{m \to \infty} \sqrt[m]{\|b_m\|_Y}$ for the genealogy $\{b_m\}$ is independent of the starting distribution b_0.

From the above argument, we conclude that the NGO of the DHM definition is acting on the b-state space E of aggregated generation distributions. Since the E-norm of the aggregated generation distribution Tb_m gives the total size of the generation (Y-norm of b_m), the generational interpretation completely holds, and actually means that the total size of each generation grows asymptotically with per generation growth rate $r(K_E) = R_0$.

The generational interpretation (2.19) and the sign relation (2.7) are two essential norms for R_0, which should be shared among possible extensions.

3 The BG definition in a periodic environment

Next let us review the BG definition of R_0 in a periodic environment. Let $\theta > 0$ be a period of vital and environmental parameters. Then the basic renewal process is given as

[10] Equation (2.16) is already shown in Inaba and Nishiura (2008a) to interpret the next generation operator.

[11] For infinite-dimensional positive operator theory, the reader may refer to Marek (1962), Sawashima (1964), Marek (1970) and Schaefer and Wolff (1999), where the classical Krein–Rutman theory is extended as it can be applied to a positive cone without interior point.

$$b(t) = g(t) + \int_0^t \Psi(t, \tau) b(t - \tau) d\tau, \quad t > 0, \tag{3.1}$$

where $\Psi(t, \tau)$ is a linear positive operator on E_+ defined by

$$(\Psi(t, \tau) f)(\zeta) := \int_{\Omega_b} A(t, \tau, \zeta, \eta) f(\eta) d\eta.$$

Then $\Psi(t, \tau)$ maps the density vector of newborns produced at time $t - \tau$ to the density of their children produced at time t. From the periodicity of environmental parameters, we assume that Ψ has a period $\theta > 0$ as

$$\Psi(t + \theta, \tau) = \Psi(t, \tau), \quad t \in \mathbf{R}, \quad \tau > 0.$$

Bacaër and his collaborators (Bacaër and Guernaoui 2006; Bacaër and Ouifki 2007; Bacaër 2007, 2009; Bacaër and Abdurahman 2008; Bacaër and Ait Dads 2011a,b) defined R_0 for the periodic case by the unique real number such that there is a positive θ-periodic continuous E-valued function $f(t)$ satisfying

$$R_0 f(t) = \int_0^\infty \Psi(t, \tau) f(t - \tau) d\tau, \tag{3.2}$$

so R_0 for the periodic case is given by the spectral radius of the positive integral operator defined by

$$f \to \int_0^\infty \Psi(t, \tau) f(t - \tau) d\tau, \quad f \in C_\theta(\mathbf{R}; E), \tag{3.3}$$

where C_θ is the set of θ-periodic, continuous E-valued functions.

Let $K_\theta(\lambda)$ ($\lambda \in \mathbf{C}$) be the integral operator on C_θ defined by

$$(K_\theta(\lambda) f)(t) := \int_0^\infty e^{-\lambda\tau} \Psi(t, \tau) f(t - \tau) d\tau, \quad f \in C_\theta(\mathbf{R}; E), \tag{3.4}$$

so the operator (3.3) is given by $K_\theta(0)$. According to the periodic renewal theorem (Thieme 1984; Jagers and Nerman 1985), the solution of (3.1) satisfies $b(t) \sim e^{\lambda_0 t} \psi_0(t)$, $(t \to \infty)$, where $\psi_0 \in C_\theta$ is a positive eigenvector of $K_\theta(\lambda_0)$ associated with eigenvalue unity and the asymptotic growth rate λ_0 is a real number such that $r(K_\theta(\lambda_0)) = 1$. Moreover, it holds that

$$\text{sign}(\lambda_0) = \text{sign}(r(K_\theta(0)) - 1), \tag{3.5}$$

which shows that the BG definition $R_0 = r(K_\theta(0))$ is reasonable from the real-time perspective, because the sign relation holds.[12]

Different from the constant environment case, however, it is clear that the state space of $K_\theta(0)$ cannot be interpreted as the space of generation distributions aggregated by the operator T, because $K_\theta(0)$ is acting on the space of periodic functions. In fact, we can calculate the genealogy as follows:

$$b_0(t) = g(t), \quad b_m(t) = \int_0^t \Psi(t, \tau) b_{m-1}(t - \tau) d\tau, \quad m = 1, 2, \ldots, \tag{3.6}$$

Integrating both sides of the above iterative relation, we have

$$\begin{aligned}\int_0^\infty b_m(t)dt &= \int_0^\infty \int_0^t \Psi(t, \tau) b_{m-1}(t - \tau) d\tau dt \\ &= \int_0^\infty \int_0^\infty \Psi(s + \tau, s) ds b_{m-1}(\tau) d\tau.\end{aligned}$$

Therefore, in the time-dependent case, we cannot define a generation evolution operator acting between two successive time-aggregated generation distributions. However, another aggregation is possible for the periodic case.

Newborns are identified by the time at birth and h-state variable, however, for the periodic case, if $t_1 \equiv t_2 \pmod{\theta}$, time t_1 and time t_2 plays the same rule as h-state variable, because individuals born at t_1 and t_2 will experience the same life cycle due to the periodicity of environment. This observation suggests that the next generation operator could be defined on the space of θ-periodic functions. Then the time parameter in the extended h-state space is no longer a real chronological time, but it is an index to indicate a season (with mod θ) at which newborns occur.[13]

In order to formulate the above perspective under the L^1-setting,[14] first we define a space Y_θ (the periodic b-state space) as the set of locally integrable θ-periodic E-valued functions with norm

$$\|f\|_{Y_\theta} := \int_0^\theta \|f(t)\|_E dt = \int_0^\theta dt \int_{\Omega_b} |f(t, \zeta)| d\zeta,$$

[12] Another approach of mathematical justification for (3.5) may be found in Michel et al. (2005) and Thieme (2009).

[13] This kind of idea is already well known in the context of matrix population models (Caswell 2001; Bacaër 2009).

[14] Since L^1-norm of the density function gives the size of population, it is a most natural metric for population dynamics.

and, according to the BG definition, define the next generation operator K_θ given by

$$(K_\theta f)(t) := \int_0^\infty \Psi(t,\tau) f(t-\tau) d\tau, \quad f \in Y_\theta.$$

On the other hand, for the periodic case, we define the generation evolution operator (GEO) as follows:

$$(K_Y f)(t) := \int_0^t \Psi(t,\tau) f(t-\tau) d\tau, \quad f \in Y_+. \tag{3.7}$$

Then (3.6) is again expressed as the iteration process in Y_+ as $b_m = K_Y b_{m-1}$. Here we assume that K_Y defines a map from Y_+ into itself, although we examine the condition to guarantee that K_Y with time-dependent kernel Ψ defines a bounded linear operator in Y in the next section.

To aggregate the generation distributions, we introduce a periodization operator $U : Y \to (Y_\theta)_+$ by

$$(Uf)(t) := \sum_{n=-\infty}^{+\infty} |f^*(t+n\theta)|, \quad t \in \mathbf{R},$$

where $f^* \in L^1(\mathbf{R} \times \Omega_b)$ such that $f^*(t) = f(t)$ for $t \geq 0$ and $f^*(t) = 0$ for $t < 0$. Then the periodization operation U is seen as an aggregation of generation distributions by identifying $f \in Y_+$ with its θ-shifted distributions $f^*(t+n\theta)$.

Lemma 3 *It holds that*

$$\|f\|_Y = \|Uf\|_{Y_\theta}, \tag{3.8}$$

then the operator norm of U is unity. Moreover, it follows that

$$UK_Y f = K_\theta U f, \quad f \in Y_+. \tag{3.9}$$

Proof If $f \in Y_+$, it follows that

$$\begin{aligned} \|Uf\|_{Y_\theta} &= \int_0^\theta dt \int_{\Omega_b} d\zeta \sum_{n=-\infty}^{+\infty} f^*(t+n\theta) = \sum_{n=-\infty}^{+\infty} \int_{n\theta}^{(n+1)\theta} dt \int_{\Omega_b} d\zeta f^*(t) \\ &= \sum_{n=0}^{+\infty} \int_{n\theta}^{(n+1)\theta} dt \int_{\Omega_b} d\zeta f(t) = \int_0^\infty \|f(t)\|_E dt = \|f\|_Y. \end{aligned}$$

For general $f \in Y$, we have $f = f_+ - f_-$ and

$$\|f\|_Y = \|f_+\|_Y + \|f_-\|_Y = \|Uf_+\|_{Y_\theta} + \|Uf_-\|_{Y_\theta}.$$

On other hand, we observe that

$$\begin{aligned}(Uf)(t) &= \sum_{n=-\infty}^{+\infty} |f^*(t+n\theta)| \\ &= \sum_{n=-\infty}^{+\infty} f_+^*(t+n\theta) + \sum_{n=-\infty}^{+\infty} f_-^*(t+n\theta) \\ &= (Uf_+)(t) + (Uf_-)(t),\end{aligned}$$

which shows that

$$\|Uf\|_{Y_\theta} = \|Uf_+\|_{Y_\theta} + \|Uf_-\|_{Y_\theta}.$$

Then we obtain that $\|f\|_Y = \|Uf\|_{Y_\theta}$. Next let us show (3.9). Observe that for $f \in Y$

$$(K_Y f)^*(t) = \int_0^\infty \Psi(t,s) f^*(t-s) ds.$$

Therefore if $f \in Y_+$, we obtain

$$\begin{aligned}(UK_Y f)(t) &= \sum_{n=-\infty}^{+\infty} \int_0^\infty \Psi(t+n\theta, s) f^*(t+n\theta-s) ds \\ &= \int_0^\infty \Psi(t,s)(Uf)(t-s) ds,\end{aligned}$$

which shows that (3.9) holds. □

Now the generation evolution process in Y-space (3.6) is reduced to an iteration process in Y_θ-space. In fact, if we apply U to $b_m = K_Y b_{m-1}$ and use (3.9), we have

$$Ub_m = UK_Y b_{m-1} = K_\theta U b_{m-1}. \tag{3.10}$$

That is, the evolution process $b_m = K_Y b_{m-1}$ in the real generation distribution space Y is reduced to the evolution on the periodic b-state space so that the size of generation is preserving as $\|b_m\|_Y = \|Ub_m\|_{Y_\theta}$. From (3.10), it is reasonable to call K_θ the next generation operator, because it evolves the time-aggregated generation distributions in a sense.

