When can a population spreading across sink habitats persist ?

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Abstract

We consider populations with time-varying growth rates living in sinks. Each population, when isolated, would become extinct. Dispersal-induced growth (DIG) occurs when the populations are able to persist and grow exponentially when dispersal among the populations is present. We provide a mathematical analysis of this surprising phenomenon, in the context of a deterministic model with periodic variation of growth rates and non-symmetric migration which are assumed to be piecewise continuous. We also consider a stochastic model with random variation of growth rates and migration. This work extends existing results of the literature on the DIG effects obtained for periodic continuous growth rates and time independent symmetric migration.
Keywords. Dispersal-induced growth. Periodic linear cooperative systems. Principal Lyapunov exponent. Averaging. Singular perturbations. Perron root. Metzler matrices. Sinks. Stochastic environment. Markov Feller process.

Contents

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1 Introduction

Many plant and animal populations live in separate patches which have different environmental conditions, that are connected by dispersal. The study of the interaction between organism dispersal and environmental heterogeneity, both spatial and temporal, to determine population growth is a central theme of ecological theory [2, 16]. A patch is called a *source* when, in the absence of dispersion, the environmental conditions lead to the persistence of the population, and a *sink* when, on the contrary, they lead to the extinction of the population. A basic insight of source-sink theory is that populations in sinks may be sustained, as a result of immigration from source patches [33]. A more surprising phenomenon is that of populations that can *persist in an environment consisting of sink habitats only* as announced in the title of [22]. In fact, this somewhat paradoxical effect of dispersal has already been pointed by Holt [19] on particular systems and called *inflation* [20]. Since it is possible for populations in a set of patches, with dispersal among them, to persist and grow despite the fact that all these patches are sinks, this phenomenon was called *dispersal-induced growth* (DIG) by Katriel [23]. For further details and complements on the mathematical modelling of this phenomenon and the biological motivations, the reader is referred to [4, 23] and the references therein.

Katriel [23] considered the model of populations of sizes $x_i(t)$ $(1 \leq i \leq n)$, inhabiting n patches, and subject to time-periodic local growth rates $r_i(t/T)$ $(1 \leq i \leq n)$, where it is assumed that $r_i(\tau)$ are 1-periodic continuous functions, so that $r_i(t/T)$ are periodic with period $T > 0$. The dispersal among the patches i and j $(i \neq j)$ is at rate $m\ell_{ij}$ where the parameter $m \geq 0$ measures the strength, and the numbers

$$\ell_{ij} = \ell_{ji}, \qquad (i \neq j) \tag{1}$$

encode the topology of the dispersal network and the relative rates of dispersal among different patches: If $\ell_{ij} = 0$, there is no migration between the patches i and j, if $\ell_{ij} > 0$, there is a migration. We then have the differential equations

$$\frac{dx_i}{dt} = r_i(t/T)x_i + m\sum_{j\neq i}\ell_{ij}\left(x_j - x_i\right), \quad 1 \leq i \leq n. \tag{2}$$

Katriel [23] proved that in the irreducible case (any two patches are connected by migration, either directly, or through other patches), any solution of (2) with $x_i(0) > 0$ for $1 \leq i \leq n$ satisfies $x_i(t) > 0$ for all $t > 0$ so that we can define the Lyapunov exponents $\Lambda[x_i] = \lim_{t\to\infty} \frac{1}{t}\ln(x_i(t))$, provided this limit exists. It is shown in [23] that, when $m > 0$, the Lyapunov exponents $\Lambda[x_i]$ of all components $x_i(t)$ are equal, and moreover they do not depend on the initial condition. The common value of the Lyapunov exponents $\Lambda[x_i]$ is called the growth rate of the system (2) and denoted $\Lambda(m, T)$. The main results in [23] are on the asymptotic properties of $\Lambda(m, T)$ when $T \to 0$ and $T \to \infty$. An important result, which play a significant role in the proofs of the main results of [23] is that for all $m > 0$, the function $T \mapsto \Lambda(m, T)$ is increasing. Actually, it is strictly increasing except in the case that all $r_i(\tau)$ are equal, where it is a constant function, see [23, Lemma 2]. This result follows from general results of Liu et al. [26] on the principal eigenvalue of a periodic linear system. Indeed, the growth rate $\Lambda(m, T)$ can be seen as a principal eigenvalue of a linear periodic problem, to which the results of [26] apply, see [23, Lemma 3.1].

Our objective in this paper is to remove the assumption (1) of symmetry of the migration made by [23] since it is rather restrictive in the context of population dynamics. In addition, we allow the migration to be time dependent. Moreover, we also consider two classes of local growth rates $r_i(\tau)$ that are more general than continuous functions. We consider first the case where $r_i(\tau)$ are only piecewise continuous, which contains the important examples of piecewise constant growth functions. We also consider the case where the growth rates are random, given as continuous functions of a Markov process. Except the important result that le map $T \mapsto \Lambda(m, T)$ is increasing, all the results of [23] are generalized in this more general setting.

The paper is organized as follows. In Section 2 we consider a periodic environment where the growth rates and the migration matrix are periodic functions.

The formulation of our main results, with some proofs, are given in Section 3. Technical aspects of some proofs of the results in this section are postponed to Appendix D. In Section 4, by means of numerous numerical illustrations of the cases with 2 and 3 patches (where formal calculus software makes it possible to exploit explicit formulas) we tried to synthesize by images our principal results. In Section 5 we consider a stochastic environment where the growth rates and the migration matrix depend on a Markov process. The results presented in Section 3 on the existence of the growth rate $\Lambda(m,T)$ and its asymptotic formulas for $T\to 0$ and $T\to\infty$, are special cases of more general results which are true for any irreducible cooperative linear T-periodic system. We present and prove these general results in Section 6. In Section 7 we discuss the results in more detail and propose some questions for further research. In Appendix A we provide some consequences of the Perron-Frobenius theorem which are needed thorough the paper. In Appendix B we provide some results which are needed in Section 6. In Appendix C we provide a statement of the theorem of Tikhonov on singular perturbations which is used to prove the asymptotic behaviour of the growth rate when the period is large ($T\to\infty$, see Section 6.3) or the migration rate is large ($m\to\infty$, see Section 6.5).

2 Periodic environment

2.1 The model

We do not consider a time independent symmetric migration as in (2). We denote by $\ell_{ij}(\tau)\geq 0$ the migration term, from patch j to patch i. At time τ, there is a migration from patch j to patch i if and only if $\ell_{ij}(\tau)>0$. The differential equations (2) become

$$\frac{dx_i}{dt}=r_i(t/T)x_i+m\sum_{j\neq i}\left(\ell_{ij}(t/T)x_j-\ell_{ji}(t/T)x_i\right),\quad 1\leq i\leq n. \tag{3}$$

We make the following assumption

Hypothesis 1. The functions $\tau\mapsto r_i(\tau)$ and $\tau\mapsto \ell_{ij}(\tau)$ are piecewise continuous 1-periodic functions, with a finite set of discontinuity points on each period. Moreover, they have left and right limits at the discontinuity points.

Therefore the solutions of (3) are continuous and piecewise $\mathcal{C}^1$ functions satisfying (3) except at the points of discontinuity of the functions r_i and ℓ_{ij}. The matrix $L(\tau)$ whose off diagonal elements are $\ell_{ij}(\tau)$, $i\neq j$, and diagonal elements $\ell_{ii}(\tau)$ are given by

$$\ell_{ii}(\tau)=-\sum_{j\neq i}\ell_{ji}(\tau),\quad 1\leq i\leq n, \tag{4}$$

is called the migration or dispersal matrix. Using the matrix $L(\tau)$, (3) can be written as

$$\frac{dx}{dt}=A(t/T)x,\qquad A(\tau)=R(\tau)+mL(\tau) \tag{5}$$

where $x=(x_1,\cdots,x_n)^\top$ and $R(\tau)=\operatorname{diag}\left(r_1(\tau),\cdots,r_n(\tau)\right)$. In addition to the assumptions that $L(\tau)$ has non-negative off diagonal elements ($\ell_{ij}(\tau)\geq 0$ for $i\neq j$), we also make the following assumption

Hypothesis 2. For all τ, $L(\tau)$ is *irreducible.*

This assumption, which is very usual in this topic, means that at each time, every patch is reachable from every other patch, either directly or by a path through other patches.

2.2 The growth rate

We use the following notations: for $x \in \mathbb{R}^n$, $x \geq 0$ means that for all i, $x_i \geq 0$, $x > 0$ means that $x \geq 0$ and $x \neq 0$, and $x \gg 0$ means that for all i, $x_i > 0$.

If $m > 0$ we have the property that if at $t = 0$ the population is present in at least one patch, then it will be present in all patches for all $t > 0$. Indeed, since $\ell_{ij}(\tau) \geq 0$ for $i \neq j$ and $L(\tau)$ is irreducible, for all $m > 0$ and $t \geq 0$, the matrix $A(t/T)$ in (5) is an irreducible cooperative matrix. Hence, using a classical result on irreducible cooperative linear systems (see [18, Theorem 1.1] or [36, Lemma]), $x(0) > 0$ implies $x(t) \gg 0$ for all $t > 0$.

The previous result needs that the migration matrix $L(\tau)$ is irreducible and that dispersal is present. Indeed, in the absence of dispersal ($m = 0$) the population in each patch would evolve independently, and the differential equations are solved to yield

$$x_i(t) = x_i(0)e^{\int_0^t r_i(s/T)ds}, \qquad 1 \leq i \leq n. \tag{6}$$

Given a function $u : [0, \infty) \to (0, \infty)$ we will denote its Lyapunov exponent by

$$\Lambda[u] = \lim_{t\to\infty} \frac{1}{t} \ln(u(t)),$$

provided this limit exists. Note that $\Lambda[u] > 0$ corresponds to exponential growth, while $\Lambda[u] < 0$ corresponds to exponential decay - leading to extinction. Therefore, as shown by (6), we have

$$\text{If } m = 0 \text{ then } \Lambda[x_i] = \lim_{t\to\infty} \frac{1}{t} \int_0^t r_i(s/T)ds = \overline{r}_i, \tag{7}$$

where

$$\overline{r}_i = \int_0^1 r_i(\tau)d\tau, \qquad 1 \leq i \leq n \tag{8}$$

are the *local* average growth rates in each of the patches.

If $m > 0$, for any solution of (5) with $x(0) > 0$, we have $x_i(t) > 0$ for all $t > 0$, so that we can define the Lyapunov exponents $\Lambda[x_i]$, for $1 \leq i \leq n$. However, the formula (7) giving $\Lambda[x_i]$ is no longer true. The study of $\Lambda[x_i]$ when the patches are coupled by dispersion ($m > 0$) is more difficult than in the uncoupled case, because equations (5) cannot be solved as in the case where $m = 0$.

Since the system (5) is a periodic system, its study reduces to the study of its monodromy matrix $\Phi(T)$, where $\Phi(t)$ is the fondamental matrix solution, i.e. the solution of the matrix equation $\frac{dX}{dt} = A(t/T)X$ associated to (5), with initial condition $X(0) = Id$, the identity matrix. Since the matrix $A(\tau)$ has off diagonal nonnegative entries (such a matrix is usually called *Metzler* or *cooperative*), the monodromy matrix $\Phi(T)$ of (5) has positive entries, and by the Perron theorem, it has a dominant eigenvalue (an eigenvalue of maximal modulus, called the *Perron root*), which is positive, see Theorem 20 in Appendix A. We denote it by $\mu(m,T)$, to emphasize its dependence on m and T. We have the following result.

Proposition 1. *Assume that Hypotheses 1 and 2 are satisfied. Suppose $m > 0$ and $T > 0$. Let $\mu(m,T)$ be the Perron root of the monodromy matrix $\Phi(T)$ of* (5)*. If $x(t)$ is a solution of* (5) *such that $x(0) > 0$, then for all i*

$$\Lambda[x_i] = \Lambda(m,T) := \frac{1}{T}\ln\left(\mu(m,T)\right). \tag{9}$$

Proof. The result is a particular case of Proposition 15 in the Section 6. □

Hence, the fundamental fact is that, when dispersal is present, the Lyapunov exponents $\Lambda[x_i]$ of all components $x_i(t)$ are equal, and moreover they do not depend on the initial condition. Following [23] we adopt the following definition.

Definition 1. The growth rate of the system (5) is the common value $\Lambda(m,T)$ given by (9) of the Lyapunov exponents $\Lambda[x_i]$ of all components of any solution $x(t)$ such that $x(0) > 0$.

The main problem is to study the dependence of $\Lambda(m,T)$ in m and T. In contrast to autonomous systems, studying the Perron root of the monodromy matrix of periodic systems analytically is challenging, and rarely possible. Thus, the formula (9) is of little practical interest. However, much can be said on the asymptotics of $\Lambda(m,T)$, for large and small m or T, as shown in Section 3.2.

For piecewise constant local growths and migration rates, it is possible to compute the monodromy matrix and select its largest eigenvalue in modulus, and use the formula (9) to plot the graph of the function $(m,T) \mapsto \Lambda(m,T)$. For details and complements, see [4] and Section 4.

2.3 The DIG threshold

Following [23] we adopt the following definition.

Definition 2. We say that *dispersal-induced growth* (DIG) occurs if all patches are sinks ($\bar{r}_i < 0$ for $1 \le i \le n$), but $\Lambda(m,T) > 0$ for some values of m and T.

This means that each of the populations would become extinct if isolated, but dispersal, at an appropriate rate, induces exponential growth in all patches. The following number was defined by Katriel [23] and plays an important role

$$\chi := \int_0^1 \max_{1\le i\le n} r_i(\tau)d\tau. \tag{10}$$

We have the following result

Theorem 2. *For all $m > 0$ and $T > 0$ we have $\Lambda(m,T) \le \chi$. Therefore if $\chi \le 0$ then $\Lambda(m,T) \le 0$ for all $m > 0$ and $T > 0$, so that DIG cannot occur.*

Proof. We define $r_{max}(\tau) = \max_{1\le i\le n} r_i(\tau)$. From (3) we have

$$\frac{dx_i}{dt} \le r_{max}(t/T)x_i + m\sum_{j\ne i}\left(\ell_{ij}(t/T)x_j - \ell_{ji}(t/T)x_i\right), \qquad 1 \le i \le n.$$

Adding these equations and setting $\rho = \sum_{i=1}^{n} x_i$ we have

$$\frac{d\rho}{dt} \leq r_{max}(t/T)\rho(t),$$

which implies

$$\begin{aligned}\Lambda(m,T) = \Lambda[x_i] = \lim_{t\to\infty} \frac{1}{t}\ln(x_i(t)) &\leq \limsup_{t\to\infty} \frac{1}{t}\ln(\rho(t)) \\ &\leq \limsup_{t\to\infty} \frac{1}{t}\int_0^t r_{max}(s/T)ds = \int_0^1 r_{max}(\tau)d\tau = \chi.\end{aligned}$$

This proves the theorem. □

Remark 1. Consider an idealized habitat whose growth rate at any time, is that of the habitat with maximal growth at this time. Hence χ, defined by (10), is the average growth rate in this idealized habitat. If the population does not grow exponentially in this idealized habitat (i.e. if $\chi \leq 0$), then from Theorem 2 we deduce that DIG cannot occur.

One of our main results is that the condition $\chi > 0$ which is necessary for DIG to occur is also sufficient, i.e. as soon as $\chi > 0$ then there are values of m and T for which $\Lambda(m,T) > 0$. For this reason we call χ the *DIG threshold*. To prove this result we will study the asymptotic behavior of $\Lambda(m,T)$ when m and T are infinitely small or infinitely large.

3 Results

3.1 Definitions and notations

For the statement of results, it is necessary to recall some classical results. If a matrix A is *Metzler* and irreducible, from the Perron-Frobenius theorem, we know that its spectral abscissa, i.e. the maximum of the real parts of its eigenvalues, is an eigenvalue of A, usually called its *dominant eigenvalue*, or the *Perron-Frobenius root* and denoted $\lambda_{max}(A)$, see Theorem 22 in Appendix A. If A is symmetric, then $\lambda_{max}(A)$ is simply the maximal eigenvalue of A.

We also need the following result, which is well known in the literature, see for example [9, Lemma 1], [1, Lemma 1], [10, Lemma 4.1] or [11, Lemma 3.1].

Lemma 3. *If a matrix L is Metzler irreducible and its colums sum to* 0*, then,* 0 *is a simple eigenvalue of L and all non-zero eigenvalues of L have negative real part. Moreover, the null space of the matrix L is generated by a positive vector. If the matrix L is symmetric, then this vector is $\delta = (1, ..., 1)^\top$.*

This result follows from Theorem 22 in Appendix A and the fact that the spectral abscissa of L is $\lambda_{max}(L) = 0$.

Remark 2. A positive vector $\delta = (\delta_1, \ldots, \delta_n)^\top$ which generates the null space of the matrix L is given explicitly by $\delta_i = (-1)^{n-1}L^*_{ii}$, where L^*_{ii} is the cofactor of the i-th diagonal entry l_{ii} of L, see [15, Lemma 2.1] or [14, Lemma 3.1].

The following notations are used:

- If $u(\tau)$ is any 1-periodic object (number, vector, matrix...), we denote by $\overline{u} = \int_0^1 u(\tau)d\tau$ its average on one period. Therefore the number (10) of Katriel is denoted $\chi := \overline{\max_{1\le i\le n} r_i}$.
- For all $\tau \in (0,1)$, $p(\tau) \gg 0$ is the unique positive eigenvector of $L(\tau)$, such that $L(\tau)p(\tau) = 0$, $\sum_{i=1}^n p_i(\tau) = 1$ (exists according to Lemma 3, since $L(\tau)$ is Metzler irreducible and its colums sum to 0). If the matrix $L(\tau)$ is symmetric, then $p_i(\tau) = 1/n$ for all i.
- Similarly, $q \gg 0$ is the unique positive eigenvector of $\overline{L}$ such that $\overline{L}q = 0$ and $\sum_{i=1}^n q_i = 1$ (exists according to Lemma 3, since $\overline{L}$ is Metzler irreducible and its colums sum to 0). It should be noticed that, in general, we do not have $q = \overline{p}$, where $p(\tau)$ is the positive eigenvector of $L(\tau)$.
- For all $\tau \in [0,1]$, $\lambda_{max}(R(\tau) + mL(\tau))$ is the dominant eigenvalue of the matrix $R(\tau) + mL(\tau)$ (exists, since $R(\tau) + mL(\tau)$ is Metzler irreducible).
- Similarly, the dominant eigenvalue $\lambda_{max}\left(\overline{R + mL}\right)$ is also well defined.

3.2 Asymptotics of $\Lambda(m,T)$ for large or small m and T

We have the following result on the limits of $\Lambda(m,T)$ as $T \to 0$, $T \to \infty$, $m \to 0$ or $m \to \infty$.

Theorem 4. *The growth rate* $\Lambda(m,T)$ *of* (5) *satisfies the following properties*

1. **(Fast regime)** *For all* $m > 0$ *we have*
$$\lim_{T\to 0} \Lambda(m,T) = \lambda_{max}\left(\overline{R + mL}\right). \tag{11}$$
2. **(Slow regime)** *For all* $m > 0$ *we have*
$$\lim_{T\to \infty} \Lambda(m,T) = \overline{\lambda_{max}(R + mL)}. \tag{12}$$
3. **(Slow migration)** *For all* $T > 0$ *we have*
$$\lim_{m\to 0} \Lambda(m,T) = \max_{1\le i\le n} \overline{r}_i. \tag{13}$$
4. **(Fast migration)** *For all* $T > 0$ *we have*
$$\lim_{m\to \infty} \Lambda(m,T) = \sum_{i=1}^n \overline{p_i r_i}. \tag{14}$$

Proof. The formula (11) is a particular case of Theorem 17 in Section 6.3. It follows from the averaging method [34]. The formula (12) is a particular case of Theorem 18 in Section 6.4. The formula (14) is a particular case of Proposition 19 in Section 6.5. The proofs of (12) and (14) use the theorem of Tikhonov [37] on singular perturbations, see Appendix C. We give here only the proof of (13) which is easy and follows from the continuous dependence of the solutions of (5) in the parameter m. Let $x(\tau,m)$ be the solution of the system

$$\frac{dx}{d\tau} = T(R(\tau) + mL(\tau))x, \tag{15}$$

with initial condition $x(0,m) = x^0 \geq 0$. This system is equivalent to (5) except that is is written with time $\tau = t/T$ instead of time t. Let

$$\xi_i(\tau) = x_i^0 e^{T\int_0^\tau r_i(s)ds}, \quad 1 \leq i \leq n,$$

be the solution, with initial condition $\xi(0) = x^0$, of the diagonal system,

$$\frac{d\xi}{d\tau} = TR(\tau)\xi, \tag{16}$$

obtained from (15) by letting $m = 0$. Recall that the matrix $A(\tau) = R(\tau) + mL(\tau))$ has a finite number of discontinuity points τ_k, $1 \leq k \leq p$ in the interval $[0,1]$. Using the continuous dependence of the solutions on the parameter m, in each sub interval $[\tau_k, \tau_{k+1}]$ on which the matrix $A(\tau)$ is continuous, we deduce that

$$\lim_{m\to 0} x_i(\tau,m) = \xi_i(\tau), \quad 1 \leq i \leq n, \quad \text{uniformly for} \quad \tau \in [0,1].$$

Therefore, if $\Phi(m,T)$ is the monodromy matrix of (15), as $m \to 0$, we have

$$\lim_{m\to 0} \Phi(m,T) = \mathrm{diag}(e^{T\overline{r}_1}, \ldots, e^{T\overline{r}_n}),$$

where the diagonal matrix is the fundamental matrix of (16). The dominant eigenvalue of this diagonal matrix is $e^{T\max_{1\leq i\leq n}\overline{r}_i}$. Using the continuity of the Perron root [29], we have $\lim_{m\to 0}\mu(m,T) = e^{T\max_{1\leq i\leq n}\overline{r}_i}$. Using (9), we have $\lim_{m\to 0}\Lambda(m,T) = \lim_{m\to 0}\frac{1}{T}\ln(\mu(m,T)) = \max_{1\leq i\leq n}\overline{r}_i$. □

We denote the limits of $\Lambda(m,T)$ as $T \to 0$ or $T \to \infty$ by

$$\Lambda(m,0) := \lim_{T\to 0}\Lambda(m,T) \quad \text{and} \quad \Lambda(m,\infty) := \lim_{T\to\infty}\Lambda(m,T), \tag{17}$$

respectively. We have the following results.

