The basic reproduction number R_0 in time-heterogeneous environments

Hisashi Inaba Graduate School of Mathematical Sciences The University of Tokyo

1 Introduction

Although the well-known traditional definition of the basic reproduction number R_0 for structured populations [3] have been originally established in a constant environment, after the epoch-making results by Bacaër and Guernaoui [2], it has been extended to the threshold index for population growth in timeheterogeneous environments [10].

The essential important point of extension in time-heterogeneous environments is that R_0 should keep its biological feature as the asymptotic per generation growth factor and the sign relation for the Malthusian parameter if it exists. In [5], we introduced a new definition of R_0 based on the generation evolution operator (GEO), which has intuitively clear biological meaning and can be applied to structured populations in any heterogeneous environment. Using the GEO, we have shown that the traditional definition based on the next generation operator (NGO) completely allow the generational interpretation and the spectral radius of GEO equals the spectral radius of NGO in at most periodic environments.

Although the new definition is a complete extension of the traditional definition, we have not yet proved that R_0 given by the new definition is calculated as the spectral radius of GEO. In the following, using the mathematical theory related to the cone spectral radius, we show that our definition of R_0 gives the local spectral radius of GEO, and in fact, it is the spectral radius of GEO in the time-state space. As is shown by Thieme [10], the sign relation holds between R_0 and the growth bound of the evolutionary family associated with the linearized population evolution equation. Then as far as we consider linear population dynamics, our R_0 is a threshold value for population extinction and persistence in time-heterogeneous environments. Next we prove that even for nonlinear system, our R_0 plays a role of a threshold value for population extinction in time-heterogeneous environments. For periodic system, we can show that supercritical condition $R_0 > 1$ implies existence of periodic solution. Finally using the idea of R_0 in time-heterogeneous environment, we examine existence and stability of periodic solution in the age-structured SIS epidemic model with time-periodic parameters.

2 Linear renewal process

2.1 Renewal equation

In the following, we state our theory based on terminologies of demographic models, while the reader can easily interpret the basic model as an epidemic model, if we read childbearing as reproduction of new infection. Although our exposition for structured population models is intuitive and not completely universal, the reader may refer to [4] for more general formulation.

Suppose that the individuals are characterized by a variable $\zeta \in \Omega$, which is called the *i-state variable* (*i* for heterogeneity of individuals). The set $\Omega \subset \mathbf{R}^n$ is the *i*-state space. Define $A(t, \tau, \zeta, \eta)$ to be the expected number of newborns with *i*-state ζ at time *t* produced per unit time by an individual which was born τ units of time ago at *i*-state η . Let $b(t, \zeta), \zeta \in \Omega_b$ denote the density of newborns at time *t*, where $\Omega_b \subset \Omega$ is the set of *states-of-birth* [?], which are the *i*-states at which newborns can have. Then the real-time development of newborns (in the linear phase) is described by a renewal integral equation:

$$b(t,\zeta) = \int_0^\infty \int_{\Omega_b} A(t,\tau,\zeta,\eta) b(t-\tau,\eta) d\eta d\tau, \quad t \in \mathbf{R}.$$
 (2.1)

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

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

Then $\Psi(t,\tau)$, which we call the *net reproduction operator*, is a positive linear operator that maps the density (distribution) of newborns at $t-\tau$ to the density of their children produced at time t.

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

$$b(t) = \int_0^\infty \Psi(t,\tau) b(t-\tau) d\tau, \quad t \in \mathbf{R}.$$
 (2.2)

Then we can rewrite (2.2) as a Volterra-type integral equation (initial value problem):

$$b(t) = b_0(t) + \int_0^t \Psi(t,\tau)b(t-\tau)d\tau, \quad t > 0,$$
(2.3)

where

$$b_0(t) := \int_t^\infty \Psi(t,\tau) b(t-\tau) d\tau$$

If a history of births for t < 0 is once given, $b_0 \in Y_+$ becomes an initial data and we can compute b(t) for t > 0 as $b(t) = \sum_{m=0}^{\infty} b_m(t)$ where the successive generation distributions of newborns is given by

$$b_m(t) = \int_0^\infty \Psi(t,\tau) b_{m-1}(t-\tau) d\tau, \quad m = 0, 1, 2, ...,$$
(2.4)

where the domain of $b_m(t)$ is extended as $b_m(t) = 0$ for t < 0, and $b(t) = \sum_{m=0}^{\infty} b_m(t)$ is in fact a finite sum if the individual reproductive period is finite.