To apply the positive operator theory, let us carry out the second aggregation. By using the periodicity, K_θ is reduced to an integral operator on $Z := L^1([0,\theta]; E)$.[15] Define a positive operator $K_Z : Z \to Z$ as follows:

$$(K_Z\phi)(t) := \int_0^\theta \Pi(t,s)\phi(s)ds, \quad t \in [0,\theta), \quad \phi \in Z, \tag{3.11}$$

where

$$\Pi(t,s) := \begin{cases} \sum_{n=0}^{\infty} \Psi(t, t-s+n\theta), & t > s, \\ \sum_{n=1}^{\infty} \Psi(t, t-s+n\theta), & t < s. \end{cases}$$

Let $V : Y_\theta \to Z$ be an operator such that $(Vf)(t) = f(t)$ for $t \in [0,\theta]$. Then we have

Lemma 4 *It holds that*

$$\|f\|_{Y_\theta} = \|Vf\|_Z, \tag{3.12}$$

then the operator norm of V is unity. Moreover it follows that

$$VK_\theta = K_Z V. \tag{3.13}$$

If we define $V^{-1} : Z \to Y_\theta$ as the operator which maps $\phi \in Z$ to its periodization in Y_θ, then V becomes a bijection from Y_θ to Z. Therefore we have $K_\theta = V^{-1}K_Z V$ and

Lemma 5 *It holds that*

$$r(K_Z) = r(K_\theta). \tag{3.14}$$

Now from (3.13), the iteration process (3.10) is reduced to an iteration process in the space Z:

$$VUb_m = VK_\theta Ub_{m-1} = K_Z VUb_{m-1}. \tag{3.15}$$

The function space Z is the set of state vectors in which the time parameter does not play a role as a chronological time, but a heterogeneity parameter to indicate a season at which newborns are produced.

Since we can usually expect that K_Z is a compact, positive nonsupporting operator, we can again apply the positive operator theory to conclude that

$$VUb_m = K_Z^m VUb_0 \sim \langle F_Z, VUb_0\rangle r(K_Z)^m f_Z, \quad m \to \infty, \tag{3.16}$$

[15] Since the reduction of K_θ to K_Z is introduced in Bacaër (2007), we omit the proof.

where $F_Z \in Z_+^*$ denotes the dual eigenfucntional with respect to the positive eigenvalue $r(K_Z)$ associated with the positive eigenfunction $f_Z \in Z_+$ and $\langle F_Z, \phi \rangle$ denotes the value of F_Z at $\phi \in Z$. From (3.8), (3.12), (3.14) and (3.16), we have

$$\lim_{m\to\infty} \sqrt[m]{\|VUb_m\|_Z} = r(K_Z) = r(K_\theta)$$
$$= \lim_{m\to\infty} \sqrt[m]{\|Ub_m\|_{Y_\theta}} = \lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}. \tag{3.17}$$

Equations (3.5) and (3.17) show that if we choose $r(K_\theta)$ as the basic reproduction number, both the sign relation and the generational interpretation hold completely:

Proposition 2 *The basic reproduction number R_0 by the BG definition allows the generational interpretation as*

$$R_0 = r(K_\theta) = \lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}. \tag{3.18}$$

Remark 1 Based on another type of argument, Bacaër and Ait Dads (2011a) proved

$$\limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} = r(K_\theta), \tag{3.19}$$

and they left an open question whether "lim sup" in (3.19) can be replaced by "lim", that is, the complete generational interpretation holds or not for the BG definition of R_0 in a periodic environment. In a recent manuscript (Bacaër and Ait Dads 2011b), they gave an affirmative answer to their own question based on a discrete model and a finite-dimensional renewal integral equation model. Our result (3.18) resolve their question. However, as is shown in the next section, their argument to lead (3.19) is very important by itself, in fact, it is my starting point for the new definition of R_0 applicable in general heterogeneous environments.

Remark 2 In this section, in order to induce the NGO K_θ of the BG definition, we have adopted tow-step aggregation of the space Y ($Y \to Y_\theta \to Z$), however one-step aggregation $Y \to Z$ is also possible, which is adopted in Bacaër and Ait Dads (2011b). Here we sketch this aggregation procedure by using our theoretical framework. Let us define a one-side aggregation operator $U_+ : Y \to Z$ as follows:

$$(U_+ f)(t) := \sum_{n=0}^{+\infty} |f(t+n\theta)|, \quad t \in [0,\theta), \quad f \in Y.$$

Then it is again easy to see that $\|U_+ f\|_Z = \|f\|_Y$. Observe that for $f \in Y_+$,

$$\begin{aligned}(U_+ K_Y f)(t) &= \sum_{n=0}^{\infty} \int_0^{t+n\theta} \Psi(t+n\theta, \tau) f(t+n\theta-\tau)d\tau \\ &= \sum_{n=0}^{\infty} \int_0^{t+n\theta} \Psi(t, t-z+n\theta) f(z)dz \\ &= \int_0^t \Psi(t, t-z) f(z)dz + \sum_{n=1}^{\infty} \left\{ \int_{n\theta}^{t+n\theta} + \int_0^{n\theta} \right\} \Psi(t, t-z+n\theta) f(z)dz,\end{aligned}$$

where

$$\int_{n\theta}^{t+n\theta} \Psi(t, t-z+n\theta) f(z) dz = \int_0^t \Psi(t, t-z) f(z+n\theta) dz,$$

$$\int_0^{n\theta} \Psi(t, t-z+n\theta) f(z) dz = \sum_{m=1}^{n} \int_{(m-1)\theta}^{m\theta} \Psi(t, t-z+n\theta) f(z) dz$$

$$= \sum_{m=1}^{n} \int_0^{\theta} \Psi(t, t-z+(n-m+1)\theta) f(z+(m-1)\theta) dz.$$

Therefore we have

$$(U_+ K_Y f)(t) = \int_0^t \Psi(t, t-z) \sum_{n=0}^{\infty} f(z+n\theta) dz$$
$$+ \sum_{n=1}^{\infty} \sum_{m=1}^{n} \int_0^{\theta} \Psi(t, t-z+(n-m+1)\theta) f(z+(m-1)\theta) dz$$

By changing the order of summation, it holds that

$$\sum_{n=1}^{\infty} \sum_{m=1}^{n} \int_0^{\theta} \Psi(t, t-z+(n-m+1)\theta) f(z+(m-1)\theta) dz$$
$$= \int_0^{\theta} \sum_{m=1}^{\infty} \Psi(t, t-z+m\theta) \sum_{n=0}^{\infty} f(z+n\theta) dz.$$

Thus we arrive at the conclusion:

$$(U_+ K_Y f)(t) = \int_0^t \Psi(t, t-z)(U_+ f)(z) dz + \int_0^{\theta} \sum_{m=1}^{\infty} \Psi(t, t-z+m\theta)(U_+ f)(z) dz$$
$$= \int_0^{\theta} \Pi(t, z)(U_+ f)(z) dz = (K_Z U_+ f)(t),$$

which shows that

$$U_+ K_Y f = K_Z U_+ f, \quad f \in Y_+.$$

That is, the evolution process $b_m = K_Y b_{m-1}$ is reduced to the evolution process $U_+ b_m = K_Z U_+ b_{m-1}$ on the space Z of aggregated generation distributions, then we can prove that

$$r(K_Z) = \lim_{m\to\infty} \sqrt[m]{\|U_+ b_m\|_Z} = \lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}.$$

In this case, K_Z is the next generation operator acting on the extended b-state space Z and $R_0 = r(K_Z)$.