Proposition 5. *The functions $\Lambda(m,0)$ and $\Lambda(m,\infty)$ defined by* (17) *satisfy the following properties.*

$$\lim_{m\to 0}\Lambda(m,0) = \max_{1\leq i\leq n}\overline{r}_i, \quad \lim_{m\to\infty}\Lambda(m,0) = \sum_{i=1}^n q_i\overline{r}_i. \tag{18}$$

$$\lim_{m\to 0}\Lambda(m,\infty) = \chi, \quad \lim_{m\to\infty}\Lambda(m,\infty) = \sum_{i=1}^n \overline{p_i r_i}. \tag{19}$$

Moreover, we have

$$\frac{d}{dm}\Lambda(m,0) \leq 0, \qquad \frac{d^2}{dm^2}\Lambda(m,0) \geq 0, \tag{20}$$

and equalities hold if an only if $\overline{r}_i = \overline{r}$, for all i, in which $\Lambda(m,\infty) = \overline{r}$ for all $m > 0$ and we have

$$\frac{d}{dm}\Lambda(m,\infty) \leq 0, \qquad \frac{d^2}{dm^2}\Lambda(m,\infty) \geq 0, \tag{21}$$

and equalities hold if an only if $r_i(\tau] = r(\tau)$, for all i, in which $\Lambda(m,T) = \overline{r}$ for all $m > 0$ and $T > 0$.

In the constant migration case, for all $m > 0$ and $T > 0$, we have

$$\Lambda(m, 0) \leq \Lambda(m, T), \tag{22}$$

and hence $\Lambda(m, 0) \leq \Lambda(m, \infty)$, for all $m > 0$.

Proof. The proof is given in Section D □

The formulas (11) and (19) gives the limits of $\Lambda(m, 0)$ and $\Lambda(m, \infty)$ as $m \to 0$ or $m \to \infty$. The formulas (20) and (21) assert that the functions $m \to \Lambda(m, 0)$ and $m \to \Lambda(m, \infty)$ are decreasing, in contrast with the functions $m \to \Lambda(m, T)$, for $T > 0$, which are not always decreasing, see the figures in Section 4. The last formula (22) asserts that when the migration matrix L is time independent, then $\Lambda(m, 0)$ is a lower bound of $\Lambda(m, T)$. This property is not true in the case where the migration matrix is time dependent, see Figures 3(c), 8(a) and 10(c) in Sections 4.

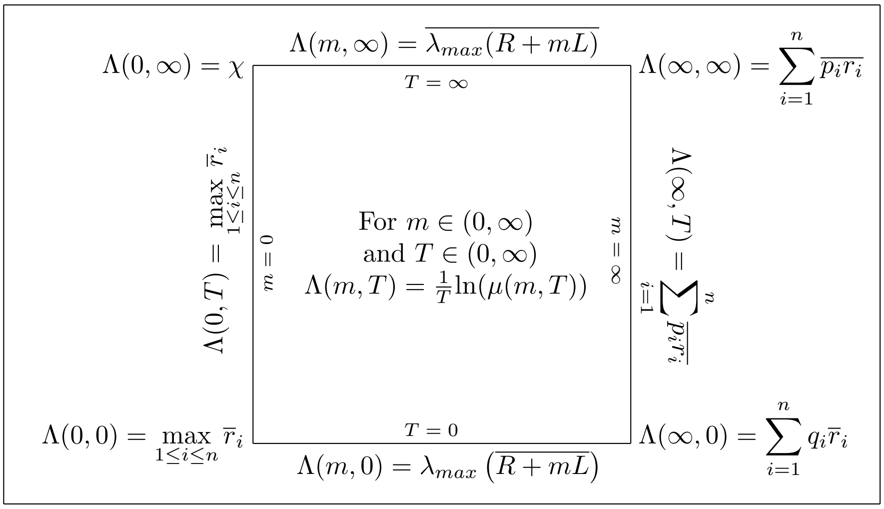


Figure 1: The definition of $\Lambda(m, T)$ and its limit values when T tends to 0 or ∞ and/or m tends to 0 or ∞.

The results of Theorems 4 and Proposition 5 are summarized in Figure 1, where, in addition to the notations (17), we use the following notations for the limits and double limits.

$$\begin{array}{rclrcl}
\Lambda(0,T) & := & \lim_{m\to 0} \Lambda(m,T), & \Lambda(\infty,T) & := & \lim_{m\to\infty} \Lambda(m,T), \\
\Lambda(0,0) & := & \lim_{m\to 0} \Lambda(m,0), & \Lambda(\infty,0) & := & \lim_{m\to\infty} \Lambda(m,0), \\
\Lambda(0,\infty) & := & \lim_{m\to 0} \Lambda(m,\infty), & \Lambda(\infty,\infty) & := & \lim_{m\to\infty} \Lambda(m,\infty).
\end{array}$$

Note that $\Lambda(0, 0) = \Lambda(0, T)$ and $\Lambda(\infty, \infty) = \Lambda(\infty, T)$, for all $T > 0$. However, in general $\chi \neq \max_{1\leq i\leq n} \overline{r}_i$, so that

$$\chi = \Lambda(0, \infty) \neq \lim_{T\to\infty} \Lambda(0, T) = \Lambda(0, T) = \max_{1\leq i\leq n} \overline{r}_i.$$

On the other hand, in general $\sum_{i=1}^{n} q_i\overline{r}_i \neq \sum_{i=1}^{n} \overline{p_i r_i}$, so that

$$\sum_{i=1}^{n} q_i\overline{r}_i = \Lambda(\infty, 0) \neq \lim_{T\to 0} \Lambda(\infty, T) = \Lambda(\infty, T) = \sum_{i=1}^{n} \overline{p_i r_i}.$$

Remark 3. In the case of time independent migration, for all i we have $q_i = p_i$ where $p \gg 0$ is the positive eigenvector of L such that $\sum_{i=1}^n p_i = 1$ and $Lp = 0$. Hence, for all $T > 0$, $\Lambda(\infty, 0) = \Lambda(\infty, \infty) = \Lambda(\infty, T) = \sum_{i=1}^n p_i \overline{r}_i$.

Remark 4. In the case where the matrix of migrations $L(\tau)$ is symmetric we have $p_i(\tau) = 1/n$, so that $\Lambda(\infty, 0) = \Lambda(\infty, \infty) = \Lambda(\infty, T) = \frac{1}{n} \sum_{i=1}^n \overline{r}_i$.

In the case where the migration matrix is constant and symmetric, and the local growth rates $r_i(\tau)$ are continuous functions, (11) was given in [23, Lemma 8], (12) was given in [23, Lemma 5], (18) was given in [23, Lemma 9(i,ii)], (19) was given in [23, Theorem 1 and Lemma 7(ii)]. The results of items *(iv)* and *(v)* of Theorem 4 were not considered in [23].

3.3 The DIG phenomenon

Let χ be the DIG threshold defined by (10). An immediate consequence of

$$\Lambda(m, T) \leq \chi \quad \text{and} \quad \lim_{m \to 0} \lim_{T \to \infty} \Lambda(m, T) = \chi, \tag{23}$$

proved in Theorem 2, and (19), respectively, is the following result.

Theorem 6. *We have* $\sup_{m,T} \Lambda(m, T) = \chi$*. Therefore, if* $\overline{r}_i < 0$ *for all* i*, DIG occurs if and only if* $\chi > 0$*.*

This result is a first answer to the question posed in the title of the paper: a population spreading across sink habitats can grow exponentially if and only if $\chi > 0$. As stated in Remark 1, $\chi = \overline{\max_i r_i}$ is the average growth rate of an idealized habitat whose growth rate at any time is that of the habitat with maximal growth. Hence, the population can survive if and only it would survive in this idealized habitat. Moreover, thanks to Theorem 4 and Proposition 5, we can answer more precisely, as stated in the following remark.

Remark 5. If $\chi > 0$ and $\max_i \overline{r_i} < 0$ then the population is growing exponentially if the environment is slowly varying and if the dispersal rate across the patch is small, but not too small. Indeed from $\lim_{m \to 0} \Lambda(m, T) = \max_i \overline{r_i} < 0$ we deduce that if T is fixed and m is very small then $\Lambda(m, T) < 0$ and from the double limit in (23) we deduce that if T is large enough and m is small enough then $\Lambda(m, T) > 0$.

We can give a more precise description of the set of m and T for which DIG occur.

Proposition 7. *Assume that* $\chi > 0$ *and* $\max_{1 \leq i \leq n} \overline{r}_i < 0$*. Two cases must be distinguished.*
1. If $\sum_{i=1}^n \overline{p_i r_i} < 0$*, then the equation* $\Lambda(m, \infty) = 0$ *has a unique solution* $m = m^* > 0$*, and we have*

- *If* $m \in (0, m^*)$ *then for any* T *sufficiently large (depending on* m*), we have* $\Lambda(m, T) > 0$ *(growth) and for any* T *sufficiently small (depending on* m*), we have* $\Lambda(m, T) < 0$ *(decay).*

- *If* $m \geq m^*$ *then for any* T *sufficiently small or sufficiently large (depending on* m*), we have* $\Lambda(m, T) < 0$ *(decay).*

2. If $\sum_{i=1}^n \overline{p_i r_i} \geq 0$, then $\Lambda(m,\infty) > 0$ for all $m > 0$ and for any T sufficiently large (depending on m), we have $\Lambda(m,T) > 0$ (growth) and for any T sufficiently small (depending on m), we have $\Lambda(m,T) < 0$ (decay).

Proof. Assuming $\chi > 0$ and $\overline{r}_i < 0$, Proposition 5 tells us that $\Lambda(m,0)$ is a decreasing function from $\Lambda(0,0) = \max_{1\leq i\leq n} \overline{r}_i < 0$ to $\Lambda(\infty,0) = \sum_{i=1}^n q_i \overline{r}_i < 0$. We conclude that $\Lambda(m,0) < 0$ for all $m > 0$. On the other hand $\Lambda(m,\infty)$ is a strictly decreasing function from $\Lambda(0,\infty) = \chi > 0$ to $\Lambda(\infty,\infty) = \sum_{ii=1}^n \overline{p_i r_i}$.

In the first case we have $\Lambda(\infty,\infty) < 0$ so that the equation $\Lambda(m,\infty) = 0$ has a unique solution $m = m^* > 0$ and $\Lambda(m,\infty) > 0$ for $m \in (0,m^*)$, $\Lambda(m,\infty) < 0$ for $m > m^*$. Therefore, (17) tells us that if $m \in (0,m^*)$, then for sufficiently large T we have $\Lambda(m,T) > 0$ and for sufficiently small T we have $\Lambda(m,T) < 0$. If $m \geq m^*$, then for sufficiently large T and for sufficiently small T we have $\Lambda(m,T) < 0$.

In the second case we have $\Lambda(\infty,\infty) \geq 0$ so that $\Lambda(m,\infty) > 0$ for all $m > 0$. Therefore, (17) tells us that for sufficiently large T we have $\Lambda(m,T) > 0$ and for sufficiently small T we have $\Lambda(m,T) < 0$. □

Remark 6. If the migration matrix is time independent, then the second case in Proposition 7 never occur because $\sum_{i=1}^n \overline{p_i r_i} = \sum_{i=1}^n p_i \overline{r}_i < 0$, if $\overline{r}_i < 0$ for all i. It does not occur either when $L(\tau)$ is symmetric since in this case we have $p_i(\tau) = 1/n$, so that $\sum_{i=1}^n \overline{p_i r_i} = \frac{1}{n}\sum_{i=1}^n \overline{r}_i < 0$, if $\overline{r}_i < 0$ for all i. An example showing the behaviour depicted in the second case of Proposition 7 is provided in Section 4.1.4.

We have the more precise statement for the result of Proposition 7.

Remark 7. Assume that $\chi > 0$, $\max_{1\leq i\leq n} \overline{r}_i < 0$ and $\sum_{ii=1}^n \overline{p_i r_i} < 0$. Consider the functions $T_1, T_2 : (0,m^*) \to (0,\infty)$ given by

$$T_1(m) = \sup\{T_1 > 0 : \Lambda(m,T) < 0 \text{ for all } T \in (0,T_1)\},$$

$$T_2(m) = \inf\{T_2 > 0 : \Lambda(m,T) > 0 \text{ for all } T \in (T_2,\infty)\},$$

and the functions $T_3, T_4 : [m^*,\infty) \to [0,\infty]$ given by

$$T_3(m) = \sup\{T_3 > 0 : \Lambda(m,T) < 0 \text{ for all } T \in (0,T_3)\},$$

$$T_4(m) = \inf\{T_4 > 0 : \Lambda(m,T) < 0 \text{ for all } T \in (T_4,\infty)\}.$$

If $m \in (0,m^*)$ then for $T > T_2(m)$, we have $\Lambda(m,T) > 0$ (growth) and for $T < T_1(m)$, we have $\Lambda(m,T) < 0$ (decay). If $m \geq m^*$ then for $T < T_3(m)$ or $T > T_4(m)$, we have $\Lambda(m,T) < 0$ (decay). Note that $T_1(m) \leq T_2(m)$ for all $m \in (0,m^*)$ and $\lim_{m\to m^*} T_1(m) = T_3(m^*)$.

If $\sum_{ii=1}^n \overline{p_i r_i} \geq 0$ then we consider the functions $T_1, T_2 : (0,\infty) \to (0,\infty)$ given as above. Then for $T > T_2(m)$, we have $\Lambda(m,T) > 0$ (growth) and for $T < T_1(m)$, we have $\Lambda(m,T) < 0$ (decay).

Note that the function T_1 and T_3 are lower semicontinuous, while the functions T_2 and T_4 are upper semicontinuous, and, since $\Lambda(0,T) = \max_{i=1}^n \overline{r}_i < 0$, we have

$$\lim_{m\to 0} T_1(m) = \lim_{m\to 0} T_2(m) = \infty.$$

If the function $T \mapsto \Lambda(m,T)$ is strictly increasing for all $m>0$ then the functions T_i, $i=1,2,3,4$ defined in Remark 7 satisfy the following properties:

$$T_1(m)=T_2(m) \text{ for } m\in(0,m^*), \text{ and } T_3(m)=\infty, T_4(m)=0 \text{ for } m\geq m^*.$$

In Section 3.6 we will consider the problem of monotonicity of the function $T\mapsto\Lambda(m,T)$ when the migration matrix L is time independent.

3.4 The variables ρ and θ

A crucial step in the description and the proofs of our main results is to reduce the linear system (5) to the $n-1$ simplex

$$\Delta := \left\{x\in\mathbb{R}^n_+ : \textstyle\sum_{i=1}^n x_i = 1\right\}$$

of $\mathbb{R}^n_+$. Indeed, the change of variables

$$\rho=\textstyle\sum_{i=1}^n x_i, \quad \theta=\frac{x}{\rho}, \tag{24}$$

transforms the differential equation (5) into

$$\tfrac{d\rho}{dt}=\rho\textstyle\sum_{i=1}^n r_i(t/T)\theta_i, \quad \tfrac{d\theta}{dt}=F(t/T,\theta) \tag{25}$$

where, for $1\leq i\leq n$, $F_i(\tau,\theta)$ is given by

$$F_i(\tau,\theta)=r_i(\tau)\theta_i+m\sum_{j=1}^n \ell_{ij}(\tau)\theta_j-\theta_i\sum_{j=1}^n r_j(\tau)\theta_j.$$

For $\sum_{i=1}^n\theta_i=1$ we have $\sum_{i=1}^n\frac{d\theta_i}{dt}=0$ which proves that the second equation in (25) can be considered as an $n-1$ dimensional system on Δ.

Remark 8. The variables ρ and θ defined by (24) are interpreted as follows: ρ is the total population present in all patches and $\theta_i=x_i/\rho$ is the fraction of the population on patch i.

By the Perron theorem the monodromy matrix $\Phi(T)$ of (5) has a positive eigenvector $\pi(m,T)\in\Delta$, called the *Perron vector*, corresponding to the its Perron root $\mu(m,T)$, which was used in (9) to define $\Lambda(m,T)$, see Theorem 20 in Appendix A. We know, see Proposition 16 in Section 6, that the solution $\theta^*(t,m,T)$ of the second equation in (25) with initial condition $\theta^*(0,m,T)=\pi(m,T)$, is a T-periodic solution. We denote it by $\theta^*(t,m,T)$, to recall its dependence on the period parameters m and T. We have the following result.

Theorem 8. *The T-periodic solution $\theta^*(t,m,T)$ of the second equation in* (25) *is globally asymptotically stable, that is to say, for any solution $\theta(t)$ of* (25)*, we have $\lim_{t\to\infty}\|\theta(t)-\theta^*(t,m,T)\|=0$. Moreover, we have*

$$\Lambda(m,T)=\int_0^1\sum_{i=1}^n r_i(\tau)\theta_i^*(T\tau,m,T)d\tau. \tag{26}$$

Proof. The existence, uniqueness and global asymptotic stability of the T-periodic $\theta^*(t,m,T)$ of (25) is a particular case of Proposition 16 in Section 6. Using Proposition 16 and since the columns of $L(\tau)$ sum to 0, we have

$$\Lambda(m,T)=\int_0^1\langle A(\tau)\theta^*(T\tau,m,T),\mathbf{1}\rangle d\tau=\int_0^1\sum_{i=1}^n r_i(\tau)\theta_i^*(T\tau,m,T)d\tau.$$

This proves (26). □

Formula (26) gives us an integral representation of the growth rate $\Lambda(m, T)$. It will play a major role when we study the limits of $\Lambda(m, T)$ when T is small or large, or when m is large, see Section 6.

3.5 Time independent migration

When the migration matrix is time independent, we have a new formula for the growth rate $\Lambda(m, T)$.

Theorem 9. *Assume that the migration matrix $L = (\ell_{ij})$ is time independent. Let p be the positive eigenvector of L such that $Lp = 0$ and $\sum_{i=1}^n p_i = 1$ (Recall that $p_i = 1/n$ is the symmetric case). We have*

$$\Lambda(m, T) = \sum_{i=1}^{n} p_i \bar{r}_i + m \int_0^1 h\left(\theta^*(T\tau, m, T)\right) d\tau, \tag{27}$$

where $h(x) = \sum_{i=1}^n \left(\sum_{j=1}^n \ell_{ij} x_j\right) \frac{p_i}{x_i}$.

Proof. We use the following variable $U = \ln(x_1^{p_1} \cdots x_n^{p_n}) = \sum_{i=1}^n p_i \ln x_i$. We have

$$\frac{dU}{dt} = \sum_{i=1}^{n} p_i r_i(t/T) + mh(x),$$

where $h(x) = \langle Lx, p/x \rangle$, and $p/x = (p_1/x_1, \cdots, p_n/x_n)^\top$. We have

$$h(x) = \langle Lx, p/x \rangle = \langle L\rho\theta, p/(\rho\theta) \rangle = \langle L\theta, p/\theta \rangle = h(\theta).$$

Therefore

$$\frac{dU}{dt} = \sum_{i=1}^{n} p_i r_i(t/T) + mh(\theta). \tag{28}$$

Let $x(t)$ the solution of (5) with initial condition $x(0) = \pi(m, T)$, where $\pi(m, T)$ is the Perron vector of the monodromy matrix $X(T)$ of (5). Since $\rho(0) = 1$, the corresponding solution of (25) has initial condition $\theta(0) = \pi(m, T)$. Hence, it is the periodic solution $\theta^*(t, m, T)$. Consider now $U(t) = \sum_{i=1}^n p_i \ln x_i(t)$. We have

$$\lim_{t\to\infty} \frac{U(t)}{t} = \sum_{i=1}^{n} p_i \lim_{t\to\infty} \frac{1}{t} \ln x_i(t) = \sum_{i=1}^{n} p_i \Lambda[x_i].$$

Using now that the $\Lambda[x_i]$ are equal to $\Lambda(m, T)$, we have

$$\lim_{t\to\infty} \frac{U(t)}{t} = \sum_{i=1}^{n} p_i \Lambda[x_i] = \Lambda(m, T) \sum_{i=1}^{n} p_i = \Lambda(m, T).$$

Since $U(t)$ is a solution of (28), we have the following integral representation of $U(t)$

$$U(t) = U(0) + \sum_{i=1}^{n} p_i \int_0^t r_i(s/T) ds + m \int_0^t h(\theta^*(s, m, T)) ds.$$

Therefore

$$\Lambda(m, T) = \lim_{t\to\infty} \frac{U(t)}{t} = \sum_{i=1}^{n} p_i \bar{r}_i + +m \int_0^1 h(\theta^*(T\tau, m, T)) d\tau$$

This proves (27). $\square$

Formula (27) for $\Lambda(m,T)$ is given in [23] uniquely in the two-patch case, when the migration is symmetric and the growth rates $r_1(\tau)$ and $r_2(\tau)$ are continuous, see [23, Lemma 4].

