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Population growth on a time varying network.

Michel Benaim ^{*} Claude Lobry [†] Tewfik Sari [‡]
 Edouard Strickler [§]

November 13, 2024

Abstract

We consider a population spreading across a finite number of sites. Individuals can move from one site to the other according to a network (oriented links between the sites) that vary periodically over time. On each site, the population experiences a growth rate which is also periodically time varying. Recently, this kind of models have been extensively studied, using various technical tools to derive precise necessary and sufficient conditions on the parameters of the system (ie the local growth rate on each site, the time period and the strength of migration between the sites) for the population to grow. In the present paper, we take a completely different approach: using elementary comparison results between linear systems, we give sufficient condition for the growth of the population. This condition is easy to check and can be applied in a broad class of examples. In particular, in the case when all sites are sinks (ie, in the absence of migration, the population become extinct in each site), we prove that when our condition of growth is satisfied, the population grows when the time period is large and for values of the migration strength that are exponentially small with respect to the time period, which answers positively to a conjecture stated by Katriel in [24].

1 Introduction

An habitat where a population resides is called a "source" when, in the absence of migration, environmental conditions ensure population growth, and called a "sink" otherwise. When "sources" and "sinks" are connected in a network through which migrations occur, population growth on the network depends on various factors: the "environmental conditions" at each site of the network, the structure of the network and the intensity of migrations. All these factors depend on time, in a

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more or less random way. Determining the growth conditions of a population on a network is a central theme in ecology, both for theoretical and practical reasons (see [2, 14]) described in [7] which we quote below :

In the real world, patches of habitat vary greatly in the resources they provide for animals and in the disturbance they experience. Consequently, some populations can be regarded as ‘sources’ that produce a net surplus of animals that are available as potential colonists to other habitat patches. On the other hand, ‘sinks’ are those populations in which mortality exceeds natality and the persistence of the population depends on a regular influx of immigrants (...). There are, as yet, limited data on the relative frequency of sources and sinks in natural environments but theoretical models suggest that the relative proportions of each and the level of dispersal between them, may have a significant influence on regional population dynamics and species conservation.

The present paper is a contribution to the theoretical models mentioned above.

As early as 1997 and 1998 it was noticed by Holt [17] and Jansen and Yoshimura [23] a paradoxical effect, later called *inflation* by Gonzalez and Holt [18] :

When environmental conditions vary over time, it can happen that two habitats that are "sinks" in isolation can become "sources" when linked by migration.

This paradoxical effect has motivated theoretical studies on continuous and discrete time models, deterministic and stochastic, for instance [25, 29, 31, 11, 32] (see [3], [4] and the references therein for more information).

Recently Katriel [24] and the authors of the present paper [3, 4, 5, 6] started a detailed mathematical study of the linear continuous time model when the local growth rate on each site is periodic [24], periodic or stochastic [3, 4, 5, 6]. In [24] Katriel suggests renaming the inflation phenomenon *Dispersal Induced Growth* (DIG). Since this expression is more mathematically meaningful, we’ll use it here. In all these articles, the inflation phenomenon is characterized in terms of the dominant eigenvalue $\lambda(m, T)$ of certain positive matrices associated with the model, depending on parameters such as the migration intensity m and the period T . Thanks to mathematical results on certain symmetric positive operators [24], Tychonov’s theorem on singular perturbations of differential equations and Perron Frobenius’ theorem [3, 4, 5, 6] it is then possible to describe the behavior of $\lambda(m, T)$ according to various assumptions on the migration process (see also [27] for asymptotic development of $\lambda(m, T)$, as T goes to 0 or infinity).

In the present paper, we take a completely different approach. Instead of trying to characterize the values of the parameters m and T for which inflation occurs, in a less ambitious way, we simply look for sufficient conditions that can cause the phenomenon. This allows us to consider migration networks that are much more general, and therefore more realistic, than those imposed by the mathematical tools used previously. We consider a model where migration is described by a succession $\mathcal{N}^1, \mathcal{N}^2, \dots$ of oriented graphs on a set of sites representing an evolution over the

time of the structure of the migration network. This approach, although absolutely elementary, explains, in our view, the reasons for the inflation phenomenon. Moreover it also answers a question raised in [24, 3, 4] about the order of magnitude of the m -threshold at which the phenomenon appears.

A suitable mathematical framework for describing our model is that of dynamic networks, increasingly considered in computer science and social network modelling (see for example [8],[10]) and recently appearing in theoretical ecology (see for instance [26]). Unfortunately, in the field of population dynamics, we know of no reference directly applicable to our situation. We therefore devote Section 2 to a detailed description of our model using notations close to those of graph theory. Section 3 is the mathematical description of our central result. In Section 4 we apply our technique to solve some questions raised in [24, 3, 4, 6] and, finally, in Section 5 we show briefly how our techniques apply to random systems.

