

## On the basic reproduction number in a random environment

Nicolas Bacaër · Mohamed Khaladi

Received: 13 July 2012 / Revised: 13 October 2012 / Published online: 23 October 2012  
© Springer-Verlag Berlin Heidelberg 2012

**Abstract** The concept of basic reproduction number  $R_0$  in population dynamics is studied in the case of random environments. For simplicity the dependence between successive environments is supposed to follow a Markov chain.  $R_0$  is the spectral radius of a next-generation operator. Its position with respect to 1 always determines population growth or decay in simulations, unlike another parameter suggested in a recent article (Hernandez-Suarez et al., Theor Popul Biol, doi:[10.1016/j.tpb.2012.05.004](https://doi.org/10.1016/j.tpb.2012.05.004), 2012). The position of the latter with respect to 1 determines growth or decay of the population's expectation.  $R_0$  is easily computed in the case of scalar population models without any structure. The main emphasis is on discrete-time models but continuous-time models are also considered.

**Keywords** Basic reproduction number · Markov chain · Population dynamics · Random environment

**Mathematics Subject Classification (2000)** 60J20 · 92D25

### 1 Introduction

In this article we consider population models of the form

$$p(t+1) = X(t)p(t), \quad X(t) = A(t) + B(t), \quad t = 0, 1, \dots$$

---

N. Bacaër (✉)  
Research group UMMISCO, IRD and University Paris 6, Paris, France  
e-mail: nicolas.bacaer@ird.fr

M. Khaladi  
Department of Mathematics, University Cadi Ayyad, Marrakech, Morocco

with  $p(0)$  given in  $\mathbb{R}^m$ .  $p(t)$  is the population vector while  $A(t)$  and  $B(t)$  are non-negative square matrices of size  $m$  for all  $t$ :  $A(t)$  is a birth matrix, while  $B(t)$  is a survival matrix. For simplicity, we assume that the nonnegative matrices  $(A(t), B(t))$  are chosen in a finite list of environments  $(A^{(k)}, B^{(k)})_{1 \leq k \leq K}$ , there being a probability  $M_{i,j}$  that an environment of type  $i$  is followed by an environment of type  $j$  ( $1 \leq i, j \leq K$ ). There is also a probability  $\mu_i$  that  $(A(0), B(0))$  is of type  $i$ . The matrix  $M = (M_{i,j})$  of this Markov chain is supposed to be irreducible. For the survival matrices to make sense biologically, we assume that  $\sum_i B_{i,j}^{(k)} \leq 1$  for all  $j$  and all  $k$ . We also assume: (H1) there exists  $\kappa$  such that  $\|B^{(\kappa)}\|_1 = \max_j \sum_i B_{i,j}^{(\kappa)} < 1$ ; (H2) the projection matrices  $A^{(k)} + B^{(k)}$  form an ergodic set (see e.g. Caswell 2001). For example, primitive matrices with a common incidence matrix form an ergodic set. Some of the assumptions above may be relaxed.

A large literature exists concerning such population models in a random environment (Lewontin and Cohen 1969; Tuljapurkar 1990 and references therein). In particular, writing  $|p(t)| = \sum_i p_i(t)$  and  $\|\cdot\|$  for any matrix norm, it is known that with the assumptions above the almost sure limit

$$r = \lim_{t \rightarrow +\infty} (\log |p(t)|)/t = \lim_{t \rightarrow +\infty} (\log \|X(t-1)X(t-2) \cdots X(0)\|)/t \quad (1)$$

exists and is independent of  $p(0)$  and of the particular sequence of environments randomly chosen following the Markov chain (Tuljapurkar 1990, p. 26). To stress the dependence of the growth rate  $r$  on the matrices  $A(t)$  and  $B(t)$ , we shall write  $r = r(A, B)$ . If for example the population vector is a scalar and if  $M_{i,j} = m_j$  for all  $i$  and  $j$ , which means that the environments are independent and identically distributed (i.i.d.), then it is known that

$$r(A, B) = \sum_k m_k \log(A^{(k)} + B^{(k)}) \quad (2)$$

(see, e.g., Haccou et al. 2005, § 2.9.2).