As it was stated in Remark 3, when the migration matrix is time independent for all $T>0$, we have $\Lambda(\infty,0)=\Lambda(\infty,\infty)=\Lambda(\infty,T)=\sum_{i=1}^n p_i\overline{r}_i$. Let us prove that this limit is actually the infimum of $\Lambda(m,T)$. This property is true uniquely in the case of time independent migration.

Proposition 10. *If the migration matrix is time independent then*

$$\inf_{m,T}\Lambda(m,T)=\sum_{i=1}^n p_i\overline{r}_i.$$

Proof. In the time independent migration case, we have the formula (27) for $\Lambda(m,T)$. If we prove that the function h is non negative on the positive cone then, for all $m>0$ and $T>0$

$$\Lambda(m,T)\geq\sum_{i=1}^n p_i\overline{r}_i.$$

Using Remark 3 we deduce then that the infimum of $\Lambda(m,T)$ is equal to $\sum_{i=1}^n p_i\overline{r}_i$. Let us prove that the function h is non negative on the positive cone. Observe that $h(x)=\langle Lx,p/x\rangle$, where $p/x=(p_1/x_1,\cdots,p_n/x_n)^\top$ and $\langle\cdot,\cdot\rangle$ is the usual Euclidean scalar product in $\mathbb{R}^n$. Let R denote the transpose of L. Then, for all $x\in\mathbb{R}^n$,

$$(Rx)_i=\sum_j R_{ij}x_j=\sum_j R_{ij}(x_j-x_i).$$

Observe that for all $x\in\mathbb{R}^n$

$$\langle p,Rx\rangle=\langle Lp,x\rangle=0 \tag{29}$$

because p is in the kernel of L. By convexity, for all $x\in\mathbb{R}^n$ with positive entries,

$$\ln(x_j)-\ln(x_i)\leq\frac{x_j-x_i}{x_i}.$$

Thus

$$R(\ln(x))_i\leq\sum_j R_{ij}(\frac{x_j-x_i}{x_i})=\frac{(Rx)_i}{x_i}.$$

That is $R(\ln(x))\leq\frac{Rx}{x}$ componentwise, where $\ln(x)$ stands for the vector defined as $\ln(x)_i=\ln(x_i)$. Hence, using (29),

$$0=\langle p,R(\ln(x))\rangle\leq\langle p,\tfrac{Rx}{x}\rangle.$$

Let $y=\frac{p}{x}$. We have

$$h(y)=\langle Ly,\tfrac{p}{y}\rangle=\langle L\tfrac{p}{x},x\rangle=\langle\tfrac{p}{x},Rx\rangle=\langle p,\tfrac{Rx}{x}\rangle\geq 0.$$

This proves that $h(y)\geq 0$ whenever y has positive entries. $\square$

3.6 The monotonicity of $\Lambda(m, T)$ with respect to T

As said in the introduction, when the matrix migration is time independent and symmetric, the growth rate $\Lambda(m, T)$ is strictly increasing with respect to T, see [23, Lemma 2]. When the migration is time dependent, the monotonicity is no longer true, see Sections 4.1.3 and 4.2. We were not able to prove the monotonicity of the function $T \mapsto \Lambda(m, T)$ in the non symmetric time independent migration case. However, owing to the property $\Lambda(m, 0) \leq \Lambda(m, T)$ given in (22) and the numerous numerical simulations we have done with constant non-symmetric matrices (see Sections 4.1.2 and 4.1.6), we formulate the following conjecture.

Conjecture 1. If the matrix migration is time independent, then the function $T \mapsto \Lambda(m, T)$ is strictly increasing for all m (except in the case where all $r_i(\tau)$ are equal).

If the migration matrix is time independent, $\chi > 0$ and $\max_{1 \leq i \leq n} \overline{r}_i < 0$ then as shown in Remark 6, the value m^* for which $\Lambda(m, \infty) = 0$ exists. We have the following result.

Proposition 11. *Assume that the migration matrix is time independent. Assume that $\chi > 0$ and $\max_{1 \leq i \leq n} \overline{r}_i < 0$. Let m^* be the unique solution of $\Lambda(m, \infty) = 0$. If Conjecture 1 is true (which thanks to [23] is the case when the migration is symmetric), there exist an analytic function $T_c : (0, m^*) \to (0, \infty)$ such that $\lim_{m \to 0} T_c(m) = \lim_{m \to m^*} T_c(m) = \infty$ and $\Lambda(m, T) > 0$ if and only if $T > T_c(m)$. In other words the critical curve $T = T_c(m)$ separates the parameters plane (m, T) in two regions : above it, DIG occurs, below it, DIG does not occur.*

Proof. For all $m > 0$ we have $\Lambda(m, 0) < 0$. If $m \geq m^*$, then $\Lambda(m, \infty) < 0$ and by the monotonicity of $\Lambda(m, T)$ with respect to T, for all $T > 0$ we have $\Lambda(m, T) < 0$. If $m \in (0, m^*)$, then $\Lambda(m, \infty) > 0$ and by the monotonicity of $\Lambda(m, T)$ with respect to T, there exists a unique value $T = T_c(m)$ such that $\Lambda(m, T) > 0$ if $T > T_c(m)$ and $\Lambda(m, T) < 0$ if $T < T_c(m)$.

Using Proposition 15, the function $\Lambda(m, T)$ is analytic in T. It is analytic in m because the monodromy matrix $\Phi(m, T)$ is also analytic in m. Indeed, the solutions of a differential equation which depends analytically on a parameter are also analytic in this parameter, and $A(\tau) = R(\tau) + mL(\tau)$ is analytic in m. Therefore $\Lambda(m, T)$ is analytic in m and T. The implicit function theorem implies that $T = T_c(m)$ is analytic in m since it is the solution of equation $\Lambda(m, T) = 0$. □

Examples where the critical curve $T = T_c(m)$ exists are provided in Section 4.1. The time independence of the migration matrix is not a necessary condition for the existence of the critical curve $T = T_c(m)$, see Sections 4.1.3 and 4.1.4. Note that in the symmetric case we have $T_c(m) = 1/\nu_c(m)$, where $\nu_c(m)$ is the critical curve of Katriel, see [23, Theorem 1(II)].

Remark 9. For time independent migration, and if Conjecture 1 is true, as a consequence of Proposition 11, DIG can occur only if $m < m^*$. In contrast, in the time dependent migration case, if $T_3(m) < T_4(m)$, for some $m \in (m^*, \infty)$, then we can have $\Lambda(m, T) > 0$ (growth) for some $T \in (T_3(m), T_4(m))$. Therefore DIG can occur even for $m > m^*$. Examples showing this behaviour are provided in Section 4.2.

3.7 Explicit formulas for the two-patch case

In the simplest two-patch case ($n = 2$) the system (3) is

$$\begin{aligned} \tfrac{dx_1}{dt} &= r_1(t/T)x_1 + m(\ell_{12}(t/T)x_2 - \ell_{21}(t/T)x_1), \\ \tfrac{dx_2}{dt} &= r_2(t/T)x_2 + m(\ell_{21}(t/T)x_1 - \ell_{12}(t/T)x_2). \end{aligned} \tag{30}$$

In this case, it is easy to compute the dominant eigenvalue $\lambda_{max}(R(\tau)+mL(\tau))$ and find that

$$\lambda_{max}(R(\tau) + mL) = \tfrac{1}{2}\left(r_1(\tau)+r_2(\tau)+\sqrt{D(r_1(\tau), r_2(\tau))}\right) - m\tfrac{\ell_{12}(\tau)+\ell_{21}(\tau)}{2},$$

where

$$D(r_1, r_2) = (r_1 - r_2 + m(\ell_{12}(\tau) - \ell_{21}(\tau)))^2 + 4m^2\ell_{12}(\tau)\ell_{21}(\tau) \tag{31}$$

We obtain the following explicit formulas for $\Lambda(m, 0)$ and $\Lambda(m,\infty)$:

$$\begin{aligned} \Lambda(m, 0) &= \tfrac{1}{2}\left(\overline{r}_1 + \overline{r}_2 + \sqrt{D(\overline{r}_1, \overline{r}_2)}\right) - m\tfrac{\overline{\ell}_{12}+\overline{\ell}_{21}}{2}, \\ \Lambda(m,\infty) &= \tfrac{1}{2}\left(\overline{r}_1 + \overline{r}_2 + \int_0^1 \sqrt{D(r_1(\tau), r_2(\tau))}d\tau\right) - m\tfrac{\overline{\ell}_{12}+\overline{\ell}_{21}}{2}. \end{aligned}$$

In the symmetric constant migration case ($\ell_{12}(\tau) = \ell_{21}(\tau) = 1$) we obtain the formulas

$$\begin{aligned} \Lambda(m, 0) &= \tfrac{1}{2}\left(\overline{r}_1 + \overline{r}_2 + \sqrt{(\overline{r}_1 - \overline{r}_2)^2 + 4m^2}\right) - m, \\ \Lambda(m,\infty) &= \tfrac{1}{2}\left(\overline{r}_1 + \overline{r}_2 + \int_0^1 \sqrt{(r_1(\tau) - r_2(\tau))^2 + 4m^2}d\tau\right) - m. \end{aligned}$$

These formulas were given by Katriel [23], see the formula (12) and the formula preceding (17) in [23].

When the migration is constant, but not necessarily symmetric, the growth rate of (30), as shown in (27), is given by

$$\Lambda(m, T) = \frac{\ell_{12}\overline{r}_1 + \ell_{21}\overline{r}_2}{\ell_{12} + \ell_{21}} + \frac{m}{T}\int_0^T \frac{(\ell_{12}\theta_2^*(t, T) - \ell_{21}\theta_1^*(t, T))^2}{\theta_1^*(t, T)\theta_2^*(t, T)(\ell_{12} + \ell_{21})}dt.$$

In the symmetric case ($\ell_{12} = \ell_{21} = 1$) we obtain the formula

$$\Lambda(m, T) = \frac{\overline{r}_1 + \overline{r}_2}{2} + m\left(\frac{1}{2T}\int_0^T \left(\frac{\theta_2^*(t, T)}{\theta_1^*(t, T)} + \frac{(\theta_1^*(t, T)}{\theta_2^*(t, T)}\right) dt - 1\right).$$

Using, as in [23], the variable $z = x_2/x_1 = \theta_2/\theta_1$, we obtain

$$\Lambda(m, T) = \frac{\overline{r}_1 + \overline{r}_2}{2} + m\left(\frac{1}{2T}\int_0^T \left(z^*(t, T) + \frac{1}{z^*(t, T)}\right) dt - 1\right).$$

which is the same formula as [23, Formula (26)].

4 Numerical illustrations

We consider the system (3), with piecewise constant 1-periodic growth rates given by

$$r_i(\tau) = \begin{cases} a_i \text{ if } 0 \le \tau < \alpha \\ b_i \text{ if } \alpha \le \tau < 1 \end{cases}, \quad 1 \le i \le n, \tag{32}$$

where $\alpha \in (0,1)$ and a_i and b_i, are real numbers. Thus, during a time of duration αT the ith population grows with a rate a_i, then, during a time of duration $(1-\alpha)T$ the population grows with a rate b_i. We also assume that the migration terms $\ell_{ij}(\tau)$ are piecewise constant. For simplicity we assume the discontinuity arises at the same value of time as the growth rates (32):

$$\ell_{ij}(\tau) = \begin{cases} h_{ij} \text{ if } 0 \le \tau < \alpha \\ k_{ij} \text{ if } \alpha \le \tau < 1 \end{cases}, \quad 1 \le i \ne j \le n, \tag{33}$$

where h_{ij} and k_{ij}, $i \ne j$, are non negative real numbers such that the matrices $H = (h_{ij})$ and $K = (k_{ij})$, whose diagonal elements are defined as in (4), are irreducible. This simplest case is already of much interest, since it illustrates all behaviors depicted in the preceding section. The monodromy matrix is given by

$$\Phi(T) = e^{(1-\alpha)TB} e^{\alpha TA}, \tag{34}$$

where the matrices $A = \mathrm{diag}(a_i) + mH$ and $B = \mathrm{diag}(b_i) + mK$, are time independent matrices. Hence, we can compute the Perron root $\mu(m,T)$ of the matrix $\Phi(T)$ and use the formula (9) to compute $\Lambda(m,T) = \frac{1}{T}\ln(\mu(m,T))$.

In (32) and (33) we have only two discontinuities on each period of time. In Section 4.2.1 we will consider a case with three discontinuities.

4.1 DIG occurs only if $m < m^*$

4.1.1 The ± 1 model

This model corresponds to the two-patch case (30), with constant symmetric migration $\ell_{12} = \ell_{21} = 1$ and piecewise constant growth rates $r_i(\tau)$ given by (32), with $a_1 = b_2 > 0$, $b_1 = a_2 < 0$ and $-b_1 > a_1$. The matrices A and B in (34) are given by

$$A = \begin{bmatrix} a_1 - m & m \\ m & b_1 - m \end{bmatrix}, \quad B = \begin{bmatrix} b_1 - m & m \\ m & a_1 - m \end{bmatrix}.$$

Therefore $\bar{r}_1 = \bar{r}_2 = \frac{a_1+b_1}{2} < 0$ and $\chi = a_1 > 0$. Hence, we have two identical sinks, that are in phase opposition and DIG can occur. This model can be reduced to the simpler form $a_1 = b_2 = 1-\varepsilon$, $b_1 = a_2 = -1-\varepsilon$, with $0 < \varepsilon < 1$, see [4, Remark 3]. Using the theoretical formulas depicted in Figure 1 and Section 3.7, we have

$$\Lambda(0,T) = \Lambda(m,0) = \Lambda(\infty,T) = -\varepsilon, \quad \Lambda(0,\infty) = 1+\varepsilon,$$
$$\Lambda(m,\infty) = -\varepsilon + \sqrt{1+m^2} - m.$$

All these formulas were already obtained in [4] by using explicit computation of $\Lambda(m,T)$. Note that in the two-patch case, a computer program like Maple is able to compute analytically the monodromy matrix (34) for any constant matrices

A and B, and then determine its Perron root, since this computation requires only the solution of a second degree algebraic equation. However, the formula obtained for $\Lambda(m,T)$ is so complicated that we cannot exploit it mathematically. It turns out that in the particular case of the ± 1 model, we can obtain an explicit formula, which is simple enough to be exploited mathematically and to deduce the properties of $\Lambda(m,T)$.

In this special case we gave in [4] some properties that are not extended to the general case considered in the present work. We proved in particular that the threshold of the dispersal rate at which DIG appears is exponentially small with the period. For a more detailed discussion on this issue, see Section 4.1.5.

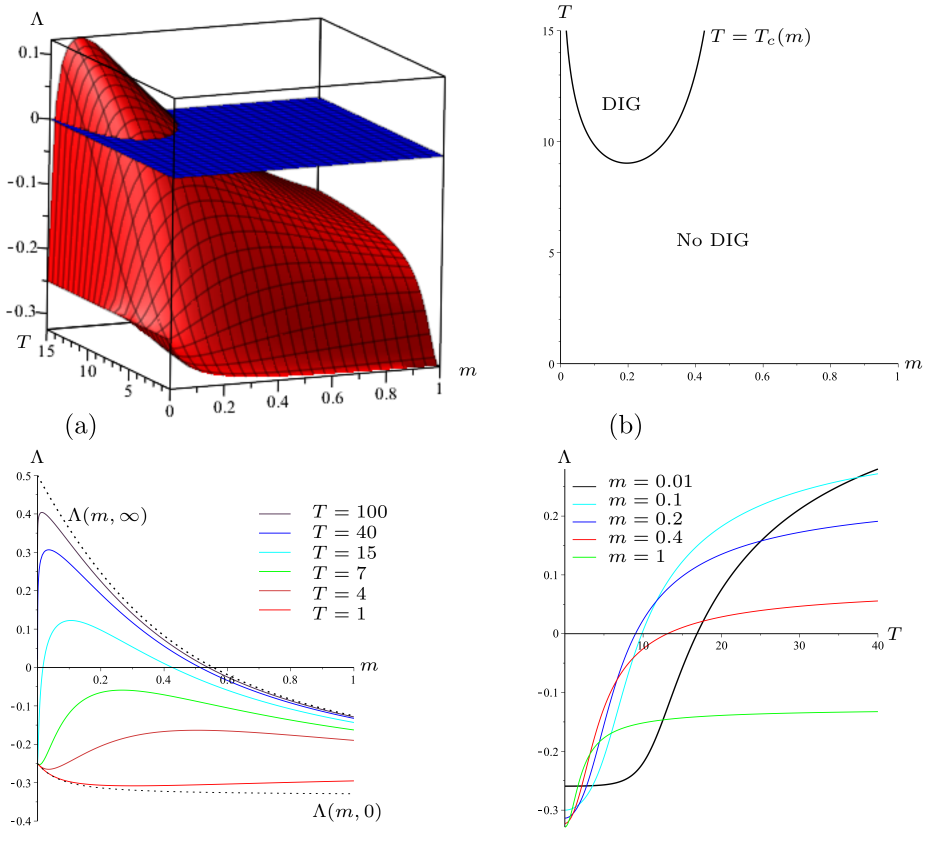


Figure 2: (a) The graph of $(m,T) \mapsto \Lambda(m,T)$. (b) The set $\Lambda(m,T) = 0$. (c) Graphs of $m \mapsto \Lambda(m,T)$ with the indicated values of T. (d) Graphs of $T \mapsto \Lambda(m,T)$ with the indicated values of m. Here we used the two patch model corresponding to the matrices (35) and $\alpha = 0.5$.

Table 1: Limits of $\Lambda(m,T)$ for the parameters values used in Figure 2

$\Lambda(0,\infty)=1/2, \quad \Lambda(0,0)=\Lambda(0,T)=-1/4$
$\Lambda(\infty,0)=\Lambda(\infty,T)=\Lambda(\infty,\infty)=-1/3$
$\Lambda(m,0)=-\frac{3}{8}-\frac{3}{2}m+\frac{1}{8}\sqrt{1+8m+144m^2}$
$\Lambda(m,\infty)=-\frac{3}{8}-\frac{3}{2}m+\frac{1}{4}\sqrt{4+4m+9m^2}+\frac{1}{8}\sqrt{9-12m+36m^2}$
$\Lambda(m,\infty)=0$ for $m=m^*=5/9$.

4.1.2 Time independent migration

We show in Figure 2(a) the plot of $\Lambda(m,T)$ (obtained by the Maple software) in the case where the matrices A and B in (34) are given by

$$A=\begin{bmatrix} 1/2-m & 2m \\ m & -3/2-2m \end{bmatrix}, \quad B=\begin{bmatrix} -1-m & 2m \\ m & 1/2-2m \end{bmatrix}. \tag{35}$$

The migration is time independent. For the parameter values used in the figure, we have $\chi=1/2$, $\overline{r}_1=-1/4$ and $\overline{r}_2=-1/2$. Therefore, the patches are sinks and DIG can occur. Using Remark 2, we have $p_1=2/3$ and $p_2=1/3$. Using the theoretical formulas depicted in Figure 1 and Section 3.7, we obtain the expressions shown in Table 1.

Comments on Figure 2. The strictly decreasing functions $m\mapsto\Lambda(m,0)$ and $m\mapsto\Lambda(m,\infty)$, are depicted in dotted line on panel (c) of the figure. Panels (a,d) of the figure show that for all $m>0$, the functions $T\mapsto\Lambda(m,T)$ are strictly increasing, supporting then Conjecture 1. Hence, there exists a critical curve $T=T_c(m)$ defined for $0<m<m^*$ such that DIG occurs if and only if $T>T_c(m)$, as depicted in panel (b) of the figure. Panel (c) of the Figure shows the graphs of functions $m\mapsto\Lambda(m,T)$ and illustrates their convergence toward $\Lambda(m,0)$ and $\Lambda(m,\infty)$ as T tends to 0 and ∞, respectively. Notice that for $0<T<\infty$, the functions $m\mapsto\Lambda(m,T)$ are not monotonic.

