

THE MALTHUSIAN PARAMETER AND R_0 FOR HETEROGENEOUS POPULATIONS IN PERIODIC ENVIRONMENTS

HISASHI INABA

Graduate School of Mathematical Sciences, University of Tokyo
3-8-1 Komaba Meguro-ku, Tokyo 153-8914, Japan

(Communicated by Yang Kuang)

ABSTRACT. Since the classical stable population theory in demography by Sharpe and Lotka, the sign relation $\text{sign}(\lambda_0) = \text{sign}(R_0 - 1)$ between the basic reproduction number R_0 and the Malthusian parameter (the intrinsic rate of natural increase) λ_0 has played a central role in population theory and its applications, because it connects individual's average reproductivity described by life cycle parameters to growth character of the whole population. Since R_0 is originally defined for linear population evolution process in a constant environment, it is an important extension if we could formulate the same kind of 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 so that it can be applied to population dynamics in periodic environments. In particular, the definition of R_0 in a periodic environment by Bacaër and Guernaoui (*J. Math. Biol.* 53, 2006) is most important, because their definition of R_0 in a periodic environment can be interpreted as the asymptotic per generation growth rate, so from the generational point of view, it can be seen as a direct extension of the most successful definition of R_0 in a constant environment by Diekmann, Heesterbeek and Metz (*J. Math. Biol.* 28, 1990).

In this paper, we propose a new approach to establish the sign relation between R_0 and the Malthusian parameter λ_0 for linear structured population dynamics in a periodic environment. Our arguments depend on the uniform primitivity of positive evolutionary system, which leads the weak ergodicity and the existence of exponential solution in periodic environments. For typical finite and infinite dimensional linear population models, we prove that a positive exponential solution exists and the sign relation holds between the Malthusian parameter, which is defined as the exponent of the exponential solution, and R_0 given by the spectral radius of the next generation operator by Bacaër and Guernaoui's definition.

1. Introduction. Since the brilliant study for the stable population theory by Alfred Lotka and his collaborators, the threshold condition for population growth formulated by the basic reproduction number R_0 and the Malthusian parameter (the intrinsic rate of natural increase), denoted by λ_0 here, have been recognized as a most important result in population dynamics and its applications. For example, the basic reproduction number for infectious diseases is essential to quantify the

2000 *Mathematics Subject Classification.* Primary: 92D30; Secondary: 92D25.

Key words and phrases. Basic reproduction number, Malthusian parameter, periodic environments, weak ergodicity, uniform primitivity, exponential solutions.

disease prevention policy, and the Malthusian parameter is seen as a measure of fitness of mutant population in evolutionary biology.

In the stable population theory, the basic population system has a positive exponential solution with the growth rate λ_0 which dominates the asymptotic behavior of the population, and the following *sign relation* holds:

$$\text{sign}(\lambda_0) = \text{sign}(R_0 - 1), \quad (1)$$

where the basic reproduction number R_0 is the asymptotic growth factor of the size of successive generations (the *generational interpretation*).

Therefore R_0 can play a role of the threshold condition for population growth based on parameters capturing the average behavior of individuals, that is, it connects individual life cycle parameters to growth character of the whole population. Then we can summarize the essential feature of this threshold theory of population growth as follows:

1. There exists a positive dominant exponential solution, whose exponent gives the Malthusian parameter λ_0 of the population,
2. The basic reproduction number R_0 that allows the generational interpretation can be defined and the sign relation (1) holds between R_0 and λ_0 .

The above threshold theory was successfully established for heterogeneous populations in constant environments by Diekmann, Heesterbeek and Metz ([20], it is called the DHM definition here for short). Then it would be an important extension if we could formulate the same kind of threshold theory for structured populations in time-heterogeneous environments.

During the last two decades, in the context of infectious disease epidemiology, several authors ([2]–[7], [27], [28], [49], [52]) proposed some ideas to extend the definition of R_0 so that it can be applied to population dynamics in periodic environments. In particular, the definition of R_0 in periodic environments by Bacaër and Guernaoui ([2]) (which is called the BG definition for short in the following) is most important, because as is shown by Bacaër and Ait Dads ([6], [7]) and Inaba ([37]), their definition of periodic R_0 allows the generational interpretation, that is, it is interpreted as the asymptotic ratio of successive generation size, so it is a direct extension of the DHM definition of R_0 in a constant environment.

Although the threshold property of the BG definition of R_0 has been proved by several authors ([46], [38], [49]), here we propose an another approach to establish the sign relation for R_0 and λ_0 in a periodic environment by focusing the existence of exponential solution.

First we briefly review the DHM definition of R_0 and the sign relation between the Malthusian parameter and R_0 in a constant environment. Second, we review basic results for the BG definition of R_0 when the state space is finite-dimensional, that is, the basic population evolution process is formulated by an ordinary differential equation system with periodic coefficients. Thirdly we formulate the definition of R_0 for an age-dependent population with periodic parameters (the multistate periodic Lotka–McKendrick population model) and show that a dominant positive exponential solution exists and the sign relation holds between its exponent and the BG definition of R_0 . Finally, as a more complex example, we introduce the BG definition of R_0 for the age-duration dependent SIR epidemic model with periodic coefficients. We again show that there exists a dominant positive exponential solution and the sign relation holds between its exponent and R_0 . Through those

examples, our basic recipe is as follows: First we construct the solution evolutionary system and prove its uniform primitivity under appropriate conditions. The uniform primitivity of the periodic evolutionary system guarantees the existence of a dominant exponential solution, so we can define the Malthusian parameter by its exponent. Subsequently we introduce Bacaër and Guernaoui-type next generation operator to establish the sign relation between its spectral radius and the Malthusian parameter. In Appendix (section 7), we summarize the positive operator theory and show some new results for uniformly primitive periodic evolutionary system in addition to classical results by G. Birkhoff ([8]–[14]) and Inaba ([32]).

2. Preliminary: The Malthusian parameter and R_0 in a constant environment. First we review the definition of the basic reproduction number R_0 for heterogeneous population with finite i -state space in a constant environment. Although the definition of R_0 for heterogeneous population in a constant environment has been studied by demographers since 1970s ([36]), it was first successfully established by Diekmann, Heesterbeek and Metz in 1990 ([20], [21]) for epidemic models and it is still evolving ([50], [35], [49], [22]).

Suppose that the state space of individuals, denoted by $\Omega = \{1, 2, \dots, N\}$, is a finite set and we neglect age structure. A subspace $\Omega_b \subset \Omega$ is called the *birth state space*¹ if individuals can be born at state $j \in \Omega_b$.

Let $p_k(t)$, $k \in \Omega$ be the size of population in k -th state and $p(t) = (p_1(t), \dots, p_N(t))^T$ be the density vector of multistate population. For the finite-dimensional autonomous case, the basic population evolution equation is given by

$$\frac{dp(t)}{dt} = Ap(t) = (Q + M)p(t), \quad (2)$$

where $A = Q + M$, M is a $N \times N$ nonnegative, nonzero matrix called the *reproduction matrix* whose (j, k) -th entry m_{jk} denotes the number of newborns produced at state j per unit time and per individual at state k , and Q is a $N \times N$ *transition intensity matrix* whose (j, k) -th entry $q_{jk} \geq 0$ ($j \neq k$) denotes the transition intensity from k -th state to j -th state. The diagonal element $q_{kk}(t)$ of Q is given by

$$q_{kk} = -\mu_k - \sum_{j \neq k} q_{jk},$$

where μ_k denotes the removal rate (by death or other causes) at k -th state. Then we assume that Q is a nonzero *essentially nonnegative matrix*, that is, all off-diagonal entries are nonnegative². Then the *survival rate matrix* is given by $L(t) = \exp(Qt)$.

If a square matrix A is irreducible and essentially nonnegative, it is called *essentially positive*. Then the following holds:

¹If we consider epidemic models, the birth state is called the *state-at-infection* ([22]).

²An essentially nonnegative nonzero matrix is also called the *quasi-positive* ([49]). Here we write $A > 0$ if all entries a_{ij} of a “matrix” $A = (a_{ij})$ are positive, while we write $A \geq 0$ if $a_{ij} \geq 0$ for all i and j . According to the standard definition, here a matrix A is called *nonnegative* if $A \geq 0$, while A is called *positive* if $A > 0$ ([51], Definition 2.1). On the other hand, as is shown in section 7, in the context of positive operator theory, a bounded linear “operator” leaving a positive cone invariant is called *positive*. Therefore the linear operator $x \mapsto Ax$ in \mathbb{R}^n is a “positive” operator if a matrix A is nonnegative, while the linear operator $x \mapsto Ax$ in \mathbb{R}^n is a “strongly positive” operator if a matrix A is positive. For any elements x and y in a positive cone, the notation $x < y$ implies that $y - x \geq 0$ and $y - x \neq 0$.

Lemma 2.1 ([51], Section 8.2). *A matrix A is essentially positive if and only if $A + sI_d$ ³ is nonnegative, irreducible and primitive matrix for all sufficiently large $s > 0$.*

Proof. Since “if” part is clear, we show “only if” part. If a matrix A is essentially positive, it is clear that $A + sI_d$ is nonnegative and irreducible for all sufficiently large $s > 0$. Then we can assume that $A + (s - 1)I_d$ is a nonnegative and irreducible $n \times n$ matrix for a large $s > 0$. From a well-known result ([25], Chapter XIII, Lemma 1; [51], Lemma 2.2), we have $(A + sI_d)^{n-1} = [(A + (s - 1)I_d) + I_d]^{n-1} > 0$, which implies that $A + sI_d$ is primitive⁴. \square

Lemma 2.2 ([9], Lemma 2, Lemma 4; [51], Theorem 8.2). *A square matrix A is essentially nonnegative if and only if $e^{At} \geq 0$ for all $t \geq 0$, and A is essentially positive if and only if $e^{At} > 0$ for all $t > 0$.*

Let $s(Q)$ be the spectral bound of matrix Q , that is, $s(Q) := \max_{\lambda \in \sigma(Q)} \Re \lambda$ where $\sigma(Q)$ is the set of eigenvalues of Q . Then it is natural to assume $s(Q) < 0$, because individuals die out as time evolves. Then the following holds (see [21], Lemma 6.12):

Lemma 2.3. *$s(Q) < 0$ if and only if $-Q$ is nonnegatively invertible, that is, $(-Q)^{-1}$ exists and $(-Q)^{-1} \geq 0$.*

Applying the variation-of-constants formula to (2), we have

$$p(t) = e^{Qt}p(0) + \int_0^t e^{Q(t-\tau)}Mp(\tau)d\tau.$$

Multiplying M from the left hand side, we obtain a renewal equation formulation of system (2):

$$\begin{aligned} Mp(t) &= Me^{Qt}p(0) + \int_0^t Me^{Q(t-\tau)}Mp(\tau)d\tau, \\ &= ML(t)p(0) + \int_0^t \Psi(\tau)Mp(t-\tau)d\tau, \end{aligned}$$

where $Mp(t)$ gives a vector of newborns at time t and $\Psi(\tau) := ML(\tau)$ is the net reproduction matrix.

Let $v(t) := Mp(t)$ be the birth rate vector of newborns. Then we obtain

$$v(t) = g(t) + \int_0^t \Psi(\tau)v(t-\tau)d\tau, \quad (3)$$

where $g(t) = ML(t)p(0)$. Since $g(t)$ is the density of newborns produced by the initial population $p(0)$, we can define the successive generation of newborns by

$$v_1(t) = g(t), \quad v_{m+1}(t) = \int_0^t \Psi(\tau)v_m(t-\tau)d\tau, \quad m = 1, 2, \dots,$$

Then the solution of the renewal equation (3) is given by the generation expansion

$$v(t) = \sum_{m=1}^{\infty} v_m(t),$$

where $v_m(t)$ is the density of newborns produced as the m -th generation at time t .

³ I_d denotes the identity matrix.

⁴A nonnegative matrix A is primitive if and only if there exists an integer n such that $A^n > 0$.

Integrating both sides of the above iterative relation from 0 to ∞ , we have

$$\begin{aligned} \int_0^\infty v_{m+1}(t)dt &= \int_0^\infty \int_0^t \Psi(\tau)v_m(t-\tau)d\tau dt \\ &= \int_0^\infty \Psi(\tau)d\tau \int_0^\infty v_m(t)dt. \end{aligned}$$

Then if we define the time-aggregated density vector of m -th generation by

$$\phi_m := \int_0^\infty v_m(t)dt,$$

it follows that

$$\phi_{m+1} = K\phi_m = K^m\phi_1,$$

where

$$K := \int_0^\infty \Psi(\tau)d\tau = \int_0^\infty Me^{Q\tau}d\tau = M(-Q)^{-1}.$$

The (i, j) -th entry of $(-Q)^{-1} = \int_0^\infty e^{Q\tau}d\tau$ denotes the expected sojourn time that an individual born in state j spends in i -th state, so $M(-Q)^{-1}$ maps a time-aggregated density vector of newborns of m -th generation to a time-aggregated density vector of the next generation of newborns.

If K is a nonnegative, irreducible and primitive matrix, it follows from the Perron-Frobenius Theorem that

$$\lim_{m \rightarrow \infty} r(K)^{-m}\phi_m = \frac{v_0^T\phi_1}{v_0^T u_0}u_0,$$

where u_0 and v_0 are the right and left positive eigenvectors of K associated with the dominant eigenvalue $r(K)$. Therefore we have

$$\lim_{m \rightarrow \infty} \sqrt[m]{|\phi_m|} = \lim_{m \rightarrow \infty} \sqrt[m]{\|v_m\|} = r(K),$$

where $|\phi_m| = \sum_{j=1}^N |\phi_j^m|$ is the norm of N -vector $\phi_m := (\phi_1^m, \dots, \phi_N^m)^T$ and

$$\|v_m\| = \int_0^\infty |v_m(t)|dt.$$

Since $\|v_m\|$ gives the total size of the m -th generation, the size of each generation asymptotically grows with geometric growth rate $r(K)$, which is called the *generational interpretation*. Then K is called the *next generation matrix* ([20], [21]), if every state is the birth state ($\Omega = \Omega_b$)⁵.

Recently, several authors established the following relation between $r(K)$ and the spectral bound of A ([22] Theorem A.1.; [49] Theorem 2.3; [50] Theorem 2):

Proposition 2.4. *Suppose that M is a nonnegative matrix, Q is an essentially nonnegative matrix with $s(Q) < 0$ and $K = M(-Q)^{-1}$. Let $R_0 = r(K)$. Then it follows that*

$$\text{sign}(s(A)) = \text{sign}(R_0 - 1). \tag{4}$$

From Proposition 2.4, we know that the stability of the trivial steady state (the steady state corresponding to population extinction) can be formulated by the spectral radius of the next generation matrix K . Based on the generational interpretation and the sign relation (4), the basic reproduction number R_0 for multistate (heterogeneous) populations is defined by $R_0 = r(K)$. Although there are often

⁵If the state space is larger than the birth state space, K is called the *next generation matrix with large domain* ([22]).

surrogate threshold parameters which share the same kind of sign relation with R_0 ([29]), $R_0 = r(K)$ is distinguished from other indices by its generational interpretation.