The classical concept of basic reproduction number (also called net reproductive rate)  $R_0$  has been extended from constant environments to periodic environments by Bacaër and Guernaoui (2006). This  $R_0$  is an asymptotic per generation growth rate (Bacaër and Ait Dads 2011, 2012). The case of nonperiodic continuous-time deterministic environments was considered by Thieme (2009, § 5.1) and Inaba (2012). In a recent article, Hernandez-Suarez et al. (2012) suggested an adaptation of  $R_0$  to models with random environments. It seems however that the position of their “ $R_0$ ” with respect to 1 does not always decide between population growth and population decay (a counter-example will be given below). In the present article, we explain how  $R_0$  should be computed so that it gives the right threshold: it is the unique solution of the equation

$$r(A/R_0, B) = 0. \quad (3)$$

In other words,  $R_0$  is the number by which all birth rates should be divided to bring the population to the critical situation where neither exponential growth nor exponential

decay occurs. Such a characterization of  $R_0$  was emphasized for constant environments by Li and Schneider (2002, Theor. 3.1) and for periodic environments either in a continuous-time or discrete-time setting by Bacaër (2007, Sect. 3.4, 2009, Sect. 4).

In Sect. 2,  $R_0$  is defined as the spectral radius of a “next-generation operator” following the terminology of Diekmann and Heesterbeek (2000). Proposition 1 shows that  $R_0 > 1$  if and only if  $r > 0$ . Proposition 2 shows that  $R_0$  may be computed using Eq. (3). The formula for  $R_0$  obtained for periodic environments by Bacaër (2009) is in fact a special case of the approach of the present article. Section 3 shows that the parameter recently introduced by Hernandez-Suarez et al. (2012) determines growth or decay of the population’s expectation. Section 4 focuses on the scalar case, for which  $R_0$  is easily computed. Some numerical examples are presented in Sect. 5. Continuous-time models are briefly discussed in Sect. 6 in order to make the link with a recent article by Artalejo et al. (2012). The conclusion explains that the difference between our  $R_0$  and the “ $R_0$ ” of Hernandez-Suarez et al. (2012) is the same as the difference between the expected growth rate of the population and the growth rate of the expected population, which has often been discussed (Lewontin and Cohen 1969; Tuljapurkar 1990).

## 2 Definition and properties of $R_0$

As in the periodic case (Bacaër and Ait Dads 2011, 2012), let us split the population in generations. Let  $q(n, t)$  be the population vector belonging to generation  $n$  at time  $t$ : for all  $t \geq 0$  and  $n \geq 0$ ,

$$\begin{aligned} q(0, 0) &= p(0), & q(0, t + 1) &= B(t)q(0, t) \\ q(n + 1, 0) &= 0, & q(n + 1, t + 1) &= A(t)q(n, t) + B(t)q(n + 1, t). \end{aligned} \tag{4}$$

Note that the zero on the right side of the equation  $q(n + 1, 0) = 0$  stands for the zero vector in  $\mathbb{R}^m$ . Then  $p(t) = \sum_{n \geq 0} q(n, t)$  satisfies  $p(t + 1) = (A(t) + B(t))p(t)$  for all  $t \geq 0$ . Let  $L = \ell^1(\mathbb{N}, \mathbb{R}^m)$  be the vector space of sequences  $(x(0), x(1), \dots)$  with  $x(t) \in \mathbb{R}^m$  for all  $t \geq 0$  such that  $\|x\| = \sum_{t \geq 0} \sum_{i=1}^m |x_i(t)| < +\infty$ . Then  $L$  is a Banach space. Notice that (4) may be written as

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

Let us introduce the operators  $\mathcal{A} : L \rightarrow L$ ,  $\mathcal{B} : L \rightarrow L$ , and the identity operator  $\mathcal{I} : L \rightarrow L$  such that for all  $x \in L$  and  $t \geq 0$ ,

$$\begin{aligned} (\mathcal{A}x)(0) &= 0, & (\mathcal{A}x)(t + 1) &= A(t)x(t), \\ (\mathcal{B}x)(0) &= 0, & (\mathcal{B}x)(t + 1) &= B(t)x(t), \\ (\mathcal{I}x)(t) &= x(t). \end{aligned}$$

Since  $A(t)$  and  $B(t)$  are chosen among a finite set of matrices, it is clear that  $\mathcal{A}x \in L$  and  $\mathcal{B}x \in L$  if  $x \in L$ . Moreover  $\mathcal{A}$  and  $\mathcal{B}$  are bounded linear operators.