4.1.3 Time dependent migration

We show in Figure 3(a) the plot of $\Lambda(m,T)$ in the case where the matrices A and B in (34) are given by

$$A=\begin{bmatrix} 1/2-2m & m \\ 2m & -3/2-m \end{bmatrix}, \quad B=\begin{bmatrix} -1-m & 2m \\ m & 1/2-2m \end{bmatrix}. \tag{36}$$

The migration is time dependent. For the parameter values used in the figure, we have $\chi=1/2$, $\overline{r}_1=-1/4$ and $\overline{r}_2=-1/2$. Therefore, the patches are sinks and DIG can occur. Using Remark 2, we have $q_1=q_2=1/2$ and

$$p_1(\tau)=\begin{cases} 1/3 \text{ if } 0\le\tau<1/2 \\ 2/3 \text{ if } 1/2\le\tau<1 \end{cases}, \quad p_2(\tau)=\begin{cases} 2/3 \text{ if } 0\le\tau<\alpha \\ 1/3 \text{ if } \alpha\le\tau<1 \end{cases}.$$

Using the theoretical formulas depicted in Figure 1 and Section 3.7, we obtain the expressions shown in Table 2. Since $\Lambda(\infty,T)<\Lambda(\infty,0)$, for m large enough, the condition $\Lambda(m,T)>\Lambda(m,0)$ cannot be satisfied. Note that according to

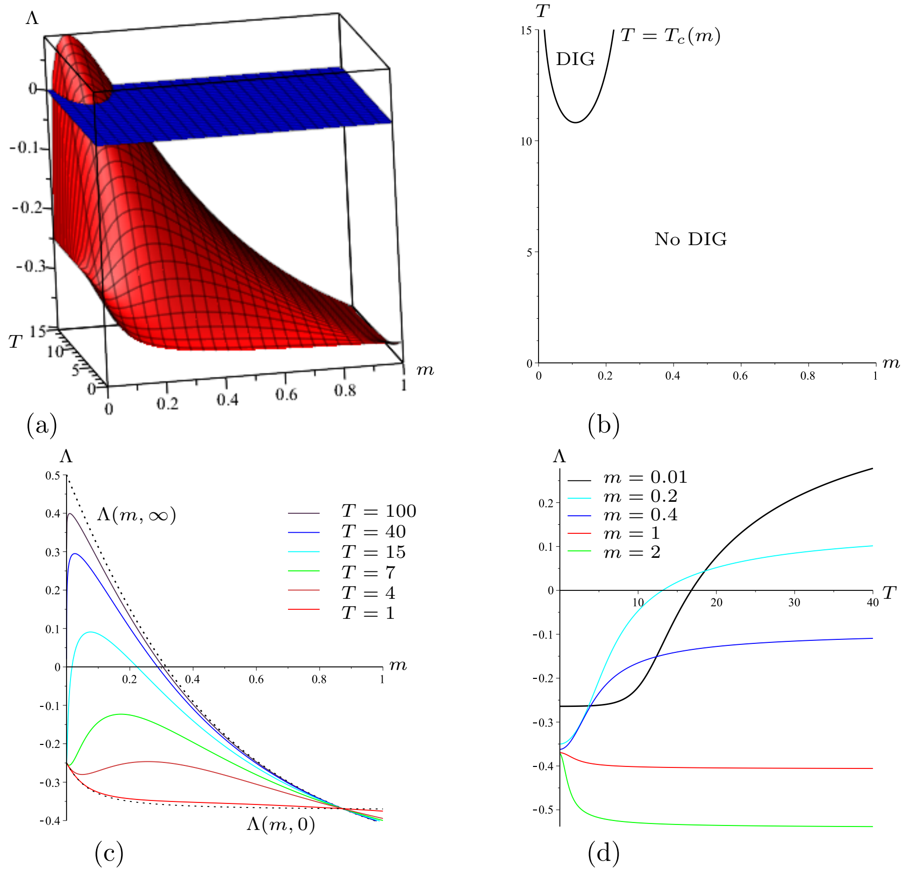


Figure 3: (a) The graph of $(m,T) \mapsto \Lambda(m,T)$. (b) The set $\Lambda(m,T) = 0$. (c) Graphs of $m \mapsto \Lambda(m,T)$ with the indicated values of T. (d) Graphs of $T \mapsto \Lambda(m,T)$ with the indicated values of m. Here we used the two patch model corresponding to the matrices (36) and $\alpha = 0.5$.

(22), this condition is always true in the case of time independent migration. Therefore, Conjecture 1 is not true in general for time dependent migration.

We can make the same comments on Figure 3, as those made in the previous section on Figure 2, except that, in contrast with Figure 2(c), for m large enough, we have $\Lambda(m,T) < \Lambda(m,0)$ and the function $T \mapsto \Lambda(m,T)$ is decreasing instead of increasing. Since this function is increasing for all $m \in (0, m^*)$ and negative for all $m > m^*$, we also have a critical curve $T = T_c(m)$ defined for $0 < m < m^*$ such that DIG occurs if and only if $T > T_c(m)$.

4.1.4 Time dependent migration where DIG occurs for all $m > 0$

We show in Figure 4(a) the plot of $\Lambda(m,T)$ in the case where the matrices A and B in (34) are given by

$$A = \begin{bmatrix} 1/2 - m & 5m \\ m & -3/2 - 5m \end{bmatrix}, \quad B = \begin{bmatrix} -1 - 5m & m \\ 5m & 1/2 - m \end{bmatrix}. \tag{37}$$

Table 2: Limits of $\Lambda(m,T)$ for the parameters values used in Figure 3

$\Lambda(0,\infty)=1/2, \quad \Lambda(0,0)=\Lambda(0,T)=-1/4$
$\Lambda(\infty,0)=-3/8, \quad \Lambda(\infty,T)=\Lambda(\infty,\infty)=-2/3$
$\Lambda(m,0)=-\frac{3}{8}-\frac{3}{2}m+\frac{1}{8}\sqrt{1+144m^2}$
$\Lambda(m,\infty)=-\frac{3}{8}-\frac{3}{2}m+\frac{1}{4}\sqrt{4-4m+9m^2}+\frac{1}{8}\sqrt{9-12m+36m^2}$
$\Lambda(m,\infty)=0$ for $m=m^*\approx 0.315$.

Table 3: Limits of $\Lambda(m,T)$ for the parameters values used in Figure 4

$\Lambda(0,\infty)=1/2, \quad \Lambda(0,0)=\Lambda(0,T)=-1/4$
$\Lambda(\infty,0)=-3/8, \quad \Lambda(\infty,T)=\Lambda(\infty,\infty)=5/24$
$\Lambda(m,0)=-\frac{3}{8}-3m+\frac{1}{8}\sqrt{1+576m^2}$
$\Lambda(m,\infty)=-\frac{3}{8}-3m+\frac{1}{2}\sqrt{1+4m+9m^2}+\frac{1}{8}\sqrt{9+48m+144m^2}$
$\Lambda(m,\infty)>0$ for all $m\geq 0$.

The migration is time dependent. For the parameter values used in the figure, we have $\chi=1/2$, $\overline{r}_1=-1/4$ and $\overline{r}_2=-1/2$. Therefore, the patches are sinks and DIG can occur. Using Remark 2, we have $q_1=q_2=1/2$ and

$$p_1(\tau)=\begin{cases} 5/6 \text{ if } 0\leq\tau<1/2 \\ 1/6 \text{ if } 1/2\leq\tau<1 \end{cases}, \quad p_2(\tau)=\begin{cases} 1/6 \text{ if } 0\leq\tau<\alpha \\ 5/6 \text{ if } \alpha\leq\tau<1 \end{cases}.$$

Using the theoretical formulas depicted in Figure 1 and Section 3.7, we obtain the expressions shown in Table 3. Since for any $T>0$, $\Lambda(\infty,T)>0$, for fixed T and m large enough, the condition $\Lambda(m,T)>0$ is satisfied, so that DIG occurs. We can make similar comments on Figure 4, as those made in the previous sections, except that, in contrast with Figures 2 and 3, the critical curve $T=T_c(m)$ is defined for all $m>0$ and DIG occurs if and only if $T>T_c(m)$.

4.1.5 The set where DIG occurs in the (m,ν) parameter-plane

In Figure 5 we display the set where DIG occurs in the (m,ν) parameter-plane, where $\nu=1/T$ is the frequency. The figure shows that the critical curve $\nu=\nu_c(m)$, where $\nu_c(m):=1/T_c(m)$, is tangent to the ν-axis at the origin, i.e. $\lim_{m\to 0}\nu_c'(m)=-\infty$. This property was already numerically observed in the symmetric migration case by Katriel [23]. This property was established in [4], for the ± 1 model considered in Section 4.1.1. Using the explicit expression of $\Lambda(m,T)$ we showed that when $\nu\to 0$, the threshold $m^*(\nu)=\inf_{\nu>0}\{m:\Lambda(m,1/\nu)>0\}$ at which DIG occurs is of order $e^{-(1-\varepsilon)/\nu}$, see [4, Proposition 2.9]. Therefore the critical curve $\nu=\nu_c(m)$ has asymptotic behavior of the form $m\sim e^{-k/\nu}$, that is m becomes exponentially small in $1/\nu$ near the origin.

The difference between the models considered in Figures 2, 3 and 4 is in the migration matrix which is assumed to be independent of time in the first figure whereas it depends on it in the two following ones.

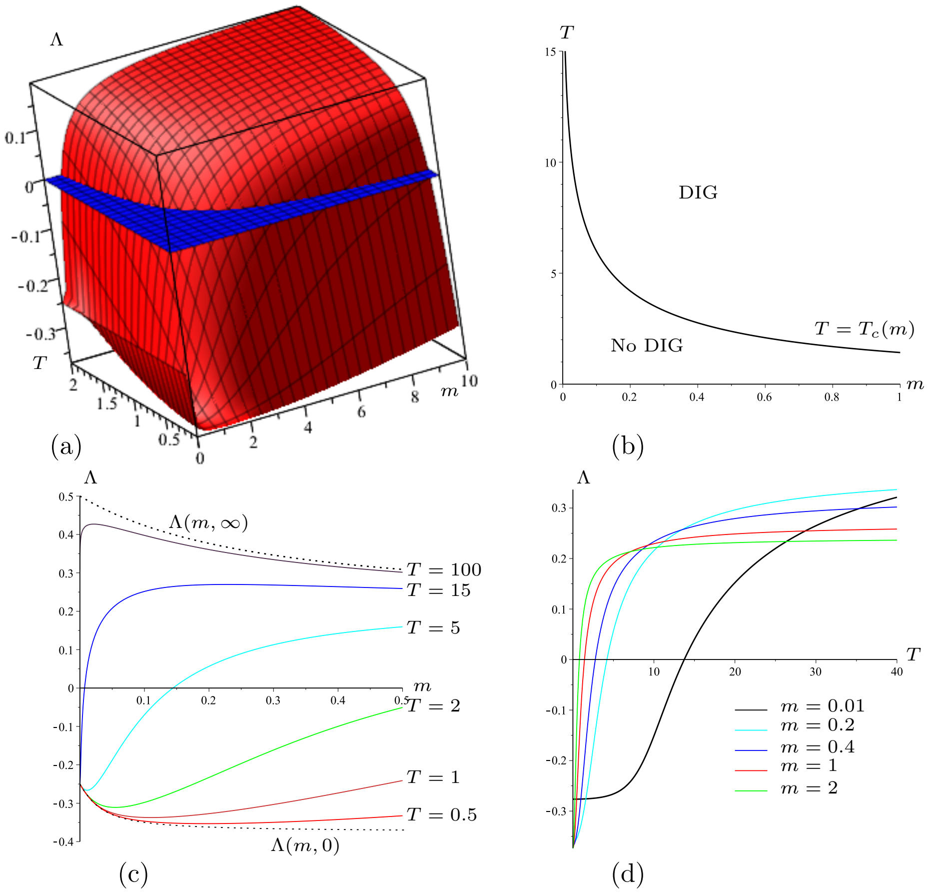


Figure 4: (a) The graph of $(m,T) \mapsto \Lambda(m,T)$. (b) The set $\Lambda(m,T) = 0$. (c) Graphs of $m \mapsto \Lambda(m,T)$ with the indicated values of T. (d) Graphs of $T \mapsto \Lambda(m,T)$ with the indicated values of m. Here we used the two patch model corresponding to the matrices (36) and $\alpha = 0.5$.

Note that in the second case the migration is always stronger towards the most unfavorable patch. As expected, and as illustrated in Figure 5(b), the region of the (m,ν) for which DIG occurs is narrowed, but it still remains present. In the third case the migration is always stronger towards the most favorable patch. As expected, and as illustrated in Figure 5(c), the region of the (m,ν) for which DIG occurs is bigger. Since $\Lambda(m,\infty) > 0$ in this case, DIG occurs for all $m > 0$.

4.1.6 The three patch case

Our objective in this section is to show numerical simulations with three patches that illustrate all our findings and also corroborate our Conjecture 1. We show in Figure 6(a) the plot of $\Lambda(m,T)$ in the three patch case with time independent migration given by $\ell_{12} = \ell_{23} = \ell_{31} = 0$ and $\ell_{21} = \ell_{32} = \ell_{13} = 1$, which corresponds to a circular migration $1 \to 2 \to 3 \to 1$. We consider the piecwise constant growth rates $r_1(\tau) = 0.15$ if $\tau < 1/2$, $r_1(\tau) = -0.45$ if $1/2 \leq \tau < 1$,

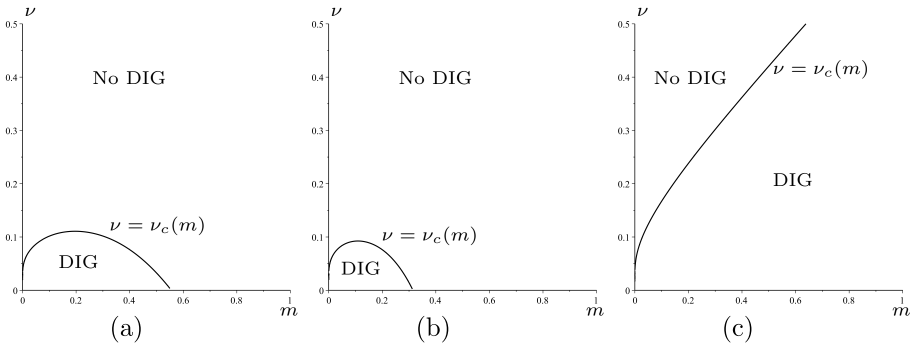


Figure 5: The set where DIG occurs in the (m, ν) parameter-plane. (a) Parameters values of Figure 2. (b) Parameters values of Figure 3. (c) Parameters values of Figure 4

$r_2(\tau) = r_1(\tau - 1/2)$ and $r_3(\tau) = -0.2$ for $\tau \in [0, 1]$. Hence, the matrices A and B in (34) are given

$$\begin{aligned} A &= \begin{bmatrix} 0.15 - m & 0 & m \\ m & -0.45 - m & 0 \\ 0 & m & -0.2 - m \end{bmatrix}, \\ B &= \begin{bmatrix} -0.45 - m & 0 & m \\ m & 0.15 - m & 0 \\ 0 & m & -0.2 - m \end{bmatrix}. \end{aligned} \tag{38}$$

For these parameter values, we have $\chi = 0.15$, $\overline{r}_1 = \overline{r}_2 = -0.15$ and $\overline{r}_3 = -0.2$. Therefore the patches are sinks and DIG can occur. Using Remark 2, we have $p_1 = p_2 = p_3 = 1/3$. Using the theoretical formulas depicted in Figure 1, we have

$$\begin{aligned} &\Lambda(0,0) = \Lambda(0,T) = -0.15, \quad \Lambda(0,\infty) = 0.15, \\ &\Lambda(\infty,0) = \Lambda(\infty,T) = \Lambda(\infty,\infty) = -1/6. \end{aligned}$$

We can make the same comments on Figure 6, as those made in Section 4.1.2 on Figure 2. Panels (a,d) of the figure are supporting then Conjecture 1.

4.2 DIG can also occur for $m > m^*$

4.2.1 The two patch case

In this section we consider the following example of two-patches (30), with piecewise constant 1-periodic growth rates and migration terms, having three discontinuities on each period of time, and given by

$$r_1(\tau) = \begin{cases} 0 \text{ if } 0 \le \tau < \frac{1}{3} \\ -\frac{4}{5} \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ \frac{1}{2} \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}, \quad r_2(\tau) = \begin{cases} -\frac{1}{10} \text{ if } 0 \le \tau < \frac{1}{3} \\ \frac{3}{2} \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ -2 \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}, \tag{39}$$

$$\ell_{12}(\tau) = \begin{cases} \frac{1}{10} \text{ if } 0 \le \tau < \frac{1}{3} \\ 2 \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ \frac{1}{100} \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}, \quad \ell_{21}(\tau) = \begin{cases} 1 \text{ if } 0 \le \tau < \frac{1}{3} \\ \frac{1}{5} \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ \frac{1}{100} \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}. \tag{40}$$

The monodromy matrix is given by

$$\Phi(T) = e^{\frac{T}{3}C} e^{\frac{T}{3}B} e^{\frac{T}{3}A}, \tag{41}$$

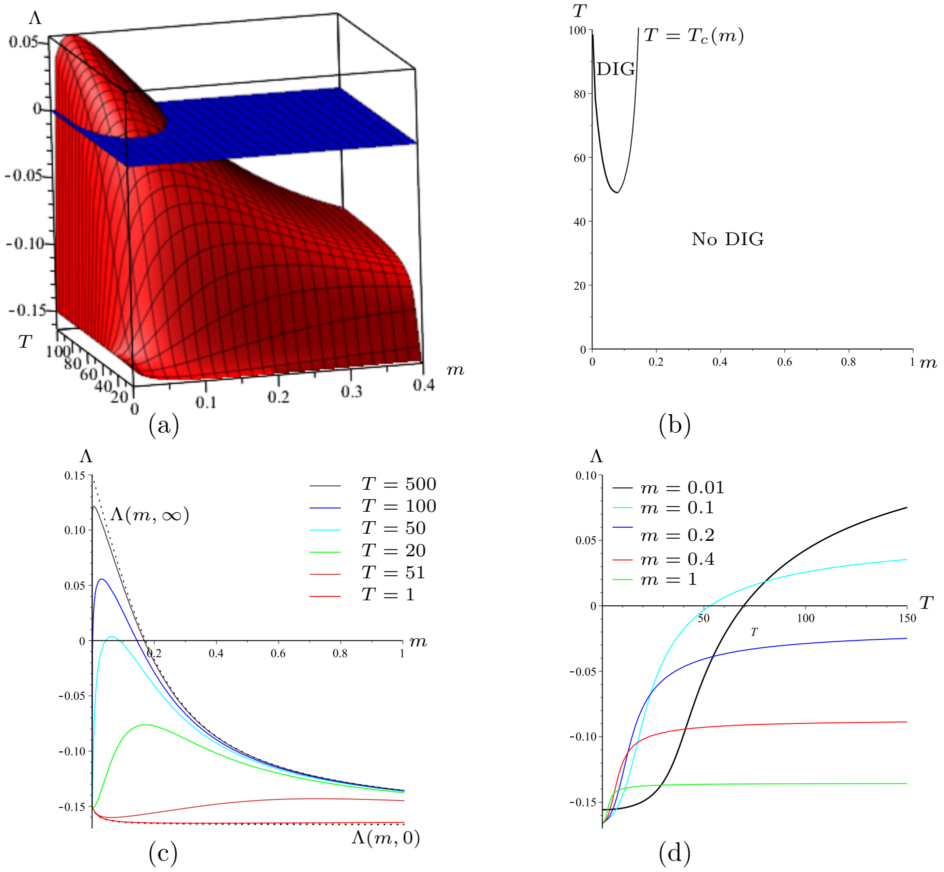


Figure 6: (a) The graph of $(m,T) \mapsto \Lambda(m,T)$. (b) The set $\Lambda(m,T) = 0$. (c) Graphs of $m \mapsto \Lambda(m,T)$ with the indicated values of T. (d) Graphs of $T \mapsto \Lambda(m,T)$ with the indicated values of m. We considers the three patch model given by the matrices (38). We have $\Lambda(m,\infty) = 0$ for $m = m^* = 0.172$.

where the matrices A, B and C are defined by

$$A = \begin{bmatrix} -m & \frac{m}{10} \\ m & -\frac{1}{10} - \frac{m}{10} \end{bmatrix}, \quad B = \begin{bmatrix} -\frac{4}{5} - \frac{m}{5} & 2m \\ \frac{m}{5} & \frac{3}{2} - 2m \end{bmatrix}, \\ C = \begin{bmatrix} \frac{1}{2} - \frac{m}{100} & \frac{m}{100} \\ \frac{m}{100} & -2 - \frac{m}{100} \end{bmatrix}. \tag{42}$$

We can compute the Perron root $\mu(m,T)$ of the matrix $\Phi(T)$ and plot the graph of $\Lambda(m,T) = \frac{1}{T}\ln(\mu(m,T))$, which is shown in Figure 7. For the parameter values used in the figure, we have $\chi = \frac{2}{3}$, $\bar{r}_1 = -\frac{1}{10}$ and $\bar{r}_2 = -\frac{1}{5}$. Therefore, the patches are sinks and DIG can occur. Using Remark 2, we have $q_1 = \frac{211}{332}$, $q_2 = \frac{121}{332}$ and

$$p_1(\tau) = \begin{cases} \frac{1}{11} \text{ if } 0 \le \tau < \frac{1}{3} \\ \frac{10}{11} \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ \frac{1}{2} \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}, \quad p_2(\tau) = \begin{cases} \frac{10}{11} \text{ if } 0 \le \tau < \frac{1}{3} \\ \frac{1}{11} \text{ if } \frac{1}{3} \le \tau < \frac{2}{3} \\ \frac{1}{2} \text{ if } \frac{2}{3} \le \tau < 1 \end{cases}.$$

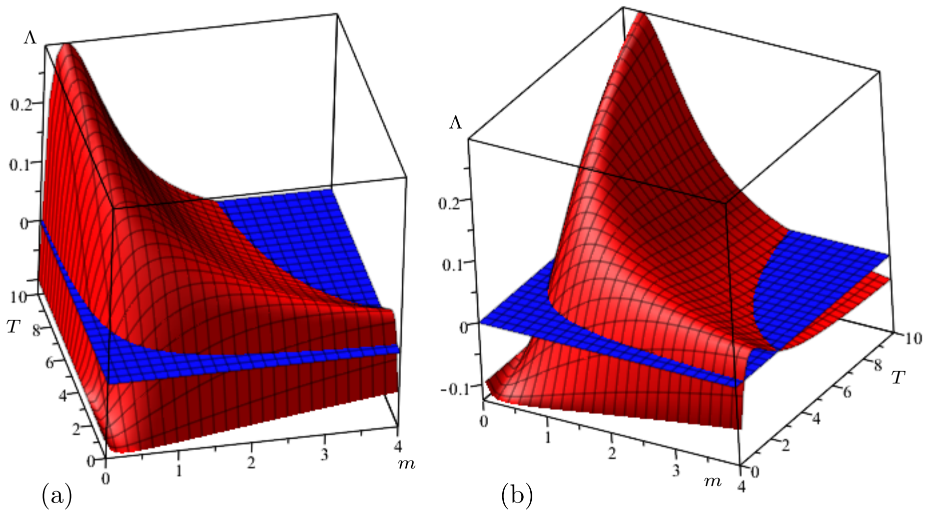


Figure 7: The graph of $(m,T) \mapsto \Lambda(m,T)$ corresponding to the matrices (42), seen from left (a) and right (b), showing the non monotonicity of $T \mapsto \Lambda(m,T)$.