Now we focus on the generation evolution process (2.4). We can see the time variable t as a kind of *i*-state variable, $\mathbf{R} \times \Omega_b$ may be called the *birth* coordinates [4]. Let Y be a function space of newborn distributions on $\mathbf{R} \times \Omega_b$, called the *time-state space*, and let Y_+ be its positive cone. Then $b_m \in Y_+$ gives the density of *m*-th generation of newborns at $(t, \zeta) \in \mathbf{R} \times \Omega_b$, called the *generation distribution*.

Although there exist several choices for the state space of generation distributions, from the biological meaning, it is most reasonable to assume that

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

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

$$\|b_m\|_Y := \int_{\mathbf{R}} \|b_m(t)\|_E dt = \int_{\mathbf{R}} \int_{\Omega_b} |b_m(t,\zeta)| d\zeta dt.$$

Then $||b_m||_Y$ gives the total size of *m*-th generation (total number of newborns produced as the *m*-th generation), and the asymptotic *per-generation growth* factor of the genealogy is given by

$$\lim_{n \to \infty} \sqrt[m]{\|b_m\|_Y}.$$
 (2.5)

Although we have introduced the generation evolution operator on the half line in [5], here we use the generation evolution operator on the line by a positive integral operator $K_Y : Y \to Y$ leaving the cone $Y_+ = L^1_+(\mathbf{R}, E_+)$ invariant as follows, since it would be more suitable for evolution semigroup setting:

Definition 2.1. Let $\Psi(t,\tau)$ be the net reproduction operator from the b-state space $E_+ = L^1_+(\Omega_b)$ into itself. Then the generation evolution operator on the line associated with the net reproduction operator $\Psi(t,\tau)$ is the positive integral operator acting on the time-state space Y_+ defined by

$$(K_Y f)(t) = \int_0^\infty \Psi(t,\tau) f(t-\tau) d\tau, \quad f \in Y_+.$$
(2.6)

2.2 Cone and orbital spectral radius

Here we introduce basic results in positive operator theory according to [11] and [12]. Let X_+ be a cone of a normed real vector space X. The cone X_+ is called

reproducing (or generating) if $X = X_+ - X_+$ and total if X is the closure of $X_+ - X_+$. A cone X_+ is called *normal* if there exists some $\delta > 0$ such that $||x + z|| \ge \delta$ whenever $x \in X_+$, $z \in X_+$ and ||x|| = ||z|| = 1. A map B on X with $B(X_+) \subset X_+$ is called a positive map.

Let X be an ordered normed vector space with cone X_+ . A map $B: X_+ \to X_+$ is called *homogeneous* (of degree one) if $B(\alpha x) = \alpha B x$ for all $\alpha \in \mathbf{R}_+$ and $x \in X_+$. For a homogeneous map $B: X_+ \to X_+$, we define

$$||B||_{+} = \sup \{ ||Bx|| : x \in X_{+}, ||x|| \le 1 \},\$$

and call B bounded if $||B||_+ \in \mathbf{R}$. Then the cone spectral radius

$$r_{+}(B) := \inf_{n \in \mathbf{N}} \|B^{n}\|_{+}^{\frac{1}{n}} = \lim_{n \to \infty} \|B^{n}\|_{+}^{\frac{1}{n}},$$
(2.7)

exists. The *local spectral radius* of B at $x \in X_+$ is defined by

$$\gamma_B(x) := \limsup_{n \to \infty} \|B^n x\|^{\frac{1}{n}}, \quad x \in X_+,$$
(2.8)

and the *orbital spectral radius* of B is defined by

$$r_o(B) := \sup_{x \in X_+} \gamma_B(x).$$
(2.9)

Proposition 2.2 ([8], [11]). Let X be an ordered normed vector space with cone X_+ and $B: X_+ \to X_+$ be continuous, homogeneous and order preserving. Then $r_+(B) \ge r_o(B) \ge \gamma_B(x)$ for any $x \in X_+$. If X_+ is complete and normal, $r_+(B) = r_o(B)$.

The following lemma is proved in [6], Theorem 1.5 as the non-flatness of reproducing wedge:

Lemma 2.3. Let X be an ordered Banach space and X_+ be reproducing. Then for any $x \in X$, there always exist $u \in X_+$ and $v \in X_+$ such that x = u - v with $||u|| \le c||x||$ and $||v|| \le c||x||$, where c > 0 is a constant independent of x.

Proposition 2.4 ([9], [11]). Let X be an ordered Banach space and X_+ be reproducing. Then any linear positive operator $B: X \to X$ that is bounded on X_+ is bounded, and $r_+(B) = r(B)$.