4 A new definition of R_0 in heterogeneous environments

From the above arguments, we know that the generation evolution process in the extended b-state space Y; $b_m = K_Y b_{m-1}$ plays an essential role to determine the basic reproduction number. Hence, in order to define R_0 for general heterogeneous environments, we again introduce the generation evolution operator (GEO) as follows:

Definition 1 Let $\Psi(t, \tau)$ be the net reproduction operator from the b-state space $E_+ = L^1_+(\Omega_b)$ into itself. Then the *generation evolution operator* (GEO) associated with the net reproduction operator $\Psi(t, \tau)$ is the positive integral operator acting on the extended b-state space $Y_+ = L^1_+(\mathbf{R}_+; E_+) \simeq L^1_+(\mathbf{R}_+ \times \Omega_b)$ defined by

$$(K_Y f)(t) = \int_0^t \Psi(t, \tau) f(t-\tau) d\tau, \quad f \in Y_+. \tag{4.1}$$

First we check a condition to guarantee that $K_Y(Y_+) \subset Y_+$. Let us introduce the *cohort net reproduction operator* on E as

$$K_\tau \phi := \int_0^\infty \Psi(s+\tau, s)\phi ds, \quad \phi \in E.$$

Then we have

$$\begin{aligned} \|K_\tau \phi\|_E &= \int_{\Omega_b} d\zeta \left| \int_0^\infty (\Psi(s+\tau, s)\phi)(\zeta) ds \right| \\ &\le \int_0^\infty \|\Psi(s+\tau, s)\phi\|_E ds \\ &\le \int_0^\infty \|\Psi(s+\tau, s)\|_{\mathcal{L}(E)} ds \|\phi\|_E. \end{aligned}$$

Hence K_τ is a bounded positive linear operator from E into itself and it follows that

$$\|K_\tau\|_{\mathcal{L}(E)} \le \int_0^\infty \|\Psi(s+\tau, s)\|_{\mathcal{L}(E)} ds.$$

Note that $K_\tau \phi$ gives the "cumulative" density of children ever produced by the newborns ϕ at time τ. Then the average family size produced by a newborn is finite, if $\sup_{\tau \ge 0} \|K_\tau\|_{\mathcal{L}(E)} < \infty$. Therefore it is biologically reasonable to assume that

Assumption 1

$$\bar{K} := \sup_{\tau \ge 0} \int_0^\infty \|\Psi(s+\tau, s)\|_{\mathcal{L}(E)} ds < \infty, \tag{4.2}$$

which is a generalization of the condition (2.11).

Proposition 3 *Under the condition* (4.2), K_Y *is a bounded linear operator from* Y *into itself leaving the cone* Y_+ *invariant. Moreover,* $K_Y(Y_+ \backslash \{0\}) \subset Y_+ \backslash \{0\}$ *if* $K_\tau(E_+ \backslash \{0\}) \subset E_+ \backslash \{0\}$ *for almost all* $\tau \ge 0$.

Proof Observe that for $f \in Y_+$,

$$\begin{aligned} \|K_Y f\|_Y &= \int_0^\infty dt \int_{\Omega_b} d\zeta \int_0^t (\Psi(t, t-\tau) f(\tau))(\zeta) d\tau \\ &= \int_0^\infty dt \int_0^t d\tau \|\Psi(t, t-\tau) f(\tau)\|_E \\ &= \int_0^\infty d\tau \int_\tau^\infty dt \|\Psi(t, t-\tau) f(\tau)\|_E \\ &\le \int_0^\infty d\tau \int_0^\infty ds \|\Psi(s+\tau, s)\|_{\mathcal{L}(E)} \|f(\tau)\|_E \le \bar{K} \|f\|_Y. \end{aligned}$$

For any $f \in Y$, we have an expression $f = f_+ - f_-$, $f_\pm \in Y_+$. Then we have $\|K_Y f\|_Y \le \|K_Y f_+\|_Y + \|K_Y f_-\|_Y \le \bar{K} \|f\|_Y$. Therefore we have $\|K_Y\|_{\mathcal{L}(Y)} \le \bar{K}$ and $K_Y(Y_+) \subset Y_+$. Next observe that if $K_Y f = 0$ for $f \in Y_+$, it follows that

$$\int_0^\infty dt (K_Y f)(t) = \int_0^\infty dt \int_0^t \Psi(t, t-\tau) f(\tau) d\tau = 0.$$

By changing the order of integrals, we obtain

$$\int_0^\infty \int_0^\infty \Psi(s+\tau, s) ds f(\tau) d\tau = \int_0^\infty K_\tau f(\tau) d\tau = 0,$$

which implies that $K_\tau f(\tau) = 0$ for almost all $\tau \geq 0$. Hence, if $K_\tau(E_+ \backslash \{0\}) \subset E_+ \backslash \{0\}$ for almost all $\tau \geq 0$, $K_Y f = 0$ implies $f(\tau) = 0$ for almost all $\tau \geq 0$. □

Since $K_Y \in \mathcal{L}(Y)$, the generation evolution operator K_Y produces a birth genealogy $\{b_0, b_1, b_2, \ldots\} \subset Y_+$, by the iteration process $b_m = K_Y b_{m-1}$. Then $\|b_m\|_Y$ gives the total size of mth generation (total number of newborns produced as the mth generation), and the asymptotic per-generation growth factor is defined by $\lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}$ if it exists.

For any $t > 0$, the density of newborns at time t is given by a generation expansion:

$$b(t) = \sum_{m=0}^{\infty} (K_Y^m b_0)(t) = \sum_{m=0}^{\infty} b_m(t), \tag{4.3}$$

where $b_0 \in Y_+$ is the zero-th generation distribution.[16] Moreover (4.3) solves the renewal equation:

$$b(t) = g(t) + (\Psi(t) * b)(t), \quad g(t) = b_0(t). \tag{4.4}$$

where $\Psi(t)$ is an operator-valued function defined by $\Psi(t)(\tau) = \Psi(t, \tau)$, and $*$ denotes the convolution defined as

$$(\Psi(t) * b)(t) := \int_0^t \Psi(t, \tau) b(t-\tau) d\tau.$$

Observe that in (4.3), K_Y^m is given by

$$(K_Y^m f)(t) = (\Psi^{(m)}(t) * f)(t),$$

where the kernel $\Psi^{(m)}$ is defined iteratively as follows:

$$\Psi^{(1)} := \Psi, \quad \Psi^{(m+1)} := \Psi \diamond \Psi^{(m)},$$

and $\diamond$ denotes the two-parameter convolution defined by

$$(\Psi \diamond \Psi^{(m)})(t, \tau) = \int_0^\tau \Psi(t, \zeta) \Psi^{(m)}(t-\zeta, \tau-\zeta) d\zeta.$$

[16] From Lemma 7, we know that under the Assumption 2, for a fixed t, only finitely many $b_m(t)$ are not zero, so (4.3) becomes a finite sum and the generation expansion (4.3) is well-defined.

Then the resolvent kernel is given by

$$\Phi(t,\tau)=\sum_{m=1}^{\infty}\Psi^{(m)}(t,\tau),$$

which satisfies the resolvent equation:

$$\Phi=\Psi+\Psi\diamond\Phi,$$

and (4.3) is also expressed as

$$b(t)=g(t)+(\Phi(t)*g)(t).$$

As a biologically reasonable assumption for an overlapping generation model in a heterogeneous environment, we adopt the following assumption:

Assumption 2 There exist the *core* reproduction schedule $\Psi_1(\tau)$ and the *upper* reproduction schedule $\Psi_2(\tau)$ such that $\Psi_1(\tau)\le\Psi(t,\tau)\le\Psi_2(\tau)$ for all t and τ. The support of Ψ_2 is a finite interval $[\tau_1,\tau_2]$ with $\tau_1>0$ and there exists a nonsupporting and compact operator A on E such that $\Psi_1(\tau)=A$ for $\tau\in[\eta_1,\eta_2]$ with $\eta_2<2\eta_1$ and $\Psi_1(\tau)=0$ for $\tau\notin[\eta_1,\eta_2]$.

For biological individuals, there are the maximum age of reproduction and the minimum age of reproduction (maturation period), so it is reasonable to assume that there exists an upper reproduction schedule. On the other hand, although it is also reasonable for many cases, the existence of a fixed core reproductive schedule is a more restrictive assumption, but it is a useful technical assumption to show the uniform primitivity of the underlying population evolution process (Inaba 1989).

Corresponding to the core schedule and the upper schedule, we can define the core and the upper mth generation kernel as follows: $\Psi_j^{(1)}:=\Psi_j,\ \Psi_j^{(m+1)}:=\Psi_j*\Psi_j^{(m)}$. Then we have

$$\Psi_1^{(m)}(\tau)\le\Psi^{(m)}(t,\tau)\le\Psi_2^{(m)}(\tau).$$

Hence if $b_j(t)$ is the solution of the renewal equation $b(t)=g(t)+(\Psi_j*b)(t)$, then $b_1(t)\le b(t)\le b_2(t)$. We call $b_1(t)$ the *lower solution* and $b_2(t)$ the *upper solution* of (4.4). Since $\hat{\Psi}_j(\lambda),\ \lambda\in\mathbf{R}$ is a nonsupporting compact operators on $E,\ b_j$ is asymptotically proportional to an exponential solution, which implies that $b(t)$ is eventually positive and growing at most exponentially.

Under the above assumption, we can obtain information for the support of the generation distribution, which is used to estimate its average value. Here we define the support of a nonnegative operator $\Psi(\tau)$ by the closure of the set of τ such that $\Psi(\tau)$ is a positive (that is, non-zero and nonnegative) operator, and the support of a E-valued function $f(t)$ is the closure of the set of t such that $\|f(t)\|_E>0$. Roughly speaking, the support of $b_m(t)$ is increasing at most arithmetically and its length is larger than a positive constant. Proofs of the following Lemmas 6–7 are technical, they are given in Appendix:

Lemma 6 *Under the Assumption 2, the support of* $\Psi^{(m)}(t,\cdot)$ *is included in the interval* $[m\tau_1, m\tau_2]$ *for all* t *and it includes the interval* $[m\eta_1, m\eta_2]$. *Moreover, the support of* $b_m(\cdot)$ *is included in the interval* $[m\tau_1, (m+1)\tau_2]$ *for all* t.