Table 4: Limits of $\Lambda(m,T)$ for the parameters values used in Figure 7

$\Lambda(0,\infty) = 2/3, \quad \Lambda(0,0) = \Lambda(0,T) = -1/4$
$\Lambda(\infty,0) = -453/3320, \quad \Lambda(\infty,T) = \Lambda(\infty,\infty) = -21/44$
$\Lambda(m,0) = -\frac{3}{20} - \frac{83}{150}m + \frac{1}{300}\sqrt{225 + 1350m + 27556m^2}$
$\Lambda(m,\infty) = -\frac{3}{20} - \frac{83}{150}m + \frac{1}{60}\sqrt{1 - 18m + 121m^2}$ $+\frac{1}{60}\sqrt{529 - 828m + 484m^2} + \frac{1}{300}\sqrt{15625 + m^2}$
$\Lambda(m,\infty) = 0$ for $m = m^* \approx 1.764$.

Using the theoretical formulas depicted in Figure 1 and Section 3.7, we obtain the expressions shown in Table 4. Since, as in Figure 3, $\Lambda(\infty,T) < \Lambda(\infty,0)$, for m large enough, the condition $\Lambda(m,T) > \Lambda(m,0)$ cannot be satisfied. Note that the functions $m \mapsto \Lambda(m,T)$ can take values greater than $\Lambda(m,\infty)$, see Figure 8(a,c). In contrast with Figure 3, the functions $T \mapsto \Lambda(m,T)$ can be increasing then decreasing, see Figure 8(b,d). Hence we do not have a critical curve $T = T_c(m)$, defined for $0 < m < m^*$, such that DIG occurs if and only if $T > T_c(m)$. The set of parameter values where DIG occur behaves as in Remarks 7 and 9. Indeed, the functions $T_i(m)$ for $i = 1,2,3,4$ defined in Remark 7 satisfy

$$T_1(m) = T_2(m), \quad 0 < T_3(m) < T_4(m) < \infty.$$

Let $T_c^1 : (0,\infty) \to (0,\infty)$ and $T_c^2 : (m^*,\infty) \to (0,\infty)$ defined by

$$T_c^1(m) = \begin{cases} T_1(m) \text{ if } 0 < m < m^*, \\ T_3(m) \text{ if } m \geq m^*, \end{cases} \quad , \quad T_c^2(m) = T_4(m) \text{ if } m > m^*.$$

Then, see Figure 9(a), DIG occur if and only if

$$T_c^1(m) < T < T_c^2(m).$$

Therefore, DIG can occur for $m > m^*$. In Figure 9(b) we display the set where DIG occurs in the (m,ν), where $\nu = 1/T$. We observe that the critical curve $\nu = 1/T_c^1(m)$ is tangent to the ν-axis at the origin.

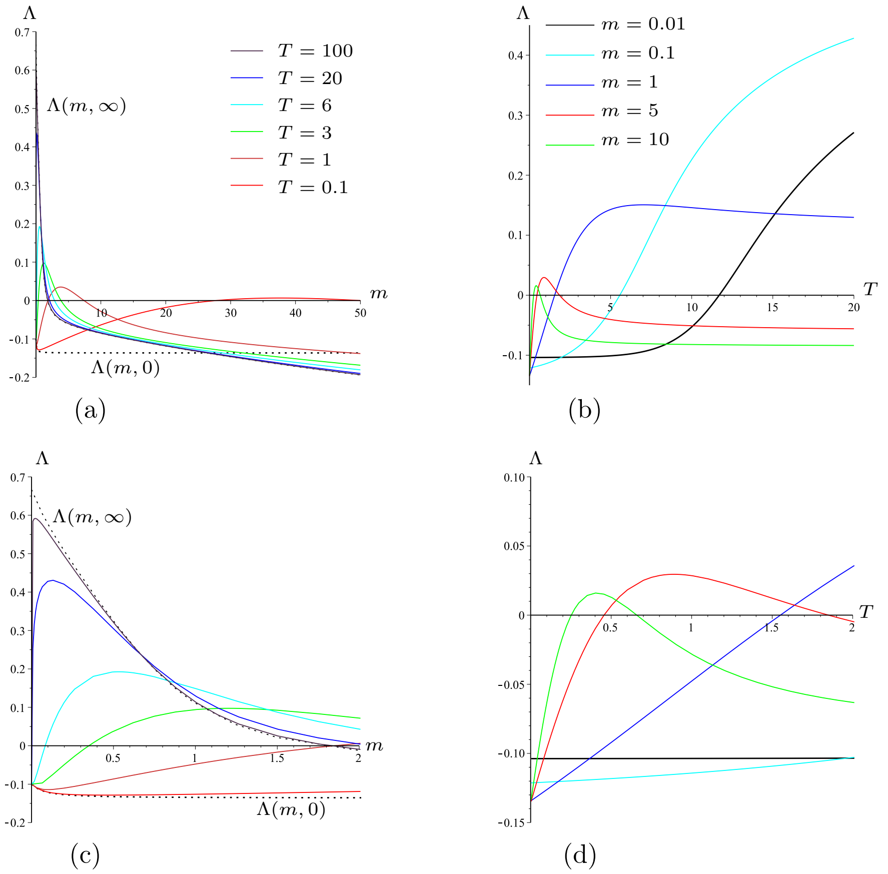


Figure 8: (a) Graphs of $m \mapsto \Lambda(m,T)$, with the indicated values of T. (b) Graphs of $T \mapsto \Lambda(m,T)$ with the indicated values of m. (c) and (d) are zooms of (a) and (b) respectively. The parameter values correspond to Figure 7.

4.2.2 The three patch case

Our objective in this section is to show numerical simulations with three patches that illustrate the non monotonicity of $\Lambda(m,T)$ with respect to T. We consider the case where $\alpha = 1/2$ and the matrices A and B in (34) are given by:

$$
\begin{aligned}
A_\varepsilon(m) &= \begin{bmatrix} 9-(10+\varepsilon_1)m & \varepsilon_2 m & \varepsilon_3 m \\ 10m & -1-(\varepsilon_2+\varepsilon_4)m & \varepsilon_5 m \\ \varepsilon_1 m & \varepsilon_4 m & -10-(\varepsilon_3+\varepsilon_5)m \end{bmatrix}, \\
B_\delta(m) &= \begin{bmatrix} -10-(\delta_1+\delta_4)m & \delta_2 m & 10m \\ \delta_1 m & -(10+\delta_2)m & \delta_3 m \\ \delta_4 m & 10m & 9-(10+\delta_3)m \end{bmatrix},
\end{aligned} \tag{43}
$$

with $\varepsilon = (\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4, \varepsilon_5) \geq 0$ and $\delta = (\delta_1, \delta_2, \delta_3, \delta_4) \geq 0$ such that the corresponding migration matrices are irreducible. Our theory applies to this example. For these parameter values, we have $\chi = 9$ and $\overline{r}_1 = \overline{r}_2 = \overline{r}_3 = -1/2$. Therefore all patches are sinks and DIG can occur. We have the following result

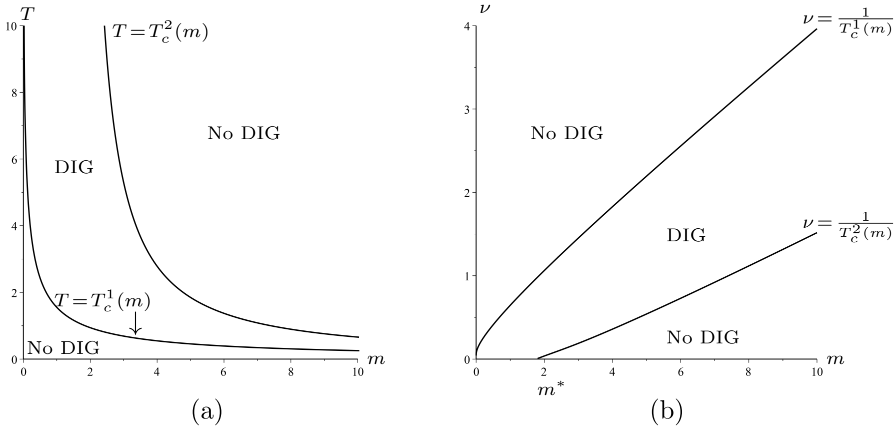


Figure 9: (a) The set $\Lambda(m,T) = 0$. (b) The set $\Lambda(m,\nu) = 0$. Here we use the parameter values of Figure 7 ($m^* = 1.764$)

Proposition 12. *Let $\Lambda_{\varepsilon,\delta}(m,T)$ the growth rate corresponding to the piecewise constant system defined by the matrices* (43)*. For ε and δ small enough, we have*

$$\Lambda_{\varepsilon,\delta}(1,0) < 0, \quad \Lambda_{\varepsilon,\delta}(1,\infty) < 0, \quad \Lambda_{\varepsilon,\delta}(1,2) > 0,$$

so that the function $T \mapsto \Lambda_{\varepsilon,\delta}(1,T)$ is not monotonous.

Proof. For $m = 1$, $\epsilon = 0$ and $\delta = 0$ we get $A_0(1) = A$ and $B_0(1) = B$, where A and B are given by

$$A = \begin{bmatrix} -1 & 0 & 0 \\ 10 & -1 & 0 \\ 0 & 0 & -10 \end{bmatrix}, \quad B = \begin{bmatrix} -10 & 0 & 10 \\ 0 & -10 & 0 \\ 0 & 10 & -1 \end{bmatrix}.$$

These matrices have been proposed in [12] as a counterexample to the conjecture that a PLS (*positive linear switched system*) is GUAS (*globally uniformly asymptotically stable*) if every matrix in the convex hull of the matrices defining the subsystems of the PLS is Hurwitz, i.e. its spectral abscissa is negative. Indeed, it is proved in [12] that every matrix in $\mathrm{co}(A,B) = \{kA + (1-k)B : k \in [0,1]\}$ is Hurwitz and a calculation reveals that the matrix $e^A e^B$ has one real eigenvalue $\mu \approx 1.669 > 1$. Thus the PLS defined by the matrices A and B is not GUAS. From these observations we deduce that

$$\lambda_{max}(A) < 0, \quad \lambda_{max}(B) < 0, \quad \lambda_{max}\left(\tfrac{A+B}{2}\right) < 0,$$

and the Perron root of $e^A e^B$ is stricly greater than 1.

Using the continuity of the spectral abscissa and the continuity of the Perron root we deduce that for ε and δ small enough, we have

$$\lambda_{max}\left(A_\varepsilon(1)\right) < 0, \quad \lambda_{max}\left(B_\delta(1)\right) < 0, \quad \lambda_{max}\left(\tfrac{A_\varepsilon(1)+B_\delta(1)}{2}\right) < 0,$$

and the Perron root of $e^{A_\varepsilon(1)} e^{B_\delta(1)}$ is stricly greater than 1.

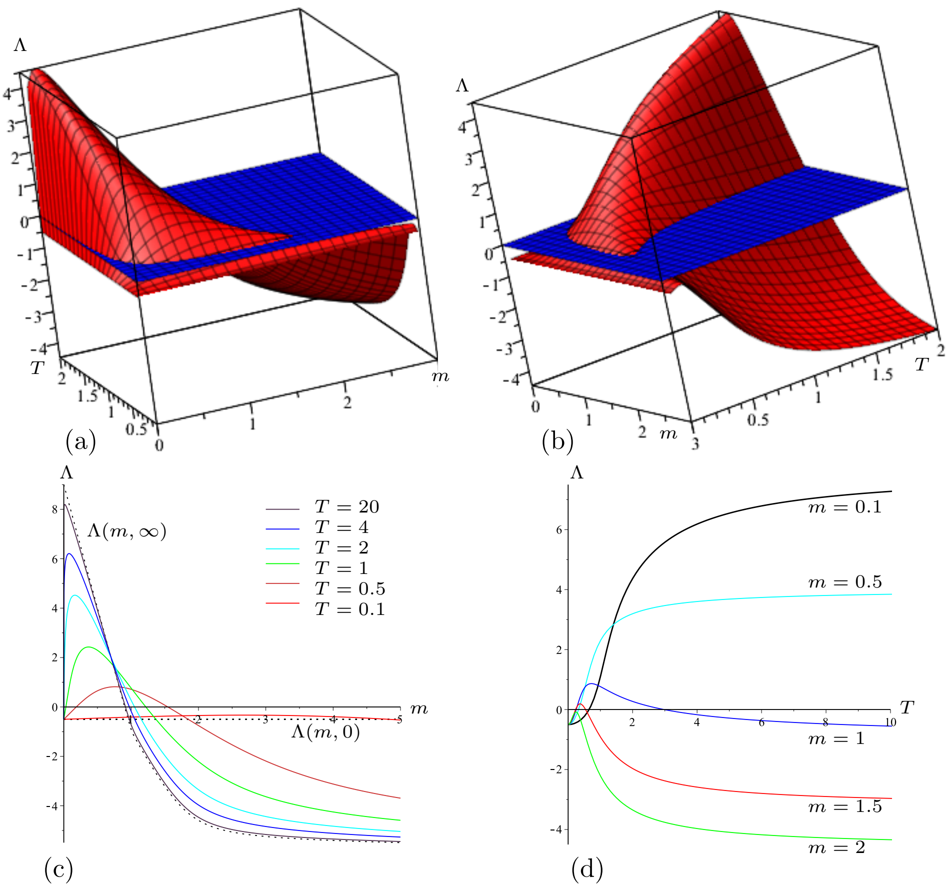


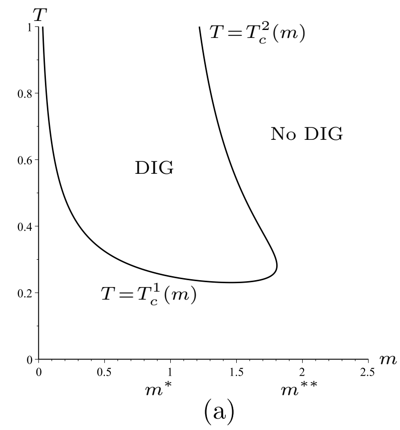
Figure 10: (a,b) The graph of $(m, T) \mapsto \Lambda(m, T)$ corresponding to the matrices (43) and $\varepsilon_3 = \varepsilon_4 = 0.1$, $\varepsilon_1 = \varepsilon_2 = \varepsilon_5 = 0$, $\delta_1 = 0.1$, $\delta_2 = \delta_3 = \delta_4 = 0$, seen from left and right. (c) Graphs of $m \mapsto \Lambda(m, T)$ with the indicated values of T. (d) Graphs of $T \mapsto \Lambda(m, T)$ with the indicated values of m. We have $\Lambda(m, \infty) = 0$ for $m = m^* = 0.172$.

Therefore, using (11) and (12) we have

$$\Lambda_{\varepsilon,\delta}(1, 0) = \lambda_{max}\left(\frac{A_\varepsilon(1)+B_\delta(1)}{2}\right) < 0,$$
$$\Lambda_{\varepsilon,\delta}(1, \infty) = \frac{1}{2}\left(\lambda_{max}\left(A_\varepsilon(1)\right) + \lambda_{max}\left(B_\delta(1)\right)\right) < 0.$$

Let μ be the Perron root of $e^{A_\varepsilon(1)}e^{B_\delta(1)}$. Using the definition (9) of $\Lambda(m, T)$, we have $\Lambda_{\varepsilon,\delta}(1, 2) = \frac{1}{2}\ln(\mu) > 0$. $\square$

We show in Figure 10 the plot of $\Lambda_{\varepsilon,\delta}(m, T)$ for the particular choice of ε and δ indicated in the caption of the figure. For this choice of ε and δ the migration



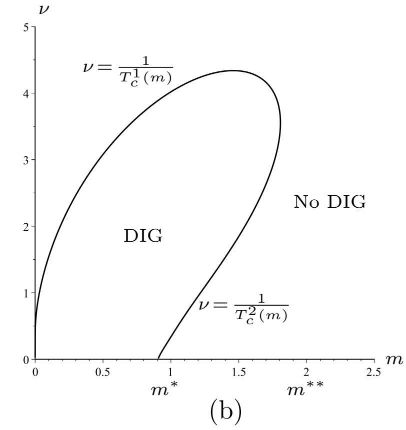


Figure 11: (a) The set $\Lambda(m,T) = 0$. (b) The set $\Lambda(m,\nu) = 0$. The parameter values are those of Figure 10. We have $m^* \approx 0.904$ and $m^{**} \approx 1.807$.

matrix is irreducible and corresponds to the circular migrations

$$\begin{aligned} &1 \xrightarrow{10} 2 \xrightarrow{0.1} 3 \xrightarrow{0.1} 1, \qquad \text{for } \tau \in [0,1/2), \\ &1 \xrightarrow{0.1} 2 \xrightarrow{10} 3 \xrightarrow{10} 1, \qquad \text{for } \tau \in [1/2,1). \end{aligned}$$

Using Remark 2, we have $q_1 = q_2 = q_3 = 1/3$ and

$$p_1(\tau) = \begin{cases} \frac{1}{201} \text{ if } 0 \le \tau < \frac{1}{2} \\ \frac{50}{51} \text{ if } \frac{1}{2} \le \tau < 1 \end{cases}, \quad p_2(\tau) = p_3(\tau) = \begin{cases} \frac{100}{201} \text{ if } 0 \le \tau < \frac{1}{2} \\ \frac{1}{102} \text{ if } \frac{1}{2} \le \tau < 1 \end{cases}.$$

Using the theoretical formulas depicted in Figure 1, we have

$$\begin{aligned} &\Lambda(0,\infty) = 9, \quad \Lambda(0,0) = \Lambda(0,T) = \Lambda(\infty,0) = \Lambda(m,0) = -1/2, \\ &\Lambda(\infty,T) = \Lambda(\infty,\infty) = -34497/4556 \approx -7.572. \end{aligned}$$

As in Figures 3 and 8, we have $\Lambda(\infty,T) < \Lambda(\infty,0)$ and hence, for m large enough we should have $\Lambda(m,T) < \Lambda(m,0)$, so that $\Lambda(m,T)$ is not increasing with respect to T. Actually, the behaviour predicted by Proposition 12 occurs in this case since for $m = 1$ the map $T \mapsto \Lambda(m,T)$ is increasing and then decreasing, see Figure 10(d). We can make comments on the critical set $\Lambda(m,T) = 0$ which are similar to those made on Figure 8. Indeed, the set of parameter values where DIG occur behaves as in Remarks 7 and 9: the functions $T_i(m)$ for $i = 1,2,3,4$ defined in Remark 7 satisfy $T_1(m) = T_2(m)$ for all $m \in (0,m^*)$ and there exists $m^{**} > m^*$ such that

$$\begin{aligned} &0 < T_3(m) < T_4(m) < \infty \text{ for } m \in [m^*,m^{**}), \quad T_3(m^{**}) = T_4(m^{**}) \\ &T_3(m) = \infty, \quad T_4(m) = 0 \text{ for } m > m^{**}. \end{aligned}$$

Let $T_c^1 : (0,\infty) \to (0,\infty)$ and $T_c^2 : (m^*,\infty) \to (0,\infty)$ defined by

$$T_c^1(m) = \begin{cases} T_1(m) \text{ if } 0 < m < m^*, \\ T_3(m) \text{ if } m^* \le m \le m^{**}, \end{cases}, \quad T_c^2(m) = T_4(m) \text{ if } m^* < m \le m^{**}.$$

Then, see Figure 11(a), DIG occur if and only if $T_c^1(m) < T < T_c^2(m)$. Therefore, DIG can occur for $m > m^*$. In Figure 11(b) we display the set where DIG occurs in the (m, ν), where $\nu = 1/T$. We observe that the critical curve $\nu = 1/T_c^1(m)$ is tangent to the ν-axis at the origin.