2.3 The definition of R_0

In [5], we have defined the basic reproduction number R_0 as

$$R_0 = \limsup_{m \to \infty} \sqrt[m]{\|b_m\|_Y}, \qquad (2.10)$$

and we have shown that it is a biologically reasonable threshold value for population extinction and persistence independent of the initial value, and it can be seen as the extension of existing definitions in constant or periodic environments. Using the above mathematical definitions of cone spectral radius, we can reformulate our definition as follows: **Definition 2.5.** For any initial data $b_0 \in Y_+$, the local reproduction number for a birth genealogy with initial data b_0 is defined by

$$R_0(b_0) = \gamma_{K_Y}(b_0) = \limsup_{m \to \infty} \sqrt[m]{\|b_m\|_Y} = \limsup_{m \to \infty} \sqrt[m]{\|K_Y^m b_0\|_Y}.$$
 (2.11)

Then the basic reproduction number is defined by the orbital spectral radius:

$$R_0 = r_o(K_Y) = \sup\{R_0(b_0) : b_0 \in Y_+\}.$$
(2.12)

As was shown in [5], in fact, we can show that $r_o(K_Y) = \gamma_{K_Y}(b_0)$ for nontrivial initial data if the population evolution process is weakly ergodic, that is, any two orbits are eventually comparable. Then R_0 is computed by the local spectral radius associated with a nontrivial data. Moreover, it follows from Proposition 2.2 and 2.4, we have $r_o(K_Y) = r_+(K_Y) = r(K_Y)$, because the time-state space is complete, normal and reproducing. Then we have

Proposition 2.6. The basic reproduction number is given by the spectral radius of the generation evolution operator:

$$R_0 = r(K_Y). (2.13)$$

3 Evolution semigroups and R_0 in linear dynamics

In this section, we prove that the well-known recipe to compute the the basic reproduction number based on differential equation systems can be also applied to calculate R_0 in time-heterogeneous environments, and it play a role as a threshold value for population extinction and persistence.

3.1 Evolution semigroup

A family $\{U(t,s)|t,s \in \mathbf{R}, t \geq s\}$ of (possibly nonlinear) operators acting on a Banach space E is called *evolutionary system* if it satisfies the following conditions:

1. U(s,s)x = x for all $s \in \mathbf{R}$ and $x \in E$,

2.
$$U(t,s)U(s,r) = U(t,r)$$
 for all $t \ge s \ge r$.

The evolutionary system is called *continuous* if it satisfies the conditions:

1. There exist K > 0 and $\alpha \in \mathbf{R}$ such that

$$||U(t,s)x - U(t,s)y|| \le Ke^{\alpha(t-s)} ||x - y||,$$

for all $t \ge s$ and $x, y \in E$,

2. U(t, s)x is continuous jointly with respect to t, s and x.

The exponential growth bound of the evolutionary system U is defined as

$$\omega(U) := \inf \left\{ \alpha : \exists M \ge 1, \forall s \in \mathbf{R}, t \ge 0, \|U(s+t,s)\| \le M e^{\alpha t} \right\}.$$
(3.1)

For exponentially bounded evolutionary system U, it follows that (see [10])

$$\omega(U) = \lim_{t \to \infty} \sup_{s \in \mathbf{R}} \frac{\log \|U(s+t,s)\|}{t}.$$
(3.2)

In the following, by $C_u(\mathbf{R}, E)$ we mean the space of all bounded, uniformly continuous functions from \mathbf{R} to E equipped with the supremum norm, while $C_0(\mathbf{R}, E)$ denotes the subspace of functions $f \in C_u(\mathbf{R}, E)$ with the property $\lim_{|t|\to\infty} ||f(t)||_E = 0$. We assume that Y denotes $L^p(\mathbf{R}, E)$ $(1 \le p < \infty)$, $C_u(\mathbf{R}, E)$ or $C_0(\mathbf{R}; E)$.

The evolution semigroup on the line $T_U(\sigma)$ on a Banach space Y associated with the evolutionary system $U(t, s), t \geq s$ on E is given by

$$(T_U(\sigma)v)(t) = U(t, t - \sigma)v(t - \sigma), \quad \forall t \in \mathbf{R},$$
(3.3)

where v belongs to the domain of T_U . The following proposition is given as Proposition 1 in [1]:

Proposition 3.1. Assume that U(t,s), $t \ge s$ is a continuous evolutionary system on E such that U(t,s)0 = 0 for all $t \ge s$. Then the associated evolution semigroup $T_U(\sigma)$, $\sigma \ge 0$ is strongly continuous in Y.