Lemma 7 *Suppose that there exists a time interval* $(\alpha, \beta) \subset (0, \tau_2)$ *such that* $g(t) > 0$ *for* $t \in (\alpha, \beta)$. *Then, for large* m, *the support of* $b_m(\cdot)$ *includes the interval* $[\eta_1+(m-1)(\eta+\delta)+\alpha, \eta_2+(m-1)(\eta_2-\delta)+\beta]$, *where* δ *is a number such that* $\delta \in (0, \frac{1}{2}(\eta_2-\eta_1))$

If we see the renewal equation (4.4) as a linear equation $b = g + K_Y b$ in Y, then it is solved as $b = (I - K_Y)^{-1} g \in Y_+$ if $r(K_Y) < 1$, which suggests that $r(K_Y) < 1$ is a sufficient condition for population extinction, because $b \in Y_+$ means the total size of children produced in the future is finite. That is, R_0 should be related to the solvability of $b = g + K_Y b$ in Y. In the following, let us elaborate our argument.

From (4.3), we obtain

$$\|b\|_Y = \sum_{m=0}^{\infty} \|b_m\|_Y, \tag{4.5}$$

because b_m $(m = 0, 1, 2, \ldots)$ are nonnegative measurable functions in Y. Using the well-known Cauchy's criterion for convergence of a positive series, it follows that

$$\limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} < 1 \Longrightarrow \|b\|_Y = \sum_{m=0}^{\infty} \|b_m\|_Y < \infty, \tag{4.6}$$

$$\limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} > 1 \Longrightarrow \|b\|_Y = \sum_{m=0}^{\infty} \|b_m\|_Y = \infty. \tag{4.7}$$

Based on the above observation, we introduce the following definition of R_0 in a general heterogeneous environment:

Definition 2 For nontrivial initial data $b_0 \in Y_+ \setminus \{0\}$, the basic reproduction number for a birth genealogy produced by the generation evolution operator K_Y is defined by

$$R_0 = \limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} = \limsup_{m\to\infty} \sqrt[m]{\|K_Y^m b_0\|_Y}. \tag{4.8}$$

From the well-known extension of Cauchy–Hadamard Theorem in a Banach space, the definition (4.8) can be written as

$$R_0 = \frac{1}{\rho}, \tag{4.9}$$

where ρ is the radius of convergence of a power series in Y:

$$\sum_{m=0}^{\infty} b_m z^m = \sum_{m=0}^{\infty} (z^m K_Y^m) b_0, \quad z \in \mathbf{C}. \tag{4.10}$$

Then the power series (4.10) solves a linear equation with a parameter z:

$$y = b_0 + zK_Y y, \quad y \in Y, \tag{4.11}$$

in Y if $|z| < 1/R_0$, while it does not have a solution in Y if $|z| > 1/R_0$. This is another characterization of R_0.

Here we should note that the radius of convergence ρ is greater than the radius of convergence $1/r(K_Y)$ of the Neumann series in $\mathcal{L}(Y)$:

$$\sum_{m=0}^{\infty} z^m K_Y^m,$$

which converges to $(I - zK_Y)^{-1}$ if $|z| < 1/r(K_Y)$. In fact, we can observe from $\|b_m\|_Y \le \|K_Y^m\|_{\mathcal{L}(Y)}\|b_0\|_Y$ that

$$\limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} \le \limsup_{m\to\infty} \sqrt[m]{\|K_Y^m\|_{\mathcal{L}(Y)}} \limsup_{m\to\infty} \sqrt[m]{\|b_0\|_Y} = r(K_Y).$$

Therefore we have

$$R_0 = \limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} \le r(K_Y), \tag{4.12}$$

that is, we obtain $\rho \ge 1/r(K_Y)$. It should be noted that we do not know whether $R_0 = 1/\rho = r(K_Y)$ holds or not in general, however, as we see below, it holds for constant and periodic environments.

For our new definition of R_0 in a general heterogeneous environment, let us check supporting facts that it gives a kind of threshold value for population "growth", since it is not yet clear for us what the population "growth" means in a heterogeneous environment.[17] In the next section, we discuss possible extensions of the Malthusian parameter.

If $R_0 < 1$, there exist a number $r > 0$ and an integer m_0 such that $\sqrt[m]{\|b_m\|_Y} < r < 1$ for $m_0 < m$. Then the population will got to extinction in a sense that the size of each generation is geometrically decreasing:

$$\lim_{m\to\infty} \|b_m\|_Y \le \lim_{m\to\infty} r^m = 0.$$

Next it follows from $\|b\|_Y < \infty$ that

$$\lim_{t\to\infty} \int_t^{\infty} \|b(\zeta)\|_E d\zeta = 0,$$

[17] As is pointed out by Hans Metz (personal communications), it is difficult to characterize the population growth or decline in a heterogeneous environment only by using the size of generation distributions. For example, even when the generation size is decreasing, the value of the mth generation birth rate $\|b_m(t)\|_E$ could be increasing if the support of $\|b_m(t)\|_E$ is rapidly decreasing.

which shows that the size of newborns goes to extinction in L^1-sense. Thirdly, observe that the time average of the mth generation birth rate $\|b_m(t)\|_E$ is given by

$$A_m := \frac{1}{|\Omega_m|}\int_{\Omega_m} \|b_m(t)\|_E dt = \frac{\|b_m\|_Y}{|\Omega_m|},$$

where Ω_m denotes the support of $b_m(\cdot)$ and $|\Omega_m|$ is its length. From Lemma 7, we have $|\Omega_m| \geq \eta_2 - \eta_1 + \beta - \alpha$, so

$$A_m \leq \frac{r^m}{\eta_2 - \eta_1 + \beta - \alpha} \to 0 \quad (m \to \infty),$$

which shows that the average value of the mth generation birth rate $\|b_m(t)\|_E$ decreasing geometrically. In summary, $R_0 < 1$ is a sufficient condition for population extinction.[18]

If $R_0 > 1$, there exists a number $r > 0$ and integers $m(k)$, $k = 1, 2, \dots$ such that $m(1) < m(2) < \cdots \to +\infty$, $\sqrt[m(k)]{\|b_{m(k)}\|_Y} > r > 1$. Then we obtain that for any $m(k)$,

$$\|b\|_Y \geq \|b_{m(k)}\|_Y \geq r^{m(k)},$$

which implies

$$\lim_{k\to\infty} \|b_{m(k)}\|_Y = +\infty,$$

so there is a diverging series of the density of newborns and $\|b\|_Y = +\infty$. From Lemma 7, we have $|\Omega_m| \leq m(\tau_2 - \tau_1) + \tau_2$, so $|\Omega_m|$ is growing at most arithmetically. Therefore we can observe that

$$A_{m(k)} \geq \frac{r^{m(k)}}{m(k)(\tau_2 - \tau_1) + \tau_2} \to \infty \quad (k \to \infty),$$

which shows that the average value of $\|b_{m(k)}(t)\|_E$ has an asymptotic geometrical growth factor larger than unity. From the above observation, we can conclude that the population persists and grows in a sense if $R_0 > 1$, although we do not yet know whether there exists a positive Malthusian parameter when $R_0 > 1$.

Finally if $R_0 = 1$, it is inconclusive whether the population is persistent or extinction. In fact, both convergence and divergence of the positive series $\sum_{m=0}^{\infty} \|b_m\|_Y$ can occur when $\limsup_{m\to\infty} \sqrt[m]{\|b_m\|_Y} = 1$.

Next let us check that the definition of R_0 by (4.8) is independent from the choice of initial data b_0. Two elements $b_1,\ b_2$ in $Y_+\backslash\{0\}$ are called *comparable* if there exist numbers $\mu > 0$ and $\alpha \geq 1$ such that $\mu b_1 \leq b_2 \leq \alpha\mu b_1$. A subset of a positive cone Y_+ is called a *connected component* if any two elements of this subset are comparable.

[18] From (4.12), $r(K_Y) < 1$ is also a sufficient condition for population extinction.