5 Stochastic environment

In this section, we briefly explain why most of our results remain valid if the growth rates are stochastic. More precisely, we consider a Markov Feller process $(\omega_t)_{t\geq 0}$ on a compact state S. For precise definition, the reader is referred to [5]. For each $1 \leq i \leq n$ we consider a continuous function $r_i : S \to \mathbb{R}$. We also consider for each $s \in S$ a matrix $L(s) = (l_{ij}(s))_{ij}$ which satisfies (4) and we assume that $s \mapsto L(s)$ is continuous on S. We then have the system of differential equations

$$\frac{dx_i}{dt} = r_i(\omega_t)x_i + m\sum_{j\neq i}\left(\ell_{ij}(\omega_t)x_j - \ell_{ji}(\omega_t)x_i\right), \qquad 1 \leq i \leq n, \tag{44}$$

We assume that $(\omega_t)_{t\geq 0}$ has a unique stationary distribution μ on S. This a the consequence that, for all bounded continuous function $f : S \to \mathbb{R}$, with probability one,

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t f(\omega_u)du = \int_S f(s)\mu(ds) \tag{45}$$

In particular, in analogy with the periodic case, we let

$$\overline{r}_i = \int_S r_i(s)\mu(ds)$$

be the local average growth rate in each patch in the absence of migration ($m = 0$). Formula (45) implies that when $m = 0$, for each $1 \leq i \leq n$, with probability one,

$$\lim_{t\to\infty}\frac{1}{t}\ln(x_i(t)) = \lim_{t\to\infty}\frac{1}{t}\int_0^t r_i(\omega_u)du = \overline{r}_i.$$

For $s \in S$, we let $R(s) = \mathrm{diag}(r_1(s), \ldots, r_n(s))$, $A(s) = R(s) + mL(s)$ and for a function f defined on S and with values in $\mathbb{R}$ or in the set of matrices, we let $\overline{f} = \int_S f(s)\mu(ds)$. Setting $x(t) = (x_1(t), \cdots, x_n(t))^\top$, Equation (44) can be rewritten as

$$\frac{dx(t)}{dt} = A(\omega_t)x,$$

By Proposition 1 in [5], we have:

Proposition 13. *There exists $\Lambda \in \mathbb{R}$ such that, for all $x(0) > 0$, with probability one,*

$$\lim_{t\to\infty}\frac{\ln(\|x(t)\|)}{t} = \Lambda. \tag{46}$$

For all $T > 0$, we let $\omega_t^T = \omega_{t/T}$. We let $\Lambda(m, T)$ denote the Lyapunov exponent given by (46), when $(\omega_t)_{t\geq 0}$ is replaced by $(\omega_t^T)_{t\geq 0}$ in (44). We can prove the following results:

Theorem 14. *The Lyapunov exponent $\Lambda(m,T)$ satisfies the following properties*

1. *For all $m, T > 0$,*
$$\Lambda(m,T) \leq \chi := \int_S \max(r_i(s))\mu(ds). \tag{47}$$

2. *For all $m > 0$,*
$$\lim_{T\to 0} \Lambda(m,T) = \lambda_{\max}(\overline{R+mL}). \tag{48}$$

3. *For all $m > 0$,*
$$\lim_{T\to\infty} \Lambda(m,T) = \int_S \lambda_{\max}(R(s)+mL(s))\mu(ds). \tag{49}$$

4. *We have*
$$\lim_{m\to 0}\lim_{T\to\infty} \Lambda(m,T) = \chi \tag{50}$$
In particular, $\sup_{m,T}\Lambda(m,T) = \chi$.

5. *We have*
$$\lim_{m\to 0}\lim_{T\to 0} \Lambda(m,T) = \max(\overline{r}_i). \tag{51}$$

6. *We have*
$$\lim_{m\to\infty}\lim_{T\to\infty} \Lambda(m,T) = \sum_i \overline{p_i r_i}, \quad \lim_{m\to\infty}\lim_{T\to 0} \Lambda(m,T) = \sum_i q_i \overline{r_i} \tag{52}$$

Proof. The proof of the upper bound (47) is exactly the same as in the periodic case, except that we use (45) to justify the convergence of the temporal mean. The limits (48) and (49) are consequence, respectively of Propositions 4 and 5 in [5]. The double limits (50), (51) and (52) are proven as in the periodic case, using Lemma 29. □

Example 1. (Periodic case) The continuous periodic case corresponds to $S = \mathbb{R}/\mathbb{Z}$ identified with the unit circle and $\omega_t = s + t \,(\mathsf{mod}\, 1)$ for some $s \in S$.

Example 2. (PDMP case) Let $S = \{1, \dots, N\}$ a finite set, and $(\omega_t)_{t\geq 0}$ a continuous time Markov chain on S. Then, $(\omega_t)_{t\geq 0}$ is a Markov Feller process. The process $(x_t, \omega_t^T)_{t\geq 0}$ is a Piecewise Deterministic Markov Process (PDMP). The case where $N = 2$ and $n = 2$ has been investigated in [4]. Theorem 14 extend to the case of general N and n the results found in [4].

Remark 10. The results given here all rely on results proved in [5]. In this paper, we have used the fact that the couple $(x_t, \omega_t)_{t\geq 0}$ is a Feller Markov process (see [5, Lemma 7]). This is the reason why we assumed that $s \to R(s)$ and $s \mapsto L(s)$ are continuous functions, in contrast with Section 2, where these functions can have discontinuities.

The proofs of the asymptotic formulas for $\Lambda(m,T)$ when T tends to 0 or T tends to infinity are done in quite different ways, in the periodic case (Theorem 4) and the random case (Theorem 14). In the random case, these formulas are special cases of the results given in [5] for a general irreducible cooperative linear system. In the periodic case, these are also special cases of general results that deal with an irreducible linear cooperative system and are given in the Section 6 of this paper. Moreover, as for the periodic case, one could also give in the random case asymptotic formulas for $\Lambda(m,T)$ when m tends to 0 or m tends to infinity, which are similar to those given in items 3 and 4 of Theorem 4.

6 Cooperative linear T-periodic systems

The existence of the growth rate (see Proposition 1) and the results presented in Theorem 4 on the fast regime ($T \to 0$), and the slow regime ($T \to \infty$), are special cases of more general results which are true for any irreducible cooperative linear T-periodic system. The objective of this section is to discuss and prove these results in this more general framework. Consider the linear T-periodic system

$$\frac{dx}{dt} = A(t/T)x, \tag{53}$$

where $A(\tau)$ is not necessarily equal to $R(\tau) + mL(\tau)$ as in the system (5). We only assume that

Hypothesis 3. The function $A : \tau \mapsto A(\tau)$ is a piecewise 1-periodic continuous function, with a finite number of discontinuities on $[0, 1)$ and has left and right limits at the discontinuity points. Moreover, for each $\tau \geq 0$, $A(\tau)$ is an irreducible Metzler matrix.

The solutions of (53) are continuous and piecewise $\mathcal{C}^1$ functions satisfying (74) excepted on the discontinuity points of $A(\tau)$. The fundamental matrix solution $X(t)$ of (53) is the solution of the matrix valued differential equation

$$\frac{dX}{dt} = A(t/T)X, \tag{54}$$

with initial condition $X(0) = Id$, the identity matrix. By changing time, we can return to the case where the period is 1 and make T appear as a parameter of the system. Indeed, the change of variables

$$t/T = \tau, \quad y(\tau) = x(T\tau), \quad Y(\tau) = X(T\tau)$$

transforms (53) and (54) into the equations

$$\frac{dy}{d\tau} = TA(\tau)y, \qquad \frac{dY}{d\tau} = TA(\tau)Y. \tag{55}$$

In order not to burden the presentation, the results on the existence of the growth rate for the system (55), and the formulas that give it, are discussed in Appendix B. The main result of Appendix B is the Theorem 26 which shows that the system (55) admits a growth rate, noted $\Lambda(T)$ to recall its dependence on the parameter T in the system (55). This theorem also provides two formulas to compute $\Lambda(T)$, one using the Perron root $\mu(T)$ of the monodromy matrix $Y(1) = X(T)$ and the other using a periodic GAS solution of the equation associated with system (55) in the simplex Δ. The existence and global asymptotic stability of this periodic solution is given in Proposition 24 in Appendix B.

In the remainder of this section we use Proposition 24 and Theorem 26 of Appendix B, which concern the 1-periodic systems (55), to derive analogous results which concern the equivalent systems (53,54).

6.1 The growth rate

We have the following result.

Proposition 15. *Let $x(t)$ be a solution of* (53) *such that $x(0) > 0$. For all $t > 0$ we have $x(t) \gg 0$. For all i we have*

$$\Lambda[x_i] = \Lambda(T) := \frac{1}{T}\ln(\mu(T)),$$

where $\mu(T)$ is the Perron root of the monodromy matrix $X(T)$ of (53)*. The function Λ is analytic in T.*

Proof. Using Theorem 26 of Appendix B, for any solution $y(\tau)$ of (55), such that $y(0) > 0$, we have

$$\lim_{\tau\to\infty}\frac{1}{\tau}\ln(y_i(\tau)) = \ln(\mu(T)),$$

where $\mu(T)$ is the Perron root of the monodromy matrix $Y(1) = X(T)$. On the other hand we have

$$\lim_{\tau\to\infty}\frac{1}{\tau}\ln(y_i(\tau)) = \lim_{t\to\infty}\frac{1}{t/T}\ln(x_i(t)) = T\lim_{t\to\infty}\frac{1}{t}\ln(x_i(t)).$$

Hence we have $\Lambda[x_i] = \Lambda(T)$, where $\Lambda(T) = \frac{1}{T}\ln(\mu(T))$.

We prove now that $\Lambda(T)$ is analytic in T. The monodromy matrix $X(T)$ is analytic in T. Indeed, the solutions of the differential equation (55), which is analytic in the parameter T are analytic in this parameter. Hence $X(T)$ is analytic in T. So is its Perron root $\mu(T)$, since it is a simple root of the characteristic polynomial, see [6]. Therefore $\Lambda(T)$ is analytic in T. $\square$

6.2 The variables ρ and θ

As we said in Section 3.4 about the particular system (5) the variables $\rho = \sum_i x_i$ and $\theta = x/\rho$ play a major role in the description of our results. Let us show in this section how these variables are used in the general case of system (53). In these variables, the system (53) is written

$$\begin{array}{rcl}\frac{d\rho}{dt} & = & \langle A(t/T)\theta, \mathbf{1}\rangle\rho \\ \frac{d\theta}{dt} & = & A(t/T)\theta - \langle A(t/T)\theta, \mathbf{1}\rangle\theta\end{array} \tag{56}$$

The second equation in (56) is a differential equation on the simplex Δ. We have the following result.

Proposition 16. *Let $\theta^*(t,T)$ be the solution of the second equation in* (56) *with initial condition $\theta^*(0,T) = \pi(T)$, where $\pi(T)$ is the Perron vector of the monodromy matrix $X(T)$. Then $\theta^*(t,T)$ is a T-periodic solution, and is globally asymptotically stable. Moreover, the growth rate $\Lambda(T) := \frac{1}{T}\ln(\mu(T))$ of equation* (53) *satisfies*

$$\Lambda(T) = \int_0^1 \langle A(\tau)\theta^*(T\tau, T), \mathbf{1}\rangle d\tau. \tag{57}$$

Proof. Using the change of variable

$$\tau = t/T, \quad \sigma(\tau) = \rho(T\tau), \quad \eta(\tau) = \theta(T\tau),$$

the system (56) becomes

$$\begin{array}{rcl} \frac{d\sigma}{d\tau} & = & T\langle A(\tau)\eta, \mathbf{1}\rangle\sigma \\ \frac{d\eta}{d\tau} & = & TA(\tau)\eta - T\langle A(\tau)\eta, \mathbf{1}\rangle\eta \end{array} \tag{58}$$

According to Proposition 24 of Appendix B, the second equation in (58), has a periodic solution, denoted $\eta^*(\tau, T)$ to emphasize its dependence on the parameter T, which is globally asymptotically stable. Recall that $\eta^*(\tau, T)$ is the solution of initial condition $\eta^*(0, T) = \pi(T)$, where $\pi(T)$ is the Perron vector of the monodromy matrix $X(T)$. Therefore, $\theta^*(t, T) := \eta^*(t/T, T)$ is a T-periodic solution of the second equation in (56). It is globally asymptotically stable. As a consequence of Theorem 26 of Appendix B, we have the formula (57) for the growth rate $\Lambda(T)$ of the equation (53). $\square$

6.3 Fast regime

Our aim is to determine the limit of $\Lambda(T)$ as $T \to 0$. We use the averaging method [34]. The averaged system of (53) consists in the following linear system

$$\frac{dx}{dt} = \overline{A}x. \tag{59}$$

In contrast with (53), the system (59) is an autonomous linear systems whose solutions can be computed analytically. We have

$$x(t) = e^{\overline{A}t}x(0).$$

Since $\overline{A}$ is a an irreducible Metzler matrix, its spectral abscissa, denoted $\lambda_{max}(\overline{A})$, is a simple real eigenvalue, called the dominant eigenvalue of $\overline{A}$. Therefore the growth rate of the averaged system (59) is equal to $\lambda_{max}(\overline{A})$. We have the following result which asserts that when $T \to 0$, the limit of the growth rate of the original system (53) is equal to the growth rate of the averaged system (59).

Theorem 17. *Let $\lambda_{max}(\overline{A})$ be the dominant eigenvalue of $\overline{A}$. We have*

$$\lim_{T\to 0} \Lambda(T) = \lambda_{max}(\overline{A}).$$

Proof. Using Proposition 16, the growth rate of the equation (53), satisfies

$$\Lambda(T) = \int_0^1 \langle A(\tau)\theta^*(T\tau, T), \mathbf{1}\rangle d\tau.$$

where $\theta^*(t, T)$ is the T-periodic solution of the second equation in (56). Let $\theta(t, T)$ be the solution of the second equation in (56), with initial condition $\theta(0, T) = \theta_0$. From the averaging theorem we deduce that, as $T \to 0$, $\theta(t, T)$ is approximated by the solution $\overline{\theta}(t)$ of the averaged equation

$$\frac{d\theta}{dt} = \overline{A}\theta - \langle \overline{A}\theta, \mathbf{1}\rangle\theta, \tag{60}$$

with the same initial condition $\overline{\theta}(0) = \theta_0$. The averaged equation (60) has a globally asymptotically stable equilibrium in Δ. Indeed, let $w = (w_1, \cdots, w_n)^\top$ be the Perron-Frobenius vector of $\overline{A}$, i.e., the unique positive eigenvector corresponding to the eigenvalue $\lambda_{max}\left(\overline{A}\right)$ of the matrix $\overline{A}$, such that $\langle w, \mathbf{1}\rangle = 1$. We have $w \in \Delta$ and w is the unique positive equilibrium of (60). Using Proposition 25 in Appendix B, w is GAS for (60) in the simplex Δ. Since the averaged equation has an attractive equilibrium w, as $T \to 0$, the T-periodic solution $\theta^*(t, T)$ of the second equation in (56) converges toward w. Hence, using Proposition 16, as $T \to 0$, we have

$$\Lambda(T) = \int_0^1 \langle A(\tau)\theta^*(T\tau, T), \mathbf{1}\rangle d\tau = \int_0^1 \langle A(\tau)w, \mathbf{1}\rangle d\tau + o(1)$$

Using $\overline{A}w = \lambda_{max}\left(\overline{A}\right) w$ and $\langle w, \mathbf{1}\rangle = 1$, we have

$$\begin{aligned} \textstyle\int_0^1 \langle A(\tau)w, \mathbf{1}\rangle d\tau &= \langle \left(\textstyle\int_0^1 A(\tau)d\tau\right) w, \mathbf{1}\rangle = \langle \overline{A}w, \mathbf{1}\rangle \\ &= \lambda_{max}\left(\overline{A}\right)\langle w, \mathbf{1}\rangle + = \lambda_{max}\left(\overline{A}\right). \end{aligned}$$

Therefore, as $T \to 0$, $\Lambda(T) = \lambda_{max}\left(\overline{A}\right) + o(1)$.

□

6.4 Slow regime

Our aim in this section is to determine $\lim_{T\to\infty} \Lambda(T)$. Since $A(\tau)$ is an irreducible cooperative matrix, the Perron-Frobenius theorem for irreducible Metzler matrices implies that its stability modulus is a simple real eigenvalue of the matrix $A(\tau)$, denoted $\lambda_{max}(A(\tau))$. We have the following result, which has already been proved by Carmona [7], in the case where the matrix $A(\tau)$ is continuous. Hence the next theorem is an extension of [7, Theorem 2.1] to the case where the matrix $A(\tau)$ is piecewise continuous.

Theorem 18. *Let $\lambda_{max}(A(\tau))$ be the spectral abscissa of the matrix $A(\tau)$. We have*

$$\lim_{T\to\infty} \Lambda(T) = \overline{\lambda_{max}(A)}$$

Proof. As shown by (56), the equation on the simplex Δ is

$$\begin{aligned} \tfrac{d\theta}{dt} &= A(\tau)\theta - \langle A(\tau)\theta, \\ \tfrac{d\tau}{dt} &= \tfrac{1}{T} \end{aligned} \tag{61}$$

We use the change of variable $\tau = t/T$ and $\eta(\tau) = \theta(T\tau)$. The equation (61) becomes

$$\frac{1}{T}\frac{d\eta}{d\tau} = A(\tau)\eta - \langle A(\tau)\eta \tag{62}$$

When $T \to \infty$ this is a singularly perturbed equation whose study is achieved using Tikhonov's theorem, see Appendix C. The systems (61) and (62) are equivalent. The first one is written using the fast time t, while the second one is written using the slow time τ. These systems have $n - 1$ fast variables θ and one slow variable τ. The fast dynamics, obtained from (61) by letting $\frac{1}{T} = 0$ is

$$\tfrac{d\theta}{dt} = A(\tau)\eta - \langle A(\tau)\eta, \tag{63}$$

where τ is considered as a parameter. Let us prove that the hypotheses of the Proposition 28 in Appendix C are satisfied. The conditions H0' and H1 hold. It remains to prove that the condition H2' also hold. This is true since the fast equation (63) admits the Perron-Frobenius vector $v(\tau)$ of $A(\tau)$ as an equilibrium which is globally asymptotically stable in the simplex Δ, see Proposition 25 in Appendix B. Therefore, according to Proposition 28 (see Remark 15 following this proposition), the solution $\eta(\tau, T)$ of (62) is approximated by the slow curve $v(\tau)$. More precisely, for any $\nu > 0$, as small as we want, as $T \to \infty$, we have

$$\eta(\tau, T) = v(\tau) + o(1) \text{ uniformly on } [0, 1] \setminus \bigcup_{k=0}^{p} [\tau_k, \tau_k + \nu],$$

where $\tau_0 = 0$ and τ_k, $1 \leq k \leq p$, are the discontinuity points of $A(\tau) = R(\tau) + mL(\tau)$. Hence the unique T-periodic solution $\eta^*(t, T)$ of the second equation in (58) (see the proof of Proposition 16), satisfies

$$\eta^*(\tau, T) = v(\tau) + o(1) \text{ uniformly on } [0, 1] \setminus \bigcup_{k=1}^{p} [\tau_k, \tau_k + \nu].$$

From this formula and $\theta^*(T\tau, T) = \eta^*(\tau, T)$ we deduce that

$$\theta^*(T\tau, T) = v(\tau) + o(1) \text{ uniformly on } [0, 1] \setminus \bigcup_{i=1}^{p} [\tau_k, \tau_k + \nu].$$

Since ν can be chosen as small as we want, as $T \to \infty$, using Proposition 16, we have

$$\Lambda(T) = \int_0^1 \langle A(\tau)\theta^*(T\tau, T), \mathbf{1}\rangle d\tau = \int_0^1 \langle A(\tau)v(\tau), \mathbf{1}\rangle d\tau + o(1)$$

Using $A(\tau)v(\tau) = \lambda_{max}(A(\tau))v(\tau)$ and $\langle v(\tau), \mathbf{1}\rangle = 1$, we have

$$\textstyle\int_0^1 \langle A(\tau)v(\tau), \mathbf{1}\rangle d\tau = \int_0^1 \lambda_{max}(A(\tau))\langle v(\tau), \mathbf{1}\rangle d\tau = \int_0^1 \lambda_{max}(A(\tau))d\tau.$$

Therefore, as $T \to \infty$, $\Lambda(T) = \int_0^1 \lambda_{max}(A(\tau))d\tau + o(1) = \overline{\lambda_{max}(A)} + o(1)$. □

The behavior of $\theta^*(T\tau, T)$ as $T \to \infty$ is illustrated in Figure 12, showing the approximation of $\theta^*(T\tau, T)$ by the Perron-Frobenius vector $v(\tau)$ when T is large enough. Note that the approximation is uniform except on the small intervals $[\tau_k, \tau_k + \nu]$, where τ_k is a discontinuity of $v(\tau$. In these thin layers, the solution jumps quickly from the left limit of $v(\tau)$ at τ_k to its right limit.

6.5 Fast migration

In this section we consider the following particular case of (53)

$$\frac{dx}{dt} = R(t/T) + mL(t/T) \tag{64}$$

where the matrix $A(\tau)$ is of the form $A(\tau) = R(\tau) + mL(\tau)$, with $m > 0$ and $R(\tau)$, $L(\tau)$ are $n \times n$ matrices. In addition to Hypothesis 3 we make the following assumption.

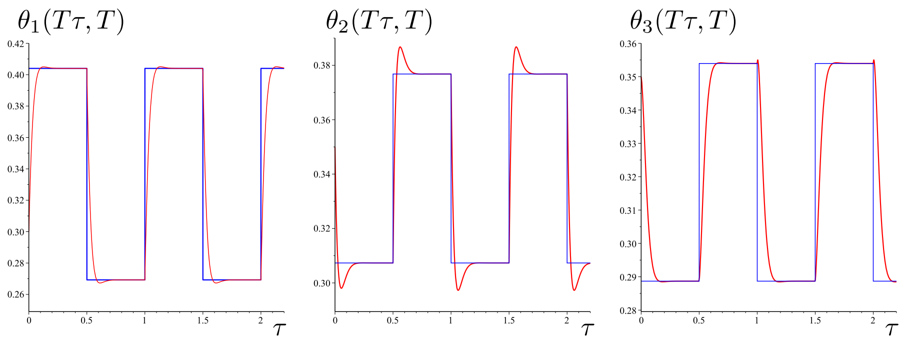


Figure 12: The figure corresponds to the example discussed in Section 4.1.6, with $m = 1$ and $T = 20$. The solution $\theta(T\tau, T)$ of the second equation in (56) with initial condition $\theta_1(0) = 0.3$, $\theta_2(0) = 0.35$, $\theta_3(0) = 0.35$ is colored in red. The Perron-Frobenius vector $v(\tau)$ of the matrix $A(\tau)$ is colored in blue.