Our main result, Proposition 3, is mathematically totally elementary, and we offer a detailed demonstration of it in an appendix which, for the reader's convenience, recalls some basic results on linear differential systems that can be found in any textbook.

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2 Model and notations

2.1 The model

Sites. We denote by

$$\Pi = \{\pi_1, \pi_2, \dots, \pi_i, \dots, \pi_n\} \quad (1)$$

a set of n sites and by $x_i(t)$ the size of the population on the i -th site at time t . We denote by

$$\mathbf{x} = (x_1, \dots, x_i, \dots, x_n)$$

the vector of the x_i ' and conversely $[x]_i$ is the i -th component of \mathbf{x} . The vector \mathbf{x} is the meta-population. If $a = \pi_i$ is some site we denote $x_a(t) = x_i(t)$.

Equations of the dynamic. We are interested in the system

$$\Sigma(r_i(\cdot), \ell_{i,j}(\cdot), m, T) = \begin{cases} \frac{dx_i}{dt} = r_i(t)x_i + m \sum_{j=1}^n \ell_{ij}(t)x_j & i = 1, \dots, n \end{cases} \quad (2)$$

where

- the functions $r_i(t)$ and $\ell_{ij}(t)$, are T -periodic,
- the matrix $(m\ell_{ij}(t))$ is a migration matrix which means that $\ell_{i,j}(t) \geq 0$ and $\ell_{i,i}(t) = -\sum_{j \neq i} \ell_{j,i}$ and thus $\sum_i \ell_{ij} = 0$. This last assumption is standing all over the paper and will not be repeated.

The system $\Sigma(r_i(\cdot), \ell_{i,j}(\cdot), m, T)$ is therefore a non-autonomous linear system of period T . The term $r_i(t)$ is the growth rate on the site π_i at time t and the term $m\ell_{ij}(t)x_j$ is the migration rate from the site π_j to the site π_i at time t .

System (2) is a linear system of the form $\frac{dx}{dt} = A(t)x$ where $A(t)$ is a matrix with positive off-diagonal elements (Metzler matrix). Solutions of (2) with positive initial conditions are positive (see appendix A.2).

We discuss the influence of parameters T and m on metapopulation growth.

Link, network. A *link* on Π is an arrow pointing from one site to another. It is noted

$$\pi_j \rightarrow \pi_i$$

The link is *outgoing* from π_j and *incoming* in π_i .

A set of links on Π is a *network*, denoted \mathcal{N} . In other words the pair (Π, \mathcal{N}) is a directed graph (di-graph) in the terminology of graph theory.

Seasonality. The following assumptions are made. The interval $[0, T]$ is the union of p intervals

$$[0, T] = [T_0 = 0, T_1] \cup [T_1, T_2] \cup \dots \cup [T_{k-1}, T_k] \cup \dots \cup [T_{p-1}, T_p = T] \quad (3)$$

Hypothesis 1 All functions $r_i(t)$ and $\ell_{ij}(t)$ are **constant** on intervals $]T_{k-1}, T_k[$ and we note

$$r_i(t) = r_i^k \quad \ell_{ij}(t) = \ell_{ij}^k \quad \text{if } t \in]T_{k-1}, T_k[\quad (4)$$

The interval $[T_{k-1}, T_k]$ is the k -th "season" and $T(t_k - t_{k-1})$ is its duration. When there is no seasonality (there is only one season), the system is said to be *static*.

The upper subscripts in r_i^k, ℓ_{ij}^k therefore indicate the season when these parameters are effective. With these notations and an obvious interpretation in terms of "switched systems" (see [3]), we can rewrite the system (2) as

$$\Sigma(r_i^k, \ell_{i,j}^k, m, T) = \begin{cases} \frac{dx_i}{dt} = r_i^k x_i + m \sum_{j=1}^n \ell_{ij}^k x_j & t \in [T_{k-1}, T_k[\\ i = 1, \dots, n & k = 1, \dots, p \end{cases} \quad (5)$$

which means that after having integrated the system (5) up to time T_k one takes $x_i(T_k)$; $i = 1 \cdot \dots \cdot n$ as initial conditions for an integration on the interval $[T_k, T_{k+1}]$.

Migrations on time varying networks.

Hypothesis 2 It is assumed that all ℓ_{ij}^k with $i \neq j$ take only 0 or 1 values.

This hypothesis, which means that if there is migration between to sites its rate is always the same, is rather restrictive. Actually we make it in order to keep the things as simple as possible but it can be relaxed (see subsection 3.1).

The ℓ_{ij}^k matrix is therefore equivalent to a \mathcal{N}^k network on Π , by

$$\pi_j \rightarrow \pi_i \in \mathcal{N}^k \iff \ell_{ij}^k = 1 \quad (6)$$

The \mathcal{N}^k network is the migration network of the k -th season. The system (5) is associated with the sequence

$$\mathcal{N}^{[1..p]} = \{ \mathcal{N}^1, \dots, \mathcal{N}^k, \dots, \mathcal{N}^p \} \quad (7)$$

of p networks. More generally a sequence, finite or not

$$\mathcal{N}^{[1..k..]} = \{ \mathcal{N}^1, \dots, \mathcal{N}^k, \dots \} \quad (8)$$

of networks is called a *time varying (or dynamic) network*; the underlying network of system (5) is a p -periodic network.