The following Lemma is given in [10]:

Lemma 3.2. Let $Y = C_0(\mathbf{R}, E)$ or $Y = L^1(\mathbf{R}, E)$. Suppose that U(t, s), $t \ge s$ is linear. Then it follows that

$$||T_U(\sigma)|| = \sup_{t \in \mathbf{R}} ||U(t+\sigma,t)||, \qquad (3.4)$$

$$\omega(T_U) = \omega(U). \tag{3.5}$$

Corollary 3.3. If $\lim_{\sigma\to\infty} ||T_U(\sigma)f||_Y = 0$ for all $f \in Y$, then $\lim_{\sigma\to\infty} ||U(r + \sigma, r)e||_E = 0$ for all $e \in E$ and all $r \in \mathbf{R}$.

3.2 Linear population dynamics

Now let us consider population dynamics described by the linearized equation formulated as an abstract differential equation in $E = L^1(\Omega_b)$:

$$\frac{dx(t)}{dt} = (A(t) + C(t))x(t), \quad t > 0,$$
(3.6)

where A(t) denotes the generator of the survival (linear) evolution process $V(t,s), t \geq s$ and C(t) denotes a bounded linear positive operator describing the birth process. We assume that $\omega(V) < 0$, because A(t) describes the population survival process without reproduction.

Let $\{W(t,s)\}_{t\geq s}$ be the evolutionary family generated by A(t) + C(t), so x(t) satisfies the variation of constants formula:

$$x(t) = W(t,0)x(0) = V(t,0)x(0) + \int_0^t V(t,\sigma)C(\sigma)x(\sigma)d\sigma.$$
 (3.7)

Let b(t) := C(t)x(t) be the density of newborns. Then we have a renewal equation

$$b(t) = C(t)V(t,0)x(0) + C(t)\int_0^t V(t,t-\sigma)b(t-\sigma)d\sigma.$$
 (3.8)

Then the generation evolution operator is given by

$$(K_Y f)(t) = C(t) \int_0^\infty V(t, t-s) f(t-s) ds, \quad f \in Y_+,$$
(3.9)

where $Y_{+} = L_{+}^{1}(\mathbf{R} \times E)$ is the time-state space. The operator (3.9) was first introduced in section 5 of [10].

Let \mathcal{A} be the infinitesimal generator of the evolution semigroup $T_V(\sigma), \sigma \geq 0$ associated with the linear evolutionary system V. Let $v, y \in Y$. Then, $v \in D(\mathcal{A})$ and $y = \mathcal{A}v$ if and only if

$$y(t) = \lim_{h \downarrow 0} \frac{1}{h} \left(V(t, t-h)v(t-h) - v(t) \right),$$
(3.10)

for almost all $t \in \mathbf{R}$. The domain of \mathcal{A} can be characterized as follows (Lemma 2.5 in [7]):

Lemma 3.4. Let $v \in Y$. Then, $v \in D(\mathcal{A})$ and $y = \mathcal{A}v$ if and only if

$$v(t) = V(t,s)v(s) - \int_s^t V(t,\zeta)y(\zeta)d\zeta.$$
(3.11)

Then it follows that

$$\mathcal{A}v(t) = -\frac{dv(t)}{dt} + A(t)v(t), \quad v \in D(\mathcal{A}).$$
(3.12)

For C_0 -semigroup T(t), $t \ge 0$, the uniform growth bound $\omega(T)$ is given by

$$\omega(T) := \inf \left\{ \alpha \in \mathbf{R} : \exists M \ge 0, \forall t \ge 0, \|T(t)\| \le M e^{\alpha t} \right\}.$$
(3.13)

Lemma 3.5. Let \mathcal{A} be the infinitesimal generator of the evolution semigroup $T_V(\sigma), \sigma \geq 0$ associated with the linear evolutionary system V. It holds that

$$s(\mathcal{A}) = \omega(T_V) = \omega(V), \qquad (3.14)$$

where $s(\mathcal{A})$ is the spectral bound of \mathcal{A} .

Let \mathcal{C} be a positive linear operator on Y_+ such that $(\mathcal{C}x)(t) = C(t)x(t)$ for $x \in Y_+$. Then $\mathcal{A} + \mathcal{C}$ becomes the infinitesimal generator of evolution semigroup $T_W(\sigma), \sigma \geq 0$. From Thieme's result [10], we have

Proposition 3.6 ([10], Theorem 5.2). The generation evolution operator for (3.6) is calculated as

$$K_Y = \mathcal{C}(-\mathcal{A})^{-1},\tag{3.15}$$

and

$$\operatorname{sign}(R_0 - 1) = \operatorname{sign}(\omega(W)). \tag{3.16}$$

Proof. Since $\omega(V) = \omega(T_V) = s(\mathcal{A}) < 0$, \mathcal{A} is invertible and

$$((-\mathcal{A})^{-1}f)(t) = \int_0^\infty V(t, t-s)f(t-s)ds.$$
(3.17)

Therefore, we have $K_Y = \mathcal{C}(-\mathcal{A})^{-1}$. Since $(\lambda - \mathcal{A})^{-1} = \int_0^\infty e^{-\lambda\sigma} T_V(\sigma) d\sigma$ and the same kind of relation holds for $\mathcal{A} + \mathcal{C}$, so \mathcal{A} and $\mathcal{A} + \mathcal{C}$ are resolvent positive operators. It follows from a theorem by Thieme (Theorem 3.5 in [10]), $s(\mathcal{A} + \mathcal{C})$ has the same sign as $r(\mathcal{C}(-\mathcal{A})^{-1})) - 1$. From Lemma 3.5, we have the sign relation (3.16).