Hypothesis 4. For any $\tau \in [0, 1]$ the matrix $L(\tau)$ is Metzler irreducible and its columns sum to 0.

If the matrix $R(\tau)$ is diagonal we obtain the system (5).

As recalled in Lemma 3, the spectral abscissa $L(\tau)$ is $\lambda_{max}(L(\tau)) = 0$. It is an eigenvalue and $L(\tau)$ has a unique positive corresponding eigenvector in the simplex Δ that we note $p(\tau)$, called its Perron-Frobenius vector, see Theorem 22 in Appendix A. We have the following result.

Proposition 19. *Let $p(\tau)$ be the Perron-Frobenius vector of $L(\tau)$. Let $\Lambda(m, T)$ be the growth rate of* (64)*. We have*

$$\lim_{m\to\infty} \Lambda(m, T) = \overline{\langle Rp, \mathbf{1}\rangle}.$$

In the particular case of (5)*, where $R(\tau) = \mathrm{diag}(r_1(\tau), \cdots, r_n(\tau))$ is diagonal, this formula becomes $\lim_{m\to\infty} \Lambda(m, T) = \sum_{i=1}^{n} \overline{p_i r_i}$.*

Proof. As shown by (56), the equation on the simplex Δ is

$$\frac{d\theta}{dt} = R(t/T)\theta + mL(t/T)\theta - \langle R(t/T)\theta, \mathbf{1}\rangle\theta - m\langle L(t/T)\theta, \mathbf{1}\rangle\theta, \tag{65}$$

Since the columns of $L(\tau)$ sum to 0 we have $\langle L(\tau)\theta, \mathbf{1}\rangle = 0$. Therefore, using the variables $\tau = t/T$ and $\eta(\tau) = \theta(T\tau)$, this equation is written

$$\frac{d\eta}{d\tau} = TR(\tau)\eta + TmL(\tau)\eta - T\langle R(\tau)\eta, \mathbf{1}\rangle\eta, \tag{66}$$

Dividing by m we obtain

$$\frac{1}{m}\frac{d\eta}{d\tau} = TL(\tau)\eta + \frac{1}{m}\left[TR(\tau)\eta - T\langle R(\tau)\eta, \mathbf{1}\rangle\eta\right]. \tag{67}$$

When $m \to \infty$ this is a singularly perturbed equation with $n - 1$ fast variables θ and one slow variable τ. Using the fast time $s = m\tau$, this equation is written

$$\begin{aligned} \tfrac{d\eta}{ds} &= TL(\tau)\eta + \tfrac{1}{m}\left[TR(\tau)\eta - T\langle R(\tau)\eta, \mathbf{1}\rangle\eta\right], \\ \tfrac{d\tau}{ds} &= \tfrac{1}{m} \end{aligned} \tag{68}$$

Therefore, the fast dynamics, obtained by letting $\frac{1}{m}=0$ in (68) is

$$\tfrac{d\eta}{ds}=TL(\tau)\eta, \tag{69}$$

where τ is considered as a parameter. Let us prove that the hypotheses of the Proposition 28 in Appendix C are satisfied. The conditions H0' and H1 hold. It remains to prove that the condition H2' also hold. This is true since the Perron-Frobenius vector $p(\tau)$ of $L(\tau)$, is the unique positive equilibrium of (69) and is GAS in the simplex Δ, as shown in the Proposition 25 in Appendix B. Therefore, according to Proposition 28 (see Remark 15 following this proposition), the solution $\theta(\tau,m)$ of (67) is approximated by the slow curve $p(\tau)$. More precisely, for any $\nu>0$, as small as we want, as $T\to\infty$, we have

$$\eta(\tau,T)=p(\tau)+o(1) \text{ uniformly on } [0,1]\setminus\bigcup_{k=0}^{p}[\tau_k,\tau_k+\nu],$$

where $\tau_0=0$ and τ_k, $1\le k\le p$, are the discontinuity points of $A(\tau)=R(\tau)+mL(\tau)$. Hence the unique T-periodic solution $\theta^*(t,T)$ of (65) satisfies

$$\theta^*(T\tau,m)=p(\tau)+o(1) \text{ uniformly on } [0,1]\setminus\bigcup_{i=1}^{p}[\tau_k,\tau_k+\nu].$$

From Proposition 16, we have $\Lambda(m,T)=\int_0^1\langle R(\tau)\theta^*(T\tau,T),\mathbf{1}\rangle d\tau$. Since ν can be chosen as small as we want, as $m\to\infty$, we have

$$\textstyle\int_0^1\langle R(\tau)\theta^*(T\tau,T),\mathbf{1}\rangle d\tau=\int_0^1\langle R(\tau)p(\tau),\mathbf{1}\rangle d\tau+o(1)=\overline{\langle Rp,\mathbf{1}\rangle}+o(1).$$

Therefore, as $m\to\infty$, $\Lambda(m,T)=\overline{\langle Rp,\mathbf{1}\rangle}+o(1)$. If R is diagonal we obtain $\Lambda(m,T)=\sum_{i=1}^n\overline{p_ir_i}+o(1)$. □

7 Discussion

Non-autonomous linear differential systems of the form

$$\frac{dx}{dt}=R(t/T)x+mL(t/T)x, \tag{70}$$

where $R(\tau)$ and $L(\tau)$ are 1-periodic, R is a diagonal matrix, representing the local growths on the patches, and L represents the migration between the patches, are the simplest models to address the question of population dynamics subject to temporal fluctuations (the system is not autonomous), and spatial fluctuations encoded in the migration matrix L.

Motivated by the pioneering remarks of [19] and [22] and some others (see [4] for a more detailed historical review) on the paradoxical effect of DIG (or inflation) a thorough mathematical study has been undertaken to clarify the origin and characteristics of this phenomenon by [4], in the case of two patches, and by [23], in the more ambitious case of n patches. The natural way to do so is to study the properties of the growth rate $\Lambda(m,T)$ which can be associated to the linear system (70) when the matrix $L(\tau)$ is irreducible for any τ (see Proposition 1). Indeed, we prove that when $m>0$, the Lyapunov exponents $\Lambda[x_i]$ of all components $x_i(t)$ of the solutions of (70) are equal, and moreover they do not depend on the initial condition. The common value of the Lyapunov exponents $\Lambda[x_i]$ is called the growth rate of the system (70) and denoted $\Lambda(m,T)$. It is given by $\Lambda(m,T) = \frac{1}{T}\ln(\mu(m,T)$, where $\mu(m,T)$ is the Perron root of the monodromy matrix associated to (70). This result is not obvious, neither in the case of a symmetric and constant migration matrix, considered by Katriel [23], nor in the one considered here when the migration matrix is neither symmetric nor constant.

In [23] the migration matrix L is time independent and symmetric and the matrix $R(t)$ is a continuous. The existence of the growth rate $\Lambda(m,T)$ is demonstrated, see [23, Section 3.1], and its properties are described:

1. Asymptotic behavior of $\Lambda(m,T)$ for T tending to 0 or ∞.
2. Monotonicity of $T \mapsto \Lambda(m,T)$.

These results of [23] follow from general results of Liu et al. [26] on the principal eigenvalue of a periodic linear system.

Using rather elementary methods, the theorem of Perron-Frobenius, the method of averaging and Tikhonov's theorem on singular perturbations, we have generalized the results of point 1 to the case where the matrix L is not symmetric and can depend on time and the functions $R(t)$ and $L(t)$ can have discontinuities. We gave the asymptotic behavior of $\Lambda(m,T)$ for m and T tending to 0 or ∞ (Theorem 4).

We have shown, as in [23], that if all patches are sinks (i.e. $\max_i \overline{r_i} < 0$) then DIG occurs (i.e. $\Lambda(m,T) > 0$, see Definition 2) if and only if $\chi := \overline{\max_i r_i} > 0$ (see Theorem 6) and we characterized the set of m and T for which $\Lambda(m,T) > 0$ (see Proposition 7 and Remark 7). The properties of $\Lambda(m,0)$ and $\Lambda(m,\infty)$, defined as the limits of $\Lambda(m,T)$, when T tends to 0 or ∞ respectively, are important in this study. As in [23], it appears that these limits are decreasing with respect of m (see Proposition 5). Among the new properties we obtain when the matrix $L(\tau)$ depends on time or is not symmetric, we can mention the following facts.

- If $\max_i \overline{r_i} < 0$ and $\chi := \overline{\max_i r_i} > 0$ then there is not necessarily any m^* for which $\Lambda(m^*,\infty) = 0$, so that $\Lambda(m,\infty) > 0$ for any $m > 0$ and DIG can occur, when T is large enough, for any $m > 0$ not only for $0 < m < m^*$ as in the constant symmetric migration case, see Section 4.1.4. This behavior cannot occur if L is constant or $L(\tau)$ is symmetric, see Remark 6.
- When m^* such that $\Lambda(m^*,\infty) = 0$ exists, DIG does not occur only for $T > T_c(m)$, where $T = T_c(m)$ is the critical curve defined for $0 < m < m^*$, as in [23]. The set of (m,T) for which DIG can occur is more complicated, see Section 4.2.
- When the migration matrix $L(\tau)$ is time dependent then the function $T \mapsto \Lambda(m,T)$ is not always strictly increasing, see Sections 4.1.3 and 4.2. The DIG phenomenon can occur for $m > m^*$, precisely because of this non-monotonicity.

The extension to a non symmetric time dependent migration seems important to us because the symmetry assumptions are not very realistic and the dispersal patterns can also be seasonal. The possibility that $R(t)$ and $L(t)$ have discontinuities is not a simple desire for mathematical generality. Indeed, it opens the way to thinking, for example in the piecewise constant case, about stochastic models (PDMP) as we sketched in the Section 5. Note that even if we assume in Section 5 that R and L are continuous, this does not contradict the fact that in our deterministic study we found it important to extend the results to the non-continuous case, since for a realization $t \mapsto \omega_t$ of many reasonable stochastic processes, $t \mapsto R(\omega_t) + mL(\omega_t)$ is discontinuous. We refer to [4] and [5] for further analysis of these issues.

In the random case, the asymptotic formulas for $\Lambda(m, T)$ when T tends to 0 or T tends to infinity given in Theorem 14 are special cases of the formulas given in [5] for a general cooperative linear system. In the periodic case, these formulas, given in Theorem 4 are special cases of the results given in Section 6 of the present paper.

There remains the second point of the results of Katriel, the monotony of $T \mapsto \Lambda(m, T)$ that we have not been able to re-demonstrate with our methods. The clarification of this last point seems to require new ideas insofar as we think that it is still true in the non-symmetric time independent case, but that it is no longer true as soon as L depends on time as we have seen.

In this article, and in its title, we focused on the case where all patches are sinks (the all-sink case). However, the theoretical results obtained on the growth rate $\Lambda(m, T)$ and its limits when m or T tends to 0 or to ∞ allow us to study also the case when some patches are sources (the source-sink case). For example, if there is at least one source (one of the $\bar{r}_i$'s is positive) then the formula $\lim_{m\to 0} \Lambda(m, T) = \max_{1\leq i\leq n} \bar{r}_i$, established in Theorem 4, shows that for m small enough $\Lambda(m, T)$ will be positive, in contrast with the all-sink case, where it is negative. The source-sink case has been analyzed in detail by Katriel [23, Section 2.4] when the migration matrix is constant. The extension of his results to the case where the migration matrix is time dependent is an important question which deserves more development and will be the subject of future work.

It seems likely that these results remain true for more realistic models including density dependent growth rates and dispersions along the lines proposed in [4], but the work remains to be done. It also remains to be addressed, still from the point of view of the combined effect of dispersal intensity and temporal fluctuations, for more complex models of population dynamics, structured populations, population interaction etc...

A The Perron Frobenius theorem

The Perron theorem, implies the following result.

Theorem 20. *Let X be a matrix with positive entries. The matrix X has a unique positive real eigenvalue, denoted μ and a unique corresponding eigenvector, denoted π, called respectively the* Perron root *and the* Perron vector*, such that*

$$X\pi = \mu\pi, \qquad \pi_i > 0 \quad \textit{and} \quad \|\pi\|_1 = \textstyle\sum_{i=1}^{n} \pi_i = 1. \tag{71}$$

Moreover

$$\lim_{k\to\infty} (X/\mu)^k = G, \tag{72}$$

where G is the projector onto the nullspace $N(M)$ along the range $R(M)$ of the matrix $M = X - \mu I$.

The matrix G is called the *Perron projection.* We have the explicit formula $G = vw^\top / w^\top v$, where v and $w^\top$ are left and right positive eigenvectors of X, with eigenvalue μ, i.e. $Xv = \mu v$ and $w^\top X = \mu w^\top$. However, we don't need here this explicit formula. For details and complements, see [28]. We have the following result.

Lemma 21. *Let X be a matrix with positive entries and π its Perron vector. For all $x \neq 0$ in $\mathbb{R}^n_+$ we have*

$$\lim_{k\to\infty} \frac{X^k x}{\|X^k x\|_1} = \pi.$$

Proof. Let $x \neq 0$ in $\mathbb{R}^n_+$. Using (72), we have

$$\lim_{k\to\infty} \frac{X^k x}{\|X^k x\|_1} = \lim_{k\to\infty} \frac{(X/\mu)^k x}{\|(X/\mu)^k x\|_1} = \frac{Gx}{\|Gx\|_1},$$

where G is the Perron projection of X. Since $Gx \in N(X - \mu I)$, which is generated by π, we have $\frac{Gx}{\|Gx\|_1} = \pi$. $\square$

The Perron Frobenius theorem extends the Perron theorem to irreducible matrices with nonnegative entries, see [28]. This theorem implies the following result.

Theorem 22. *Let A be an irreducible Metzler matrix (i.e. the matrix A has off diagonal nonnegative entries). The matrix A has a unique real eigenvalue, denoted $\lambda_{max}(A)$ and a unique corresponding eigenvector, denoted u, called respectively the* Perron-Frobenius root *and the* Perron-Frobenius vector*, such that*

$$Ap = \lambda_{max} p, \qquad p_i > 0 \quad \textit{and} \quad \|p\|_1 = \textstyle\sum_{i=1}^n p_i = 1. \tag{73}$$

Moreover any other eigenvalue λ of A satisfies $\Re(\lambda) < \lambda_{max}(A)$.

This result is obtained by applying the Perron-Frobenius theorem to the matrix $X = A + rId$ where r is chosen such that X has nonnegative entries.

B Cooperative linear 1-periodic systems

We consider the linear differential equation

$$\frac{dx}{dt} = A(t)x. \tag{74}$$

We assume that Hypotheis 3 of Section 6 is satisfied, i.e. the function $A : t \mapsto A(t)$ is a piecewise 1-periodic continuous function, with a finite number of discontinuities on $[0, 1)$ and having left and right limits at the discontinuity points. and, for each $t \geq 0$, $A(t)$ is an irreducible Metzler matrix. Therefore the solutions of (74) are continuous and piecewise $\mathcal{C}^1$ functions satisfying (74) excepted on the discontinuity points of $A(t)$. Moreover, the positive cone is positively invariant for (74). More precisely, since $A(t)$ is cooperative and irreducible then, as a consequence of [18, Theorem 1.1] or [36, Lemma], we have the following result.

Lemma 23. *Suppose that $x : [0 + \infty) \to \mathbb{R}^n$ is a solution of* (74) *such that $x(0) > 0$. Then $x(t) \gg 0$ for all $t > 0$.*

Recall that the solution $x(t, x_0)$ to (74) such that $x(0, x_0) = x_0$ writes

$$x(t, x_0) = \Phi(t)x_0 \tag{75}$$

where $\Phi(t)$, called the *fundamental matrix solution*, is the solution to the matrix valued differential equation

$$\frac{dX}{dt} = A(t)X, \qquad X(0) = Id. \tag{76}$$

From Lemma 23 we deduce that for all $t > 0$, $\Phi(t)$ has positive entries.

Let $\Delta := \left\{x \in \mathbb{R}^n_+ : \sum_{i=1}^n x_i = 1\right\}$ be the unit $n - 1$ simplex of $\mathbb{R}^n_+$. Every $x \neq 0$ in $\mathbb{R}^n_+$ can be written as

$$x = \rho\theta, \quad \text{with} \quad \rho = \textstyle\sum_{i=1}^n x_i \quad \text{and} \quad \theta = \frac{x}{\rho} \in \Delta. \tag{77}$$

The flow (75) of (74) induces a flow on Δ, given by

$$\Psi(t, \theta) = \frac{\Phi(t)\theta}{\langle\Phi(t)\theta, \mathbf{1}\rangle}. \tag{78}$$

Here $\mathbf{1} = (1, \ldots, 1)^\top$ and $\langle x, \mathbf{1}\rangle = \|x\|_1 = \sum_{i=1}^n x_i$ is the usual Euclidean scalar product of vectors x and $\mathbf{1}$. We have the following result.

Proposition 24. *Let $\pi \in \Delta$ the Perron vector of $\Phi(1)$. Then $t \mapsto \Psi(t, \pi)$ is a periodic orbit in Δ. It is globally asymptotically stable, i.e. for any $\theta \in \Delta$*

$$\lim_{t\to\infty} \|\Psi(t, \theta) - \Psi(t, \pi)\| = 0.$$

Proof. The Perron vector π of $\Phi(1)$ is a fixed point for the induced flow $\Psi(1, \theta)$ on Δ. Indeed, using (71) and(78), we have

$$\Psi(1, \pi) = \frac{\Phi(1)\pi}{\langle\Phi(1)\pi, \mathbf{1}\rangle} = \frac{\mu\pi}{\mu\langle\pi, \mathbf{1}\rangle} = \pi.$$

Therefore $\Psi(t, \pi)$ is a periodic orbit in Δ. Using (78) and Lemma 21 we have

$$\begin{aligned}\lim_{t\to\infty} \|\Psi(t, \theta) - \Psi(t, \pi)\| &= \lim_{k\to\infty} \|\Psi(k, \theta) - \Psi(k, \pi)\| \\ &= \lim_{k\to\infty} \left\| \frac{\Phi(1)^k\theta}{\|\Phi(1)^k\theta\|_1} - \pi \right\| = 0.\end{aligned}$$

This proves the global asymptotic stability of $\Psi(t, \pi)$. $\square$

Let us write the differential equation on Δ corresponding to the flow (78). Using the decomposition (77), the differential equation (74), with initial condition $x(0) > 0$, rewrites:

$$\frac{d\rho}{dt} = \langle A(t)\theta, \mathbf{1}\rangle\rho \tag{79}$$

$$\frac{d\theta}{dt} = A(t)\theta - \langle A(t)\theta, \mathbf{1}\rangle\theta \tag{80}$$

with initial conditions $\rho(0) = \langle x(0), \mathbf{1}\rangle$ and $\theta(0) = \frac{x(0)}{\langle x(0),\mathbf{1}\rangle}$. For any $\theta_0 \in \Delta$, the solution $\theta(t)$ of of (80) with initial condition $\theta(0) = \theta_0$ is given by $\theta(t, \theta_0) = \Psi(t, \theta_0)$, where Ψ is given by (78). We can also express the solution $x(t, x_0)$ by using the solution $\theta(t, \theta_0)$, as shown in the following remark.

Remark 11. Let $\theta(t, \theta_0)$ be the solution of (80) with initial condition θ_0. The solution $x(t, x_0)$ of (74) with initial condition x_0 is given by

$$x(t, x_0) = \theta\left(t, x_0/\rho_0\right) \rho_0 e^{\int_0^t \langle A(s)\theta(s,x_0/\rho_0),\mathbf{1}\rangle ds}, \tag{81}$$

where $\rho_0 = \langle x_0, \mathbf{1}\rangle$.

We have the following result which is the particular case of Proposition 24 when the matrix A is constant. We state it here because it is used several times in the proofs of our results, see Sections 6.3, 6.4, and 6.5.

Proposition 25. *Let A be an irreducible Metzler matrix. Let $\lambda_{max}(A)$ be its spectral abscissa. Let $p \in \Delta$ be the Perron Frobenius vector associated to $\lambda_{max}(A)$. Then p is an equilibrium point of the differential equation*

$$\frac{d\theta}{dt} = A\theta - \langle A\theta, \mathbf{1}\rangle\theta \tag{82}$$

on the simplex Δ associated to the autonomous linear equation $\frac{dx}{dt} = Ax$. It is GAS in the simplex Δ.