Example. In the paper [26] *A periodic Markov model to formalize animal migration on a network*, A. Költz and al. consider migration networks that change with seasons. In Figure 1 we see on the left a scheme extracted from Figure 1 of the paper [26]. It represents four sites where birds are living. In summer (season 1) there is no migration (and most of the population is on site 1), in autumn there is migration to sites 3 and 4 through site 2, in winter (season 3) no migration and in spring (season four) migration back from sites 3 and 4 to site 1. On the right of our Figure 1 one sees the representation of this dynamic network in the style that we use in our paper.

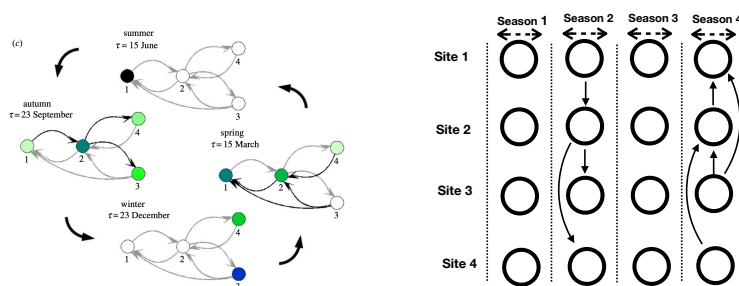


Figure 1: A migration network from [26] .

2.2 Terminology : paths, circuits.

Path A simple path (without loops) in a network \mathcal{N} is sequence of links γ_i , all different, such that the origin of γ_{i+1} is the extremity of γ_i , never returning to a previously visited site. Precisely :

A simple path $a\Gamma b$ of length $l(a\Gamma b)$ of the network \mathcal{N} is a sequence

$$a\Gamma b = \{a = \pi_{i(0)} \rightarrow \pi_{i(1)} \rightarrow \dots \rightarrow \pi_{i(j)} \rightarrow \dots \rightarrow \pi_{i(l)} = b\} \quad (9)$$

of all **different sites** $\pi_{i(j)}$ of Π linked by $\pi_{i(j-1)} \rightarrow \pi_{i(j)}$. The index l is the length $l(a\Gamma b)$ of the path $a\Gamma b$.

If there exists a path $\pi_j\Gamma\pi_i$ the site π_j is said "upstream" of π_i and π_i is said "downstream" of π_j .

Time varying path. Let $\mathcal{N}^{[1\dots k\dots]} = \{\mathcal{N}^1, \dots, \mathcal{N}^k, \dots\}$ be a time varying network.

A *simple time varying path* of $\mathcal{N}^{[1 \dots k \dots]}$ is a sequence

$$a_0 \Gamma^1 a_1 \Gamma^2 a_2 \dots a_{k-1} \Gamma^k a_k \dots \quad (10)$$

where each $\dots a_{k-1} \Gamma^k a_k$ is a simple path of \mathcal{N}^k .

T-simple-circuit. A T-simple-circuit (T-circuit in short) of the periodic time varying network $\mathcal{N}^{[1 \dots p]}$ of period p is a time varying simple path

$$a_0 \Gamma^1 a_1 \Gamma^2 a_2 \dots a_{k-1} \Gamma^k a_k \dots a_{p-1} \Gamma^p a_p \quad (11)$$

such that $a_p = a_0$.

Figure 2 shows an example of a time varying network (5 sites and 3 seasons) with a T-circuit issued from site 3 in red.

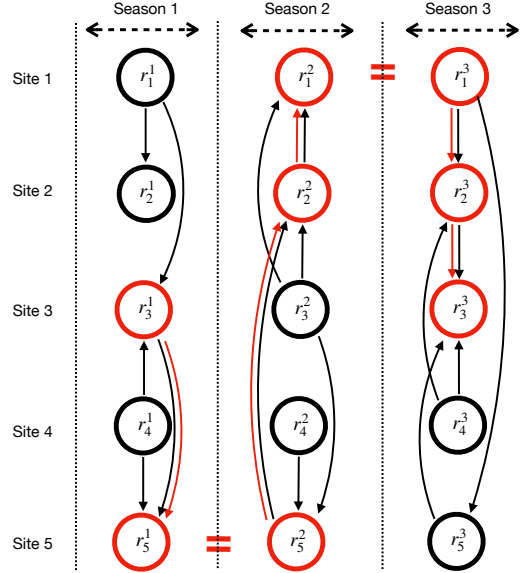


Figure 2: In red a T-circuit in a time varying network (black arrows).