Lemma 2.5. *Under the assumption of Proposition 2.4, there exists a nonnegative exponential solution $e^{\lambda_0 t} \phi_0$ for the basic system (2), where ϕ_0 is a nonnegative eigenvector of A associated with eigenvalue $\lambda_0 = s(A)$.*

Proof. Since A is essentially nonnegative, there exists $\alpha > 0$ such that $A + \alpha I \geq 0$. From the Perron–Frobenius Theorem, there exists a nonnegative eigenvector ϕ such that $(A + \alpha I)\phi = r(A + \alpha I)\phi$. Since $\lambda \in \sigma(A + \alpha I)$ if and only if $\lambda - \alpha \in \sigma(A)$, we have $s(A) = r(A + \alpha I) - \alpha \in \sigma(A)$ and ϕ is its corresponding eigenvector. Therefore we know that (1) has a nonnegative exponential solution $e^{s(A)t} \phi$. \square

If we ensure the existence of a positive dominant⁶ exponential solution, we need additional conditions:

Proposition 2.6 (Birkhoff [9]). *If A is essentially positive, it has a unique (up to a constant factor) strictly positive eigenvector ϕ_0 associated with a real, simple eigenvalue λ_0 such that $\lambda_0 > \Re \lambda$ for any $\lambda \in \sigma(A) \setminus \{\lambda_0\}$. Then the basic system (2) has a positive dominant exponential solution $e^{\lambda_0 t} \phi_0$.*

We remark that if $e^{Qt} > 0$, that is, an individual born in any state can reach every state, Q is essentially positive, hence A is also essentially positive and there exists a dominant positive exponential solution.

In the following, if a dominant positive exponential solution exists, we call its exponent λ_0 the *Malthusian parameter* (the intrinsic rate of natural increase) of the heterogeneous population in a sense that every state-specific population asymptotically grows with a common exponent λ_0 .

3. Finite-dimensional periodic evolutionary system. Now we assume that individuals' reproduction and survival parameters are changing with time. If we consider the case that density-dependent effects can be neglected, $p(t)$ satisfies a linear differential equation system as follows⁷.

$$\frac{dp(t)}{dt} = A(t)p(t) = (Q(t) + M(t))p(t), \quad p(0) = p_0 \in \mathbb{R}_+^N, \quad (5)$$

Define the survival rate matrix $L(t)$ as the solution of a matrix differential equation

$$\frac{dL(t)}{dt} = Q(t)L(t), \quad L(0) = I_d,$$

where I_d denotes the $N \times N$ identity matrix. In other words, $L(t)$ is the fundamental matrix of the N -dimensional nonhomogeneous ODE system $dx(t)/dt = Q(t)x(t)$, so it is invertible. Let $\ell_{ij}(t)$ be the (i, j) -th entry of $L(t)$. Then $\ell_{ij}(t)$ for $j \in \Omega_b$ is the probability that a newborn produced at state j and time zero will survive in state i and time t .

⁶If any solution of the basic equation (2) is asymptotically proportional to the exponential solution, we call it the dominant exponential solution.

⁷For the basic definitions and results about nonautonomous differential equation systems describing linear population dynamics, the reader may refer to [26], [40], [49] and [53].

Define a 2-parameter system (the transition matrix) $L(t, s) := L(t)L(s)^{-1}$, $t \geq s$. Then it forms an *evolutionary system*⁸ generated by $Q(t)$, that is, the following properties hold:

$$\begin{aligned} \frac{\partial}{\partial t}L(t, s) &= Q(t)L(t, s), \\ L(t, s)L(s, r) &= L(t, r), \quad r \leq s \leq t, \quad L(s, s) = I_d. \end{aligned}$$

In the following, we call $\{L(t, s) : t \geq s\}$ the *survival evolutionary system*.

The transition matrix is nonnegative; $L(t, s) \geq 0$, since $Q(t)$ is essentially non-negative. The *exponential growth bound* of the evolutionary system $L(t, s)$ is defined by

$$\omega(L) := \inf\{\omega : \text{there exists a } \bar{L} \geq 1 \text{ such that } |L(\tau + s, s)| \leq \bar{L}e^{\omega\tau}, \forall s \in \mathbb{R}, \tau \geq 0\},$$

where $|A|$ denotes the norm of a matrix A .

In this paper, we adopt the following assumption:

Assumption 3.1. *We assume that $Q(t)$ and $M(t)$ are uniformly bounded and continuous on \mathbb{R} , so $\bar{Q} := \sup_{t \in \mathbb{R}} |Q(t)| < \infty$ and $\bar{M} := \sup_{t \in \mathbb{R}} |M(t)| < \infty$. For the survival evolutionary system, we assume that $\omega(L) < 0$.*

The above assumption $\omega(L) < 0$ is biologically reasonable, because it implies that a closed population goes to extinction if there is no reproduction. For example, if we assume that $\inf_{j,t} \mu_j(t) =: \underline{\mu} > 0$, then we can observe that $|L(t, \tau)| \leq e^{-\underline{\mu}(t-\tau)}$, $t \geq \tau$, so it follows that $\omega(L) \leq -\underline{\mu}$.

Next let $U(t, s)$, $t \geq s$ be the evolutionary system associated with the generator $A(t)$. By using a fundamental matrix $\Phi(t)$ of (5), we have $U(t, s) = \Phi(t)\Phi(s)^{-1}$. Then the solution of (5) is given by $p(t) = U(t, s)p(s)$ and $\{U(t, s) : t \geq s\}$ is an evolutionary system acting on \mathbb{R}^n such that

$$\begin{aligned} \frac{\partial}{\partial t}U(t, s) &= A(t)U(t, s), \\ U(t, s)U(s, r) &= U(t, r), \quad r \leq s \leq t, \quad L(s, s) = I_d. \end{aligned}$$

Applying the variation-of-constants formula, we have

$$U(t, s) = L(t, s) + \int_s^t L(t, \sigma)M(\sigma)U(\sigma, s)d\sigma, \quad t \geq s.$$

Then $L(t, s) \geq 0$ implies $U(t, s) \geq 0$, so $\{U(t, s) : t \geq s\}$ is a positive evolutionary system. Moreover, we note that $U(t, s)$ is strongly positive if $L(t, s)$ is strongly positive⁹.

Under some additional conditions, a positive evolutionary system becomes *weakly ergodic*, that is, every positive solutions are asymptotically proportional to each other (see Appendix). A useful sufficient condition to guarantee the weak ergodicity is *uniform primitivity* (see section 7.3). Here we show a simple condition to guarantee the uniform primitivity of the evolutionary system $U(t, s)$ associated with the ODE system (5) ([53]):

⁸Evolutionary system is also called the *multiplicative process* ([12], [13], [14]).

⁹For the definition of strongly positive operator, the reader may refer to section 7. Based on our convention (footnote 2), if $L(t, s)$ is a positive “matrix”, $x \mapsto L(t, s)x$ is a strongly positive “operator” on \mathbb{R}^n .

Proposition 3.2. *Suppose that there exists an essentially positive matrix B such that $B \leq A(t)$ for all $t \in \mathbb{R}$ ¹⁰. Then the positive evolutionary system $U(t, s)$, $t > s$ is uniformly primitive.*

Proof. From our assumption here and the assumption 3.1, there exists an essentially positive matrix C such that $A(t) \leq C$ for all $t \in \mathbb{R}$. From the variation-of-constants formula, we can observe that

$$\begin{aligned} U(t, s) &= e^{(t-s)C} + \int_s^t e^{C(t-\sigma)}(A(\sigma) - C)U(\sigma, s)d\sigma \\ &= e^{(t-s)B} + \int_s^t e^{C(t-\sigma)}(A(\sigma) - B)U(\sigma, s)d\sigma \end{aligned}$$

Then we obtain $0 < e^{(t-s)B} \leq U(t, s) \leq e^{(t-s)C}$. Therefore if $p(0) > 0$, then $p(t) > 0$ for all $t > 0$ and it is easy to see that the projective diameter of $U(s+1, s)$ is uniformly bounded, so $U(t, s)$ forms a uniformly primitive multiplicative process in the sense of G. Birkhoff. \square

In the following, let us consider the periodic case. Define the state space $E := C_\theta(\mathbb{R}; \mathbb{R}^n)$, which is a Banach space of all θ -periodic continuous functions from \mathbb{R} to \mathbb{R}^n equipped with maximum norm. Let E_+ be its positive cone. Suppose that $Q(t)$ and $M(t)$ are θ -periodic (matrix-valued) functions. Then it follows that

$$L(t + \theta, \tau + \theta) = L(t, \tau), \quad U(t + \theta, \tau + \theta) = U(t, \tau).$$

If there exist a number $\lambda \in \mathbb{C}$ and $\phi \in E \setminus \{0\}$ such that $e^{\lambda t}\phi(t)$ satisfies (5) for all $t \in \mathbb{R}$, we call it the *exponential solution* with *exponent* λ . If the basic system (5) has a positive exponential solution and any solution is asymptotically proportional to the exponential solution, we call the exponent of the exponential solution the *Malthusian parameter* (or the intrinsic rate of natural increase).

For the weakly ergodic evolutionary system, if there exists a positive exponential solution, any positive solution is asymptotically proportional to the exponential solution by the weak ergodicity, so the positive exponential solution necessarily dominates the asymptotic behavior of the evolutionary system, and the exponent of the positive exponential solution is the Malthusian parameter.

From Proposition 3.2 and general results Proposition 7.19 and Proposition 7.24, we have

Corollary 3.3. *Under the assumption of Proposition 3.2, the basic system (5) with periodic coefficients has a positive exponential solution and every positive solutions are asymptotically proportional to the exponential solution.*

If the periodic system (5) has a positive exponential solution $e^{\lambda_0 t}\phi(t)$, the monodromy matrix $U(s + \theta, s)$ has a positive eigenvector $\phi(s)$ associated with a positive eigenvalue $e^{\lambda_0 \theta}$, because $e^{\lambda_0(s+\theta)}\phi(s + \theta) = U(s + \theta, s)e^{\lambda_0 s}\phi(s)$ and $\phi(s + \theta) = \phi(s)$. If $U(s + \theta, s)$ is primitive, it follows from Perron–Frobenius theory that $e^{\lambda_0 \theta} = r(U(s + \theta, s))$, so λ_0 is the dominant Floquet exponent. Then the following sign relation holds:

$$\text{sign}(\lambda_0) = \text{sign}(r(U(s + \theta, s)) - 1).$$

¹⁰If there exists an essentially positive matrix B such that $Q(t) \geq B$, the assumption of Proposition 3.2 is satisfied, so the population evolution process can be uniformly primitive even if there exists a non-reproductive season as $M(t) = 0$.

From the dominant property of the exponential solution and the above sign relation, we know that $r(U(s + \theta, s))$ is “the most obvious choice as threshold quantity for periodic system” ([21], p. 149), so several authors developed this type of approach to R_0 ([27], [28], [4]). However, the monodromy operator is not the next generation operator, so $r(U(s + \theta, s))$ does not have the generational interpretation and we can not see $r(U(s + \theta, s))$ as an extension of the DHM definition of R_0 in a constant environment.

Instead of the monodromy matrix approach, Bacaër and his collaborators ([2]–[7]) have developed a definition of R_0 in periodic environments based on the theory of periodic renewal equation theory ([46], [38]). For our ODE model (5), the next generation operator K_θ in the Bacaër–Guernaoui definition is defined as follows:

$$(K_\theta\phi)(t) = \int_0^\infty M(t)L(t, t - \sigma)\phi(t - \sigma)d\sigma,$$

where K_θ is acting on $E = C_\theta(\mathbb{R}; \mathbb{R}^n)$. The basic reproduction number in a periodic environment by the BG definition is the spectral radius of the positive operator K_θ .

As is shown in separate papers ([6], [7], [37]), the basic reproduction number given by $r(K_\theta)$ satisfies the generational interpretation, that is, it gives the asymptotic ratio of successive generation size. Thus it is reasonable to define R_0 by $r(K_\theta)$ from the generational point of view. In the following, we show that the sign relation (1) holds between the Malthusian parameter λ_0 , whose existence is guaranteed by Corollary 3.3, and R_0 given by the BG definition¹¹.

First observe that $e^{\lambda t}\phi$ is an exponential solution of (5) if and only if the following eigenvalue problem has a solution $(\lambda, \phi) \in \mathbb{C} \times E$ ¹²:

$$\tilde{A}\phi := \left(-\frac{d}{dt} + A(t)\right)\phi = \lambda\phi, \quad \phi \in E, \quad \lambda \in \mathbb{C}. \tag{6}$$

According to the standard split of the population generator ([21], [40], [50]), we define

$$(\tilde{A}_1\phi)(t) := -\frac{d\phi(t)}{dt} + Q(t)\phi(t), \quad (\tilde{A}_2\phi)(t) := M(t)\phi(t),$$

where $\phi \in E$.

Consider the resolvent equation as

$$(\lambda - \tilde{A}_1)^{-1}\psi = \phi.$$

For any $s < t$, by using the variation of constants formula, we have

$$\phi(t) = e^{-\lambda(t-s)}L(t, s)\phi(s) + \int_s^t e^{-\lambda(t-\sigma)}L(t, \sigma)\psi(\sigma)d\sigma.$$

Observe that there exists a number $M \geq 1$ such that

$$e^{-\lambda(t-s)}|L(t, s)| \leq Me^{-(\lambda-\omega(L))(t-s)}.$$

Then if we let $s \rightarrow -\infty$ with $\Re\lambda > \omega(L)$, we have

$$\phi(t) = \int_{-\infty}^t e^{-\lambda(t-\sigma)}L(t, \sigma)\psi(\sigma)d\sigma = \int_0^\infty e^{-\lambda\sigma}L(t, t - \sigma)\psi(t - \sigma)d\sigma.$$

¹¹Thieme ([49]) shows the sign relation between R_0 by the BG definition and the growth bound of U by using the evolution semigroup method.

¹²The operator \tilde{A} is the generator of the evolution semigroup associated with the evolution system $U(t, s)$ ([49]).

Therefore the resolvent operator exists for $\Re\lambda > \omega(L)$ and it is positive for real $\lambda > \omega(L)$ ¹³:

$$(R(\lambda, \tilde{A}_1)\psi)(t) = ((\lambda - \tilde{A}_1)^{-1}\psi)(t) = \int_0^\infty e^{-\lambda\sigma} L(t, t - \sigma)\psi(t - \sigma)d\sigma.$$

For $\Re\lambda > \omega(L)$, let $\tilde{K}(\lambda)$ be an operator¹⁴ defined by

$$\begin{aligned} (\tilde{K}(\lambda)\phi)(t) &:= ((\lambda - \tilde{A}_1)^{-1}\tilde{A}_2\phi)(t) \\ &= \int_0^\infty e^{-\lambda\sigma} L(t, t - \sigma)M(t - \sigma)\phi(t - \sigma)d\sigma. \end{aligned}$$

Using the operator $\tilde{K}(\lambda)$, we can rewrite the eigenvalue problem (6) as follows:

$$\phi = \tilde{K}(\lambda)\phi, \quad \Re\lambda > \omega(L).$$

On the other hand, we can also introduce a similar operator $K(\lambda)$ as follows:

$$(K(\lambda)\psi)(t) := (\tilde{A}_2(\lambda - \tilde{A}_1)^{-1}\psi)(t) = \int_0^\infty e^{-\lambda\sigma} M(t)\psi(t - \sigma)d\sigma.$$

Then we know that if

$$\psi = K(\lambda)\psi, \quad \Re\lambda > \omega(L),$$

then $\phi := (\lambda - \tilde{A}_1)^{-1}\psi$ gives the eigenfunction of (6) associated with eigenvalue λ . Then it holds that $P_\sigma(K(\lambda)) = P_\sigma(\tilde{K}(\lambda))$ and $r(K(\lambda)) = r(\tilde{K}(\lambda))$, although we omit the proof.