**Lemma 1** *The spectral radius  $\rho(\mathcal{A} + \mathcal{B})$  is equal to  $e^{r(A, B)}$ .*

*Proof* Set  $\mathcal{X} = \mathcal{A} + \mathcal{B}$ . For all  $x \in L$  and  $\tau \geq 1$ , we have  $(\mathcal{X}^\tau x)(t) = 0$  for  $0 \leq t \leq \tau - 1$  and  $(\mathcal{X}^\tau x)(t) = X(t - 1)X(t - 2) \cdots X(t - \tau)x(t - \tau)$  if  $t \geq \tau$ . From (1) and from the spectral radius formula we see that

$$\rho(\mathcal{X}) = \lim_{\tau \rightarrow +\infty} \|\mathcal{X}^\tau\|^{1/\tau} = e^{r(A, B)},$$

where  $\|\cdot\|$  is the operator norm associated with the vector norm in  $L$ . □

**Lemma 2**  *$r(0, B) < 0$ : the population dies out if there are no births.*

*Proof* We have  $\|B^{(k)}\|_1 \leq 1$  for all  $k$  and  $\|B^{(k)}\|_1 < 1$ . The environment  $\kappa$  occurs (as  $t \rightarrow +\infty$ ) in a positive fraction  $\pi_\kappa$  of the  $t$  terms of the matrix product of Eq. (1) because the Markov chain is assumed irreducible. But  $\|\cdot\|_1$  is a sub-multiplicative norm. So we get  $r(0, B) \leq \pi_\kappa \log \|B^{(\kappa)}\|_1 < 0$ . □

Since  $r(0, B) < 0$ , Lemma 1 shows that  $\rho(B) < 1$ . So  $\mathcal{I} - B$  is invertible: if  $y = (\mathcal{I} - B)x$ , then  $x = (\mathcal{I} - B)^{-1}y = y + By + B^2y + \cdots$ , i.e.,

$$x(t) = \sum_{\tau=0}^t B(t - 1)B(t - 2) \cdots B(\tau)y(\tau)$$

for all  $t \geq 0$ . For all  $n \geq 0$ , set  $q_n = (q(n, t))_{t \geq 0}$ . Equation (5) is equivalent to  $(\mathcal{I} - B)q_{n+1} = \mathcal{A}q_n$ , i.e.,  $q_{n+1} = (\mathcal{I} - B)^{-1}\mathcal{A}q_n$ . Since  $q_0 \in L$ , we have  $q_n \in L$  for all  $n \geq 1$ . Now set  $g_n = \mathcal{A}q_n$ . In this way  $g_n(t + 1) = A(t)q(n, t)$  is the birth vector due to generation  $n$  between time  $t$  and  $t + 1$ . We arrive at the following conclusion:

$$g_{n+1} = \mathcal{A}q_{n+1} = \mathcal{A}(\mathcal{I} - B)^{-1}g_n.$$

More explicitly, we have  $g_{n+1}(0) = 0$  and the renewal equation for the births

$$g_{n+1}(t + 1) = \sum_{\tau=0}^t A(t)B(t - 1)B(t - 2) \cdots B(\tau)g_n(\tau) \tag{6}$$

for all  $t \geq 0$  and  $n \geq 0$ .

**Definition 1** The spectral radius of the next-generation operator  $\mathcal{A}(\mathcal{I} - B)^{-1}$  is called  $R_0$ .

Notice the analogy between Definition 1 and the presentation of  $R_0$  for continuous-time models in time-heterogeneous environments by Thieme (2009, § 5.1) and Inaba (2012). As for the growth rate  $r(A, B)$  in Sect. 1, we shall write  $R_0(A, B)$  to stress the dependence with respect to the sequence of matrices  $A(t)$  and  $B(t)$ .

**Proposition 1**  *$R_0(A, B) > 1$  if  $r(A, B) > 0$ ,  $R_0(A, B) = 1$  if  $r(A, B) = 0$ , and  $R_0(A, B) < 1$  if  $r(A, B) < 0$ .*

*Proof* Applying a result by Thieme (2009, Theor. 3.10), we know that  $R_0(A, B) - 1$  has the same sign as  $\rho(\mathcal{A} + \mathcal{B}) - 1$ . But Lemma 1 showed that  $\rho(\mathcal{A} + \mathcal{B}) = e^{r(A, B)}$ . So  $R_0(A, B) - 1$  has the same sign as  $r(A, B)$ .  $\square$

**Proposition 2** *Assume that  $R_0(A, B) > 0$ . Then  $R_0(A, B)$  is the unique solution of the equation  $r(A/R, B) = 0$  on the interval  $R \in (0, +\infty)$ .*