The sign relation (3.16) shows that the basic reproduction number $R_0 = r(K_Y)$ plays a role as a threshold value for extinction and persistence of population.

Remark 3.7. Although the generation evolution operator K_Y acting on the time-state space $Y = L^1(\mathbf{R}, E)$ is most suitable for biological interpretation, we also use the generation evolution operator acting one $C_0(\mathbf{R}, E)$ and $C_u(\mathbf{R}, E)$. Let K_0 denotes GEO acting on $Y = C_0(\mathbf{R}, E)$ and let K_u be GEO acting on $Y = C_u(\mathbf{R}, E)$. Because Proposition 3.6 holds again when the time-state space is $Y = C_0(\mathbf{R}, E)$ or $Y = C_u(\mathbf{R}, E)$, so we obtain

$$\operatorname{sign}(r(K_Y) - 1) = \operatorname{sign}(\omega(W)) = \operatorname{sign}(r(K_0) - 1) = \operatorname{sign}(r(K_u) - 1). \quad (3.18)$$

Then we have

$$\operatorname{sign}(R_0 - 1) = \operatorname{sign}(r(K_0) - 1) = \operatorname{sign}(r(K_u) - 1).$$
(3.19)

That is, $r(K_0)$ and $r(K_u)$ are surrogate indices for the basic reproduction number R_0 , while $Y = C_0(\mathbf{R}, E)$ or $Y = C_u(\mathbf{R}, E)$ is often more convenient to discuss the role of R_0 in nonlinear dynamics.

4 The role of R_0 in nonlinear dynamics

4.1 Linearized stability

From Proposition 3.6, if $R_0 < 1$, the zero solution of the linear system (3.6) is asymptotically exponentially stable. If (3.6) can be seen as a linearized equation at the zero equilibrium point of a nonlinear system, then it is expected that $R_0 < 1$ is a sufficient condition for local stability of the zero steady state of the original nonlinear system. To see this fact, here we consider a semilinear system:

$$\frac{dx(t)}{dt} = (A(t) + F(t))x(t), \quad t > 0,$$
(4.1)

where $x(t) = x(t, \cdot)$ is a vector-valued function from **R** to $E = L^1_+(\Omega_b)$. In the following, we adopt the following assumption:

- **Assumption 4.1.** 1. The linear equation dx(t)/dt = A(t)x(t) is well-posed, that is, there exists a continuous evolutionary system V(t, s), $t \ge s \ge 0$ on E such that for every $s \in \mathbf{R}$ and $x \in D(A(s))$, the linear equation dx/dt =A(t)x with x(s) = x has the unique solution given by x(t) = V(t, s)x.
 - 2. Let F(t) be a nonlinear operator on E such that F(t)x = f(t, x), where the nonlinear function $f : \mathbf{R} \times E \to E$ is jointly continuous with respect to $t \in \mathbf{R}$ and $x \in E$, Lipschitz continuous with respect to x uniformly for t and f(t, 0) = 0 for all $t \in \mathbf{R}$.

Every solution of the integral equation

$$x(t) = V(t,s)x + \int_{s}^{t} V(t,\xi)F(\xi)x(\xi)d\xi, \quad t \ge s,$$
(4.2)

is called a *mild solution* of the semilinear problem (4.1) starting from x at t = s. If for every $x \in E$, (4.2) has a unique solution x(t) with x(s) = x, it generates an evolutionary system U(t, s), $t \ge s$ such that x(t) = U(t, s)x. Under our assumptions, equation (4.2) has a unique mild solution.

Proposition 4.2 ([1], Proposition 2). Let $Y = L^p(\mathbf{R}, E)$ or $Y = C_0(\mathbf{R}, E)$. The semilinear problem (4.1) generates a continuous evolutionary process U(t, s), $t \ge s$ whose associated evolution semigroup $T_U(\sigma)$, $\sigma \ge 0$ on Y is strongly continuous and has an infinitesimal generator of the form $\mathcal{A} + \mathcal{F}$, where \mathcal{A} is the infinitesimal generator of the linear evolution semigroup $T_V(\sigma)$, $\sigma \ge 0$ associated with V(t, s), $t \ge s$ in Y and \mathcal{F} is the operator from Y into itself defined by $(\mathcal{F}v)(t) = f(\cdot, v(\cdot))$ for $v \in Y$.