Lemma 8 *Suppose that $K_Y(Y_+\backslash\{0\}) \subset Y_+\backslash\{0\}$. Then the definition (4.8) gives a unique R_0 for initial data b_0 belonging to a connected component.*

Proof If $u, v \in Y_+\backslash\{0\}$ and there exists positive numbers $0 < \alpha < \beta$ such that $\alpha u \le v \le \beta u$, it holds that

$$\alpha(K_Y)^m u \le (K_Y)^m v \le \beta(K_Y)^m u.$$

Therefore we have

$$\alpha\|(K_Y)^m u\|_Y \le \|(K_Y)^m v\|_Y \le \beta\|(K_Y)^m u\|_Y,$$

which implies that

$$\begin{aligned}
\limsup_{m\to\infty} \|(K_Y)^m u\|_Y^{1/m} &\le \limsup_{m\to\infty} \left(\frac{1}{\alpha}\right)^{1/m} \limsup_{m\to\infty} \|(K_Y)^m v\|_Y^{1/m},\\
\limsup_{m\to\infty} \|(K_Y)^m v\|_Y^{1/m} &\le \limsup_{m\to\infty} \beta^{1/m} \limsup_{m\to\infty} \|(K_Y)^m u\|_Y^{1/m}.
\end{aligned}$$

Thus we know that

$$\limsup_{m\to\infty} \|(K_Y)^m u\|_Y^{1/m} = \limsup_{m\to\infty} \|(K_Y)^m v\|_Y^{1/m},$$

which shows that R_0 is independent of the choice among comparable initial data. □

In order to show that it is not loss of generality for R_0 to consider initial data b_0 belonging to a connected component, let us introduce the age-density function of the underlying population evolution process, denoted by $p(t, \tau, \eta)$. Suppose that newborns $b(t, \zeta)$ is produced by the birth law as

$$b(t, \zeta) = \int_0^\infty d\tau \int_{\Omega_b} M(t, \tau, \zeta, \eta) p(t, \tau, \eta) d\eta,$$

and p and b are related by the survival law as

$$p(t, \tau, \eta) = \int_{\Omega_b} \Lambda(t, \tau, \eta; t-\tau, 0, \xi) b(t-\tau, \xi) d\xi,$$

where $M(t, \tau, \zeta, \eta)$ denotes the fertility rate at time t that an individual at age τ and state η produces newborns with state ζ, and $\Lambda(t+h, \tau+h, \zeta; t, \tau, \xi)$, $h \ge 0$ is the survival rate that an individual at time t, age τ and state ξ will survive to age $\tau + h$

and state ζ. Under the above setting, we have

$$(\Psi(t,\tau)f)(\zeta) = \int_{\Omega_b} d\xi \int_{\Omega_b} d\eta M(t,\tau,\zeta,\eta)\Lambda(t,\tau,\eta;t-\tau,0,\xi)f(\xi)$$
$$= \int_{\Omega_b} A(t,\tau,\zeta,\xi)f(\xi)d\xi,$$

and the starting function $g(t)$ of the renewal equation (4.4) is given as follows:

$$g(t) = \int_t^\infty d\tau \int_{\Omega_b} d\eta M(t,\tau,\zeta,\eta)p(t,\tau,\eta)$$
$$= \int_t^\infty d\tau \int_{\Omega_b} d\eta M(t,\tau,\zeta,\eta) \int_{\Omega_b} d\xi \Lambda(t,\tau,\eta;0,\tau-t,\xi)p(0,\tau-t,\xi)$$
$$= \int_t^\infty d\tau \int_{\Omega_b} d\xi \int_{\Omega_b} d\eta M(t,\tau,\zeta,\eta)\Lambda(t,\tau,\eta;0,\tau-t,\xi)p(0,\tau-t,\xi),$$

which shows that the initial data $b_0 = g$ is in a connected component if the initial population distribution $p(0,\tau,\xi)$ is in a connected component.

If the age-dependent population is time-evolved by a *uniformly primitive* evolutionary system (see Inaba 1989), any nontrivial age distributions[19] starting from two different initial distributions are going into a connected component after a finite time interval, that is, any age-distributions are eventually comparable.[20] Since the starting functions produced from comparable population distributions are also comparable, we can define a unique R_0 by (4.8) for any nontrivial initial data if we reset the time origin at the moment that any age-distributions have become comparable.

Subsequently let us examine relation between the new definition of R_0 and the spectral radius of GEO. Since we have not yet known general conditions such that the equality holds in the inequality (4.12), we cannot yet state that "the spectral radius of GEO is the basic reproduction number". Moreover, we do not know whether "lim sup" is replaced by "lim" in our new definition (4.8), so the generational interpretation is not complete.

However, at least for the case of constant and periodic environments, our new definition is seen as an extension of the DHM and BG definitions in the sense that $r(K_Y)$ gives R_0 of the DHM definition or of the BG definition and the generational interpretation holds:

[19] The initial age distribution p is called nontrivial if $g \neq 0$.

[20] More strongly, we can state that any age-distributions evolved by a uniformly primitive evolutionary system are asymptotically proportional to each other (*weak ergodicity*).

Proposition 4 *If the net reproduction operator Ψ is time independent, it holds that*

$$r(K_Y) = r(K_E) = \lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}. \tag{4.13}$$

Proof It follows from (2.18) and (4.12) that $r(K_E) \le r(K_Y)$. Then it is sufficient to show that $r(K_E) \ge r(K_Y)$. For $f \in Y_+$, observe that

$$\begin{aligned}
\|K_Y f\|_Y &= \int_{\Omega_b} d\zeta \int_0^\infty dt \int_0^t \Psi(s) f(t-s) ds \\
&= \int_{\Omega_b} d\zeta \int_0^\infty ds \int_s^\infty \Psi(s) f(t-s) dt = \int_{\Omega_b} d\zeta \int_0^\infty \Psi(s) ds \int_0^\infty f(t) dt \\
&= \int_{\Omega_b} d\zeta K_E T f = \|K_E T f\|_E.
\end{aligned}$$

Moreover, if $\|K_Y^n f\|_Y = \|K_E^n T f\|_E$ for $f \in Y_+$, we have

$$\|K_Y^{n+1} f\|_Y = \|K_Y^n (K_Y f)\|_Y = \|K_E^n T K_Y f\|_E = \|K_E^n K_E T f\|_E = \|K_E^{n+1} T f\|_E,$$

where we have used (2.15). By mathematical induction, it holds that

$$\|K_Y^n f\|_Y = \|K_E^n T f\|_E, \quad n = 1, 2, \ldots$$

Therefore, for any $f \in Y$, we obtain

$$\|K_Y^n f\|_Y \le \|K_Y^n f_+\|_Y + \|K_Y^n f_-\|_Y = \|K_E^n T f_+\|_E + \|K_E^n T f_-\|_E. \tag{4.14}$$

Here we can observe that

$$\|K_E^n T f\|_E = \|K_E^n T f_+\|_E + \|K_E^n T f_-\|_E, \tag{4.15}$$

because $Tf = Tf_+ + Tf_-$ and $\|K_E^n (f+g)\|_E = \|K_E^n f\|_E + \|K_E^n g\|_E$ if $f, g \in E_+$. From (4.14) and (4.15), we have

$$\|K_Y^n f\|_Y \le \|K_E^n T f\|_E.$$

Using the fact (2.14), we obtain for $f \ne 0$

$$\frac{\|K_Y^n f\|_Y}{\|f\|_Y} \le \frac{\|K_E^n T f\|_E}{\|T f\|_E}.$$

Note that $Tf \neq 0$ if $f \neq 0$. Therefore it follows that

$$\begin{aligned}\|K_Y^n\|_{\mathcal{L}(Y)} &= \sup_{f\in Y\setminus\{0\}} \frac{\|K_Y^n f\|_Y}{\|f\|_Y} \leq \sup_{f\in Y\setminus\{0\}} \frac{\|K_E^n Tf\|_E}{\|Tf\|_E} \\ &\leq \sup_{\phi\in E\setminus\{0\}} \frac{\|K_E^n \phi\|_E}{\|\phi\|_E} = \|K_E^n\|_{\mathcal{L}(E)},\end{aligned}$$

which shows that

$$r(K_Y) = \lim_{n\to\infty} \sqrt[n]{\|K_Y^n\|_{\mathcal{L}(Y)}} \leq \lim_{n\to\infty} \sqrt[n]{\|K_E^n\|_{\mathcal{L}(E)}} = r(K_E).$$

□

Proposition 5 *If the net reproduction operator* Ψ *is* θ*-periodic with respect to time* t*, it holds that*

$$r(K_Y) = r(K_\theta) = \lim_{m\to\infty} \sqrt[m]{\|b_m\|_Y}. \tag{4.16}$$

Proof It follows from (3.18) and (4.12) that $r(K_\theta) \leq r(K_Y)$. Then it is sufficient to show that $r(K_\theta) \geq r(K_Y)$. For $f \in Y_+$, observe that

$$\begin{aligned}\|K_Y f\|_Y &= \int_{\Omega_b} d\zeta \int_0^\infty dt \int_0^t \Psi(t,s) f(t-s) ds \\ &= \int_{\Omega_b} d\zeta \int_0^\infty dt \int_0^\infty \Psi(t,s) f^*(t-s) ds \\ &= \int_{\Omega_b} d\zeta \sum_{n=-\infty}^{\infty} \int_{n\theta}^{(n+1)\theta} dt \int_0^\infty \Psi(t,s) f^*(t-s) ds \\ &= \int_{\Omega_b} d\zeta \int_0^\theta dx \int_0^\infty \sum_{n=-\infty}^{\infty} \Psi(n\theta + x, s) f^*(n\theta + x - s) ds \\ &= \int_{\Omega_b} d\zeta \int_0^\theta dx \int_0^\infty \Psi(x,s) \sum_{n=-\infty}^{\infty} f^*(n\theta + x - s) ds \\ &= \int_{\Omega_b} d\zeta \int_0^\theta dx \int_0^\infty \Psi(x,s)(Uf)(x-s) ds \\ &= \int_{\Omega_b} d\zeta \int_0^\theta dx K_\theta Uf = \|K_\theta Uf\|_{Y_\theta}.\end{aligned}$$