*Proof* Since the basic reproduction number depends linearly on the set of birth rates, we have  $R_0(A/R_0(A, B), B) = 1$ . So  $r(A/R_0(A, B), B) = 0$  because of Proposition 1. Hence the equation  $r(A/R, B) = 0$  has at least one solution. Given Eq. (1), the mapping  $R \mapsto r(A/R, B)$  is obviously nonincreasing on the interval  $R \in (0, +\infty)$ . It is easily checked, by taking the second derivative, that for every  $(i, j)$  the mapping  $R \mapsto A_{i,j}(t)/R + B_{i,j}(t)$  is either identically zero or log-convex [this point was already used by Bacaër and Ait Dads (2012, Appendix C)]. It follows from the results of Cohen (1980, Theor. 1) that the mapping  $R \mapsto r(A/R, B)$  is convex. So the equation  $r(A/R, B) = 0$  cannot have more than one solution. Indeed if it had two distinct solutions  $R_1$  and  $R_2$  with  $R_1 < R_2$ , the nonincreasing and convex function  $R \mapsto r(A/R, B)$  would be constant equal to 0 not only on the interval  $(R_1, R_2)$ , but for all  $R \geq R_1$ . This function from  $(0, +\infty)$  to  $\mathbb{R}$  being convex, it is also continuous. So  $r(A/R, B) \rightarrow r(0, B) < 0$  as  $R \rightarrow +\infty$ . We have thus reached a contradiction.  $\square$

*Remark 1* Proposition 2 shows that, in general, computing  $R_0$  is as difficult as computing  $r$ , and requires slightly more computer time because a dichotomy method has to be used.

*Remark 2* For periodic environments where the sequence is  $(1, 2, \dots, K)$ , Bacaër (2009) showed that  $R_0$  was the spectral radius of

$$\begin{pmatrix} A^{(1)} & 0 & \dots & 0 \\ 0 & A^{(2)} & & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & A^{(K)} \end{pmatrix} \begin{pmatrix} -B^{(1)} & I & 0 & \dots & 0 \\ 0 & -B^{(2)} & I & & 0 \\ 0 & \ddots & \ddots & & \vdots \\ \vdots & \ddots & \ddots & 0 & I \\ I & \dots & 0 & 0 & -B^{(K)} \end{pmatrix}^{-1} \tag{7}$$

Bacaër and Ait Dads (2012, Prop. 3) emphasized that this  $R_0$  is the unique solution of the equation

$$\rho\left(\left(\frac{A^{(K)}}{R} + B^{(K)}\right) \dots \left(\frac{A^{(1)}}{R} + B^{(1)}\right)\right) = 1.$$

Given Eq. (1), the left side above is obviously equal to  $e^{r(A/R, B)}$ . So we can conclude from Proposition 2 that the  $R_0$  of Bacaër (2009) is the same as the  $R_0$  of Definition 1 in the special case of periodic environments ( $M_{i,j} = 1$  if  $j = i + 1$  and  $1 \leq i \leq K - 1$ ,

$M_{K,1} = 1$ , and  $M_{i,j} = 0$  otherwise). To emphasize this, it is convenient to present  $R_0$  in a periodic environment as the spectral radius of

$$\left( \begin{array}{cccccc} 0 & 0 & \dots & 0 & A^{(K)} & \\ A^{(1)} & 0 & & & 0 & \\ 0 & \ddots & \ddots & & \vdots & \\ \vdots & \ddots & \ddots & 0 & 0 & \\ 0 & \dots & 0 & A^{(K-1)} & 0 & \end{array} \right) \left( \begin{array}{cccccc} I & 0 & \dots & 0 & -B^{(K)} & \\ -B^{(1)} & I & & & 0 & \\ 0 & \ddots & \ddots & & \vdots & \\ \vdots & \ddots & \ddots & I & 0 & \\ 0 & \dots & 0 & -B^{(K-1)} & I & \end{array} \right)^{-1}, \tag{8}$$

which is easily shown to be the same as the spectral radius of (7) (see Hernandez-Suarez et al. 2012, Sect. 5). The fact that this spectral radius coincides with the spectral radius of  $A(I - B)^{-1}$  (Cushing and Zhou 1994; Caswell 2001) when the environment is constant (with  $A^{(k)} = A$  and  $B^{(k)} = B$  for all  $k$ ) was already shown by Bacaër and Ait Dads (2012).

**Proposition 3** *The definition of  $R_0$  above is independent of the particular random sequence  $(A(t), B(t))_{t \geq 0}$  of environments following the Markov chain with matrix  $M$ . So  $R_0$  may be called the basic reproduction number of the model.*

*Proof* Let  $(A(t), B(t))$  and  $(A'(t), B'(t))$  be two sequences of environments following the Markov chain with matrix  $M$ . Let  $R_0(A, B)$  and  $R_0(A', B')$  be the corresponding basic reproduction numbers. We wish to show that  $R_0(A, B) = R_0(A', B')$ . From Proposition 2, we know that  $r(A/R_0(A, B), B) = 0$  and that  $r(A'/R_0(A', B'), B') = 0$ . But growth rates are independent of the particular sequence of environments (Tuljapurkar 1990). So  $0 = r(A/R_0(A, B), B) = r(A'/R_0(A, B), B')$ . We see that both  $R_0(A, B)$  and  $R_0(A', B')$  are solutions of  $r(A'/R, B') = 0$ . Proposition 2 implies that  $R_0(A, B) = R_0(A', B')$ . □