Corollary 4.3. The infinitesimal generator $\mathcal{A}+\mathcal{F}$ of the evolutionary semigroup $T_U(\sigma), \sigma \geq 0$ is closed and densely defined in Y.

Then the operator $\mathcal{A} + \mathcal{F}$ generates a semigroup $S(\sigma), \sigma \geq 0$ of nonlinear operators on X in the Crandall-Liggett sense [14]. That is,

$$\lim_{\sigma \to 0+} \frac{S(\sigma)x - x}{\sigma} = (\mathcal{A} + \mathcal{F})x, \quad x \in D(\mathcal{A} + \mathcal{F}).$$
(4.3)

Under additional conditions, this semigroup coincides with the evolution semigroup $T_U(\sigma)$, $\sigma \geq 0$ associated with U(t,s), $t \geq s$, that is, the evolution semigroup $T_U(\sigma)$, $\sigma \geq 0$ gives the solution semiflow of a semilinear Cauchy problem with the generator $\mathcal{A} + \mathcal{F}$ on the time-state space Y. Now we state a Webb's result using our notations: **Theorem 4.4** ([14], Proposition 4.16). Let \mathcal{A} denote the infinitesimal generator of the linear semigroup $T_V(\sigma), \sigma \geq 0$. Let $\mathcal{F} : v \to f(\cdot, v(\cdot))$ be a nonlinear operator from a Banach space Y to Y such that \mathcal{F} is continuously Fréchet differentiable on Y. Then the following hold:

(i) For each $x \in Y$ there exists a maximal interval of existence $[0, \sigma_x)$ and unique continuous function $u : \sigma \to u(\sigma; x)$ from $[0, \sigma_x)$ to Y such that

$$u(\sigma; x) = T_V(\sigma)x + \int_0^{\sigma} T_V(\sigma - \zeta) \mathcal{F}u(\zeta; x) d\zeta, \qquad (4.4)$$

for all $\sigma \in [0, \sigma_x)$ and either $\sigma_x = \infty$ or $\lim_{\sigma \to \sigma_x} \|u(\sigma; x)\|_Y = \infty$.

- (ii) $u(\sigma; x)$ is a continuous function of x in the sense that if $x \in Y$ and $0 \le \sigma < \sigma_x$, there exist positive constant C and ϵ such that if $y \in Y$ and $||x y||_Y < \epsilon$, then $\sigma < \sigma_y$ and $||u(s; x) u(s; y)||_Y \le C||x y||_Y$ for all $0 \le s \le \sigma$.
- (iii) If $x \in D(\mathcal{A})$, then $u(\sigma; x) \in D(\mathcal{A})$ for $0 \leq \sigma < \sigma_x$ and the function $\sigma \to u(\sigma; x)$ is continuously differentiable and satisfies

$$\frac{du(\sigma;x)}{d\sigma} = \mathcal{A}u(\sigma;x) + \mathcal{F}u(\sigma;x), \quad \sigma \in [0,\sigma_x).$$
(4.5)

The following proposition is proved by the essentially same method as the proof of Theorem 1 of [1]:

Proposition 4.5. Under the assumptions of Proposition 4.2 and Theorem 4.4, it follows that

$$T_U(\sigma)x = T_V(\sigma)x + \int_0^\sigma T_V(\sigma - \zeta)\mathcal{F}T_U(\zeta)xd\zeta, \quad x \in Y.$$
(4.6)

Corollary 4.6. $v^* \in Y$ is a fixed point of the semigroup $T_U(\sigma)$, $\sigma \ge 0$ if and only if

$$\mathcal{A}v^* + \mathcal{F}v^* = 0. \tag{4.7}$$

Proof. Suppose that $T_U(\sigma)v^* = v^*$ for all $\sigma \ge 0$. As we discussed above, $\mathcal{A} + \mathcal{F}$ generates a strongly continuous semigroup $T_U(\sigma)$ satisfying the integral equation (4.6). Inserting $v^* = T_U(\sigma - \eta)v^*$ into (4.6), we have

$$v^*(\sigma) = V(\sigma, \eta)v^*(\eta) + \int_{\eta}^{\sigma} V(\sigma, z)f(z, v^*(z))dz.$$
(4.8)

From Lemma 3.4, we have $v^* \in D(\mathcal{A})$ and $\mathcal{A}v^* = -\mathcal{F}v^*$. Conversely if $\mathcal{A}v^* + \mathcal{F}v^* = 0$, v^* satisfies the integral equation (4.8), which implies $v^* = T_U(\sigma - \eta)v^*$. Then $v^* = T_U(\sigma)v^*$ for all $\sigma \geq 0$.