3 Main results

3.1 Sources and sinks in a time varying network.

Consider the T-periodic switched system (5) with the underlying time varying network

$$\mathcal{N}^{[1 \dots p]} = \{ \mathcal{N}^1, \dots, \mathcal{N}^k, \dots, \mathcal{N}^p \} \quad (12)$$

One says that, in absence of migration, a site π_i is a "source" if $\sum_{k=1}^p r_i^k(t_k - t_{k-1}) > 0$ which is equivalent to say that the solution of the T-periodic switched system

$$\frac{dx_i}{dt} = r_i^k x_i \quad t \in [Tt_{k-1}, Tt_k[\quad x_i(0) = x_o > 0 \quad (13)$$

tends to infinity as t tends to infinity. In the opposite case the site is called a "sink".

Remark 1 If we recall the definition of $r_i(t)$ (see hypothesis 1) as $r_i(t) = r_i^k$ if $t \in]Tt_{k-1}, Tt_k[$ the system (13) reads

$$\frac{dx_i}{dt} = r_i(t)x_i \quad x_i(0) = x_o > 0$$

and the condition $\sum_{k=1}^p r_i^k(t_k - t_{k-1}) > 0$ is the same as $\frac{1}{T} \int_0^T r_i(t)dt > 0$ which is the time average growth rate on the site π_i .

We extend the definition of "source" and "sink" to the whole system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ by saying that it is a "source" when, given an initial condition $x(0) > 0$ the corresponding total population $S(t, m, T, x(0)) = \sum_{i=1}^n x_i(t, m, T, x(0))$ tends to infinity when t tends to infinity. Since (due to linearity) the fact that $S(t, m, T, x(0))$ tends to infinity is independent of the positive initial condition $x(0)$ we omit it in the following.

Definition 1 Let $S(t, m, T)$ be the total population of $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. The $m(T)$ -threshold of $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ is the number

$$m^*(T) = \inf \{m : S(t, m, T) \rightarrow \infty\} \quad (14)$$

The DIG phenomenon refers to the fact that the total population growth rate can be higher than all the mean growth rates of the isolated sites. In particular we adopt the following definition from [24].

Definition 2 DIG [24]. We consider system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ for which we assume that every site is a "sink" (i.e. $\forall i : \sum_{k=1}^p r_i^k(t_k - t_{k-1}) < 0$). One says that there is DIG (Dispersal Induced Growth) for $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ if there exists values m, T such that for these values of the parameters, the whole system is a "source" (i.e. $S(t) \rightarrow \infty$) or, in other words, if there is some T such that $m^*(T) < \infty$

In [24] Katriel introduced the "growth index" :

Definition 3 Growth-index of the system.

The growth index of the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ is the number

$$\chi = \sum_{k=1}^p \left(\max_{i=1}^n r_i^k \right) (t_k - t_{k-1}) = \frac{1}{T} \int_0^T \max_{i=1}^n r_i(t) dt \quad (15)$$

Then Katriel proved the following

Proposition 1 - Necessary condition for DIG (Katriel [24]). *A necessary condition for the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ to be a "source" for some m, T , is that its growth index χ be positive. In other words, a necessary condition for the existence of DIG is that the growth index χ be positive.*

Proof. One has

$$\frac{dS}{dt} = \sum_{i=1}^n r_i(t)x_i(t) + \sum_{j=1}^n \ell_{i,j}(t)x_j(t) = \sum_{i=1}^n r_i(t)x_i(t) \leq \sum_{i=1}^n (\max_{i=1}^n r_i(t))x_i(t) = (\max_{i=1}^n r_i(t))S(t)$$

Let $\rho(t) = \max_{i=1}^n r_i(t)$, one has $\frac{dS}{dt} \leq \rho(t)S(t)$ which implies $S(T) \leq e^{\int_0^T \rho(s)ds}$ which, by definition of χ is $S(T) \leq e^{T\chi}S(0)$. Hence, if $\chi < 0$ the total population tends to 0 and the system is not a "source". \square

We introduce now the *growth of a T-circuit* which is the growth index of the system reduced on the T-circuit. Precisely

Definition 4 Growth index of a simple T-circuit.

Let

$$\mathcal{C} = a_0\Gamma^1 a_1\Gamma^2 a_2 \cdots a_{k-1}\Gamma^k a^k \cdots a_{p-1}\Gamma^p a_0 \quad (16)$$

with

$$a_{k-1}\Gamma^k a_k = \left\{ a_{k-1} = \pi_{i^k(0)} \rightarrow \pi_{i^k(1)} \rightarrow \cdots \pi_{i^k(j)} \rightarrow \pi_{i^k(l^k)} = a_k \right\}$$

be a simple T-circuit defined on the underlying time varying network of the system (5). We call growth index of the circuit \mathcal{C} the number

$$\chi^{\mathcal{C}} = \sum_{k=1}^p (t_k - t_{k-1}) \max_{\pi_i \in \Gamma^k} r_i^k \quad (17)$$

Note that the growth index of $\chi^{\mathcal{C}}$ of a T-circuit is always smaller than χ since $\max_{\pi_i \in \Gamma^k} r_i^k < \max_{i=1..n} r_i^k$.