If we assume that $\|K_Y^n f\|_Y = \|K_\theta^n U f\|_{Y_\theta}$ for $f \in Y_+$, we have

$$\|K_Y^{n+1} f\|_Y = \|K_Y^n (K_Y f)\|_Y = \|K_\theta^n U K_Y f\|_{Y_\theta} = \|K_\theta^{n+1} U f\|_{Y_\theta},$$

where we have used (3.9). By mathematical induction, it holds that for $f \in Y_+$

$$\|K_Y^n f\|_Y = \|K_\theta^n U f\|_{Y_\theta}, \quad n = 1, 2, \ldots$$

Therefore, for any $f \in Y$, we obtain

$$\|K_Y^n f\|_Y \leq \|K_Y^n f_+\|_Y + \|K_Y^n f_-\|_Y = \|K_\theta^n U f_+\|_{Y_\theta} + \|K_\theta^n U f_-\|_{Y_\theta}. \tag{4.17}$$

On the other hand, we can observe that

$$\|K_\theta^n U f\|_{Y_\theta} = \|K_\theta^n U f_+\|_{Y_\theta} + \|K_\theta^n U f_-\|_{Y_\theta}, \tag{4.18}$$

because $Uf = Uf_+ + Uf_-$ and $\|K_\theta^n (f+g)\|_{Y_\theta} = \|K_\theta^n f\|_{Y_\theta} + \|K_\theta^n g\|_{Y_\theta}$ if $f, g \in E_+$. From (4.17) and (4.18), we have

$$\|K_Y^n f\|_Y \leq \|K_\theta^n U f\|_{Y_\theta}.$$

Using the fact (3.8), we obtain for $f \neq 0$

$$\frac{\|K_Y^n f\|_Y}{\|f\|_Y} \leq \frac{\|K_\theta^n U f\|_{Y_\theta}}{\|U f\|_{Y_\theta}}.$$

Note that $Uf \neq 0$ if $f \neq 0$. Therefore it follows that

$$\begin{aligned}\|K_Y^n\|_{\mathcal{L}(Y)} &= \sup_{f \in Y \setminus \{0\}} \frac{\|K_Y^n f\|_Y}{\|f\|_Y} \leq \sup_{f \in Y \setminus \{0\}} \frac{\|K_\theta^n U f\|_{Y_\theta}}{\|U f\|_{Y_\theta}} \\ &\leq \sup_{\phi \in Y_\theta \setminus \{0\}} \frac{\|K_\theta^n \phi\|_{Y_\theta}}{\|\phi\|_{Y_\theta}} = \|K_\theta^n\|_{\mathcal{L}(Y_\theta)},\end{aligned}$$

which shows that

$$r(K_Y) = \lim_{n \to \infty} \sqrt[n]{\|K_Y^n\|_{\mathcal{L}(Y)}} \leq \lim_{n \to \infty} \sqrt[n]{\|K_\theta^n\|_{\mathcal{L}(Y_\theta)}} = r(K_\theta).$$

□

Finally remark that as the price of universal applicability, our definition of R_0 is not convenient for calculation purpose. In fact, it cannot be calculated as an eigenvalue of GEO:

Lemma 9 *K_Y has no non-zero eigenvalue.*

Proof Suppose that there exists an eigenfunction $f \in Y$ of K_Y associated with an eigenvalue λ, so it holds that

$$\lambda f(t) = \int_0^t \Psi(t,\tau) f(t-\tau) d\tau = \int_0^t \Psi(t, t-s) f(s) ds.$$

For any fixed $t_0 > 0$, define an operator $\Phi(t,s)$ such that $\Phi(t,s) = \Psi(t, t-s)$ if $t > s$ and $\Phi(t,s) = 0$ if $t < s$ for $(t,s) \in \Delta := [0, t_0] \times [0, t_0]$. Then it follows that for $t \in [0, t_0]$,

$$\lambda f(t) = \int_0^{t_0} \Phi(t,s) f(s) ds, \quad f \in L^1([0, t_0]; E),$$

which shows that λ is an eigenvalue of the Volterra type integral operator on $L^1(\Delta)$. However the Volterra type integral operator on $L^1(\Delta)$ is quasi-nilpotent (Kato 1984, pp. 153–154), so we have $\lambda = 0$. $\square$

5 The intrinsic growth rate in a heterogeneous environment

Finally let us consider possible extensions (definitions) of the Malthusian parameter in heterogeneous environments and check the sign relation.

First we note that due to the existence of the core reproduction schedule, the birth rate $\|b(t)\|_E$ is eventually positive. Then we can assume that $\|b(t)\|_E > 0$ for all large t. A first choice of the growth measure is the *Lyapunov order number*[21] for $\|b(t)\|_E$ defined by

$$\kappa := \limsup_{t \to \infty} \frac{\log \|b(t)\|_E}{t}.$$

Under the Assumption 2, it is easy to see that κ is finite, because it is less than the Malthusian parameter associated with the upper schedule.

Lemma 10 *If $R_0 > 1$, then $\kappa \geq 0$.*

Proof Suppose that $R_0 > 1$. If $\kappa < 0$, there exists a small $\epsilon > 0$ such that $\kappa + \epsilon < 0$ and there exists $t_0 > 0$ such that $\|b(t)\|_E < e^{(\kappa+\epsilon)t}$ for $t > t_0$, which implies that $\|b\|_Y = \int_0^\infty \|b(t)\|_E dt < \infty$. This contradicts $R_0 > 1$. Then we have $\kappa \geq 0$.

Suppose that $\|b(t)\|_E > 0$ for $t \geq t_0$. If $\|b(t)\|_E$ is differentiable,

$$r(t) := \frac{d}{dt} \log \|b(t)\|_E,$$

[21] See Hartman (2002).

is the growth rate at time t. Then we have

$$\int_{t_0}^{t} r(s)ds = \log\left(\frac{\|b(t)\|_E}{\|b(t_0)\|_E}\right),$$

and the average growth rate is, if it exists, calculated as

$$\lim_{t\to\infty}\frac{1}{t-t_0}\int_{t_0}^{t} r(s)ds = \lim_{t\to\infty}\frac{\log\|b(t)\|_E}{t}.$$

Then if the limit exists, we define the *average Multhusian parameter* as follows:

$$\bar{\lambda}_0 := \lim_{t\to\infty}\frac{\log\|b(t)\|_E}{t}.$$

A possible extension of the sign relation in heterogeneous environments may be

$$\text{sign}(R_0 - 1) = \text{sign}(\bar{\lambda}_0). \tag{5.1}$$

Although we have not yet known a most general condition for the existence of the average Malthusian parameter,[22] we examine the relation between R_0 and $\bar{\lambda}_0$ under the assumption that $\bar{\lambda}_0$ exists.

For this purpose, let us introduce a third measure. For $f \in Y$, we define the real Laplace transform of the E-norm of $f(t): \mathbf{R}_+ \to E$, denoted by $(Lf)(\lambda)$, as follows:

$$(Lf)(\lambda) := \int_0^{\infty} e^{-\lambda t}\|f(t)\|_E dt, \quad \lambda \in \mathbf{R}.$$

The *abscissa of absolute convergence*, denoted by σ_a, is defined as a real number such that if $\lambda > \sigma_a$, $(Lf)(\lambda) < \infty$, while $(Lf)(\lambda) = \infty$ if $\lambda < \sigma_a$. If $(Lf)(\lambda) < \infty$ for all $\lambda \in \mathbf{R}$, $\sigma_a = -\infty$, while $\sigma_a = \infty$ if $(Lf)(\lambda) = \infty$ for all $\lambda \in \mathbf{R}$.

Lemma 11 *It holds that $\sigma_a \le \kappa$. If the average Malthusian parameter exists, it holds that $\kappa = \bar{\lambda}_0 = \sigma_a$.*

Proof For any small $\epsilon > 0$, there exists $t_0 > 0$ such that $\|b(t)\|_E < e^{(\kappa+\epsilon)t}$ for $t > t_0$. Then $(Lb)(\lambda) < \infty$ for $\lambda > \kappa + \epsilon$, which means $(Lb)(\lambda) < \infty$ for $\lambda > \kappa$ and $\sigma_a \le \kappa$. Next suppose that the average Malthusian parameter exists. For any $\epsilon > 0$, there exists $t_0 > 0$ such that $e^{(\bar{\lambda}_0-\epsilon)t} < \|b(t)\|_E < e^{(\bar{\lambda}_0+\epsilon)t}$. Then we conclude that $\bar{\lambda}_0 = \sigma_a$. □

22 For example, if the birth rate $\|b(t)\|_E$ is asymptotically comparable with an exponential function, that is, if there exist numbers r and $0 < M_1 < M_2$ such that $M_1 e^{rt} \le \|b(t)\|_E \le M_2 e^{rt}$ for all large t, it is easy to see that the exponent r gives the average Malthusian parameter. This situation covers the periodic case and the asymptotically autonomous case (Inaba 1992).

In order to formulate a relation between R_0 and σ_a, first we prepare technical lemmas, whose proofs are given in Appendix:

Lemma 12 *If* $(Lf)(\lambda) < \infty$ *for* $\lambda > 0$, *it follows that*

$$\int_0^t \|f(\zeta)\|_E d\zeta = o(e^{\lambda t}). \tag{5.2}$$

Lemma 13 *If there exists a number* μ *and* M *such that*

$$\int_0^t \|f(\zeta)\|_E d\zeta \le M e^{\mu t},$$

then $(Lf)(\lambda) < \infty$ *for* $\lambda > \mu$.