Proposition 3.4. *The evolutionary system (5) has a strictly positive exponential solution if and only if there exist a number $\lambda_0 > \omega(L)$ and a strictly positive periodic function $\phi \in E^\circ$ or $\psi \in E^\circ$ such that $\phi = \tilde{K}(\lambda_0)\phi$ or $\psi = K(\lambda_0)\psi$.*

Proof. Since “if” part is clear from the above argument, we show that if the evolutionary system (5) has a strictly positive exponential solution $e^{\lambda_0 t}\phi(t)$, $\phi \in E^\circ$, then $\lambda_0 > \omega(L)$. Solving the equation $-\phi' + (M + Q)\phi = \lambda_0\phi$ by the variation of constants formula, we obtain

$$\phi(t) = e^{-\lambda_0 t} L(t, 0)\phi(0) + \int_0^t e^{-\lambda_0(t-\sigma)} L(t, \sigma)M(\sigma)\phi(\sigma)d\sigma.$$

Therefore we have $\phi(0) > e^{-\lambda_0\theta} L(\theta, 0)\phi(0)$, which shows that $e^{\lambda_0\theta} - L(\theta, 0)$ is nonnegatively invertible, so $e^{\lambda_0\theta} > r(L(\theta, 0)) = e^{\omega(L)\theta}$. Then we have $\lambda_0 > \omega(L)$ and can rewrite the eigenvalue problem (6) as $\phi = \tilde{K}(\lambda_0)\phi$. \square

In order to reduce $\tilde{K}(\lambda)$ to a compact operator, using the well-known calculation ([2], [4]), we define an integral operator $\tilde{J}(\lambda)$ on $Z := \{\phi \in C([0, \theta]; \mathbb{R}^n) : \phi(0) = \phi(\theta)\}$ by

$$(\tilde{J}(\lambda)\phi_Z)(t) = \int_0^\theta \tilde{\Theta}_\lambda(t, \sigma)\phi(\sigma)d\sigma, \quad \phi_Z \in Z,$$

where $\tilde{\Theta}(t, \sigma)$ is a function defined by

$$\tilde{\Theta}_\lambda(t, \sigma) := \begin{cases} \sum_{n=0}^\infty \tilde{\Psi}_\lambda(t, t - \sigma + n\theta) & (t > \sigma), \\ \sum_{n=1}^\infty \tilde{\Psi}_\lambda(t, t - \sigma + n\theta) & (t < \sigma), \end{cases}$$

¹³The resolvent $R(\lambda, \tilde{A}_1)$ is given by the Laplace transform of the evolution semigroup associated with the evolution system $L(t, s)$ ([49]).

¹⁴ $\tilde{K}(0)$ is introduced by Wang and Zhao ([52]) as the *next infection operator* under slightly different theoretical framework.

for $t, \sigma \in [0, \theta]$ and

$$\tilde{\Psi}_\lambda(t, \sigma) := e^{-\lambda\sigma} L(t, t - \sigma)M(t - \sigma).$$

Then $\tilde{\Psi}$ and $\tilde{\Theta}$ have a period θ . Observe that

$$|\tilde{\Psi}(t, t - \sigma + n\theta)| \leq \bar{L}\bar{M}e^{-(\lambda - \omega(L))(t - \sigma + n\theta)}.$$

Then a matrix $\tilde{\Theta}_\lambda(t, \sigma)$ is well defined for $\Re\lambda > \omega(L)$ on $(t, \sigma) \in [0, \theta] \times [0, \theta]$ and it is continuous except for $t = \sigma$. From the Ascoli-Arzelá Theorem, it follows that $\tilde{J}(\lambda)$ is a compact operator on Z .

Let $P : Z \rightarrow E$ be a periodization operator defined by

$$(P\phi_Z)(t) = \phi_Z(t - [t/\theta]\theta), \quad \phi_Z \in Z, \quad t \in \mathbb{R}.$$

As is shown by [4] and [6], we can observe that for $\phi \in E$

$$\begin{aligned} (\tilde{K}(\lambda)\phi)(t) &= (\tilde{K}(\lambda)\phi)(u) = \int_0^\infty \tilde{\Psi}_\lambda(u, \sigma)\phi(u - \sigma)d\sigma \\ &= \int_{-\infty}^u \tilde{\Psi}_\lambda(u, u - \sigma)\phi(\sigma)d\sigma = \int_0^\theta \tilde{\Theta}_\lambda(u, \sigma)\phi_Z(\sigma)d\sigma, \end{aligned}$$

where $u := t - [t/\theta]\theta \in [0, \theta)$. Then it follows that

$$\tilde{K}(\lambda)P = P\tilde{J}(\lambda), \quad r(\tilde{K}(\lambda)) = r(\tilde{J}(\lambda)).$$

Proposition 3.5. *Suppose that the basic system (5) with periodic coefficients has a positive exponential solution with exponent λ_0 . If $\tilde{J}(\lambda)$ or $J(\lambda)$ is compact and strongly positive for all $\lambda > \omega(L)$, then the sign relation holds:*

$$\text{sign}(\lambda_0) = \text{sign}(R_0 - 1),$$

where $R_0 = r(\tilde{K}(0)) = r(K(0))$.

Proof. It is sufficient to prove for the case that $\tilde{J}(\lambda)$ is compact and strongly positive for all $\lambda > \omega(L)$. From the well-known Krein-Rutman theorem and its stronger version based on the strong positivity ([17], Theorem 19.2, 19.3), $r(\tilde{J}(\lambda))$ is an eigenvalue of $\tilde{J}(\lambda)$ and $r(\tilde{J}(\lambda))$ is strictly monotone decreasing for λ , because $\tilde{J}(\lambda_1) \gg \tilde{J}(\lambda_2)$ when $\lambda_1 < \lambda_2$. Since $r(\tilde{J}(\lambda_0)) = r(\tilde{K}(\lambda_0)) = 1$ with $\lambda_0 > \omega(L)$, it is clear that $\text{sign}(\lambda_0) = \text{sign}(r(\tilde{J}(0)) - 1) = \text{sign}(r(\tilde{K}(0)) - 1)$. \square

4. Infinite-dimensional periodic evolutionary system I:

The Lotka–McKendrick age-dependent population model. If we take into account the age structure, the basic linear population system is formulated as the *multistate stable population model* (Lotka–McKendrick model), which has been developed in mathematical demography¹⁵ ([31], [32], [34], [35]). Here we introduce the definition of R_0 for the multistate Lotka–McKendrick model with time periodic parameters¹⁶ and establish the sign relation.

¹⁵Although here we consider the chronological-age dependent case (demographic model), the basic model (7) can be applied to the infection-age dependent model or the duration-dependent model in mathematical epidemiology ([35]).

¹⁶The Lotka–McKendrick model with time periodic parameters is examined in [1], [42] and [6].

In general, the age-dependent population dynamics in a heterogeneous environment is described as follows ([31], [32], [35]):

$$\begin{aligned} \frac{\partial p(t, a)}{\partial t} + \frac{\partial p(t, a)}{\partial a} &= Q(t, a)p(t, a), \\ p(t, 0) &= \int_0^\beta M(t, a)p(t, a)da, \end{aligned} \quad (7)$$

where $p(t, a) = (p_1(t, a), \dots, p_N(t, a))^T$ is the population density vector composed of the age density function $p_j(t, \tau)$ at each state $j \in \Omega$, a is the chronological age and β is the length of reproductive period, which is assumed to be finite, $Q(t, a)$ is an essentially nonnegative matrix whose (j, k) ($j \neq k$) element $q_{jk}(a)$ is the force of transition from k -th state to j -th state at age a at time t , and the diagonal element is given by

$$q_{nn}(t, a) := -\mu_n(t, a) - \sum_{j \neq n} q_{jn}(t, a), \quad (n = 1, 2, \dots, N),$$

$\mu_n(t, a)$ is the removal rate (caused by death, emigration, etc.) and $M(t, a)$ is a nonnegative matrix whose jk -th element $m_{jk}(a)$ is the age-dependent fertility rate of children with state j who are produced by individuals at state k . We assume that $M(t, a) \equiv 0$ for $a > \beta$.

First we define the *survival rate matrix* $L(x; t, a)$, $x \geq 0$ as the solution of the matrix ODE system:

$$\frac{dL(x; t, a)}{dx} = Q(t + x, a + x)L(x; t, a), \quad L(0; t, a) = I_d.$$

Integrating the McKendrick equation along the cohort line ([32]), the solution $p(t, a)$ of (7) with initial data $p(s, a)$, $s \leq t$ is given as $p(t, a) = (U(t, s)p(s, \cdot))(a)$, where two-parameter family of linear positive operators $U(t, s)$, $s \leq t$ from the state space $X_+ := L_+^1([0, \beta]; \mathbb{R}^n)$ into itself is given by

$$(U(t, s)\phi)(a) = \begin{cases} L(a; t - a, 0)B(t - s - a; \phi, s), & t - s > a, \\ L(t - s; s, a - t + s)\phi(a - t + s), & t - s \leq a, \end{cases} \quad (8)$$

where $B(\xi; \phi, s)$, $\xi > 0$ denotes the number of newborns per unit time at time $s + \xi$ with initial data ϕ at time s , it is the solution of the renewal equation:

$$B(\xi; \phi, s) = G(\xi; \phi, s) + \int_0^\xi \Psi(s + \xi, a)B(\xi - a; \phi, s)da,$$

where

$$\begin{aligned} \Psi(t, a) &:= M(t, a)L(a; t - a, 0), \\ G(\xi; \phi, s) &:= \int_\xi^\infty M(\xi + s, a)L(\xi; s, a - \xi)\phi(a - \xi)da. \end{aligned}$$

Although the expression (8) is not necessarily differentiable with respect to time and age, it has a directional derivative along the cohort line, so we consider (8) as a generalized solution of the Lotka–McKendrick system (7) with initial data $\phi \in X_+$ ([30]).

Then $U(t, s)$, $s \leq t$, forms an evolutionary system (time-inhomogeneous multiplicative process), so it satisfies the law of evolution:

$$U(t_3, t_2)U(t_2, t_1) = U(t_3, t_1), \quad t_1 \leq t_2 \leq t_3, \quad U(s, s) = I_d.$$

Moreover, here we assume that $M(t, a)$ and $Q(t, a)$ are θ -periodic with respect to time t . Then it follows that

$$L(x; t + \theta, a) = L(x; t, a), \quad U(t + \theta, s + \theta) = U(t, s).$$

For the periodic evolutionary system $U(t, s)$, if there exists a θ -periodic X_+ -valued function ϕ such that $e^{\lambda t}\phi(t) = U(t, s)e^{\lambda s}\phi(s)$ for all $t > s$, it is called the *exponential solution*. As is shown by Lemma 7.23, if U is a strictly positive evolutionary system, there exists an exponential solution with exponent λ if and only if the monodromy operator $U(s + \theta, s)$ has an eigenvector associated with a positive eigenvalue $e^{\theta\lambda}$.

In the following, we assume the following assumption:

Assumption 4.1. 1. $M(t, a)$ and $Q(t, a)$ are uniformly bounded and measurable for $(t, a) \in \mathbb{R} \times [0, \beta]$.

2. There exist nonnegative primitive matrix N and numbers $0 < \gamma_1 < \gamma_2 < \beta$ such that $\Psi(t, a) \geq N$ for all $(t, a) \in \mathbb{R} \times [\gamma_1, \gamma_2]$.

3. Let $\Phi(t, a)$ be a positive matrix¹⁷ defined by

$$\Phi(t, a) := \int_0^\beta M(t + \rho, a + \rho)L(\rho; t, a)d\rho.$$

Then $\Phi(t, a)$ is almost everywhere positive for $(t, a) \in \mathbb{R} \times [0, \beta]$.

Although we omit the proof here, the above assumption is sufficient to show the the uniform primitivity of U by using the same kind of argument as [32]:

Proposition 4.2 ([32]). *Under the assumption 4.1, U is a uniformly primitive evolutionary system in X_+ .*

From the above proposition and Proposition 7.24, we conclude that

Corollary 4.3. *Under the assumption 4.1, if U is a periodic evolutionary system on X_+ , then it has a dominant positive exponential solution.*

From the above corollary, the periodic evolutionary system U has the Malthusian parameter λ_0 . Then we establish the sign relation between the Malthusian parameter λ_0 and R_0 calculated as the spectral radius of the the next generation operator for the periodic Lotka–McKendrick system (7):

$$(K_\theta f)(t) := \int_0^\infty M(t, a)L(a; t - a, 0)f(t - a)da,$$

where f is a θ -periodic locally integrable function¹⁸.

First note that if the exponential solution $e^{\lambda t}\phi(t, a)$ satisfies the basic system (7) in the sense of generalized solution, $(\lambda, \phi) \in \mathbb{R} \times \mathbb{F}$ is a solution of the eigenvalue problem:

$$\begin{aligned} (-D + Q(t, a))\phi(t, a) &= \lambda\phi(t, a), \\ \phi(t, 0) &= \int_0^\beta M(t, a)\phi(t, a)da, \end{aligned} \tag{9}$$

¹⁷The (i, j) -th entry $\phi_{ij}(t, a)$ of $\Phi(t, a)$ gives the expected total number of children with state i produced by an individual at state j with time t and age a during the remaining life.

¹⁸In [6], the reader may find another argument to establish the sign relation between the asymptotic growth rate of the system (7) and $R_0 = r(K_\theta)$ based on the space of continuous functions. The reason of the choice of K_θ as the next generation operator is that it allows the generational interpretation ([7], [37]).

where D is a directional derivative operator defined by

$$D\phi(t, a) := \lim_{h \rightarrow 0} \frac{\phi(t+h, a+h) - \phi(t, a)}{h},$$

and \mathbb{F} is a Banach lattice composed of θ -periodic, locally integrable function $\mathbb{R} \times [0, \beta]$:

$$\mathbb{F} := \{\phi \in L^1([0, \theta] \times [0, \beta]; \mathbb{R}^n) : \phi(t, \cdot) = \phi(t + \theta, \cdot)\},$$

where its norm is given by

$$\|\phi\|_{\mathbb{F}} := \int_0^\theta dt \int_0^\beta |\phi(t, a)| da.$$

In order to formulate a next generation operator, we formally rewrite (9) as an abstract eigenvalue problem in an extended state space¹⁹ to use the standard split of the population generator as in the previous section. Let Y be a Banach lattice composed of θ -periodic, \mathbb{R}^n -valued locally integrable function on \mathbb{R} :

$$Y := \{f \in L^1([0, \theta]; \mathbb{R}^n) : f(t) = f(t + \theta)\},$$

where Y -norm is given by

$$\|f\|_Y := \int_0^\theta |f(t)| dt.$$

Let $W := Y \times \mathbb{F}$ be an extended state space for the eigenvalue problem (9). Then \mathbb{F} is identified with the subspace $W_2 := \{0\} \times \mathbb{F} \subset W$ and we write $\phi \in \mathbb{F}$ as $(0, \phi)$ when we see $\phi \in \mathbb{F}$ as an element of W_2 . Moreover, Y is identified with the subspace $W_1 := Y \times \{0\} \subset W$ and we write $f \in Y$ as $(f, 0)$ when we see $f \in Y$ as an element of W_1 .