Proposition 2 - Sufficient condition for DIG. *Consider the T-periodic system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. Assume that there exists a T-circuit \mathcal{C} of the underlying time varying network of $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ such that $\chi^{\mathcal{C}} > 0$. Then there exist T^* and $0 < a(T^*) < b(T^*)$ such that :*

$$T \geq T^* \quad m \in [a(T^*), b(T^*)] \implies \Sigma(r_i^k, \ell_{i,j}^k, m, T) \text{ is a source.}$$

Which we can rephrase as : *If $\chi^{\mathcal{C}} > 0$ we're certain that for T large enough and for m neither too small nor too large, the system is a source.*

The proof of this proposition relies on the minoration of the growth given in the following proposition.

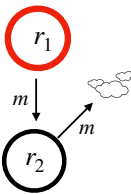
Proposition 3 Consider the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ on the underlying network (12). Consider the T -circuit \mathcal{C} defined by (80) and its growth index $\chi^{\mathcal{C}}$. Then there exist T^* and constants $C > 0$ and $\mu > 0$ (independent of m) such that

$$T > T^* \implies x_{i^1(0)}(T) \geq Cm^L e^{T(\chi^{\mathcal{C}} - \mu \times m)} x_{i^1(0)}(0) \quad (18)$$

where L is the total length of the circuit.

So, after one period, the value of the population size at the beginning site of the T -circuit is minorized by $Cm^L e^{T(\chi^{\mathcal{C}} - \mu \times m)}$ times the initial value. If this number is greater than 1 the size of the population is increasing. The proof of this proposition, which is elementary but a bit intricate, is given in appendix B. We give here the idea behind the proof.

- We isolate the T -circuit \mathcal{C} from the whole dynamic network by cutting all the links incoming from outside of \mathcal{C} and we add to each site of \mathcal{C} outgoing links *to the clouds* such that the total number of links leaving each site is $n - 1$; each link to the clouds can be considered as an added mortality rate m .
- This new dynamic network defines a new system whose solutions minorize those of $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. This is straightforward since cutting incoming links suppresses positive terms in the right hand of (5) and the addition of outgoing links adds negative ones.
- On each path Γ^k of the T -circuit the maximum r^k of the growth rates is attained some dominant site $\pi_{i^k(d)}$ and it is possible (lemma 1) to prove by direct computation that for large enough T , for all the sites which are down stream of $\pi_{i^k(d)}$ the growth rate is r^k . Actually this is straightforward in the case of two sites. In this case the system is :

$$\begin{aligned} \frac{dx_1}{dt} &= (r_1 - m)x_1 \\ \frac{dx_2}{dt} &= mx_1 + (r_2 - m)x_2 \end{aligned}$$


Integration of the first equation gives $x_1(T) = e^{T(r_1 - m)} x_1(0)$ and the second one (see appendix A.1)

$$x_2(T) = e^{T(r_2 - m)} \left\{ x_2(0) + \int_0^T e^{-s(r_2 - m)} m e^{s(r_1 - m)} x_1(0) ds \right\} \geq e^{T(r_2 - m)} \int_0^T e^{s(r_1 - r_2)} ds m x_1(0)$$

$$x_2(T) \geq e^{T(r_2 - m)} \frac{1}{r_1 - r_2} \left[e^{T(r_1 - r_2)} - 1 \right] m x_1(0) = e^{T(r_1 - m)} \frac{1 - e^{T(r_2 - r_1)}}{r_1 - r_2} m x_1(0)$$

Since $r_1 > r_2$ the term $e^{T(r_2-r_1)}$ tends to 0 when T tends to ∞ and by the way is smaller than $1/2$ for T large enough and thus

$$\exists T^* \text{ such that } T \geq T^* \implies x_2(T) > \frac{1}{r_1 - r_2} m e^{T(r_1-m)} x_1(0)$$

which looks like (18) with $\mu = 1$. Proving the general case is just a matter of notations.

- The iteration of this inequality along the paths of the T-circuit gives rise to (18).