From (4.8), a fixed point v^* of $T_U(\sigma)$, $\sigma \ge 0$ is a total trajectory of (4.1), since $v^*(t+h) = U(t+h,t)v^*(t)$ for all $h \ge 0$ and $t \in \mathbf{R}$. Let $u^* \in Y$ satisfy $(\mathcal{A} + \mathcal{F})u^* = 0$. Suppose that \mathcal{F} is continuously Fréchet differentiable and let $\mathcal{C} := \mathcal{F}'[u^*]$ be the Fréchet derivative of \mathcal{F} at $u = u^*$. Here we assume that $(\mathcal{C}u)(t) = C(t)u(t)$, where C(t) is a bounded linear operator in E. Let $W(t,s), t \ge s$ be the evolutionary system generated by linear operator A(t) + C(t) associated with the evolution semigroup $T_W(\sigma), \sigma \ge 0$. Then we have

$$T_W(\sigma)u = T_V(\sigma)u + \int_0^\sigma T_V(\sigma - \zeta)\mathcal{C}T_W(\zeta)ud\zeta, \quad u \in Y.$$
(4.9)

From Proposition 4.17 in [14], we have a result for linearized stability for the evolutionary semigroup $T_U(\sigma)$, $\sigma \ge 0$:

Theorem 4.7. Let $u^* \in Y$ satisfy $(\mathcal{A} + \mathcal{F})u^* = 0$. If $\omega(T_W) < 0$, u^* is a locally asymptotically stable equilibrium in the following sense: There exists $\epsilon > 0$, $M \ge 1$ and $\gamma < 0$ such that if $u \in Y$ and $||u - u^*||_Y \le \epsilon$, then $\sigma_x = \infty$ and $||T_U(\sigma)u - u^*||_Y \le Me^{\gamma\sigma}||u - u^*||_Y$ for all $t \ge 0$.

Proposition 4.8. Let $Y = Y_0$ or $Y = Y_u$ and let $u^* \in Y$ be a fixed point of $T_U(\sigma), \sigma \ge 0$. If $\omega(T_W) < 0, u^*$ is a locally asymptotically stable orbit of (4.1) in the following sense: There exists $\epsilon > 0, M \ge 1$ and $\gamma < 0$ such that if $x \in E$ and $||x - u^*(s)||_E \le \epsilon$, then $||U(t, s)x - u^*(t)||_E \le Me^{\gamma(t-s)}||x - u^*(s)||_E$ for all $t \ge s$.

Proof. Suppose $Y = Y_u$ and we omit the case $Y = Y_0$ because we can repeat the same kind of argument. For any $x \in E$ such that $||x - u^*(s)||_E \leq \epsilon$, define $u(\zeta) := \phi(\zeta)(x - u^*(s)) + u^*(\zeta)$ where $\phi \in C_u(\mathbf{R}, \mathbf{R})$ such that $\phi(s) = 1$ and $\sup_{\zeta \in \mathbf{R}} |\phi(\zeta)| \leq 1$. Then $u \in Y$, u(s) = x and $||u - u^*||_Y \leq \epsilon$, so there exists $M \geq 1$ and $\gamma < 0$ such that $||T_U(\sigma)u - u^*||_Y \leq Me^{\gamma\sigma}||u - u^*||_Y$ for all $t \geq$ 0. Observe that $||T_U(t - s)u - u^*||_Y = \sup_{\zeta \in \mathbf{R}} ||(T_U(t - s)u)(\zeta) - u^*(\zeta)||_E \leq$ $Me^{\gamma(t-s)}||u - u^*||_Y$. Since $(T_U(t - s)u)(t) = U(t, s)u(s)$, we have $||U(t, s)x - u^*(t)||_E \leq Me^{\gamma(t-s)} \sup_{\zeta \in \mathbf{R}} ||u(\zeta) - u^*(\zeta)||_E \leq Me^{\gamma(t-s)}||x - u^*(s)||_E$. This completes our proof.

In special, the trivial steady state $u^* = 0$ is locally asymptotically stable steady state of (4.1) if $\omega(T_W) < 0$. Since $\omega(T_W) < 0$ if $r(K_Y) < 1$, we have

Proposition 4.9. Let $K_Y = C(-A)^{-1}$. The zero solution of (4.1) is locally asymptotically stable if $R_0 = r(K_Y) < 1$.