Let $\mathbb{D}(D) := \{\phi \in \mathbb{F} : D\phi \text{ exists, } D\phi \in \mathbb{F}\}$. Define operators $A_1 : \{0\} \times \mathbb{D}(D) \rightarrow W$ and $A_2 : W_2 \rightarrow W_1$ as

$$A_1(0, \phi) = (-\phi(t, 0), -D\phi + Q(t, a)\phi), \quad A_2(0, \phi) = \left(\int_0^\beta M(t, a)\phi(t, a) da, 0 \right).$$

Then the eigenvalue problem (9) is formulated as follows:

$$(A_1 + A_2)(0, \phi) = \lambda(0, \phi).$$

Observe that for $\lambda \in \mathbb{R}$

$$(\lambda - A_1)^{-1}(f, 0) = (0, e^{-\lambda a} L(a; t - a, 0) f(t - a)).$$

Then we have

$$A_2(\lambda - A_1)^{-1}(f, 0) = \left(\int_0^\beta e^{-\lambda a} M(t, a) L(a; t - a, 0) f(t - a) da, 0 \right).$$

Therefore we can define an operator $K(\lambda) : W_1 \rightarrow W_1$ as $K(\lambda) := A_2(\lambda - A_1)^{-1}$, the eigenvalue problem (9) can be written as

$$K(\lambda)(f, 0) = (f, 0).$$

In fact, if there exists a number λ such that $K(\lambda)(f, 0) = (f, 0)$, (λ, ϕ) is a solution of the eigenvalue problem (9) where $(\lambda - A_1)^{-1}(f, 0) = (0, \phi)$.

¹⁹The reader may refer to [48] for the extended state space method by which the boundary condition is treated as a bounded perturbation of the generator.

Based on the above formal discussion, again we define a linear integral operator $K(\lambda)$ on Y by

$$(K(\lambda)f)(t) = \int_0^\infty e^{-\lambda a} \Psi(t, a) f(t - a) da, \quad f \in Y.$$

where we adopt a convention that $\Psi = 0$ for $a \in \mathbb{R} \setminus [0, \beta]$. Then we obtain

Lemma 4.4. *The periodic evolutionary system U has a positive exponential solution with exponent λ_0 if and only if $K(\lambda_0)$ has a positive eigenvector associated with eigenvalue unity.*

Proof. If there exists $f \in Y_+ \setminus \{0\}$ such that $f = K(\lambda_0)f$, then it is easy to see that

$$e^{\lambda_0 t} \phi(t, a) = e^{\lambda_0(t-a)} L(a; t - a, 0) f(t - a),$$

is a positive exponential solution of (9) with exponent λ_0 . Conversely if (7) has a positive exponential solution $e^{\lambda_0 t} \phi(t, a)$, (λ_0, ϕ) satisfies the eigenvalue problem (9). By solving the McKendrick equation of (9) along the characteristic line, we have an expression as

$$\phi(t, a) = e^{-\lambda_0 a} L(a; t - a, 0) \phi(t - a, 0),$$

Inserting the above expression into the boundary condition of (9), we conclude that $\phi(t, 0)$ is a positive eigenvector of $K(\lambda_0)$ associated with eigenvalue unity. \square

Now we define a linear operator $J(\lambda)$ on Z as

$$(J(\lambda)f_Z)(t) := \int_0^\theta \Theta_\lambda(t, \sigma) f_Z(\sigma) d\sigma, \quad f_Z \in Z, \quad t \in [0, \theta],$$

where

$$\Theta_\lambda(t, \sigma) := \begin{cases} \sum_{n=0}^{[\beta/\theta]+1} e^{-\lambda(t-\sigma+n\theta)} \Psi(t, t - \sigma + n\theta) & (t > \sigma), \\ \sum_{n=1}^{[\beta/\theta]+1} e^{-\lambda(t-\sigma+n\theta)} \Psi(t, t - \sigma + n\theta) & (t < \sigma). \end{cases}$$

Here we note that $\Psi(t, a) = 0$ for $a > \beta$, $\Theta_\lambda(t, \sigma)$ is given by a finite sum of $e^{-\lambda(t-\sigma+n\theta)} \Psi(t, t - \sigma + n\theta)$, because $t - \sigma + n\theta > \beta$ when $n \geq [\beta/\theta] + 2$. Then the matrix $\Theta_\lambda(t, \sigma)$ is well defined for all $\lambda \in \mathbb{C}$ and $(t, \sigma) \in [0, \theta] \times [0, \theta]$.

By the well known calculation based on the periodicity ([2], [4]), it follows that $PJ(\lambda) = K(\lambda)P$ from which we have $r(K(\lambda)) = r(J(\lambda))$, where P denotes the periodization operator.

By using the same kind of argument as Norton's lemma ([32], Lemma 4.1), we here prepare the following technical lemma:

Lemma 4.5. *Under the assumption 4.1, for any $\delta > 0$ such that $0 < \delta < (\gamma_2 - \gamma_1)/2$, it follows that*

$$\Psi^{(n)}(t, a) \geq N^n \delta^{n-1}, \quad n = 1, 2, \dots, \tag{10}$$

for $a \in S_n := [\gamma_1 + (n - 1)(\gamma_1 + \delta), \gamma_2 + (n - 1)(\gamma_2 - \delta)]$, where $\Psi_0^{(n)}$ is defined iteratively as follows:

$$\Psi^{(1)}(t, a) := \Psi(t, a), \quad \Psi^{(n+1)}(t, a) = \int_0^a \Psi(t, \sigma) \Psi^{(n)}(t - \sigma, a - \sigma) d\sigma.$$

Proof. From our assumption, (10) holds for $n = 1$. Assume that (10) holds for $n = k$. If we assume that $t - a \in S_k$, we have $t - a \geq \gamma_1$ and

$$\Psi_0^{(k+1)}(t, t - a) = \int_a^t \Psi_0(t, t - \sigma) \Psi_0^{(k)}(\sigma, \sigma - a) d\sigma.$$

If $t - a \geq \gamma_2$, we have

$$\Psi_0^{(k+1)}(t, t - a) \geq \int_{t-\gamma_2}^{t-\gamma_1} \Psi_0(t, t - \sigma) \Psi_0^{(k)}(\sigma, \sigma - a) d\sigma.$$

Let $I = I_1 \cap I_2$ where

$$I_1 := [t - \gamma_2, t - \gamma_1], \quad I_2 := [a + \gamma_1 + (k - 1)(\gamma_1 + \delta), a + \gamma_2 + (k - 1)(\gamma_2 - \delta)].$$

If $t - a \in S_{k+1}$, it follows that $I_2 \subset I_1$, hence the length of the interval I , denoted by $|I|$, is greater than $|I_2| \geq \gamma_2 - \gamma_1 > \delta$. Therefore we obtain

$$\Psi_0^{(k+1)}(t, t - a) \geq \int_{I_2} \Psi_0(t, t - \sigma) \Psi_0^{(k)}(\sigma, \sigma - a) d\sigma \geq N^{k+1} \delta^k,$$

since $t - \sigma \in S_1$ and $\sigma - a \in S_k$ for $\sigma \in I_2$. Next if $t - a < \gamma_2$, we have

$$\Psi_0^{(k+1)}(t, t - a) \geq \int_a^{t-\gamma_1} \Psi_0(t, t - \sigma) \Psi_0^{(k)}(\sigma, \sigma - a) d\sigma.$$

Now we define $I = I_1 \cap I_2$ where

$$I_1 := [a, t - \gamma_1], \quad I_2 := [a + \gamma_1 + (k - 1)(\gamma_1 + \delta), a + \gamma_2 + (k - 1)(\gamma_2 - \delta)].$$

Then again we have $|I| > \delta$, because $t - a - [a + \gamma_1 + (k - 1)(\gamma_1 + \delta)] > \delta$, and

$$\Psi_0^{(k+1)}(t, t - a) \geq \int_I \Psi_0(t, t - \sigma) \Psi_0^{(k)}(\sigma, \sigma - a) d\sigma \geq N^{k+1} \delta^k.$$

Therefore we conclude that (10) holds for $n = k + 1$. By mathematical induction, (10) holds for every positive integer. \square

Lemma 4.6. *Under the assumption 4.1, the operator $J(\lambda)$ is nonsupporting²⁰ for $\lambda \in \mathbb{R}$.*

Proof. Observe that for $f = Pf_Z \in Y$, $t \in [0, \theta]$

$$(J^n(\lambda)f_Z)(t) = (K^n(\lambda)f)(t) = \int_0^\infty e^{-\lambda a} \Psi_0^{(n)}(t, a) f(t - a) da.$$

where $f = Pf_Z$. From Lemma 4.5, we have

$$\int_0^\infty e^{-\lambda a} \Psi_0^{(n)}(t, a) f(t - a) da \geq N^n \delta^{n-1} e^{-|\lambda|(\gamma_2 + (n-1)(\gamma_2 - \delta))} \int_{S_n} f(t - a) da.$$

If we take a large n such that $|S_n| > \theta$ and $N^n > 0$, for each $t \in [0, \theta]$ there exists an integer k such that

$$[k\theta, (k+1)\theta] \subset [t - \gamma_2 - (n-1)(\gamma_2 - \delta), t - \gamma_1 - (n-1)(\gamma_1 + \delta)].$$

Then it follows that

$$\int_{S_n} f(t - a) da = \int_{t-\gamma_2-(n-1)(\gamma_2-\delta)}^{t-\gamma_1-(n-1)(\gamma_1+\delta)} f(a) da \geq \int_{k\theta}^{(k+1)\theta} f(a) da = \int_0^\theta f(a) da.$$

Therefore we obtain for $t \in [0, \theta]$

$$(K^n(\lambda)f)(t) \geq N^n \delta^{n-1} e^{-|\lambda|(\gamma_2 + (n-1)(\gamma_2 - \delta))} \int_0^\theta f(a) da > 0.$$

Let $F \in Z_+^*$ ²¹ be a positive functional. From the above estimate, it follows that

$$\langle F, J^n(\lambda)^n f_Z \rangle = \langle F, P^{-1} K^n(\lambda)^n f \rangle > 0,$$

²⁰For the definition of nonsupporting operators, the reader may refer to section 7.

²¹ Z^* is the dual cone of the positive cone Z_+ .

which implies that the operator $J(\lambda)$ is nonsupporting. □

Now we introduce another technical assumption:

Assumption 4.7. *The following holds uniformly for $\sigma \in [0, \theta]$:*

$$\lim_{h \rightarrow 0} \int_0^\theta |\Theta_\lambda(t+h, \sigma) - \Theta_\lambda(t, \sigma)| dt = 0,$$

where we use a convention that $\Theta_\lambda(t, \sigma) = 0$ for $t \notin [0, \theta]$.

From the well-known compactness criterion in L^1 and the assumption 4.7, it is easy to see that $J(\lambda)$ is a compact operator on Z .

Proposition 4.8. *Under the assumption 4.1 and 4.7, there exists a positive exponential solution with exponent λ_0 and the sign relation holds:*

$$\text{sign}(\lambda_0) = \text{sign}(r(K(0)) - 1). \tag{11}$$

Proof. From Lemma 4.4, $K(\lambda_0)$ and so $J(\lambda_0)$ has a positive eigenvector associated with eigenvalue unity. Since $J(\lambda_0)$ is nonsupporting and compact, its spectral radius $r(J(\lambda_0))$ is a positive dominant eigenvalue of $J(\lambda)$ associated with a (essentially unique) positive eigenvector and it is a strictly decreasing function of λ (Corollary 7.6, Proposition 7.7). Therefore we have $r(J(\lambda_0)) = r(K(\lambda_0)) = 1$ and we obtain the sign relation (11). □

Since $K_\theta = K(0)$, we conclude that the BG definition $R_0 = r(K_\theta)$ is the reasonable extension of the definition of R_0 in a constant environment in a sense that R_0 allows the generational interpretation ([7], [37]), the Malthusian parameter λ_0 is well-defined and the sign relation holds between R_0 and λ_0 .

5. Infinite-dimensional periodic evolutionary system II: The age-duration dependent SIR epidemic model. Finally, as a more complex example, let us consider an age-duration structured epidemic model with periodic coefficients.

Let us introduce $I(t, \tau; a)$ as the density of infected population at time t and infection-age τ whose chronological age at infection is a . Let $S(t, a)$ be the age density of susceptibles at time t and age a and $R(t, \tau; a)$ the density of recovered individuals at time t , duration (the time elapsed since recovery) τ and age at recovery a . Then the age-duration-dependent homogeneous SIR epidemic system is formulated as follows:

$$\begin{aligned} \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) S(t, a) &= -(\mu(a) + \kappa(t, a))S(t, a), \\ \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial \tau}\right) I(t, \tau; a) &= -(\mu(a + \tau) + \gamma(\tau; a))I(t, \tau; a), \\ \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial \tau}\right) R(t, \tau; a) &= -\mu(a + \tau)R(t, \tau; a), \\ S(t, 0) &= B, \\ I(t, 0; a) &= \kappa(t, a)S(t, a), \\ R(t, 0; a) &= \int_0^a \gamma(\tau; a - \tau)I(t, \tau; a - \tau)d\tau, \end{aligned} \tag{12}$$

where B is the number of susceptible newborns per unit time, $\mu(a)$ the force of mortality, $\gamma(\tau; a)$ the rate of recovery at infection-age τ and the age at infection a and κ is the force of infection²². We assume that the force of infection is given by

$$\kappa(t, a) = \int_0^\infty m(t, a, \sigma) \int_0^\sigma f(\tau) I(t, \tau; \sigma - \tau) d\tau d\sigma, \quad (13)$$

where $m(t, a, \sigma)$ can be interpreted as the probability that a susceptible individual with age a encounters with an infected individuals with age σ at time t , and the function $f(\tau)$ is the probability of successful transmission of infective agents from infective individuals with infection-age τ . In the expression (13), we omit the scale factor $1/N$ (N is the total host population size), because we can assume that the host population is in a demographic steady state and so N is constant.

For simplicity, we assume that demographic parameters of the host population is time-independent, but the transmission coefficient $m(t, a, \sigma)$ is θ -periodic with respect to time variable. Although this assumption is mathematically restrictive, it would be reasonable for common childhood infectious diseases with seasonally changing parameters.

Thus we can assume that the host population density, described by $P(t, a) := S(t, a) + \int_0^a I(t, \tau; a - \tau) + R(t, a)$, is in a demographic steady state as $P(t, a) = B\ell(a)$, where $\ell(a)$ is the survival rate given by $\ell(a) = \exp(-\int_0^a \mu(\sigma) d\sigma)$ and the disease-free steady state is given by $(S, I, R) = (S_0(a), 0, 0)$ with $S_0(a) := B\ell(a)$.

Now the disease invasion process is described by the linearized equation at the disease-free steady state:

$$\begin{aligned} DJ(t, \tau; a) &= -(\mu(a + \tau) + \gamma(\tau; a))J(t, \tau; a) \\ J(t, 0; a) &= S_0(a) \int_0^\infty m(t, a, \sigma) \int_0^\sigma f(\tau) J(t, \tau; \sigma - \tau) d\tau d\sigma, \end{aligned} \quad (14)$$

where $J(t, \tau; a)$ denotes the density of infected population at time t and infection-age τ whose age at infection is a in the initial invasion phase.