### 3 Another parameter

In a recent article, Hernandez-Suarez et al. (2012) suggested to call “ $R_0$ ” the spectral radius of

$$\left( \begin{array}{ccc} M_{1,1}A^{(1)} & \dots & M_{K,1}A^{(K)} \\ \vdots & & \vdots \\ M_{1,K}A^{(1)} & \dots & M_{K,K}A^{(K)} \end{array} \right) \left[ I - \left( \begin{array}{ccc} M_{1,1}B^{(1)} & \dots & M_{K,1}B^{(K)} \\ \vdots & & \vdots \\ M_{1,K}B^{(1)} & \dots & M_{K,K}B^{(K)} \end{array} \right) \right]^{-1}, \tag{9}$$

where  $I$  is an identity matrix of suitable size. To avoid any confusion, we shall call this spectral radius  $R_*$ .

In the literature on Markovian environments, it is known that

$$\log \mu = \lim_{t \rightarrow +\infty} \frac{\log \mathbb{E}[|p(t)|]}{t} \tag{10}$$

exists (recall that  $|\cdot|$  stands for the sum of components). Moreover  $\mu$  is the spectral radius of  $D(M' \otimes I)$ , where  $D$  is the block-diagonal matrix  $D = \text{diag}(A^{(1)} + B^{(1)}, \dots, A^{(K)} + B^{(K)})$ ,  $M'$  is the transpose of  $M$ , and  $I$  is the identity matrix (see Tuljapurkar 1990, p. 45, where it is called Bharucha’s formula).

**Proposition 4**  $R_* > 1$  if  $\log \mu > 0$ ,  $R_* = 1$  if  $\log \mu = 0$ , and  $R_* < 1$  if  $\log \mu < 0$ .

*Proof* Notice that the matrix  $D(M' \otimes I)$  is equal to

$$\begin{pmatrix} M_{1,1}(A^{(1)} + B^{(1)}) & \dots & M_{K,1}(A^{(K)} + B^{(K)}) \\ \vdots & & \vdots \\ M_{1,K}(A^{(1)} + B^{(1)}) & \dots & M_{K,K}(A^{(K)} + B^{(K)}) \end{pmatrix}.$$

This matrix is equal to  $A^* + B^*$ , where

$$A^* = \begin{pmatrix} M_{1,1}A^{(1)} & \dots & M_{K,1}A^{(K)} \\ \vdots & & \vdots \\ M_{1,K}A^{(1)} & \dots & M_{K,K}A^{(K)} \end{pmatrix},$$

and  $B^*$  is defined similarly by replacing  $A$  by  $B$ . Applying the result given by Thieme (2009, Theor. 3.10), we know that  $\rho(A^* + B^*) - 1$  and  $\rho(A^*(I - B^*)^{-1}) - 1$  have the same sign. But  $\mu = \rho(A^* + B^*)$  and  $R_* = \rho(A^*(I - B^*)^{-1})$ .  $\square$

*Remark 3* In a periodic environment we have  $R_0 = R_*$ , as can be seen by comparing the matrices (8) and (9).

### 4 The scalar case

If the matrices  $A(t)$  and  $B(t)$  are scalars, and if the environments are i.i.d., then it follows immediately from Eq. (2) and Proposition 2 that

$$\sum_{k=1}^K m_k \log \left( \frac{A^{(k)}}{R_0} + B^{(k)} \right) = 0,$$

or equivalently that

$$\prod_{k=1}^K \left( \frac{A^{(k)}}{R_0} + B^{(k)} \right)^{m_k} = 1.$$

Consider now the more general case of Markov dependence between successive environments. Recall that  $M = (M_{i,j})$  is the matrix of transition probabilities. The chain being irreducible, let  $\pi$  be the positive stationary distribution of the time spent in

the different environments:  $\pi_j = \sum_i \pi_i M_{i,j}$  for all  $j$  and  $\sum_j \pi_j = 1$ . As mentioned by Haccou et al. (2005, § 2.9.2) the growth rate is

$$r(A, B) = \sum_k \pi_k \log(A^{(k)} + B^{(k)})$$

[for a proof, simply notice that  $\log p(t) = \sum_{\tau=0}^{t-1} \log X(\tau) + \log p(0)$  and that, as  $t \rightarrow +\infty$ , the number of terms equal to  $\log(A^{(k)} + B^{(k)})$  in the sum over  $\tau$  is  $\pi_k t + o(t)$ ]. So Proposition 2 shows that  $R_0$  is the solution of

$$\prod_{k=1}^K \left( \frac{A^{(k)}}{R_0} + B^{(k)} \right)^{\pi_k} = 1. \tag{11}$$