Relaxation of hypothesis 2

Consider the system

$$\Sigma(r_i^k, \alpha_i^k, \ell_{i,j}^k, m, T) = \begin{cases} \frac{dx_i}{dt} = (r_i^k - m\alpha_i^k)x_i + m \sum_{j=1}^n \ell_{i,j}^k x_j & t \in [Tt_{k-1}, Tt_k[\\ i = 1, \dots, n & k = 1, \dots, p & \alpha_i^k \geq 0 \end{cases} \quad (19)$$

where the growth rate on each site decreases linearly with the parameter m . It is clear that the system

$$\Sigma(\rho_i^k, \alpha, \ell_{i,j}^k, m, T) = \begin{cases} \frac{dx_i}{dt} = (r_i^k - m\alpha)x_i + m \sum_{j=1}^n \ell_{i,j}^k x_j & t \in [Tt_{k-1}, Tt_k[\\ i = 1, \dots, n & k = 1, \dots, p & \alpha \geq 0 \end{cases} \quad (20)$$

with $\alpha = \max_{i,k} \alpha_i^k$ minorizes the system $\Sigma(r_i^k, \alpha_i^k, \ell_{i,j}^k, m, T)$. So proposition 3 is still true for this system with a new μ equal to $\mu + \alpha$.

Now we do not assume that $\ell_{i,j} \in \{0, 1\}$ in system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. Let

$$\ell = \min_{\ell_{i,j} > 0} \ell_{i,j} \quad \beta_{i,j} = 1 \text{ if } \ell_{i,j} > 0, \beta_{i,j} = 0 \text{ otherwise.}$$

For $i \neq j$ we have $m\ell_{i,j} \geq m\ell\beta_{i,j}$ and the system

$$\Sigma(r_i^k, \alpha_i^k, \beta_{i,j}^k, m, T) = \begin{cases} \frac{dx_i}{dt} = (r_i^k - m\alpha_i^k)x_i + m\ell \sum_{j=1}^n \beta_{i,j}^k x_j & t \in [Tt_{k-1}, Tt_k[\\ i = 1, \dots, n & k = 1, \dots, p \end{cases} \quad (21)$$

with $\beta_{i,i} = -\sum_{j \neq i} \beta_{i,j}^k$ and $\alpha_i^k = \sum_{i \neq j} (\ell_{i,j}^k - \ell)$, to which we can apply proposition 3 minorizes, the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. Thus we can relax hypothesis 2.

3.2 The shape of the minimizing function.

Let us see now how proposition 2 follows immediately from proposition 3. Indeed from (18), there exist T^* and C and μ such that

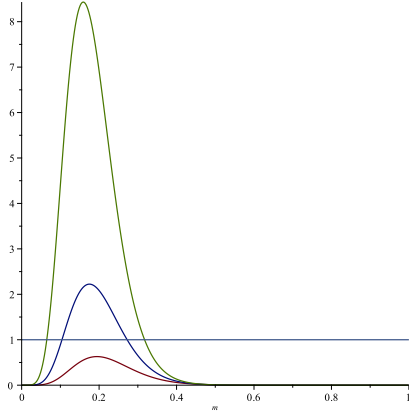
$$T > T^* \implies x_{i_0}(T) \geq C m^L e^{T(\chi^{\mathcal{G}} - \mu \times m)} x_{i_0}(0)$$

Thus $Cm^L e^{T(\chi^{\mathcal{C}} - \mu \times m)} > 1$ implies that the sequence $j \in \mathbb{N} \mapsto x_{i_0^1}(j \times T)$ tends to infinity which means that $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ is a "source".

Let us denote :

$$H(m, T) \stackrel{\text{def}}{=} m^L e^{T(\chi^{\mathcal{C}} - (n-1) \times m)}$$

the minimizing function appearing in (18). From elementary calculus it follows that when $\chi^{\mathcal{C}} > 0$

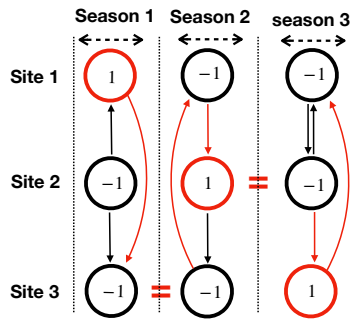


- $H(m, T)$ is positive
- the function $t \mapsto H(m, T)$ is increasing,
- the function $m \mapsto H(m, T)$ is increasing, passes through a maximum $M(T)$ and then decreases to 0,
- moreover $M(T) \rightarrow \infty$ as $T \rightarrow \infty$

(Above the graphs of the functions $m \mapsto H(m, T) = m^7 e^{T(2-4m)}$ for $T = 9$ (red), $T = 10$ (blue), $T = 11$ (green).)

Thus, for T large enough, there is an interval $[a(T), b(T)]$ where $H(m, T) > 1$. which proves the proposition 2.

3.3 An exemple.



Consider the system Σ defined by the scheme on the left and assume that each season is of duration $1/3$. Each isolated site is a "sink" (one sequence with growth rate equal to 1 against two with a decay rate of -1). Consider the T-circuit \mathcal{C} shown in red, that is :

$$\mathcal{C} = |1 \xrightarrow{\text{season1}} 3| |3 \xrightarrow{\text{season2}} 1 \xrightarrow{\text{season3}} 2| |2 \xrightarrow{\text{season3}} 3 \xrightarrow{\text{season1}} 1|$$

Since in each season the growth rate of the dominant site is $+1$ the growth index of the circuit is $\frac{1}{3} + \frac{1}{3} + \frac{1}{3} = 1$ and thus is strictly positive. From proposition 2 there is possibility of DIG. We have simulated the system Σ from the initial condition $(1, 1, 1)$ in the case $T = 24$ and increasing values of m . On figure 3 one sees the logarithm of the population size on each site as a function of time.