Therefore we can conclude that $R_0 < 1$ implies local extinction of population in time-heterogeneous environment governed by nonautonomous system (4.1). If there exists a nontrivial steady state $u^* \in Y$, we can apply Webb's Theorem II [13] (see also Corollary 2 and Theorem 1 in [1]).

Proposition 4.10. Let $Y = Y_0$ or $Y = Y_u$. Suppose that there exists real numbers α and γ such that $\alpha I - (\mathcal{A} + \mathcal{F})$ is m-accretive and $\gamma I - \mathcal{F}$ is accretive, the evolution semigroup $T_U(\sigma)$, $\sigma \geq 0$ is type $\alpha + \gamma$ as

$$||T_U(\sigma)v - T_U(\sigma)w||_Y \le e^{(\alpha + \gamma)\sigma} ||v - w||_Y, \quad v, w \in Y,$$
(4.10)

for all $\sigma \geq 0$. If $\alpha + \gamma < 0$, there exists a unique mild solution $v^* \in Y$ of equation (4.1), which is exponentially stable among mild solutions.

Proof. The first part is a result of Theorem II of [13]. If $\alpha + \gamma < 0$, $T_U(\sigma)$ is a contraction map, so there exists a unique fixed point $v^* \in Y$ such that $T_U(\sigma)v^* = v^*$. Then $||T_U(\sigma)v - v^*||_Y \leq e^{\alpha\sigma}||v - v^*||_Y$ for all $v \in Y$ and $v^*(\sigma) = V(\sigma, \eta)v^*(\eta) + \int_{\eta}^{\sigma} V(\sigma, \zeta)f(\zeta, v^*(\zeta))d\zeta$, which implies that v^* is a mild solution of (4.1) and $||T_U(\sigma)v - v^*||_Y \leq e^{(\alpha+\gamma)\sigma}||v - v^*||_Y$. Therefore we have $\sup_{t \in \mathbf{R}} ||U(t, t - \sigma)v(t - \sigma) - v^*(t)||_E \leq e^{(\alpha+\gamma)\sigma} \sup_{t \in \mathbf{R}} ||v(t) - v^*(t)||_E$, which shows that $\lim_{\sigma \to \infty} \sup_{t \in \mathbf{R}} ||U(t + \sigma, t)v(t) - v^*(t + \sigma)||_E = 0$, so v^* is globally stable among mild solutions.

4.2 The periodic case

Here we pay a special attention to a periodic solution for (4.1) with periodic parameters. Suppose that A(t) is a generator of a periodic evolutionary family $\{V(t,s)\}_{t\geq s\geq 0}$ such that $V(t+\theta, s+\theta) = V(t,s)$ with a period θ and F(t) is a periodic nonlinear operator on E such that $F(t+\theta) = F(t)$. Suppose that A(t) + F(t) generates an evolutionary process $U(t,s), t\geq s$ associated with the evolution semigroup $T_U(\sigma)$ on Y_u (Theorem 2 in [1]).

Lemma 4.11. Evolutionary process U(t,s), $t \ge s$ is θ -periodic as $U(t + \theta, s + \theta) = U(t,s)$.

Let v^* be a θ -periodic solution of (4.1). Then v^* is a total trajectory of (4.1), so it is a fixed point of $T_U(\sigma)$ for all $\sigma \ge 0$. Conversely we can expect that a fixed point of $T_U(\theta)$, if it exists in the set of periodic functions, gives to a periodic solution of (4.1):

Proposition 4.12. Let $Z_{\theta} := \{v \in Y_u : v(t + \theta) = v(t)\}$. If $T_U(\sigma), \sigma \ge 0$ has a fixed point v^* in Z_{θ} , it is a θ -periodic mild solution of (4.1).

Proposition 4.13 (Theorem 3, [1]). Let \mathcal{T} be the θ -translation in Y_u as $(\mathcal{T}v)(t) = v(t+\theta)$. Let $\Omega \subset Y_u$ be a subset such that $\mathcal{T}\Omega \subset \Omega$. If v^* is a unique fixed point of $T_U(\theta)$ in $\Omega \setminus \{0\}$, v^* is a θ -periodic mild solution of equation (4.1).

From Proposition 4.10, a θ -periodic mild solution v^* is globally exponentially stable among mild solutions in Y_u if $T_U(\sigma), \sigma \ge 0$ is type $\alpha + \gamma < 0$.

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Hisashi Inaba

Graduate School of Mathematical Sciences, The University of Tokyo 3-8-1 Komaba Meguro-ku Tokyo 153-8914 Japan E-mail address: inaba@ms.u-tokyo.ac.jp

東京大学大学院数理科学研究科 稲葉 寿