First we check the uniform primitivity ergodicity of the linear evolutionary process given by (14). Integrating (14) along the characteristic line, we can obtain the expression as

$$J(t, \tau; a) = \begin{cases} \frac{\ell(a+\tau)}{\ell(a)} \Gamma(\tau; a) J(t - \tau, 0; a), & t - \tau > 0, \\ \frac{\ell(a+\tau)}{\ell(a+\tau-t)} \frac{\Gamma(\tau; a)}{\Gamma(\tau-t; a)} J(0, \tau - t; a), & \tau - t > 0, \end{cases} \quad (15)$$

where

$$\Gamma(\tau; a) := \exp\left(-\int_0^\tau \gamma(x; a) dx\right),$$

denotes the survival rate that an infected individual with age at infection a remains in the infected status at infection-age τ .

Inserting (15) into the boundary condition of (14), we obtain an abstract renewal equation for $B(t, a) := J(t, 0; a)$ as

$$B(t, a) = G(t, a) + \int_0^t (\Psi(t, t - z) B(z, \cdot))(a) dz, \quad (16)$$

where

$$(\Psi(t, x)u)(a) := S_0(a) \int_x^\infty m(t, a, \sigma) f(x) \frac{\ell(\sigma)}{\ell(\sigma - x)} \Gamma(x; \sigma - x) u(\sigma - x) d\sigma,$$

²²The reader may refer to [34] for the origin and applications of the model (12).

$$G(t, a) := \int_t^\infty dx \int_x^\infty S_0(a)m(t, a, \sigma)f(x) \frac{\ell(\sigma)}{\ell(\sigma - t)} \frac{\Gamma(x; \sigma - x)}{\Gamma(x - t; \sigma - x)} J(0, x - t; \sigma - x) d\sigma.$$

Here we assume that the infectious period is finite, so there exists a number $\beta > 0$ (the length of the period of infectiousness) such that $f(\tau) = 0$ for $\tau > \beta$. Then $\Psi(t, x)$ is a linear positive operator on $L^1(\mathbb{R}_+)$ and $\Psi = 0$ for $x > \beta$.

Let $R(t, z)$ be the resolvent kernel (operator on L^1) corresponding to $\Psi(t, t - z)$ defined by the solution of the resolvent equation:

$$R(t, z) = \Psi(t, t - z) + \int_z^t \Psi(t, t - \zeta)R(\zeta, z)d\zeta. \tag{17}$$

Using the resolvent kernel, we can obtain the solution of (16) as follows:

$$B(t, a) = G(t, a) + \int_0^t (R(t, z)G(z, \cdot))(a)dz.$$

Since $G = 0$ for $t > \beta$, it follows that for $t > 2\beta$, $\tau \in [0, \beta]$,

$$\begin{aligned} J(t, \tau; a) &= \frac{\ell(a + \tau)}{\ell(a)} \Gamma(\tau; a)B(t - \tau, a) \\ &= \frac{\ell(a + \tau)}{\ell(a)} \Gamma(\tau; a) \int_0^\beta (R(t - \tau, z)G(z, \cdot))(a)dz. \end{aligned} \tag{18}$$

For simplicity, we here adopt the following assumption, although we could relax this positivity condition as assumption 4.1 in the previous section:

Assumption 5.1. m, γ, f and μ are bounded nonnegative measurable functions for $t \in \mathbb{R}$ and $a, \sigma, \tau \in \mathbb{R}_+$. In particular, suppose that $\underline{f} := \inf f > 0$ and $\underline{\beta} := \inf \beta > 0$.

Lemma 5.2. Under the assumption 5.1, it follows that

$$\underline{m}f(x)S_0(a)e^{-(\underline{\mu} + \underline{\gamma})x}\|u\|_{L^1} \leq (\Psi(t, x)u)(a) \leq \bar{m}f(x)S_0(a)\|u\|_{L^1}, \tag{19}$$

$$(R(t, z)u)(a) \leq \bar{m}\bar{f}S_0(a)e^{\bar{m}\bar{f}\|S_0\|_{L^1}(t-z)}\|u\|_{L^1}, \tag{20}$$

where $\bar{m} := \sup m, \bar{f} := \sup f, \bar{\mu} := \sup \mu$ and $\bar{\gamma} := \sup \gamma$.

Proof. Since (19) easily follows from the definition of Ψ , let us show (20). It follows from (19) that

$$(R(t, z)u)(a) \leq \bar{m}\bar{f}S_0(a)\|u\|_{L^1} + \int_z^t (\Psi(t, t - \zeta)R(\zeta, z)u)(a)d\zeta. \tag{21}$$

Applying (19) again, we have

$$\|R(t, z)u\|_{L^1} \leq \bar{m}\bar{f}\|u\|_{L^1}\|S_0\|_{L^1} + \bar{m}\bar{f}\|S_0\|_{L^1} \int_z^t \|R(\zeta, z)u\|_{L^1}d\zeta.$$

Therefore it follows that

$$\|R(t, z)u\|_{L^1} \leq \bar{m}\bar{f}\|u\|_{L^1}\|S_0\|_{L^1}e^{\bar{m}\bar{f}\|S_0\|_{L^1}(t-z)}.$$

Again using (19), we have

$$\begin{aligned} \int_z^t (\Psi(t, t - \zeta)R(\zeta, z)u)(a)d\zeta &\leq \bar{m}\bar{f}S_0(a) \int_z^t \|R(\zeta, z)u\|_{L^1}d\zeta \\ &\leq \bar{m}\bar{f}S_0(a) \int_z^t \bar{m}\bar{f}\|u\|_{L^1}\|S_0\|_{L^1}e^{\bar{m}\bar{f}\|S_0\|_{L^1}(\zeta-z)}d\zeta \\ &= \bar{m}\bar{f}S_0(a)\|u\|_{L^1}(e^{\bar{m}\bar{f}\|S_0\|_{L^1}(t-z)} - 1). \end{aligned}$$

Thus it follows from (21) that (20) holds. \square

Let us define the population evolution operator $U(t, s)$, $t > s$ on

$$X := L^1([0, \beta]; L^1(\mathbb{R}_+)),$$

as follows:

$$(U(t, s)\phi)(\tau; a) = \begin{cases} \frac{\ell(a+\tau)}{\ell(a)}\Gamma(\tau; a)B_s(t-s-\tau, a), & t-s-\tau > 0, \\ \frac{\ell(a+\tau)}{\ell(a+\tau-t+s)}\frac{\Gamma(\tau; a)}{\Gamma(\tau-t+s; a)}\phi(\tau-t+s; a), & \tau-t+s > 0, \end{cases}$$

where $B_s(\zeta, a)$, $\zeta > 0$ is the solution of the abstract renewal equation:

$$B_s(\zeta, a) = G_s(\zeta, a) + \int_0^\zeta (\Psi(s+\zeta, \tau)B_s(\zeta-\tau, \cdot))(a)d\tau,$$

where

$$G_s(\zeta, a) := S_0(a) \int_\zeta^\infty d\tau \int_\tau^\infty m(s+\zeta, a, \sigma) \frac{\ell(\sigma)}{\ell(\sigma-\zeta)} \frac{\Gamma(\tau; \sigma-\tau)}{\Gamma(\tau-\zeta; \sigma-\tau)} \phi(\tau-\zeta; \sigma-\tau).$$

Then the following holds:

Proposition 5.3. *Under the assumption 5.1, U is a uniformly primitive periodic multiplicative process.*

Proof. Since $U(t, s)$, $t > s$ is a solution evolution operator for (14), it forms an non-negative evolutionary system. It follows from $\Psi(t+\theta, x) = \Psi(t, x)$ and $G_{s+\theta}(\zeta, a) = G_s(\zeta, a)$ that $B_{s+\theta}(\zeta, a) = B_s(\zeta, a)$. Then we know that $U(t+\theta, s+\theta) = U(t, s)$, that is, $U(t, s)$ is a periodic multiplicative process. In order to see the uniform primitivity of $U(t, s)$, it is sufficient to show that $U(t, 0)$ has a finite projective diameter²³ for some $t > 2\beta$. In fact, if $\Delta(U(t, 0)) \leq \alpha$, then $\Delta(U(t+n\theta, n\theta)) \leq \alpha$ for all integer n by its periodicity, so U is uniformly primitive for positive time. From (17) and (18), we have

$$J(t, \tau; a) = (U(t, 0)J_0)(\tau; a) \geq \frac{\ell(a+\tau)}{\ell(a)}\Gamma(\tau; a) \int_0^\beta (\Psi(t-\tau, t-z)G(z, \cdot))(a)dz,$$

where $J_0(\tau; a) = J(0, \tau; a) \in X$ and

$$\begin{aligned} \int_0^\beta (\Psi(t-\tau, t-z)G(z, \cdot))(a)dz &\geq \underline{m}S_0(a)e^{-(\bar{\mu}+\bar{\gamma})t} \int_0^\beta f(t-z)\|G(z, \cdot)\|_{L^1}dz, \\ \int_0^\beta (\Psi(t-\tau, t-z)G(z, \cdot))(a)dz &\leq \bar{m}S_0(a) \int_0^\beta f(t-z)\|G(z, \cdot)\|_{L^1}dz. \end{aligned}$$

Let us define

$$e := \frac{\ell(a+\tau)}{\ell(a)}\Gamma(\tau; a)S_0(a), \quad \alpha := \frac{\bar{m}\bar{f}}{\underline{m}\underline{f}}e^{(\bar{\mu}+\bar{\gamma})t},$$

$$\lambda(J_0) := \underline{m}\underline{f}e^{-(\bar{\mu}+\bar{\gamma})t} \int_0^\beta \|G(z, \cdot)\|_{L^1}dz.$$

Then for $J_0 \in X$, we have

$$\lambda(J_0)e \leq U(t, 0)J_0 \leq \alpha\lambda(J_0)e.$$

For a fixed $t > 2\beta$, λ is a positive functional and e is a quasi-interior point in X_+ . Therefore we conclude that $\Delta(U(t, 0)) \leq 2\log \alpha$. Then $U(t, s)$ is a uniformly primitive multiplicative process. \square

²³The definition of the projective diameter is given in Appendix of this text.

From Proposition 5.3, we know that there exists a dominant positive exponential solution and so the Malthusian parameter λ_0 is defined as its exponent. Inserting an exponential solution $e^{\lambda t}\psi(t, \tau; a)$ into (14), we obtain the following eigenvalue problem:

$$\begin{aligned} &-(D + \mu(a + \tau) + \gamma(\tau; a))\psi(t, \tau; a) = \lambda\psi(t, \tau; a), \\ \psi(t, 0; a) &= S_0(a) \int_0^\infty \beta(t, a, \sigma) \int_0^\sigma f(x)\psi(t, x; \sigma - x) dx d\sigma \end{aligned} \tag{22}$$

where ψ is a θ -periodic X -valued function.

Let

$$Y := \{P\phi_Z : \phi_Z \in L^1([0, \theta] \times \mathbb{R}_+)\},$$

where $P : Y \rightarrow Z := L^1([0, \theta] \times \mathbb{R}_+)$ is a periodization operator defined by

$$(P\phi_Z)(t, a) = \phi_Z(t - [t/\theta]\theta, a), \quad t \in \mathbb{R},$$

and its norm is given by

$$\|\phi\|_Y = \int_0^\theta \int_0^\infty |\phi(t, a)| da dt.$$

Then it is easy to see that a function ψ given by

$$\psi(t, \tau; a) = e^{-\lambda\tau} \frac{\ell(a + \tau)}{\ell(a)} \Gamma(\tau; a) \phi(t - \tau, a),$$

satisfies the eigenvalue problem (22) if $\phi \in Y$ satisfies the boundary condition:

$$\begin{aligned} \phi(t, a) &= \int_0^\infty S_0(a)m(t, a, \sigma) \int_0^\sigma e^{-\lambda x} \frac{\ell(\sigma)}{\ell(\sigma - x)} \Gamma(x; \sigma - x) f(x) \phi(t - x, \sigma - x) dx d\sigma \\ &= \int_0^\infty dx \int_x^\infty S_0(a)m(t, a, \sigma) e^{-\lambda x} \frac{\ell(\sigma)}{\ell(\sigma - x)} \Gamma(x; \sigma - x) f(x) \phi(t - x, \sigma - x) d\sigma. \end{aligned} \tag{23}$$

The boundary value $\psi(t, 0; a) = \phi(t, a)$ denotes the density of newly produced infecteds at age a and time t .

Define a linear positive operator on $L^1(\mathbb{R}_+)$ as

$$\begin{aligned} (\Psi_\lambda(t, x)u)(a) &:= \int_x^\infty S_0(a)m(t, a, \sigma) e^{-\lambda x} \frac{\ell(\sigma)}{\ell(\sigma - x)} \Gamma(x; \sigma - x) f(x) u(\sigma - x) d\sigma \\ &= \int_0^\infty S_0(a)m(t, a, z + x) e^{-\lambda x} \frac{\ell(z + x)}{\ell(z)} \Gamma(x; z) f(x) u(z) dz, \end{aligned}$$

where $u \in L^1(\mathbb{R}_+)$.

Then (23) can be written as follows:

$$\begin{aligned} \phi(t, a) &= (K(\lambda)\phi)(t, a) = \int_0^\infty dx (\Psi_\lambda(t, x)\phi(t - x, \cdot))(a) \\ &= \int_{-\infty}^t dy (\Psi_\lambda(t, t - y)\phi(y, \cdot))(a), \end{aligned} \tag{24}$$

where $K(\lambda)$ is a linear operator on Y defined by

$$\begin{aligned} (K(\lambda)\phi)(t, a) &:= \int_0^\infty dx \int_x^\infty S_0(a)m(t, a, \sigma) \\ &\quad \times e^{-\lambda x} \frac{\ell(\sigma)}{\ell(\sigma - x)} \Gamma(x; \sigma - x) f(x) \phi(t - x, \sigma - x) d\sigma. \end{aligned}$$

If $\phi = P\phi_Z \in Y$ for $\phi \in Z$, it follows from the periodicity of ϕ and Ψ_λ that (24) can be reduced to an equation on the space Z :

$$\phi_Z(t, a) = (J(\lambda)\phi_Z)(t, a) := \int_0^\theta dy (\Theta_\lambda(t, y)\phi_Z(y, \cdot))(a).$$

where

$$\Theta_\lambda(t, y) := \begin{cases} \sum_{n=0}^{[\omega/\theta]+1} \Psi_\lambda(t, t-y+n\theta) & (t > y), \\ \sum_{n=1}^{[\omega/\theta]+1} \Psi_\lambda(t, t-y+n\theta) & (t < y). \end{cases}$$

Therefore, we have $K(\lambda)P = PJ(\lambda)$ and $r(K(\lambda)) = r(J(\lambda))$.

Now we define a bounded measurable function $\Pi_\lambda(t, a, y, z)$ for $t, y \in \mathbb{R}$ and $a, z \in \mathbb{R}_+$ as

$$\Pi_\lambda(t, a, y, z) := S_0(a)m(t, a, t-y+z)e^{-\lambda(t-y)} \frac{\ell(t-y+z)}{\ell(z)} \Gamma(t-y; z)f(t-y),$$

where we adopt a convention that $\Pi_\lambda(t, a, y, z) = 0$ if $a < 0$, $z < 0$ and $t < y$. Then we have

$$\int_0^\theta dy (\Psi_\lambda(t, y)\phi_Z(y, \cdot))(a) = \int_0^\theta \int_0^\infty \Pi_\lambda(t, a, y-n\theta, z)\phi_Z(y, z)dzdy,$$

so we can see $J(\lambda)$ as an integral operator from L^1 -space Z into itself.