Proposition 6 *Let* $b(t)$ *be the solution of* (4.4). *If* $R_0 > 1$, *then* $\sigma_a \ge 0$ *and*

$$\sigma_a = \limsup_{t\to\infty} \frac{1}{t} \log \int_0^t \|b(\zeta)\|_E d\zeta. \tag{5.3}$$

Proof If $R_0 > 1$, it follows from (4.7) that

$$\|b\|_Y = \int_0^\infty \|b(\zeta)\|_E d\zeta = \sum_{m=0}^\infty \|b_m\|_Y = \infty,$$

which means that $(Lb)(0) = \infty$ and $\sigma_a \ge 0$. Let

$$\lambda_0 := \limsup_{t\to\infty} \frac{1}{t} \log \int_0^t \|b(\zeta)\|_E d\zeta.$$

It follows from $(Lb)(0) = \infty$ that $\lambda_0 \ge 0$. First we assume that $\lambda_0 < \infty$. Then for any small $\epsilon > 0$, we can take a large $t > 0$ such that

$$\int_0^t \|b(\zeta)\|_E d\zeta < e^{(\lambda_0+\epsilon)t}.$$

From Lemma 13, $(Lb)(\lambda) < \infty$ for $\lambda > \lambda_0 + \epsilon$. Since ϵ is any small positive number, we know that $(Lb)(\lambda) < \infty$ for $\lambda > \lambda_0$, which implies that $\sigma_a \le \lambda_0$. Suppose that $\sigma_a < \lambda_0$. Then there exists a number λ' such that $0 \le \sigma_a < \lambda' < \lambda_0$ and so $(Lb)(\lambda') < \infty$. From Lemma 12, we have

$$\int_0^t \|b(\zeta)\|_E d\zeta = o(e^{\lambda' t}).$$

Thus there exists a number $M > 1$ such that

$$\int_0^t \|b(\zeta)\|_E d\zeta \le M e^{\lambda' t}.$$

Therefore we obtain that

$$\frac{1}{t} \log \int_0^t \|b(\zeta)\|_E d\zeta \le \frac{\log M}{t} + \lambda',$$

which shows that

$$\lambda_0 = \limsup_{t\to\infty} \frac{1}{t} \log \int_0^t \|b(\zeta)\|_E d\zeta \le \lambda'.$$

This contradicts the assumption $\lambda' < \lambda_0$, hence we conclude that $\sigma_a = \lambda_0$. Next we consider the case that $\lambda_0 = \infty$. If $\sigma_a < \infty$, there exists λ' such that $\sigma_a < \lambda' < \infty$ and we can repeat the above argument to arrive at a contradiction. Then $\sigma_a = \lambda_0 = \infty$. □

Lemma 14 *If* $(Lf)(\lambda) < \infty$ *for* $\lambda < 0$, *it holds that*

$$\int_t^\infty \|f(\zeta)\| d\zeta = o(e^{\lambda t}).$$

Lemma 15 *If there exists a number* μ *and* M *such that*

$$\int_t^\infty \|f(\zeta)\|_E d\zeta \le M e^{\mu t},$$

then $(Lf)(\lambda) < \infty$ *for* $\lambda > \mu$.

Proposition 7 *Let* $b(t)$ *be the solution of* (4.4). *If* $R_0 < 1$, *then* $\sigma_a \le 0$ *and*

$$\sigma_a = \limsup_{t\to\infty} \frac{1}{t} \log \int_t^\infty \|b(\zeta)\|_E d\zeta. \tag{5.4}$$

Proof If $R_0 < 1$, it follows from (4.6) that

$$\|b\|_Y = \int_0^\infty \|b(\zeta)\|_E d\zeta = \sum_{m=0}^\infty \|b_m\|_Y < \infty,$$

which means that $(Lb)(0) < \infty$ and $\sigma_a \le 0$. Let

$$\mu_0 := \limsup_{t\to\infty} \frac{1}{t} \log \int_t^\infty \|b(\zeta)\|_E d\zeta.$$

It follows from $(Lb)(0) < \infty$ that $\mu_0 \le 0$.

First we consider the case that $\mu_0 > -\infty$. Then for any small $\epsilon > 0$, we can take a large $t_0 > 0$ such that

$$\int_t^\infty \|b(\zeta)\|_E d\zeta < e^{(\mu_0+\epsilon)t}, \quad \forall t > t_0.$$

From Lemma 15, $(Lb)(\lambda) < \infty$ for $\lambda > \mu_0 + \epsilon$. Since ϵ is any small positive number, we know that $(Lb)(\lambda) < \infty$ for $\lambda > \mu_0$, which implies that $\sigma_a \le \mu_0$.

Suppose that $\sigma_a < 0$. Then there exists a number λ' such that $\sigma_a < \lambda' < 0$ and so $(Lb)(\lambda') < \infty$. From Lemma 14, we have

$$\int_t^\infty \|b(\zeta)\|_E d\zeta = o(e^{\lambda' t}).$$

Thus there exists a number $M \ge 1$ such that

$$\int_t^\infty \|b(\zeta)\|_E d\zeta \le M e^{\lambda' t}.$$

Therefore we obtain that

$$\frac{1}{t} \log \int_t^\infty \|b(\zeta)\|_E d\zeta \le \frac{\log M}{t} + \lambda',$$

which shows that

$$\mu_0 = \limsup_{t\to\infty} \frac{1}{t} \log \int_t^\infty \|b(\zeta)\|_E d\zeta \le \lambda'.$$

This implies that $\mu_0 \leq \sigma_a$, so we have $\mu_0 = \sigma_a$. Next suppose that $\sigma_a = 0$. If $\mu_0 < 0$, we have $0 = \sigma_a \leq \mu_0 < 0$, so this is a contradiction. Then we have $\mu_0 = \sigma_a = 0$.

Finally let us consider the case that $\mu_0 = -\infty$. In this case, for any $\mu < 0$, we can choose a sufficiently large t_0 such that

$$\int_t^\infty \|b(\zeta)\| d\zeta < e^{\mu t}, \quad \forall t > t_0,$$

which implies that $(Lb)(\lambda) < \infty$ for $\lambda > \mu$ (Lemma 15). Since $\mu < 0$ is any negative number, we have $\sigma_a = -\infty = \mu_0$. □

From the above observations, we know that

Proposition 8 *If the average Malthusian parameter exists,* $\bar{\lambda}_0 \geq 0$ *when* $R_0 > 1$*, while* $\bar{\lambda}_0 \leq 0$ *when* $R_0 < 1$.

6 Discussion

In this paper, first we have cleared some ambiguous points in the well-known traditional definition of R_0 in a constant environment and in its recent extension to the case of periodic environment. From our point of view, the next generation operator is useful for calculation purpose because its spectral radius is R_0 and it is calculated as the positive eigenvalue, but it is an artificial operator acting on a state space of aggregated generation distributions for both constant and periodic cases. In order to go beyond those two special cases, we have to return to elementary observation that newborns are identified by the extended h-state variables, that is, time at birth and h-state variables.

Instead of the next generation operator, we introduced the generation evolution operator (GEO) acting on the extended b-state space $Y = L^1(\mathbf{R}_+ \times \Omega_b)$. Based on the generation evolution operator, we have proposed a new definition of R_0, which is given by a reciprocal number of the radius of convergence of a power series in the extended b-state space.

As the new basic reproduction number R_0 is the upper limit of the per-generation growth factor of the generation distribution, it can be applied to population renewal process in any heterogeneous environment, while we may not yet say that the spectral radius of the generation evolution operator always gives R_0. The constant environment and the periodic environment are two special cases such that R_0 is given by the spectral radius of GEO and the generational interpretation completely holds, that is, we have

$$R_0 = r(K_Y) = \lim_{m \to \infty} \sqrt[m]{\|b_m\|_Y}, \tag{6.1}$$

and $r(K_Y)$ coincides with the spectral radius of the next generation operator. In this sense, our definition of R_0 based on GEO is an extension of the DHM definition and the BG definition. It is an open problem whether there exists a more general environment than periodicity under which (6.1) holds.

From generational point of view, if there exists a maturation time and the reproductive period is finite, there exists a subseries of generation distributions where the average value of the birth rate per unit time is geometrically growing when $R_0 > 1$. On the other hand, $R_0 < 1$ is a sufficient condition for population extinction, so our new R_0 plays a role of a threshold value for population persistence.

Finally we have shown that if the average Malthusian parameter exists, it is nonnegative when $R_0 > 1$, while it is nonpositive when $R_0 < 1$. However, it is also an open question what is a most general condition for the existence of the average Mathusian parameter such that the sign relation holds.

From practical point of view, our new definition of R_0 is not convenient for analytical computation, however it is biologically most natural definition to reveal the essential structure of population renewal process and can provide a powerful approach to extensions of the basic reproduction number. For example, the concept of generation evolution operator plays a crucial role to define the type-reproduction number in heterogeneous environments, which will be discussed in a separate paper.