- For $m = 0$ all the sites are disconnected. Unsurprisingly, since we've taken the logarithm, growth at site 1 is a straight line with a slope of $+1$ for $1/3$ of

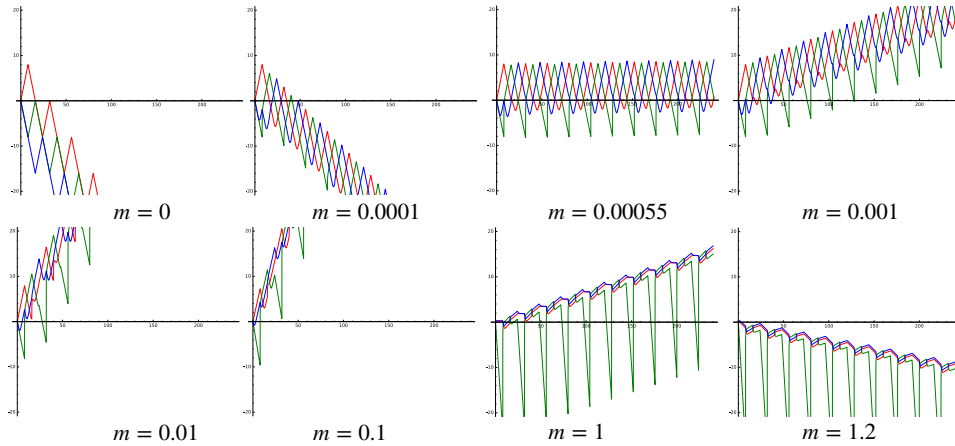


Figure 3: Simulations of Σ in the case $T = 28$. One sees the logarithm of the population on site 1 (in red), on site 2 (in green) and site 3 (in blue)

the period, followed by a slope of -1 for the remaining two-thirds. The same occurs with the two other sites with a shift in the growing period.

- For $m = 0.0001$ the total population is still decaying, while for $m = 0.001$ it is growing with a threshold around $m = 0.00055$.
- The rate of growth increases for $m = 0.01$ and $m = 0.1$ and decreases later for $m = 1$
- For $m = 1.2$ one sees that the system is again a "sink".

An interesting point in this example is that the first value for which one observes an increase of the population is around 0.00055 which is rather small compared to the parameters. This is actually a general feature that we explain in the next paragraph.

3.4 The m -threshold is exponentially small with respect to T .

Let us define $m^*(T)$ as the first value of m such that, for a given T , the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ is a source. Precisely

$$m^*(T) = \inf_m \{m \text{ such that } \Sigma(r_i^k, \ell_{i,j}^k, m, T) \text{ is a source}\} \quad (22)$$

Proposition 4 Consider the T -periodic system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$. Assume that there exists a T -circuit \mathcal{C} of the underlying time varying network of such that $\chi^{\mathcal{C}} > 0$. Then there exist T^* and $\alpha > 0$ such that

$$T > T^* \implies m^*(T) \leq e^{-\alpha T}$$

Proof. From proposition 2 we know that $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ is growing provided

$$H(m, T) = Cm^L e^{T(\chi^\ell - \mu m)} > 1$$

When $m < \frac{\chi^c}{2\mu}$ we have $H(m, T) > Cm^L e^{T\frac{\chi^\ell}{2}}$ and thus

$$Cm^L e^{T\frac{\chi^\ell}{2}} > 1 \implies \Sigma(r_i^k, \ell_{i,j}^k, m, T) \text{ is growing}$$

One easily check that

$$m \geq e^{-T\frac{\chi^\ell}{2LC^{1/L}}} \implies Cm^L e^{T\frac{\chi^\ell}{2}} > 1$$

which proves the proposition with $\alpha = \frac{\chi^\ell}{2LC^{1/L}}$. \square

This proposition says that the m threshold for DIG is exponentially small with respect to T . It answers positively to the question asked in [24, 4].