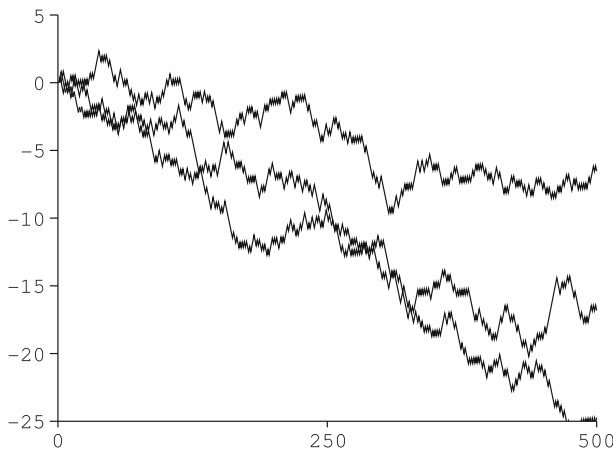
Thus  $R_0$  can be easily computed, e.g., using a dichotomy method.

### 5 Examples

As a first example, consider a scalar population ( $m = 1$ ) and suppose that there are two environments ( $K = 2$ ):

$$(A^{(1)}, B^{(1)}) = (1, 0.5), \quad (A^{(2)}, B^{(2)}) = (0.1, 0.58), \quad M = \begin{pmatrix} 0.3 & 0.7 \\ 0.6 & 0.4 \end{pmatrix}.$$

The stationary distribution is  $(\pi_1, \pi_2) = (6/13, 7/13)$ . Equation (11) gives  $R_0 \simeq 0.949 < 1$ : the population goes extinct almost surely. For such an example, Eq. (9) gives  $R_* \simeq 1.050 > 1$ . For illustration we made several simulations of the model starting from  $p(0) = 1$ . Fig. 1 suggests that the process is indeed subcritical. The parameter values were chosen precisely so that  $R_0 < 1$  while  $R_* > 1$ . However it



**Fig. 1**  $\log p(t)$  as a function of  $t$ . Here  $R_0 < 1$  while  $R_* > 1$



seems that in many other cases both parameters are on the same side of 1 and differ only very slightly, the difference often being less than 1 %. Although such a difference may appear as biologically insignificant, it does have its importance for establishing threshold results mathematically.

As a second example, let us consider a model with two stages and two environments:

$$A^{(1)} = \begin{pmatrix} 0.1 & 2 \\ 0 & 0 \end{pmatrix}, \quad B^{(1)} = \begin{pmatrix} 0 & 0 \\ 0.1 & 0 \end{pmatrix},$$

$$A^{(2)} = \begin{pmatrix} 1 & 0.3 \\ 0 & 0 \end{pmatrix}, \quad B^{(2)} = \begin{pmatrix} 0 & 0 \\ 0.7 & 0 \end{pmatrix}, \quad M = \begin{pmatrix} 0.5 & 0.5 \\ 0.5 & 0.5 \end{pmatrix}.$$

Notice that the matrices  $A^{(k)} + B^{(k)}$  for  $k = 1, 2$  are Leslie matrices and that the environments are independent and identically distributed. Formula (9) gives  $R_* = 1.01 > 1$ . If we run simulations starting for example from  $p(0) = (1 \ 1)'$ , if we estimate the growth rate  $r$  by  $\frac{1}{t} \log(|p(t)|/|p(0)|)$  with  $t = 5000$ , and if we iterate the process 1000 times, we find that the expected growth rate is  $-0.1021$  with a sample standard error of 0.0074. This suggests that  $r < 0$  and therefore that  $R_0 < 1$ . To estimate  $R_0$  numerically, we use Proposition 2: we divide  $A^{(k)}$  for  $k = 1, 2$  by  $R$  and estimate the new growth rate. With  $R = 0.84$ , we find  $r \simeq 0.0135$  with a sample standard error of 0.0072, suggesting that  $r > 0$ . With  $R = 0.88$ , we find  $r \simeq -0.0168$  with a sample standard error of 0.0071, suggesting that  $r < 0$ . So it seems that  $0.84 < R_0 < 0.88$ .