Lemma 5.4. *Suppose that the following holds uniformly for (y, z) :*

$$\lim_{h \rightarrow 0} \int_{\mathbb{R}} \int_{\mathbb{R}} |\Pi_\lambda(t+h, a+h, y, z) - \Pi_\lambda(t, a, y, z)| dt da = 0,$$

Then the operator $J(\lambda)$, $\lambda \in \mathbb{R}$ is a nonsupporting compact operator on Z .

Proof. Using the function Π_λ , we can rewrite (23) as

$$(J(\lambda)\phi_Z)(t, a) = \int_0^\theta \int_0^\infty H_\lambda(t, a, y, z)\phi_Z(y, z)dzdy,$$

where

$$H_\lambda(t, a, y, z) = \begin{cases} \sum_{n=0}^{[\omega/\theta]+1} \Pi_\lambda(t, a, y-n\theta, z), & t > y, \\ \sum_{n=1}^{[\omega/\theta]+1} \Pi_\lambda(t, a, y-n\theta, z), & t < y. \end{cases}$$

Therefore it follows from the above assumption and the well-known Fréchet-Kolmogorov compactness criterion in L^1 that $J(\lambda)$ is compact. Next we can observe that

$$\begin{aligned} (J(\lambda)\phi_Z)(t, a) &\geq \int_0^\theta dy \int_0^\infty \Pi_\lambda(t, a, y-\theta, z)\phi_Z(y, z)dz \\ &\geq S_0(a)\underline{m}f e^{-(\lambda+\bar{\mu}+\bar{\gamma})t} \|\phi_Z\|_Z. \end{aligned}$$

Then it is easy to see that $J(\lambda)$, $\lambda \in \mathbb{R}$ is a nonsupporting operator on Z . \square

By using the same kind of argument as Proposition 4.8, we can conclude as follows:

Proposition 5.5. *Under the assumption 5.1, there exists a positive dominant exponential solution with exponent λ_0 such that $r(J(\lambda_0)) = r(K(\lambda_0)) = 1$ and*

$$\text{sign}(\lambda_0) = \text{sign}(r(J(0)) - 1) = \text{sign}(r(K(0)) - 1),$$

From the above result, we know that it is reasonable to define the basic reproduction number for the periodic epidemic system (12) by the spectral radius of the integral operator $K(0)$ and we have the sign relation between λ_0 and $R_0 = r(K(0))$.

6. Conclusion. As is seen in the main text and the appendix, the asymptotic behavior of a non-autonomous linear positive system can be characterized by the positive exponential solution if it exists and the evolutionary system is weakly ergodic. Uniform primitivity is a useful sufficient condition for weak ergodicity of positive evolutionary system. If the evolutionary system is periodic and uniform primitive, we can show that there exists a dominant positive exponential solution, so the basic system has the Malthusian parameter λ_0 . Moreover, as is shown for typical cases of linear population dynamics in heterogeneous environments, we can construct the next generation operator to show the sign relation between the Malthusian parameter λ_0 and R_0 given by the spectral radius of the next generation operator. As is shown by Bacaër and Ait Dads ([7]) and Inaba ([37]), the generational interpretation holds for this BG definition of R_0 in periodic environments, that is, R_0 becomes the asymptotic growth ratio of successive generation size. Therefore, we can say that the classical threshold theory for R_0 and the Malthusian parameter in constant environments can be extended to the case of periodic environments without losing its essential features.

7. Appendix.

7.1. Theory of linear positive operators. Let E be a real or complex Banach space and let E^* be its dual space. Then E^* is a space of all linear functionals on E . In the following, we write the value of $f \in E^*$ at $\psi \in E$ as $\langle f, \psi \rangle$.

A closed subset $C \subset E$ is called the *cone* (or *positive cone*) if the following conditions hold: (1) $C + C \subset C$, (2) $\lambda \geq 0 \Rightarrow \lambda C \subset C$, (3) $C \cap (-C) = \{0\}$ and (4) $C \neq \{0\}$. With respect to the cone C , we write $x \leq y$ if $y - x \in C$, and $x < y$ if $y - x \in C^+ := C \setminus \{0\}$. If the set $\{\psi - \phi : \psi, \phi \in C\}$ is dense in E , the cone C is called *total*. If $E = C - C$, C is called a *reproducing cone*. If a cone C has nonempty interior C° , C is called a *solid cone*. Any solid cone is reproducing. We write $x \ll y$ if $y - x \in C^\circ$.

Let $B(E)$ be a set of bounded linear operators from E into itself. Let $r(T)$ be the spectral radius of $T \in B(E)$ and let $P_\sigma(T)$ be the point spectrum of T . The dual cone C^* is a subset of E^* composed of all positive linear functionals. $f \in C^*$ is called a positive linear functional if $\langle f, \psi \rangle \geq 0$ for all $\psi \in C$. $\psi \in C$ is called a *quasi-interior point* or *nonsupporting point* provided that $\langle f, \psi \rangle > 0$ for all $f \in C^* \setminus \{0\}$. A positive linear functional $f \in C^*$ is called *strictly positive* if $\langle f, \psi \rangle > 0$ for all $\psi \in C^+$. $T \in B(E)$ is called *positive* if $T(C) \subset C$ and $T \in B(E)$ is called *strictly positive* if $T(C^+) \subset C^+$ ²⁴. If $(T - S)(C) \subset C$ for $T, S \in B(E)$, we write $S \leq T$. If C is a solid cone and $T(C^+) \subset C^\circ$, T is called *strongly positive*.

Proposition 7.1 (Krein–Rutman Theorem; [39], [45]). *Suppose that C is total, a positive linear operator $T : C \rightarrow C$ is compact and $r(T) > 0$. Then $r(T)$ is an eigenvalue of T corresponding to a positive eigenvector $\psi \in C^+$.*

Proposition 7.2. *Suppose that C is a solid cone and $T : C \rightarrow C$ is a compact linear strongly positive operator. Then it follows that*

²⁴The reader should remark that in rather old papers as Birkhoff's, a positive operator is called *nonnegative*, and a strictly positive operator is called *positive*.

- (1) $r(T) > 0$, $r(T)$ is a simple eigenvalue associated with an eigenvector in C° and there is no other eigenvalue with a positive eigenvector.
- (2) $|\lambda| < r(T)$ for all eigenvalues $\lambda \neq r(T)$.

Definition 7.3 ([44], [41]). A positive operator $T \in B(E)$ is called semi-nonsupporting if for any $\psi \in C^+$ and $f \in C^* \setminus \{0\}$, there exists an integer $p = p(\psi, f)$ such that $\langle f, T^p \psi \rangle > 0$. A positive operator $T \in B(E)$ is called nonsupporting if for any $\psi \in C^+$ and $f \in C^* \setminus \{0\}$, there exists an integer $p = p(\psi, f)$ such that $\langle f, T^n \psi \rangle > 0$ for all $n \geq p$. A positive operator $T \in B(E)$ is called strictly nonsupporting if for any $\psi \in C^+$, there exists a positive integer $p = p(\psi)$ such that $T^n \psi$ is a quasi-interior point of C for all $n \geq p$.

The idea of semi-nonsupporting is an infinite-dimensional extension of indecomposability of nonnegative matrices. Krasnoselskij called it *irreducible*. The idea of nonsupporting is an infinite-dimensional extension of primitivity of nonnegative matrices.

Proposition 7.4 ([44], [41]). Suppose that the cone C is total, $T \in B(E)$ is semi-nonsupporting with respect to C and $r(T)$ is a pole of resolvent $R(\lambda, T) = (\lambda - T)^{-1}$. Then the following holds:

- (1) $r(T) \in P_\sigma(T) \setminus \{0\}$ and $r(T)$ is a simple pole of the resolvent $R(\lambda, T)$;
- (2) The eigenspace corresponding to $r(T)$ is one-dimensional and its eigenvector $\psi \in C$ is a quasi-interior point. Any eigenvector in C is proportional to ψ ;
- (3) The adjoint eigenspace corresponding to $r(T)$ is one-dimensional and its eigenfunctional $f \in C^* \setminus \{0\}$ is strictly positive.

Proposition 7.5 ([44], [41]). Suppose that the cone C is total, $T \in B(E)$ is nonsupporting with respect to C and $r(T)$ is a pole of resolvent $R(\lambda, T) = (\lambda - T)^{-1}$. Then (1)-(3) of Proposition 7.4 hold and moreover, it follows that

- (1) $r(T)$ is a dominant point of the spectrum $\sigma(T)$, that is, $|\mu| < r(T)$ for all $\mu \in \sigma(T) \setminus \{r(T)\}$;
- (2) $B_1 := \lim_{n \rightarrow \infty} r(T)^{-n} T^n$ converges in the operator norm and B_1 is a strictly nonsupporting operator given by

$$B_1 = \frac{1}{2\pi i} \int_{\Gamma_0} R(\lambda, T) d\lambda,$$

where Γ_0 is a positively oriented circle with center at $r(T)$ such that no points of the spectrum $\sigma(T)$ except $r(T)$ lie on and inside the circle Γ_0 .

From the above statement, we know that $\lim_{n \rightarrow \infty} r(T)^{-n} T^n$ converges to a projection operator on one-dimensional eigenspace spanned by the positive eigenvector associated with the dominant positive eigenvalue $r(T)$.

Combining Krein-Rutman Theorem and Sawashima's theorem, we can obtain a useful statement:

Corollary 7.6. Suppose that the cone C is total, $r(T) > 0$, T is power compact²⁵ and nonsupporting with respect to C . Then all statements of Proposition 7.4 and 7.5 hold.

Proof. Suppose that T^n is compact. Then the spectrum $\sigma(T^n)$ is a countable set with no accumulation point different from zero. From the Spectral Mapping Theorem, we have $\sigma(T^n) = \{\sigma(T)\}^n$, in particular $r(T^n) = r(T)^n > 0$ and

²⁵ $T \in B(E)$ is power compact if there is a positive integer n such that T^n is compact.

$r(T) = r(T^n)^{1/n} \in \sigma(T)$. Since T is power compact, its nonzero eigenvalue $r(T)$ is a pole of the resolvent $R(\lambda, T)$ ([23], p. 579). Therefore we can apply Proposition 7.4 to T and arrive at the conclusion. \square

Proposition 7.7 ([41]). *Let E be a Banach lattice. Suppose that $S, T \in B(E)$ are positive operators. Then the following holds:*

- (1) *If $S \leq T$, then $r(S) \leq r(T)$.*
- (2) *If S, T are semi-nonsupporting and compact, $S \leq T$, $S \neq T$ and $r(T) \neq 0$, then $r(S) < r(T)$.*

7.2. The projective metric and uniform primitivity. We here summarize some basic concepts and results of the projective metric and uniform primitivity of positive operators, as long as they are needed to discuss the weak ergodicity of evolutionary system in a Banach lattice²⁶. For omitted proofs, the reader may consult Birkhoff ([12], [13], [14]), Inaba ([32]) and its references.

Let E be a Banach lattice²⁷ with a total positive cone C . For $(x, y) \in E \times C^+$, we define $\sup(x/y) := \inf\{\lambda : x \leq \lambda y\}$ and $\inf(x/y) := \sup\{\mu : \mu y \leq x\}$, where we adopt conventions such that $\inf \emptyset = \infty$ and $\sup \emptyset = -\infty$. In C^+ , the *Hilbert projective pseudometric* is defined as follows:

$$d(x, y) := \log \left[\frac{\sup(x/y)}{\inf(x/y)} \right], \quad (x, y) \in C^+ \times C^+.$$

Then it is easy to see that $d(x, y)$ has the following properties:

Lemma 7.8. *If $x, y, z \in C^+$, then*

- (1) *$d(x, x) = 0$, $d(x, y) = d(y, x)$ and $d(x, z) \leq d(x, y) + d(y, z)$,*
- (2) *$d(x, y) = 0$ if and only if there exists a $\lambda > 0$ such that $x = \lambda y$,*
- (3) *For any $\lambda > 0$ and $\mu > 0$, $d(\lambda x, \mu y) = d(x, y)$.*

By the metric d , $\{C^+, d\}$ becomes a pseudometric space. The *connected component* in $\{C^+, d\}$ is an equivalent class composed of elements such that $d(x, y) < \infty$. The *ray* is an equivalent class composed of elements such that $d(x, y) = 0$. Two elements x, y in C^+ are called *comparable* if there exist $\mu > 0$ and $\alpha \geq 1$ such that $\mu y \leq x \leq \alpha \mu y$. Then two elements x, y of C^+ belong to the same component if and only if they are comparable.

If two elements in C^+ are comparable, images of those elements by a strictly positive linear operator A are also comparable, and it follows that

$$d(Ax, Ay) \leq d(x, y), \quad \forall (x, y) \in C^+ \times C^+.$$

Then a strictly positive linear operator is a contraction mapping with respect to the projective metric d . The *projective diameter* of a strictly positive operator A is defined by

$$\Delta(A) := \sup\{d(Ax, Ay) : (x, y) \in C^+ \times C^+\}.$$

²⁶The main results of Birkhoff's theory hold in Archimedean semi-ordered real linear space.

²⁷For a real linear space X with partial order \leq , X is called *lattice* if for any two elements $x, y \in X$, there are the least upper bound by the partial order \leq , denoted by $\sup(x, y) =: x \vee y$ and the the greatest lower bound, denoted by $\inf(x, y) =: x \wedge y$. Moreover, the partial order \leq satisfies the following condition (1) $x \leq y$, then $x + z \leq y + z$, (2) $x \leq y$ and $\lambda \geq 0$, then $\lambda x \leq \lambda y$, then X is called *vector lattice*. The absolute value of an element of a vector lattice $x \in X$ is defined by $|x| = x \vee (-x)$. A real Banach space X is called *Banach lattice* if it is a vector lattice and its norm $\|\cdot\|$ satisfies $\|x\| \leq \|y\|$ provided that $|x| \leq |y|$.

For a linear strictly positive operator A , it is called *uniformly positive* if $\Delta(A) < \infty$. If a power of A becomes uniformly positive, A is called *uniformly primitive*²⁸.

Lemma 7.9. *Let A and B be strictly positive linear operators. Then it follows that*

$$\Delta(AB) \leq \min\{\Delta(A), \Delta(B)\}.$$

Proof. From the definition, we have

$$\begin{aligned} \Delta(AB) &= \sup\{d(ABx, AB y) : (x, y) \in C^+ \times C^+\} \\ &\leq \sup\{d(Ax, Ay) : (x, y) \in C^+ \times C^+\} = \Delta(A), \end{aligned}$$

because $B(C^+) \subset C^+$. On the other hand, it follows from $d(ABx, AB y) \leq d(Bx, B y)$ that $\Delta(AB) \leq \Delta(B)$. This completes our proof. \square

Lemma 7.10 ([32]). *A strictly positive linear operator A is uniformly positive if and only if there exist $e \in C^+$, $\alpha \geq 1$ and a strictly positive functional $\lambda(x)$ such that*

$$\lambda(x)e \leq Ax \leq \alpha\lambda(x)e, \quad (25)$$

for any $x \in C$.