Proof. We obviously have $Ap - \langle Ap, \mathbf{1}\rangle p = 0$. Therefor p is an equilibrium point of (82). Since the differential equation is autonomous, the fundamental matrix of solution is $X(t) = e^{tA}$. Its Perron root is $\mu = e^{\lambda_{max}(A)}$. Since $Ap = \lambda_{max}p$ we have $e^A p = e^{\lambda_{max}A}p$, so that the Perron vector of $X(1)$ is equal to p. Recall that the flow $\Psi(t, \theta)$ of (82) is given by (78) where $\Phi(t, \theta) = e^{tA}\theta$. Hence, using Lemma 21, we have

$$\begin{aligned}\lim_{t\to\infty} \|\Psi(t, \theta) - \Psi(t, p)\| &= \lim_{k\to\infty} \|\Psi(k, \theta) - \Psi(k, p)\| \\ &= \lim_{k\to\infty} \left\| \frac{\left(e^A\right)^k \theta}{\| \left(e^A\right)^k \theta\|_1} - p \right\| = 0.\end{aligned}$$

This proves the global asymptotic stability of p. ☐

We have the following result, which asserts the existence of the growth rate of (74) and which gives us two formulas to calculate it. One uses the periodic solution whose existence was given in Proposition 24. The other uses the Perron root of the monodromy matrix of (74).

Theorem 26. *Let $\Lambda = \ln(\mu)$, where μ is the Perron root of the monodromy matrix $\Phi(1)$ of (74). Let π its Perron vector. Let $\theta^*(t) := \Psi(t, \pi)$ is the periodic solution of (80) whose existence and global asymptotic stability are proved in Proposition 24. For any solution $x(t)$ of (74), such that $x(0) > 0$, we have*

$$\lim_{t\to\infty} \frac{1}{t} \ln(x_i(t)) = \int_0^1 \langle A(t)\theta^*(t), \mathbf{1}\rangle dt = \Lambda,$$

Proof. Using (81), the Lyapunov exponent of the components of any solution $x(t,x_0)$ of (74) can be computed as follows

$$\begin{aligned}\lim_{t\to\infty}\frac{1}{t}\ln(x_i(t,x_0)) &= \lim_{k\to\infty}\frac{1}{k}\ln(x_i(k,x_0))\\ &= \lim_{k\to\infty}\frac{1}{k}\left[\ln(\theta_i(k,x_0/\rho_0)\rho_0)+\int_0^k U(s)ds\right],\end{aligned}$$

where $U(s)=\langle A(s)\theta\left(s,x_0/\rho_0\right),\mathbf{1}\rangle$. Since $\|\theta\left(t,x_0/\rho_0\right)-\theta^*(t)\|$ tends to 0, as t tends to ∞, the first term in the right hand side goes to 0. Therefore, for all $k_1\geq 0$,

$$\lim_{t\to\infty}\frac{1}{t}\ln(x_i(t,x_0))=\lim_{k\to\infty}\frac{1}{k}\left[\int_0^{k_1}U(s)ds+\int_{k_1}^k U(s)ds\right]$$

Using Proposition 24, for k_1 large enough, we can replace in the second integral $\theta\left(t,x_0/\rho_0\right)$ by $\theta^*(t)$, and then, using the fact that the first term tends to 0 as $k\to\infty$, we have

$$\begin{aligned}\lim_{t\to\infty}\frac{1}{t}\ln(x_i(t,x_0)) &= \lim_{k\to\infty}\frac{1}{k}\int_{k_1}^k\langle A(s)\theta^*(s),\mathbf{1}\rangle ds\\ &= \lim_{k\to\infty}\frac{k-k_1}{k}\int_0^1\langle A(s)\theta^*(s),\mathbf{1}\rangle ds=\int_0^1\langle A(t)\theta^*(s),\mathbf{1}\rangle ds.\end{aligned}$$

This proves the first equality. The second equality is proved as follows. Let $x(t)=\Phi(t)\pi$ be the solution of (74), with initial condition $x(0)=\pi$, where $\pi\in\Delta$ is the Perron vector of $\Phi(1)$. Since $x(1)=\Phi(1)\pi=\mu\pi$, we have $x(k)=\Phi(k)\pi=\Phi(1)^k\pi=\mu^k\pi$. Hence

$$\lim_{k\to\infty}\frac{1}{k}\ln(x_i(k))=\ln(\mu)=\Lambda,$$

which proves the formula, since all components of all solutions $x(t)$ of (74), such that $x(0)>0$, have the same Lyapunov exponents. □

Remark 12. In the Floquet theory of linear periodic systems (see [17, Section 4.6]), $\ln(\mu)$ is known as the *largest Floquet exponent*, or the *principal Lyapunov exponent*, that is, the carracteristic multiplier corresponding to the dominant eigenvalue μ of $\Phi(1)$. For further details, we refer the reader to [7] and [30, Section II.2].

C Tikhonov's theorem

Tikhonov's theorem [37] provides a mathematically rigorous basis for the quasi-steady-state approximation commonly used in the study of systems at several time scales [31, 35]. We consider the singularly perturbed initial value problem

$$\left\{\begin{array}{rcll}\varepsilon\frac{dx}{d\tau} &=& f(\tau,x,y,\varepsilon), & x(\tau_0)=x^0(\varepsilon),\\ \frac{dy}{d\tau} &=& g(\tau,x,y,\varepsilon) & y(\tau_0)=y^0(\varepsilon),\end{array}\right. \tag{83}$$

for an m vector x and an n vector y on some bounded interval, say $\tau_0\leq\tau\leq\tau_1$, where ε is a small positive parameter, $0<\varepsilon\ll 1$. We assume that

H0 The functions f and g are continuous in $\tau \in [\tau_0, \tau_1]$.

H1 The functions f, g, x^0 and y^0 are continuous in ε. The functions f and g are differentiable in their x and y arguments.

If assumptions H0 and H1 are satisfied, then the initial value problem (83) has a unique solution, denoted $x(\tau,\varepsilon)$, $y(\tau,\varepsilon)$. When $\varepsilon \to 0$, (83) is a *slow-fast* system, with m *fast variables* x, and $n+1$ *slow variables*, y and τ. According to Tikhonov's theory, the so called *fast equation* is

$$\frac{dx}{dt} = f(\tau, x, y, 0) \tag{84}$$

where τ and y are considered as parameters. Note that this equation is obtained by replacing ε by 0 in the right hand side of the system

$$\left\{\begin{array}{rcl} \frac{dx}{dt} & = & f(\tau, x, y, \varepsilon), \\ \frac{dy}{dt} & = & \varepsilon g(\tau, x, y, \varepsilon) \\ \frac{d\tau}{dt} & = & \varepsilon. \end{array}\right. \tag{85}$$

which is equivalent to the slow-fast system in (83), written with the time $t = \tau/\varepsilon$. We refer to τ as the *slow time* and to t as the *fast time*. We assume that

H2 For any y in a compact set K and $\tau \in [\tau_0, \tau_1]$, the fast equation (84) has an equilibrium $x = \xi(\tau, y)$, which is asymptotically stable with a basin of attraction that is uniform in the parameters $(\tau, y) \in [0,1] \times K$. The function ξ is continuous in τ and differentiable in y.

The *critical manifold*, also called *slow manifold*, is the set of equilibrium points $x = \xi(\tau, y)$ of the fast equation (84). The *reduced equation*, defined for $(\tau, y) \in [\tau_0, \tau_1] \times K$,

$$\frac{dy}{d\tau} = g(\tau, \xi(\tau, y), y, 0), \qquad y(t_0) = y^0(0) \tag{86}$$

is obtained by replacing ε by 0 and x by $\xi(\tau, y)$ in the second equation of (83). Since the function ξ is continuous in τ and differentiable in y, the equation (86) is well defined. Tikhonov's theorem states that the solution of (83) jumps quickly near the critical manifold and is then approximated by the solution of (86). More precisely:

Theorem 27 (Tikhonov's theorem)**.** *Assume that H0, H1 and H2 are satisfied. Assume that $y^0(0) \in K$ and $x^0(0)$ belongs to the basin of attraction of $\xi(\tau_0, y^0(0))$. Let $\overline{y}(\tau)$ be the solution of* (86)*, which is assumed to exist on the interval $[\tau_0, \tau_1]$. Let $\nu > 0$. For ε small enough, $x(\tau,\varepsilon)$ and $y(\tau,\varepsilon)$ are defined on $[\tau_0, \tau_1]$ and, as $\varepsilon \to 0$*

$$\begin{array}{lll} y(\tau,\varepsilon) = \overline{y}(\tau) + o(1) & \textit{uniformly on} & [\tau_0, \tau_1], \\ x(\tau,\varepsilon) = \xi(\tau, \overline{y}(\tau)) + o(1) & \textit{uniformly on} & [\tau_0 + \nu, \tau_1]. \end{array}$$

Remark 13. The approximation given by Tikhonov's theorem holds for all $\tau \in [\tau_0, \tau_1]$ for the slow variable $y(\tau,\varepsilon)$ and for all $\tau \in [\tau_0 + \nu, \tau_1]$ for the fast variables $x(\tau,\varepsilon)$, where ν is as small as we want. Indeed we have a *boundary layer* at $\tau = \tau_0$ since the fast variables jumps quickly from their initial conditions $x^0(\varepsilon)$ near the point $\xi(\tau_0, y_0(0))$ of the slow manifold.

This theorem was first stated by Tikhonov [37] and can be found in various forms in the classical literature, see the book by O'Malley [32, Section 2.D] and the book by Wasow [38, Section X.39]. For a statement of Tikhonov's theorem that is very close to the one given here, the reader can refer to [27] or to Khalil's book [24, Theorem 11.1]. The book by Banaisak and Lachowicz [3, Chapter 3] is also a highly recommended reference for the reader interested by applications in mathematical biology. This result remains true under less restrictive conditions on the regularity of f and g, see [27, 38]. This result was extended by Fenichel [13] in the context of *Geometric Singular Perturbation Theory*. See also [25, Chapter 3].

We want to use Tikhonov's theorem when the functions f and g have discontinuities in the variable τ. Assume that

H0' There exist a finite set $D = \{\tau_k, 1 \leq k \leq p : 0 < \tau_1 < \cdots < \tau_p < 1\}$ such that f and g are continuous on $[0,1] \setminus D$ and have right and left limits at the discontinuity points $\tau_k \in (0,1)$, $k = 1, \ldots, p$.

We extend f by its right limit at each discontinuity point, so that the fast equation (84) is defined for all $\tau \in [0,1]$. We assume that

H2' For all y in some compact set K and $\tau \in [0,1]$, the fast equation (84) has a globally asymptotically stable equilibrium $x = \xi(\tau, y)$. The function ξ is continuous for $\tau \in [0,1] \setminus D$ and differentiable in $y \in K$ and has left and right limits at the discontinuity points τ_k denoted by

$$\xi(\tau_k - 0, y) = \lim_{\tau \to \tau_k, \tau < \tau_k} \xi(\tau, y), \quad \xi(\tau_k + 0, y) = \lim_{\tau \to \tau_k, \tau > \tau_k} \xi(\tau, y), \quad (87)$$

and $\xi(\tau_k + 0, y)$ is the globally asymptotically stable equilibrium for the fast equation (84) for $\tau = \tau_k$.

Since the function ξ is continuous for $\tau \in [0,1] \setminus D$ and differentiable in $y \in K$, the equation (86) is well defined on $[0,1] \times K$.

As a consequence of Tikhonov's theorem, we have the following result, which is used in the proofs of Theorem 4(4), see Section 6.5 and Theorem 18, see Section 6.4.

Proposition 28. *Assume that H0', H1 and H2' are satisfied. Assume that $y^0(0) \in K$. Let $\overline{y}(\tau)$ be the solution of (86), which is assumed to exist on the interval $[0,1]$. Let $\nu > 0$. For ε small enough, $x(\tau,\varepsilon)$ and $y(\tau,\varepsilon)$ are defined on $[0,1]$ and, as $\varepsilon \to 0$*

$$\begin{array}{lll} y(\tau,\varepsilon) = \overline{y}(\tau) + o(1) & \textit{uniformly on} & [0,1], \\ x(\tau,\varepsilon) = \xi(\tau, \overline{y}(\tau)) + o(1) & \textit{uniformly on} & [0,1] \setminus \bigcup_{k=0}^{p} [\tau_k, \tau_k + \nu]. \end{array}$$

where $\tau_0 = 0$ and τ_k, $1 \leq k \leq p$, are the discontinuity points of f and g.

Proof. For each $0 \leq k \leq p$, we consider the system (83) on the interval $[\tau_k, \tau_{k+1}]$, where $\tau_{p+1} = 1$. We extend the functions f and g by continuity to τ_k and τ_{k+1} (such extensions exist because, according to H0', the functions have left and right limits at the discontinuity points τ_k). This system satisfies assumptions H0, H1 and H2. For the first interval ($k = 0$), we use the initial condition $x(0) = x^0(\varepsilon)$ and $y(0) = y^0(\varepsilon)$. We obtain an approximation on the interval

$[\tau_0, \tau_1]$. For the second interval ($k = 1$), we use as initial conditions $x(\tau_1, \varepsilon)$ and $y(\tau_1, \varepsilon)$, which, according to the approximation obtained in the first interval, are close to $\xi(\tau_1 - 0, \overline{y}(\tau_1))$ and $\overline{y}(\tau_1)$, respectively. Since $\xi(\tau_1 + 0, \overline{y}(\tau_1))$ is a globally asymptotically stable equilibrium for the fast equation (84), $\xi(\tau_1 - 0, \overline{y}(\tau_1))$ belongs to its basin of attraction, so that Tikhonov's theorem can be used on the interval $[\tau_1, \tau_2]$. Similarly for the following intervals. Therefore, on each interval, for any $\nu > 0$, as $\varepsilon \to 0$,

$$\begin{array}{lll} y(\tau, \varepsilon) = \overline{y}(\tau) + o(1) & \text{uniformly on} & [\tau_k, \tau_{k+1}], \\ x(\tau, \varepsilon) = \xi(\tau, \overline{y}(\tau)) + o(1) & \text{uniformly on} & [\tau_k + \nu, \tau_{k+1}]. \end{array}$$

This ends the proof of the proposition. □

Remark 14. In addition to the boundary layer at $\tau = 0$, we have now an *inner layer* at each discontinuity point τ_k, because the fast variables must jump quickly from a point close to $\xi(\tau_k - 0, y(\tau_k))$ to a point close to $\xi(\tau_k + 0, y(\tau_k))$, where the left and right limits are defined by (87). These behaviors are illustrated in Figure 12 for the limit $T \to \infty$.

Remark 15. Consider the special case where there is no slow variable y in (83), that is to say we have a singularly perturbed system of the form

$$\varepsilon \frac{dx}{d\tau} = f(\tau, x, \varepsilon),$$

where τ is the only slow variable. The critical manifold is a curve (also called the slow curve) $x = \xi(\tau)$, where $\xi(\tau)$ is the equilibrium of the fast dynamics $\frac{dx}{dt} = f(\tau, x, 0)$. In this case, the fast variable $x(\tau, \varepsilon)$ is approximated by the slow curve, i.e. the result of Proposition 28 becomes $x(\tau, \varepsilon) = \xi(\tau) + o(1)$ uniformly on each interval $[\tau_k + \nu, \tau_{k+1}]$.

D Proof of Proposition 5

We use the following Lemma:

Lemma 29. *Let B and H two Metzler matrices. For $\varepsilon \geq 0$, the function $\varepsilon \mapsto \lambda_{max}(\varepsilon) := \lambda_{max}(B + \varepsilon H)$ is continuous in a neighbourhood of 0. If furthermore B is irreducible, then $\varepsilon \mapsto \lambda_{max}(\varepsilon)$ is differentiable at $\varepsilon = 0$, and*

$$\lambda'_{max}(0) = y^\top H x, \tag{88}$$

where x and y are respectively the right- and left eigenvectors of B associated to $\lambda_{max}(B)$ such that $1^\top x = 1$ and $y^\top x = 1$.

Proof of Lemma 29. Let C be a matrix with nonnegative entries. Then, the Perron-Frobenius theorem (as stated in Section 2 of [29]) implies that the spectral radius of C, denoted $\mu(C)$, is an eigenvalue of C. Moreover, if C_n is a sequence of matrices with nonnegative entries converging to C, then Theorem 3.1 (in the case where C is irreducible) and Theorem 3.2 in [29] (in the case where C is reducible) entail that $\mu(C_n)$ converges to $\mu(C)$. Note that since $\mu(C)$ is an eigenvalue of C, then it is also its spectral abscissa, i.e. $\mu(C) = \lambda_{max}(C)$. Therefore, the aforementioned results imply the continuity of $\varepsilon \mapsto \lambda_{max}(C+\varepsilon K)$, for any matrix K with nonnegative entries. Now, let B and H two Metzler matrices. Then, there exists $\eta \geq 0$ such that $B + \varepsilon H + \eta Id$ has nonnegative entries for all $\varepsilon \in [0, 1]$. Thus, $\varepsilon \mapsto \lambda_{max}(B + \varepsilon H + \eta Id)$ is continuous on $[0, 1]$. This yields the continuity of $\varepsilon \mapsto \lambda_{max}(\varepsilon)$ since $\lambda_{max}(B + \varepsilon H + \eta Id) = \lambda_{max}(\varepsilon) + \eta$. A proof of the formula for the derivative can be found in [21, Theorem 6.3.12]. $\square$

Using $\Lambda(m, 0) = \lambda_{max}(\overline{R} + m\overline{L})$, $B = \overline{R}$ and $H = \overline{L}$, we deduce that

$$\lim_{m \to 0} \Lambda(m, 0) = \lambda_{max}(\overline{R}) = \max_{1 \leq i \leq n} \overline{r}_i.$$

Using $\Lambda(m, \infty) = \int_0^1 \lambda_{max}(R(\tau) + mL(\tau))d\tau$, $B = R(\tau)$ and $H = L(\tau)$, we deduce that

$$\lim_{m \to 0} \Lambda(m, \infty) = \int_0^1 \lambda_{max}(R(\tau))d\tau = \int_0^1 \max_{1 \leq i \leq n}(r_i(\tau))d\tau = \chi.$$

Note that we can exchange the limit and the integral by dominated convergence, since for all $\tau \in [0, 1]$,

$$\min_i r_i(\tau) \leq \lambda_{\max}(R(\tau) + mL(\tau)) \leq \max_i r_i(\tau). \tag{89}$$

Now, using (88), $B = \overline{L}$ and $H = \overline{R}$, and the fact that $\lambda_{max}(\overline{L}) = 0$, $x = q$ and $y = 1$, we have

$$\begin{array}{rcl} \lambda_{max}(\overline{R} + m\overline{L}) & = & m\lambda_{max}\left(\frac{1}{m}\overline{R} + \overline{L}\right) \\ & = & m\left(\lambda_{max}(\overline{L}) + \frac{1}{m}1^\top \overline{R}q + o\left(\frac{1}{m}\right)\right) \\ & = & \sum_{i=1}^n q_i\overline{r}_i + o(1). \end{array}$$

Therefore,

$$\lim_{m\to\infty} \Lambda(m, 0) = \lim_{m\to\infty} \lambda_{max}(\overline{R} + m\overline{L}) = \sum_{i=1}^n q_i\overline{r}_i.$$

Similarly, using (88), $B = L(\tau)$ and $H = R(\tau)$, and the fact that $\lambda_{max}(L(\tau)) = 0$, $x = p(\tau)$ and $y = 1$, we have

$$\begin{array}{rcl} \lambda_{max}(L(\tau) + mL(\tau)) & = & m\lambda_{max}\left(\frac{1}{m}R(\tau) + L(\tau)\right) \\ & = & m\left(\lambda_{max}(L(\tau)) + \frac{1}{m}1^\top R(\tau)p(\tau) + o\left(\frac{1}{m}\right)\right) \\ & = & \sum_{i=1}^n p_i(\tau)r_i(\tau) + o(1). \end{array}$$

Therefore, we obtain

$$\begin{array}{rcl} \lim_{m\to\infty} \Lambda(m, \infty) & = & \int_0^1 \lim_{m\to\infty} \lambda_{max}(R(\tau) + mL(\tau))d\tau \\ & = & \int_0^1 \sum_{i=1}^n p_i(\tau)r_i(\tau)d\tau = \sum_{i=1}^n \overline{p_i r_i}. \end{array}$$

Note that we can also exchange the limit and the integral by using (89) and dominated convergence.

By [8, Theorem 1.1], for any diagonal matrix $S = \text{diag}(s_1, \ldots, s_n)$, and Metzler irreducible matrix K whose columns sum to 0, we have

$$\frac{d}{dm}\lambda_{max}(S + mK) \leq \lambda_{max}(K) = 0, \qquad \frac{d^2}{dm^2}\lambda_{max}(S + mK) \geq 0,$$

and the equality holds if and only if $s_1 = \ldots = s_n$.

Using $\Lambda(m,0) = \lambda_{max}(\overline{R} + m\overline{L})$, $S = \overline{R}$ and $K = \overline{L}$ we deduce that (20) is true and the equality holds if and only if $\overline{r}_1 = \ldots = \overline{r}_n$. Similarly, using $\Lambda(m,\infty) = \int_0^1 \lambda_{max}(R(\tau) + mL(\tau))d\tau$, $S = R(\tau)$ and $K = L(\tau)$ we deduce that (21) is true and the equality holds if and only if $r_1(\tau) = \ldots = r_n(\tau)$ for all τ.

Finally, we prove (22). For $T > 0$, and $t \geq 0$, let $C(t) = A(t/T) = R(t/T) + mL$ (recall that we have asusmed here that the migration is constant). Then, C is a T - periodic function, with constant off-diagonal entries. By [30, Theorem II.5.3],

$$\Lambda(m,T) \geq \lambda_{\max}(\overline{C}),$$

where

$$\overline{C} = \frac{1}{T}\int_0^T C(t)dt = \overline{R} + mL.$$

By (11), $\lambda_{\max}(\overline{C}) = \Lambda(m,0)$, which concludes the proof.

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