For the same example, one can also directly use the definition of  $R_0$  as the spectral radius of the operator  $\Omega = \mathcal{A}(\mathcal{T} - \mathcal{B})^{-1}$ . Beware that this operator does not have any nonzero eigenvalue, as the continuous-time case studied by Inaba (2012, Lemma 9). But we can compute  $g_n$  for  $n$  large and estimate  $R_0$  from  $\sqrt[n]{\|g_n\|/\|g_0\|}$ . In our example notice that  $B^{(k)}B^{(k')} = 0$  for all  $k, k' = 1, 2$  and that  $g_0(t) = 0$  for all  $t \geq 3$ . It follows from the renewal equation (6) that  $g_n(t) = 0$  for all  $t \geq \tau$  implies  $g_{n+1}(t) = 0$  for all  $t \geq \tau + 2$ . So  $g_n(t) = 0$  for all  $t \geq 2n + 3$ . To compute  $g_n$ , it is therefore enough to consider the operator  $\Omega$  on the finite dimensional subspace  $\ell^1(\{0, 1, \dots, 2n + 2\}, \mathbb{R}^2)$ . For  $n = 1, 000$ , we chose 10 random sequences of environments and found estimates of  $R_0$  with a mean of 0.86 and a sample standard error of 0.015, in line with the estimate already obtained.

### 6 Continuous-time models

Let us now briefly sketch how a similar theory can be developed for linear continuous-time population models in a random ergodic environment. For example let us take a model of the form

$$dp/dt = (A(t) - B(t))p(t), \tag{12}$$

where  $p(t)$  is a vector,  $A(t)$  a nonnegative square matrix function of size  $m$ , and  $B(t)$  a matrix function of the same size with nonnegative off-diagonal coefficients. We assume for simplicity that  $(A(t), B(t))$  belongs to a finite list of environments

$((A^{(k)}, B^{(k)}))_{1 \leq k \leq K}$  and that the transition between the environments follows an inhomogeneous continuous-time Markov chain (see, e.g., Ge et al. 2006): the probability  $\Pi_k(t)$  to be in state  $k$  at time  $t$  satisfies  $d\Pi/dt = Q(t)\Pi$ , where  $Q(t)$  is irreducible,  $T$ -periodic, with nonnegative off-diagonal coefficients, piecewise continuous, and such that  $Q_{jj}(t) = -\sum_{i \neq j} Q_{ij}(t)$ . The matrix  $Q(t)$  is allowed to be periodic because many populations experience a mixture of seasonal and random effects (for discrete-time models such a mixture can be incorporated in the transition matrix  $M$  of Sect. 1). Let  $\lambda_1(A, B)$  be the largest Lyapunov exponent (see, e.g., Arnold and Wihstutz 1986) of (12). We shall assume that  $\lambda_1(0, B) < 0$ : the population tends to 0 without births.

The basic reproduction number  $R_0$  can be defined as the spectral radius of the renewal operator  $\mathcal{K}$  on  $L^1((0, \infty), \mathbb{R}^m)$  given by  $(\mathcal{K}u)(t) = \int_0^t K(t, x)u(t - x) dx$ , where the kernel is given by  $K(t, x) = A(t)C(t, x)$  and  $C(t, x)$  is the survival matrix from time  $t - x$  to time  $t$ :  $C(t, x) = Z(t)$ ,  $dZ/ds = -B(s)Z(s)$  for  $t - x < s < t$  and  $Z(t - x) = I$  (the identity matrix). Indeed it is known (Bacaër and Ait Dads 2011, Lemma 2) that the birth vector per unit of time due to generation  $n$  satisfies a recurrence relation involving the operator  $\mathcal{K}$ , which is similar to Eq. (6). For a discussion of the link between the spectral radius of this operator and  $R_0$  but for deterministic models, see Inaba (2012, Sect. 4). If  $R_0 > 0$  then  $R_0$  may once again be characterized by the fact that  $\lambda_1(A/R_0, B) = 0$ , as in Proposition 2. The spectral radius  $R_0$  of  $\mathcal{K}$  is almost surely independent of the particular random sequence of environments, as in Proposition 3.

If  $p(t)$  is a scalar population then  $\lambda_1(A, B) = \langle A \rangle - \langle B \rangle$ , where for instance  $\langle A \rangle = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t A(s) ds$ . So  $R_0 = \langle A \rangle / \langle B \rangle$  as, e.g., in the work of Córdova-Lepe et al. (2012) on a model with almost periodic coefficients. The row vector  $v = (1 \ 1 \ \dots \ 1)$  satisfies  $dv/dt = 0 = vQ(t)$ . So it can be shown, following Perthame (2007, § 6.3.2), that there is a unique  $T$ -periodic positive solution  $u(t)$  of  $du/dt = Q(t)u(t)$  such that  $\sum_i u_i(t) = 1$ . The law of large numbers for Markov chains shows that  $\langle A \rangle = \frac{1}{T} \int_0^T \sum_k u_k(s)A^{(k)} ds$ . So

$$R_0 = \frac{\int_0^T \sum_k u_k(s)A^{(k)} ds}{\int_0^T \sum_k u_k(s)B^{(k)} ds}.$$

If moreover  $Q(t)$  does not depend on  $t$  then there is a unique vector  $u$  such that  $Qu = 0$  and  $\sum_i u_i = 1$ . So  $R_0 = (\sum_k u_k A^{(k)}) / (\sum_k u_k B^{(k)})$ . This formula for  $R_0$  is the same as the one for “ $R_0^{ARA}$ ” by Artalejo et al. (2012, § 4.1).