Corollary 7.11. *If A is a uniformly primitive operator such that (25) holds for a quasi-interior point e , then A is strictly nonsupporting.*

Proof. Suppose that for some integer n , A^n satisfies (25) with a quasi-interior point e . For any $v^* \in C^* \setminus \{0\}$ and $x \in C^+$, we have $\langle v^*, A^n x \rangle \geq \lambda(x) \langle v^*, e \rangle > 0$, which shows that $A^n x$ is a quasi-interior point. \square

Corollary 7.12. *If a strictly positive linear operator A is uniformly primitive, there exists an integer n such that the range of $A^m(C^+)$ ($m \geq n$) is included in a connected component K and K is invariant with respect to A , that is, $A(K) \subset K$.*

For a strictly positive linear operator A and elements x, y such that $0 < d(x, y) < \infty$, the *projective norm* $\|A\|_p$ or the *Birkhoff contraction ratio* $k(A)$ is defined by

$$\|A\|_p = k(A) := \sup \left\{ \frac{d(Ax, Ay)}{d(x, y)} : 0 < d(x, y) < \infty, (x, y) \in C^+ \times C^+ \right\},$$

and the *oscillation ratio* $N(A)$ is defined by

$$N(A) = \inf \left\{ \lambda : \text{osc}(Ax/Ay) \leq \lambda \text{osc}(x/y), (x, y) \in C^+ \times C^+ \right\},$$

where $\text{osc}(x/y) := \sup(x/y) - \inf(x/y)$.

Proposition 7.13 ([15], [43]). *If A is a strictly positive linear operator in E , then $k(A) = N(A)$.*

Proposition 7.14 ([8]-[14]). *Suppose that A is a strictly positive linear operator in E . Then it follows that*

$$k(A) \leq \tanh \left[\frac{\Delta(A)}{4} \right].$$

²⁸The definitions of uniform positivity in 1957 ([8]) was slightly extended in the paper at 1962 ([12]) by Birkhoff so that it can be applied to not necessarily strictly positive operator. For simplicity, we limit our argument to strictly positive operators ([32]).

From the above theorem, a uniformly positive linear operator A is a strictly contractive mapping with respect to the projective metric. That is, its contraction ratio is less than $\tanh(\Delta(A)/4)$:

$$d(Ax, Ay) \leq \tanh \left[\frac{\Delta(A)}{4} \right] d(x, y).$$

Proposition 7.15 ([8]). *A connected component of a positive cone C in E is a complete pseudo metric space with respect to the projective metric.*

Proposition 7.16 (The projective contraction mapping principle). *If a strictly positive bounded linear operator A on a Banach lattice E is uniformly primitive, A has a unique fixed point (positive eigenvector) $\phi \in C^+$ with respect to d , and $A^n x$ ($n = 1, 2, \dots$) converges to ϕ for any $x \in C^+$.*

Proof. The original proof for the case of uniformly positive operator is given in [8]. Suppose that for some integer k , A^k is uniformly positive. Then $\Delta(A^k) < \infty$. For integers $m, n \geq k$, define $\alpha := \min([m/k] - 1, [n/k] - 1)$. Then it follows that

$$\begin{aligned} d(A^m x, A^n x) &\leq \left(\tanh \frac{\Delta(A^k)}{4} \right)^\alpha d(A^k A^{m-(\alpha+1)k} x, A^k A^{n-(\alpha+1)k} x) \\ &\leq \left(\tanh \frac{\Delta(A^k)}{4} \right)^\alpha \Delta(A^k) \rightarrow 0, \quad (m, n \rightarrow \infty). \end{aligned}$$

Therefore $\{A^{k+j} x\}_{j=1,2,\dots}$ is a Cauchy sequence in a complete connected component $A^k(C^+)$, so there exists $\phi \in A^k(C^+)$ such that $\lim_{j \rightarrow \infty} d(A^{k+j} x, \phi) = 0$. Observe that for $m \geq k + 1$

$$d(A\phi, \phi) \leq d(A\phi, A^m \phi) + d(A^m \phi, \phi) \leq d(\phi, A^{m-1} \phi) + d(A^m \phi, \phi) \rightarrow 0, \quad (m \rightarrow \infty),$$

which shows that ϕ is a positive eigenvector of A . □

Corollary 7.17. *Let ϕ is a positive eigenvector of a uniformly primitive operator A associated with positive eigenvalue γ . Then there exist a strictly positive linear functional v^* , a positive constant $M(x)$ and $0 < \rho < \gamma$ independent of $x \in C^+$ such that*

$$|A^n x - \langle v^*, x \rangle \gamma^n \phi| \leq M(x) \rho^n \phi, \tag{26}$$

where v^* is a strictly positive eigenfunctional of the dual operator A^* associated with the positive eigenvalue γ .

Proof. Suppose that A^k is uniformly positive. Observe that $\sup(A^n x/A^n \phi)$, $n = 1, 2, \dots$ is monotone decreasing and $\inf(A^n x/A^n \phi)$ is monotone increasing and positive for $x \in C^+$ because $A^n(C^+)$ is a connected component for $n \geq k$, and it holds that

$$\begin{aligned} 0 &\leq \text{osc}(A^n x/A^n \phi) = \sup(A^n x/A^n \phi) - \inf(A^n x/A^n \phi) \\ &\leq (e^{d(A^n x, A^n \phi)} - 1) \sup(A^k x/A^k \phi) \rightarrow 0, \quad (n \rightarrow \infty). \end{aligned}$$

Then we can define a strictly positive functional v^* as

$$\langle v^*, x \rangle := \lim_{n \rightarrow \infty} \inf(A^n x/A^n \phi) = \lim_{n \rightarrow \infty} \sup(A^n x/A^n \phi).$$

From the definition, we have

$$\begin{aligned} \inf(A^n x/A^n \phi) A^n \phi &\leq A^n x \leq \sup(A^n x/A^n \phi) A^n \phi. \\ \inf(A^n x/A^n \phi) A^n \phi &\leq \langle v^*, x \rangle A^n \phi \leq \sup(A^n x/A^n \phi) A^n \phi \end{aligned}$$

Therefore we have

$$|A^n x - \langle v^*, x \rangle \gamma^n \phi| \leq \text{osc}(A^n x / A^n \phi) \gamma^n \phi.$$

Let $\alpha := [n/k] - 1$ for $n \geq k$. Then we have

$$\text{osc}(A^n x / A^n \phi) \leq \|A^k\|_p^\alpha \text{osc}(A^k x / A^k \phi).$$

Therefore if we choose ρ and $M(x)$ as

$$\gamma \|A^k\|_p^{\alpha/n} < \rho < \gamma, \quad M(x) := \text{osc}(A^k x / A^k \phi),$$

then we arrive at (26). It follows from (26) that v^* is a continuous linear functional. Finally from (26), we obtain

$$\lim_{n \rightarrow \infty} \gamma^{-n} \langle A^n v^*, x \rangle = \langle v^*, x \rangle \langle v^*, \phi \rangle.$$

Observe that

$$\begin{aligned} \lim_{n \rightarrow \infty} \gamma^{-n} \langle (A^*)^{n+1} v^*, x \rangle &= \langle v^*, Ax \rangle \langle v^*, \phi \rangle \\ &= \gamma \lim_{n \rightarrow \infty} \gamma^{-(n+1)} \langle (A^*)^{n+1} v^*, x \rangle = \gamma \langle v^*, x \rangle \langle v^*, \phi \rangle, \end{aligned}$$

which holds for any $x \in C$, so it implies that $A^* v^* = \gamma v^*$. Then v^* is a positive eigenfunctional of A^* associated with eigenvalue γ . \square

7.3. Uniformly primitive evolutionary system. An evolutionary system (which was called the *time-inhomogeneous multiplicative process* by Birkhoff) for positive [negative] time $J = [s_0, \infty)$ [for negative time $J = (-\infty, s_0]$] on a Banach lattice E with a total cone C is a two-parameter family of positive linear operators $U(t, s)$, $t \geq s$, $t, s \in J$ satisfying the multiplicative property:

$$U(t, r)U(r, s) = U(t, s), \quad t \geq r \geq s, \quad t, r, s \in J,$$

and $U(s, s) = I_d$ where I_d is the identity operator.

A strictly positive evolutionary system for positive [negative] time is *uniformly primitive* when for some $\alpha > 0$, there exist for any $K > s_0$ [$K < s_0$] some $t > s > K$ [$s < t < K$] such that $\Delta(U(t, s)) \leq \alpha$.

A function $f(t)$ defined for all $t \in J$ and with values $f(t) \in C$ is *consistent* with the evolutionary system U when $f(t) = U(t, s)f(s)$ for all $t, s \in J$.

Let C^* be the set of linear nonnegative functionals on E and let $E^* := \{f^* - g^* : f^*, g^* \in C^*\}$. Then C^* is a positive cone of E^* and the vector space (E^*, C^*) is the dual space of (E, C) . As the dual of any Banach lattice is again a Banach lattice, we can define the *dual evolutionary system* $U^*(s, t)$, $s \leq t$ by

$$\langle U^*(s, t)v^*, \phi \rangle = \langle v^*, U(t, s)\phi \rangle,$$

where $\langle v, \phi \rangle$ denotes the value of $v \in E^*$ at $\phi \in E$. Then it is easy to see that $U^*(s, t)$ is an evolutionary system such that $U^*(s, r)U^*(r, t) = U^*(s, t)$, and it is positive if $U(t, s)$, $t \geq s$ is positive.

A function $v^*(t)$ defined for all $t \in J$ and with values $v^*(t) \in C^*$ is *consistent* with $U^*(s, t)$ when for all $s \leq t$, $s, t \in J$, $v^*(s) = U^*(s, t)v^*(t)$. Then it is easy to see that²⁹:

²⁹Birkhoff defines a consistent functional $v^*(t)$ such that (26) holds for any function $f(t)$ consistent with the process $U(t, s)$ ([13]).

Proposition 7.18. *If $f(t)$ is consistent with $U(t, s)$ and $v^*(t)$ is consistent with $U^*(s, t)$, it follows that for any $t, s \in J$*

$$\langle v^*(t), f(t) \rangle = \langle v^*(s), f(s) \rangle = \text{const.} \tag{27}$$

Let $U(t, s), t \geq s$ be a strictly positive evolutionary system for positive time on (E, C) , it is called *weakly ergodic* if for any $\psi, \phi \in C^+$,

$$\lim_{t \rightarrow \infty} d(U(t, s)\psi, U(t, s)\phi) = 0.$$

Proposition 7.19 ([13], [32]). *Let U be a strictly positive evolutionary system for positive time on (E, C) . If U is uniformly primitive for positive time, it is weakly ergodic.*

Proposition 7.20 ([13], [32]). *Let U be a weakly ergodic evolutionary system for positive time on a Banach lattice (E, C) , and let $f(t)$ and $g(t), t \in J$ be consistent with U . If $d(f(s), g(s)) < \infty$, there exists a strictly positive functional $v^*(s) \in V^*$ such that*

$$|f(t) - \langle v^*(s), f(s) \rangle g(t)| \leq |g(t)| \text{osc}(f(t)/g(t)), \tag{28}$$

where $v^*(s), s \in J$ is defined by

$$\langle v^*(s), \phi \rangle := \lim_{t \rightarrow \infty} \inf(U(t, s)\phi/g(t)) = \lim_{t \rightarrow \infty} \sup(U(t, s)\phi/g(t)).$$

The functional $v^*(s)$ is consistent with the dual process $U^*(s, t), s \leq t$ and, up to a positive constant factor, it is uniquely determined.

A strictly positive linear functional $v^*(s)$ defined in Proposition 7.20 is called *importance functional*.

Proposition 7.21 ([13]). *Let $U(t, s), t \geq s$ be a weakly ergodic time-inhomogeneous multiplicative process for positive time on a Banach lattice (E, C) . Then the importance functional is a one and essentially only one positive linear functional consistent with the dual process $U^*(s, t), t \geq s$.*

Proof. Let $v^*(s)$ be the importance functional associated with a positive consistent function $g(t)$. For any $\psi \in C^+$, due to the weak ergodicity, we can assume without loss of generality that $d(U(t, s)\psi, g(t)) < \infty$. Let $w^*(s)$ be any positive consistent functional. It follows from (28) that

$$|\langle w^*(t), U(t, s)\psi \rangle - \langle v^*(s), \psi \rangle \langle w^*(t), g(t) \rangle| \leq \langle w^*(t), g(t) \rangle \text{osc}(U(t, s)\psi/g(t)).$$

From the weak ergodicity, we have $\lim_{t \rightarrow \infty} \text{osc}(U(t, s)\psi/g(t)) = 0$. Since $\langle w^*(t), g(t) \rangle$ is constant, we conclude that

$$\langle w^*(s), \psi \rangle = \langle v^*(s), \psi \rangle \langle w^*(s), g(s) \rangle,$$

where we used (27). Therefore, we have

$$w^*(s) = v^*(s) \langle w^*(s), g(s) \rangle,$$

which shows that $w^*(s)$ is proportional to the importance functional v^* , because $\langle w^*(s), g(s) \rangle$ is a constant. \square

7.4. Periodic evolutionary system. Finally let us consider the case that a strictly positive evolutionary system $\{U(t, s)\}_{s \leq t}$ on a Banach lattice (E, C) has a periodicity. Suppose that for all $s \leq t$, there exists $\theta > 0$ such that

$$U(t + \theta, s + \theta) = U(t, s), \quad s \leq t.$$

Then it is clear that the dual process is also a periodic evolutionary system; $U^*(s + \theta, t + \theta) = U^*(s, t)$.

Lemma 7.22. *If U is a uniformly primitive θ -periodic evolutionary system, the monodromy operator $U(s + \theta, s)$ is uniformly primitive for any $s \in J$.*

Proof. From the periodicity, we have $U(s + \theta, s)^n = U(s + n\theta, s)$ for any positive integer n . From the uniform primitivity of U , for some $\alpha > 0$ there exist for any $K > s_0$ some $t > s > K$ such that $\Delta(U(t, s)) \leq \alpha$. Then we can choose a sufficiently large n such that there exists an interval $(t_1, t_2) \subset (s, n\theta)$ with $\Delta(U(t_2, t_1)) \leq \alpha$. From Lemma 7.9, we have $\Delta(U(s + n\theta, s)) \leq \Delta(U(t_2, t_1)) \leq \alpha$, which shows that $U(s + \theta, s)$ is uniformly primitive. \square

If there exists a consistent function $f(t)$ such that $f(t) = e^{\lambda t} \phi(t)$ where $\lambda \in \mathbb{R}$ and $\phi(t)$ is θ -periodic positive function, we call $f(t)$ the *exponential solution*. Then we can prove the following:

Lemma 7.23. *Suppose that U is a strictly positive periodic evolutionary system on (E, C) . Then there exists a positive exponential solution with exponent λ if and only if the monodromy operator $U(s + \theta, s)$ has a positive eigenvector associated with a positive eigenvalue $e^{\lambda\theta}$.*

Proof. If there exists an exponential solution $e^{\lambda t} \phi(t)$, it follows that $e^{\lambda t} \phi(t) = U(t, 0) \phi(0)$. Since $\phi(\theta) = \phi(0)$, we have $e^{\lambda\theta} \phi(0) = U(\theta, 0) \phi(0)$, which shows that $U(\theta, 0)$ has a positive eigenvector $\phi(0)$ associated with an eigenvalue $e^{\lambda\theta}$. Observe that

$$U(s + \theta, s)U(s, 0) = U(s + \theta, \theta)U(\theta, 0) = U(s, 0)U(\theta, 0).$$