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Appendix

Here we give proofs for technical lemmas. For Lemmas 12–15, the reader may find the original ideas in Widder (1946):

Proof of Lemma 6 To show the first part, since $\Psi_1^{(m)}(\cdot) \le \Psi^{(m)}(t,\cdot) \le \Psi_2^{(m)}(\cdot)$ for all t, it is sufficient to show that the support of $\Psi_2^{(m)}(\cdot)$ is included in the interval $[m\tau_1, m\tau_2]$. Suppose that $\Psi_2^{(m)}(\tau) = 0$ for $\tau \notin [m\tau_1, m\tau_2]$. From

$$\Psi_2^{(m+1)}(\tau) = \int_0^\tau \Psi_2(\zeta)\Psi_2^{(m)}(\tau-\zeta)d\zeta,$$

we have $\Psi_2^{(m+1)} = 0$ if $\tau < \tau_1$. If $(m+1)\tau_1 > \tau > \tau_1$, we again obtain

$$\Psi_2^{(m+1)}(\tau) = \int_{\tau_1}^\tau \Psi_2(\zeta)\Psi_2^{(m)}(\tau-\zeta)d\zeta = 0,$$

because $\tau - \zeta < m\tau_1$. Moreover if $\tau > (m+1)\tau_2$, we have

$$\Psi_2^{(m+1)}(\tau) = \int_0^{\tau_2} \Psi_2(\zeta)\Psi_2^{(m)}(\tau-\zeta)d\zeta = 0,$$

since $\tau-\zeta>m\tau_2$. By mathematical induction, we know that the support of $\Psi_2^{(m)}(\cdot)$ is included in the interval $[m\tau_1, m\tau_2]$.

Next we show that $\Psi_1^{(m)}(\tau)$ is a positive operator for $\tau\in(m\eta_1, m\eta_2)$. This statement holds for $m=1$. Suppose that it holds for $m=k$. If $\tau\in((k+1)\eta_1, (k+1)\eta_2)$, then we have

$$\Psi_1^{(k+1)}(\tau)=\int_{\eta_1}^{\eta_2}\Psi_1(\zeta)\Psi_1^{(k)}(\tau-\zeta)d\zeta=\int_{\tau-\eta_2}^{\tau-\eta_1}A\Psi_1^{(k)}(x)dx,$$

is a positive operator, because $[k\eta_1, k\eta_2]\cap[\tau-\eta_2, \tau-\eta_1]$ has a positive measure. Then by mathematical induction, we know that $\Psi_1^{(m)}(\tau)$ is a positive operator for $\tau\in(m\eta_1, m\eta_2)$. Then the support of $\Psi^{(m)}(t,\cdot)$ includes the interval $[m\eta_1, m\eta_2]$.

Finally, since $g(t)=b_0(t)=0$ for $t>\tau_2$, it follows from the relation $b_m=\Psi^{(m)}(t)*b_0$ that support $b_m\subset[m\tau_1, (m+1)\tau_2]$. □

Proof of Lemma 7 Let δ be a number such that $\delta\in(0, \frac{1}{2}(\eta_2-\eta_1))$. First we show that $\Psi_1^{(m)}(\tau)\geq A^m\delta^{m-1}$ for $\tau\in[\eta_1+(m-1)(\eta_1+\delta), \eta_2+(m-1)(\eta_2-\delta)]$. From the Assumption 2, the above statement holds for $m=1$. Suppose that the statement holds for $m=k$. For $\tau\in[\eta_1+k(\eta_1+\delta), \eta_2+k(\eta_2-\delta)]$, it holds that

$$\Psi_1^{(k+1)}(\tau)=\int_{\eta_1}^{\eta_2}\Psi_1(\zeta)\Psi_1^{(k)}(\tau-\zeta)d\zeta=\int_{\tau-\eta_2}^{\tau-\eta_1}A\Psi_1^{(k)}(x)dx.$$

Let $L_k:=[\eta_1+(k-1)(\eta_1+\delta), \eta_2+(k-1)(\eta_2-\delta)]\cap[\tau-\eta_2, \tau-\eta_1]$. Then if $\tau\in[\eta_1+k(\eta_1+\delta), \eta_2+k(\eta_2-\delta)]$, we have $|L_k|\geq\delta$, so it follows that

$$\Psi_1^{(k+1)}(\tau)\geq\int_{L_k}A\Psi_1^{(k)}(x)dx\geq A^{k+1}\delta^k,$$

because $\Psi_1^{(k)}(x)\geq A^k\delta^{k-1}$ for $x\in L_k$ from our assumption. By mathematical induction, we obtain the conclusion. Let $u_m:=\eta_1+(m-1)(\eta+\delta)$ and $v_m:=\eta_2+(m-1)(\eta_2-\delta)$. Then if $t\in[\eta_1+(m-1)(\eta+\delta)+\alpha, \eta_2+(m-1)(\eta_2-\delta)+\beta]$,

$$\begin{aligned}b_m(t)&\geq\int_{u_m}^{t\wedge v_m}\Psi_1^{(m)}(\tau)b_0(t-\tau)d\tau\\&=\int_{t-t\wedge v_m}^{t-u_m}\Psi_1^{(m)}(t-x)b_0(x)dx\geq\int_{J_m}A^m\delta^{m-1}b_0(x)dx,\end{aligned}$$

because $J_m:=(t-t\wedge v_m, t-u_m)\cap(\alpha,\beta)\neq\emptyset$, on which $\Psi_1^{(m)}(t-x)\geq A^m\delta^{m-1}$ and $A^m\delta^{m-1}b_0(x)$ becomes a quasi-interior point for large m since A is a nonsupporting operator. Then $b_m(t)$ is almost everywhere positive in $[\eta_1 + (m-1)(\eta+\delta)+\alpha, \eta_2 + (m-1)(\eta_2 - \delta) + \beta]$. □

Proof of Lemma 12 Define

$$F_\lambda(t) := \int_0^t e^{-\lambda\zeta} \|f(\zeta)\|_E d\zeta.$$

Then we observe that

$$\begin{aligned}\int_0^t \|f(\zeta)\|_E d\zeta &= \int_0^t e^{\lambda\zeta} e^{-\lambda\zeta} \|f(\zeta)\|_E d\zeta \\ &= \left[e^{\lambda\zeta} F_\lambda(\zeta)\right]_0^t - \lambda \int_0^t e^{\lambda\zeta} F_\lambda(\zeta) d\zeta = e^{\lambda t} F_\lambda(t) - \lambda \int_0^t e^{\lambda\zeta} F_\lambda(\zeta) d\zeta\end{aligned}$$

Since $F_\lambda(t) \to (Lf)(\lambda) < \infty$ as $t \to \infty$, we have

$$\begin{aligned}\lim_{t\to\infty} e^{-\lambda t} \int_0^t \|f(\zeta)\|_E d\zeta &= (Lf)(\lambda) - \lim_{t\to\infty} \lambda e^{-\lambda t} \int_0^t e^{\lambda\zeta} F_\lambda(\zeta) d\zeta \\ &= \lim_{t\to\infty} \lambda e^{-\lambda t} \int_0^t e^{\lambda\zeta} ((Lf)(\lambda) - F_\lambda(\zeta)) d\zeta = 0.\end{aligned}$$

□

Proof of Lemma 13 Using the same notation as the proof of Lemma 12, we can observe that

$$\begin{aligned}\int_0^t e^{-\lambda\zeta} \|f(\zeta)\|_E d\zeta &= \left[e^{-\lambda\zeta} F_0(\zeta)\right]_0^t + \lambda \int_0^t e^{-\lambda\zeta} F_0(\zeta) d\zeta \\ &= e^{-\lambda t} F_0(t) + \lambda \int_0^t e^{-\lambda\zeta} F_0(\zeta) d\zeta \\ &\le M e^{-(\lambda-\mu)t} + |\lambda| \int_0^t M e^{-(\lambda-\mu)\zeta} d\zeta < \infty, \quad (t \to \infty).\end{aligned}$$

□

Proof of Lemma 14 Using the same notation as the proof of Lemma 12, we have $F_0(\infty) < \infty$, since $(Lf)(0) \le (Lf)(\lambda) < \infty$. Observe that

$$F_0(\infty) - F_0(t) = \int_t^\infty e^{\lambda\zeta} e^{-\lambda\zeta} \|f(\zeta)\| d\zeta$$
$$= \left[F_\lambda(\zeta) e^{\lambda\zeta}\right]_t^\infty - \lambda \int_t^\infty e^{\lambda\zeta} F_\lambda(\zeta) d\zeta$$
$$= -F_\lambda(t) e^{\lambda t} - \lambda \int_t^\infty e^{\lambda\zeta} F_\lambda(\zeta) d\zeta.$$

Then we have

$$\lim_{t\to\infty} e^{-\lambda t}(F_0(\infty) - F_0(t)) = -F_\lambda(\infty) - \lim_{t\to\infty} \lambda e^{-\lambda t} \int_t^\infty e^{\lambda\zeta} F_\lambda(\zeta) d\zeta$$
$$= \lim_{t\to\infty} \lambda e^{-\lambda t} \int_t^\infty e^{\lambda\zeta} (F_\lambda(\infty) - F_\lambda(\zeta)) d\zeta = 0,$$

which shows that

$$F_0(\infty) - F_0(t) = \int_t^\infty \|f(\zeta)\| d\zeta = o(e^{\lambda t}).$$

□

Proof of Lemma 15 Let

$$G(t) := \int_t^\infty \|f(\zeta)\| d\zeta \le M e^{\mu t}.$$

Then we can observe that

$$\int_t^\infty e^{-\lambda\zeta} \|f(\zeta)\|_E d\zeta = \left[-e^{-\lambda\zeta} G(\zeta)\right]_t^\infty - \lambda \int_t^\infty e^{-\lambda\zeta} G(\zeta) d\zeta$$
$$= e^{-\lambda t} G(t) - \lambda \int_t^\infty e^{-\lambda\zeta} G(\zeta) d\zeta$$
$$\le M e^{-(\lambda-\mu)t} + |\lambda| \int_t^\infty M e^{-(\lambda-\mu)\zeta} d\zeta < \infty.$$

□

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