### 7 Conclusion

The difference between the  $R_0$  in the present paper and the “ $R_0$ ” (which we call  $R_*$ ) of Hernandez-Suarez et al. (2012) is similar to the difference between on one side the “stochastic” growth rate (1), which is also equal to the expected growth rate of the population

$$r = \lim_{t \rightarrow +\infty} \mathbb{E} \left[ \frac{\log |p(t)|}{t} \right],$$

and on the other side the growth rate of the expected population (10) (Lewontin and Cohen 1969; Tuljapurkar 1990). It is the position of  $r$  with respect to 0 or of our  $R_0$  with respect to 1, which decides whether the population is sub- or supercritical in simulations. However  $\log \mu$  and  $R_*$  are much easier to compute in Markovian environments with structured (non-scalar) populations: they are given by the spectral radii of simple matrices.

**Acknowledgments** We thank S. Méléard, O. Diekmann, and particularly C. Hernandez-Suarez for stimulating our interest in random environments.

## References

- Arnold L, Wihstutz V (1986) Lyapunov exponents: a survey. In: Arnold L, Wihstutz V (eds) Lyapunov exponents. Lecture Notes in Mathematics, vol 1186. Springer, Berlin, pp 1–26
- Artalejo JR, Economou A, Lopez-Herrero MJ (2012) Stochastic epidemic models with random environment: quasi-stationarity, extinction and final size. *J Math Biol*. doi:[10.1007/s00285-012-0570-5](https://doi.org/10.1007/s00285-012-0570-5)
- Bacaër N (2007) Approximation of the basic reproduction number  $R_0$  for vector-borne diseases with a periodic vector population. *Bull Math Biol* 69:1067–1091
- Bacaër N (2009) Periodic matrix population models: growth rate, basic reproduction number and entropy. *Bull Math Biol* 71:1781–1792
- Bacaër N, Ait Dads EH (2011) Genealogy with seasonality, the basic reproduction number, and the influenza pandemic. *J Math Biol* 62:741–762
- Bacaër N, Ait Dads EH (2012) On the biological interpretation of a definition for the parameter  $R_0$  in periodic population models. *J Math Biol* 65:601–621
- Bacaër N, Guernaoui S (2006) The epidemic threshold of vector-borne diseases with seasonality. *J Math Biol* 53:421–436
- Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland
- Cohen JE (1980) Convexity properties of products of random nonnegative matrices. *Proc Natl Acad Sci USA* 77:3749–3752
- Córdova-Lepe F, Robledo G, Pinto M, González-Olivares E (2012) Modeling pulse infectious events erupting into a controlled context: a SIS disease with almost periodic parameters. *Appl Math Model* 36:1323–1337
- Cushing JM, Zhou Y (1994) The net reproductive value and stability in structured population models. *Nat Res Model* 8:1–37
- Diekmann O, Heesterbeek JAP (2000) Mathematical epidemiology of infectious diseases. Wiley, Chichester
- Ge H, Jiang DQ, Qian M (2006) Reversibility and entropy production of inhomogeneous Markov chains. *J Appl Probab* 43:1028–1043
- Haccou P, Jagers P, Vatutin VA (2005) Branching processes: variation, growth, and extinction of populations. Cambridge University Press, Cambridge
- Hernandez-Suarez C, Rabinovich J, Hernandez K (2012) The long-run distribution of births across environments under environmental stochasticity and its use in the calculation of unconditional life-history parameters. *Theor Popul Biol*. doi:[10.1016/j.tpb.2012.05.004](https://doi.org/10.1016/j.tpb.2012.05.004)
- Inaba H (2012) On a new perspective of the basic reproduction number in heterogeneous environments. *J Math Biol* 65:309–348
- Lewontin RC, Cohen D (1969) On population growth in a randomly varying environment. *Proc Natl Acad Sci USA* 62:1056–1060
- Li CK, Schneider H (2002) Applications of Perron–Frobenius theory to population dynamics. *J Math Biol* 44:450–462
- Perthame B (2007) Transport equations in biology. Birkhäuser, Basel
- Thieme HR (2009) Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. *SIAM J Appl Math* 70:188–211
- Tuljapurkar S (1990) Population dynamics in variable environments. Springer, New York