Therefore it follows that

$$U(s + \theta, s)[U(s, 0)\phi(0)] = e^{\lambda\theta}[U(s, 0)\phi(0)],$$

which shows that $U(s + \theta, s)$ has an eigenvector $U(s, 0)\phi(0)$ associated with an eigenvalue $e^{\lambda\theta}$. Conversely suppose that $U(s + \theta, s)$ has a positive eigenvector $\phi(s)$ associated with a positive eigenvalue $e^{\lambda\theta}$. Let us define a positive functional $\phi(t)$ by $\phi(t) := e^{-\lambda(t-s)}U(t, s)\phi(s)$. Then it is easy to see that $\phi(t)$ has a period θ and $e^{\lambda t}\phi(t)$ is a consistent function, which is an exponential solution. \square

Proposition 7.24. *If U is a uniformly primitive periodic evolutionary system on (E, C) , it has a positive exponential solution.*

Proof. From Lemma 7.23, it is sufficient to show that $U(s + \theta, s)$ has a positive eigenvector. Since the monodromy operator $U(s + \theta, s)$ is uniformly primitive (Lemma 7.22), it has a positive eigenvector (Proposition 7.16). \square

From Corollary 7.6 and Proposition 7.23, we have another condition for existence of exponential solution:

Proposition 7.25. *Suppose that E is a real Banach space with a total cone C , U is a strictly positive periodic multiplicative process on (E, C) . If the monodromy operator $U(s + \theta, s)$ is power compact and nonsupporting, it has a positive exponential solution.*

Proposition 7.26. *Suppose that U is a uniformly primitive θ -periodic evolutionary system on (E, C) . Let $e^{\lambda t}\phi(t)$ be its exponential solution. Then there exists a positive linear functional (importance functional) $v^*(s)$ such that*

$$\lim_{t \rightarrow \infty} \|e^{-\lambda t}U(t, s)x - \langle v^*(s), x \rangle \phi(t)\| = 0. \tag{29}$$

where v^* is an exponential solution of the dual system U^* , that is, there exists a periodic functional $w^*(s)$ such that

$$v^*(s) = e^{-\lambda s}w^*(s).$$

Proof. Suppose that a uniformly primitive periodic evolutionary system U has an exponential solution $e^{\lambda t}\phi(t)$. Then it follows from (28) that there exists a positive functional $v^*(s)$ such that for any $x \in C^+$ satisfying $d(\phi(s), x) < \infty$,

$$e^{-\lambda t}U(t, s)x = \langle v^*(s), x \rangle \phi(t) + o(\|\phi(t)\|),$$

where $\phi(t)$ is a periodic function, so $\|\phi(t)\|$ is bounded. Any two consistent functions are going into a connected component after finite time, we have (29). From (29), we have

$$\begin{aligned} e^{-\lambda(t+\theta)}U(t+\theta, s+\theta)x &= \langle v^*(s+\theta), x \rangle \phi(t+\theta) + o(\|\phi(t+\theta)\|) \\ &= \langle v^*(s+\theta), x \rangle \phi(t) + o(\|\phi(t)\|) \\ &= e^{-\lambda(t+\theta)}U(t, s)x \\ &= e^{-\lambda\theta}(\langle v^*(s), x \rangle \phi(t) + o(\|\phi(t)\|)), \end{aligned}$$

which shows that $v^*(s+\theta) = e^{-\lambda\theta}v^*(s)$. If we define a functional $w^*(s)$ by $w^*(s) = e^{\lambda s}v^*(s)$, w^* is θ -periodic. Since the importance functional is consistent with the dual system, $v^*(s) = e^{-\lambda s}w^*(s)$ is the exponential solution of the dual system. \square

From (29), we know that for any function $f(t) = U(t, s)x$ consistent with a uniformly primitive periodic multiplicative process, we obtain

$$\lim_{t \rightarrow \infty} \left\| \frac{f(t)}{\|f(t)\|} - \frac{\phi(t)}{\|\phi(t)\|} \right\| = 0,$$

which shows that the normalized distribution $f(t)/\|f(t)\|$ converges to a periodic distribution $\phi(t)/\|\phi(t)\|$.

7.5. Reproductive value in a periodic environment. Bacaër and Abdurahman ([5]) proposed to define $w^*(s)$ as the reproductive value in the periodic environment. In fact, if the population vector $p(t)$ is evolved as $p(t) = U(t, s)p(s)$ and the total reproductive value is defined by $V(t) := \langle w^*(t), p(t) \rangle$, it follows from (25) that

$$V(t) = \langle w^*(t), p(t) \rangle = e^{\lambda t} \langle v^*(t), p(t) \rangle = e^{\lambda t} \langle v^*(0), p(0) \rangle = e^{\lambda t}V(0),$$

which shows that the exponential growth of the “total reproductive value”, so it is seen as an extension of Fisher’s theorem for the reproductive value in a constant environment ([31]). On the other hand, the importance functional $v^*(s)$ is seen as the *demographic potential* defined by Ediev ([24]) in the context of Lotka’s stable population model. Then Birkhoff’s result (27) implies Ediev’s observation that the *total demographic potential* $\langle v^*(t), f(t) \rangle$ is constant in the time-inhomogeneous Lotka model.

If we consider a constant environment, $v^*(s)$ becomes a (essentially) unique persistent (exponential) solution of the dual evolution system (semigroup) and $w^*(s)$ is a time-independent positive eigenvector of the generator of the dual semigroup.

Acknowledgments. I would like to thank Prof. Odo Diekmann for his kind comments on earlier ideas of this manuscript, and I also thank Dr. Nicolas Bacaër for sending me his manuscripts and comments on the historical development of the idea of R_0 for periodic case. I also thank Prof. Horst Thieme and one anonymous reviewer for their helpful comments to the first version of this paper, which are most helpful to improve the manuscript. This research is partially supported by Aihara Innovative Mathematical Modelling Project, the Japan Society for the Promotion of Science (JSPS) through its “Funding Program for World-Leading Innovative R&D on Science and Technology (FIRST Program)” and Grant-in-Aid for Scientific Research (C) (225401114).

REFERENCES

- [1] S. Anita, M. Iannelli, M.-Y. Kim and E.-J. Park, *Optimal harvesting for periodic age-dependent population dynamics*, SIAM J. Appl. Math., **58** (1998), 1648–1666.
- [2] N. Bacaër and S. Guernaoui, *The epidemic threshold of vector-borne diseases with seasonality. The case of cutaneous leishmaniasis in Chichaoua, Morocco*, J. Math. Biol., **53** (2006), 421–436.
- [3] N. Bacaër and R. Ouifki, *Growth rate and basic reproduction number for population models with a simple periodic factor*, Math. Biosci., **210** (2007), 647–658.
- [4] N. Bacaër, *Approximation of the basic reproduction number R_0 for vector-borne diseases with a periodic vector population*, Bull. Math. Biol., **69** (2007), 1067–1091.
- [5] N. Bacaër and X. Abdurahman, *Resonance of the epidemic threshold in a periodic environment*, J. Math. Biol., **57** (2008), 649–673.
- [6] N. Bacaër and E. H. Ait Dads, *Genealogy with seasonality, the basic reproduction number, and the influenza pandemic*, J. Math. Biol., **62** (2011), 741–762.
- [7] N. Bacaër and E. H. Ait Dads, *On the biological interpretation of a definition for the parameter R_0 in periodic population models*, J. Math. Biol., Online First, 11 October, 2011.
- [8] G. Birkhoff, *Extensions of Jentzsch’s theorem*, Trans. Amer. Math. Soc., **85** (1957), 219–227.
- [9] G. Birkhoff and R. S. Varga, *Reactor criticality and nonnegative matrices*, J. Soc. Indust. Appl. Math., **6** (1958), 354–377.
- [10] G. Birkhoff, *Lattices in applied mathematics*, in “1961 Proceedings of Symposia in Pure Mathematics,” Vol. 2, Amer. Math. Soc., Providence, R.I., (1961), 155–184.
- [11] G. Birkhoff, *Positivity and criticality*, in “1961 Proceedings of Symposia in Applied Mathematics,” Vol. XI, Amer. Math. Soc., Providence, RI, (1961), 116–126.
- [12] G. Birkhoff, *Uniformly semi-primitive multiplicative process*, Trans. Am. Math. Soc., **104** (1962), 37–51.
- [13] G. Birkhoff, *Uniformly semi-primitive multiplicative processes. II*, J. Math. Mech., **14** (1965), 507–512.
- [14] G. Birkhoff, “Lattice Theory,” 3rd ed., American Mathematical Society Colloquium Publications, Vol. XXV, American Mathematical Society, Providence, R.I., 1967.
- [15] P. J. Bushell, *On the projective contraction ratio for positive linear mappings*, J. London Math. Soc. (2), **6** (1973), 256–258.
- [16] C. Chicone and Y. Latushkin, “Evolution Semigroups in Dynamical Systems and Differential Equations,” Mathematical Surveys and Monographs, **70**, American Mathematical Society, Providence, RI, 1999.
- [17] K. Deimling, “Nonlinear Functional Analysis,” Springer-Verlag, Berlin, 1985.
- [18] Ph. Clément, O. Diekmann, M. Gyllenberg, H. J. A. M. Heijmans and H. R. Thieme, *Perturbation theory for dual semigroups. II. Time-dependent perturbations in the sun-reflexive case*, Proc. Royal Soc. Edinburgh Sect. A, **109** (1988), 145–172.
- [19] O. Diekmann, H. J. A. M. Heijmans and H. R. Thieme, *On the stability of the cell-size distribution. II. Time-periodic developmental rates. Hyperbolic partial differential equations, III*, Comp. Math. Appl. Part A, **12** (1986), 491–512.

- [20] O. Diekmann, J. A. P. Heesterbeek and J. A. J. Metz, *On the definition and the computation of the basic reproduction ratio R_0 in models for infectious diseases in heterogeneous populations*, J. Math. Biol., **28** (1990), 365–382.
- [21] O. Diekmann and J. A. P. Heesterbeek, “Mathematical Epidemiology of Infectious Diseases. Model Building, Analysis and Interpretation,” Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Chichester, 2000.
- [22] O. Diekmann, J. A. P. Heesterbeek and M. G. Roberts, , *The construction of next-generation matrices for compartmental epidemic models*, J. Roy. Soc. Interface **6**, **7** (2010), 873–885.
- [23] N. Dunford and J. T. Schwartz, “Linear Operators. Part I. General Theory,” With the assistance of W. G. Bade and R. G. Bartle, Pure and Applied Mathematics, Vol. 7, Interscience Publishers, Inc., New York, Interscience Publishers, Ltd., London, 1958.
- [24] D. M. Ediev, *On the definition of the reproductive value: Response to the discussion by Bacaër and Abdurahman*, J. Math. Biol., **59** (2009), 651–657.
- [25] F. R. Gantmacher, “The Theory of Matrices,” Vol. 2, Chelsea Publishing Company, New York, 1959.
- [26] J. K. Hale, “Ordinary Differential Equations,” Robert E. Krieger Pub. Co., Malabar, Florida, 1980.
- [27] J. A. P. Heesterbeek and M. G. Roberts, *Threshold quantities for helminth infections*, J. Math. Biol., **33** (1995), 415–434.
- [28] J. A. P. Heesterbeek and M. G. Roberts, *Threshold quantities for infectious diseases in periodic environments*, J. Biol. Sys., **3** (1995), 779–787.
- [29] J. M. Heffernan, R. J. Smith and L. M. Wahl, *Perspectives on the basic reproductive ratio*, J. Roy. Soc. Interface, **2** (2005), 281–293.
- [30] M. Iannelli, “Mathematical Theory of Age-Structured Population Dynamics,” Giardini Editori e Stampatori in Pisa, 1995.
- [31] H. Inaba, *A semigroup approach to the strong ergodic theorem of the multistate stable population process*, Math. Popul. Studies, **1** (1988), 49–77.
- [32] H. Inaba, *Weak ergodicity of population evolution processes*, Math. Biosci., **96** (1989), 195–219.
- [33] H. Inaba, *Threshold and stability results for an age-structured epidemic model*, J. Math. Biol., **28** (1990), 411–434.
- [34] H. Inaba and H. Nishiura, *The basic reproduction number of an infectious disease in a stable population: The impact of population growth rate on the eradication threshold*, Mathematical Modelling of Natural Phenomena, **3** (2008), 194–228.
- [35] H. Inaba and H. Nishiura, *The state-reproduction number for a multistate class age structured epidemic system and its application to the asymptomatic transmission model*, Math. Biosci., **216** (2008), 77–89
- [36] H. Inaba, *The net reproduction rate and the type-reproduction number in multiregional demography*, Vienna Yearbook of Population Research, (2009), 197–215.
- [37] H. Inaba, *On a new perspective of the basic reproduction number in heterogeneous environments*, J. Math. Biol., published online 14 August, 2011.
- [38] P. Jagers and O. Nerman, *Branching processes in periodically varying environment*, The Annals of Probability, **13** (1985), 254–268.
- [39] M. G. Kreĭn and M. A. Rutman, *Linear operators leaving invariant a cone in a Banach space*, Uspehi. Mat. Nauk. (N.S.), **3** (1948), 3–95; English translation: Ame. Math. Soc. Transl., **10** (1950), 199–325.
- [40] C.-K. Li and H. Schneider, *Applications of Perron-Frobenius theory to population dynamics*, J. Math. Biol., **44** (2002), 450–462.
- [41] I. Marek, *Frobenius theory of positive operators: Comparison theorems and applications*, SIAM J. Appl. Math., **19** (1970), 607–628.
- [42] P. Michel, S. Mischler and B. Perthame, *General relative entropy inequality: An illustration on growth models*, J. Math. Pures Appl. (9), **84** (2005), 1235–1260.
- [43] A. M. Ostrowski, *Positive matrices and functional analysis*, in “1964 Recent Advances in Matrix Theory” (ed. H. Schrecher) (Proc. Advanced Seminar, Math. Res. Center, U.S. Army, Univ. Wisconsin, Madison, Wis., 1963), Univ. of Wisconsin Press, Madison, (1964), 81–101.
- [44] I. Sawashima, *On spectral properties of some positive operators*, Nat. Sci. Report Ochanomizu Univ., **15** (1964), 53–64.
- [45] H. H. Schaefer and M. P. Wolff, “Topological Vector Spaces,” 2nd edition, Graduate Texts in Mathematics, **3**, Springer-Verlag, New York, 1999.

- [46] H. R. Thieme, *Renewal theorems for linear periodic Volterra integral equations*, J. Inte. Equ., **7** (1984), 253–277.
- [47] H. R. Thieme, *Asymptotic proportionality (weak ergodicity) and conditional asymptotic equality of solutions to time-heterogeneous sublinear difference and differential equations*, J. Diff. Equ., **73** (1988), 237–268.
- [48] H. R. Thieme, *Semiflows generated by Lipschitz perturbations of non-densely defined operators*, Differential and Integral Equations, **3** (1990), 1035–1066.
- [49] H. R. Thieme, *Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity*, SIAM J. Appl. Math., **70** (2009), 188–211.
- [50] P. van den Driessche and J. Watmough, *Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission*, Math. Biosci., **180** (2002), 29–48.
- [51] R. S. Varga, “Matrix Iterative Analysis,” 2nd Edition, Springer Series in Computational Mathematics, **27**, Springer-Verlag, Berlin, 2000.
- [52] W. Wang and X.-Q. Zhao, *Threshold dynamics for compartmental epidemic models in periodic environments*, J. Dyn. Diff. Equat., **20** (2008), 699–717.
- [53] A. D. Ziebur, *New directions in linear differential equations*, SIAM Review, **21** (1979), 57–70.

Received June 1, 2011; Accepted August 29, 2011.

E-mail address: inaba@ms.u-tokyo.ac.jp