4 Some applications

4.1 The case of irreducible migration matrices

In [4] we considered the system

$$\Sigma(r_i(\cdot), \ell_{i,j}(\cdot), m, T) \quad \frac{dx_i}{dt} = r_i(t/T)x_i + m \sum_{j=1}^n \ell_{ij}(t/T)x_j \quad i = 1, \dots, n$$

where $r_i(\tau)$ and $\ell_{ij}(\tau)$ were piecewise continuous functions of period 1, in the case where the migration matrix $M(\tau) = (\ell_{ij}(\tau))$ is irreducible for every value of τ . We proved (as a consequence of Perron-Frobenius theorem) that the Lyapunov exponent

$$\Lambda(m, T)[x_i] \stackrel{\text{def}}{=} \lim_{t \rightarrow \infty} \frac{1}{t} \log(x_i(t))$$

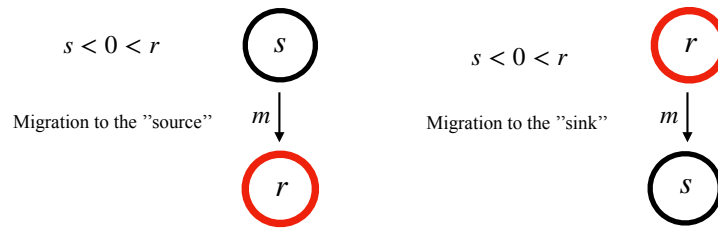
is actually independent of the site i and, by the way, is denoted $\Lambda(m, T)$. The description of the growth of the system in terms of $\Lambda(m, T)$ is more precise than the one we propose here by just minorizing the growth but relies on the stronger assumption that $M(\tau)$ is irreducible. Nevertheless, our proposition 4 answers positively (at least in the piecewise constant case) to a question that was already asked in [24, 4] : *Assume that the growth index χ is positive. Is the growth threshold exponentially small with respect to T ?* Indeed, if for any τ the migration matrix is irreducible, during any season any site is connected to every site by a patch. Then, starting from a dominant site at time 0 there exists a simple path during season 1 that connects it to one of the dominant sites of season 2, then, during season 2 there exists a simple path that connects it to a dominant site of season 3, and so on until the last season when we return to the starting site; this defines a T-circuit whose growth index is precisely χ which allows us to apply the proposition 4 which gives a positive answer to the conjecture.

4.2 Large migration rate.

As we have seen (see subsection 3.2) the minimizing function tends to 0 as T tends to ∞ but we can't draw any conclusions about the system's growth, since it's a minorization. Thus it is of interest to have a better understanding of what happens when the migration rate tends to infinity.

"Dead end-path"..

Consider the two static systems defined by the schemes below



In the case of migration to the "sink" we have the system

$$\frac{dx_1}{dt} = (r - m)x_1 \quad \frac{dx_2}{dt} = mx_1 + sx_2 \quad s < 0 < r \quad (23)$$

The system is triangular and the two eigenvalues are $r - m$ and s . So one sees that, as soon as $m > r$, the population is decaying in both sites. In the case of migration to the "source" the picture is completely different. We have the system

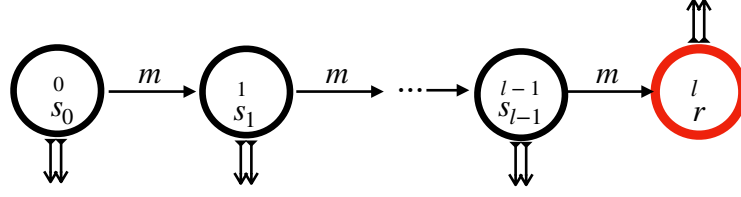
$$\frac{dx_1}{dt} = (s - m)x_1 \quad \frac{dx_2}{dt} = mx_1 + rx_2 \quad s < 0 < r \quad (24)$$

whose solutions are

$$x_1(t) = e^{t(s-m)}x_1(0) \quad x_2(t) = e^{tr} \left\{ x_2(0) + \frac{m}{r+m-s} \left(1 - e^{t(s-r-m)} \right) x_1(0) \right\} \quad (25)$$

and we see that even in the case where $x_1(0) = 0$, provided $x_2(0) > 0$, the population grows in the source site at the rate r for all the positive values of m . In fact, this is obvious without even looking at the equations: as soon as the population is non-zero at site 2, *since there is no emigration from this site*, there is growth at rate r .

This remark can be generalized as follows. Let us consider the system defined on a simple path like the one below:



where $s_i < 0 < r$. The double arrow directed upward symbolizes a positive growth while directed downward it symbolizes decay. We call such a simple path which ends by a "trap" a "dead-end path" (the concept of "trap" is important in compartmental analysis, see for instance [22]). In this case we prove the following

Proposition 5 Consider the system

$$\begin{aligned}
 \frac{dx_0}{dt} &= (s_0 - m)x_0 \\
 \frac{dx_i}{dt} &= m_{i-1}x_{i-1} + (s_i - m)x_i \quad i = 1 \cdots l-1 \\
 \frac{dx_l}{dt} &= m_{l-1}x_{l-1} + rx_l
 \end{aligned} \tag{26}$$

For every $m > 0$, as soon as one of the $x_j(0)$'s is strictly positive the population $x_l(t)$ on the last site is growing at rate r .

Proof If the initial condition $x_l(0) > 0$ we have $x_l(t) \geq x_l(0)e^{tr}$ which grows at the rate r . If it is not the case, $x_j > 0$ for some j and since the migration rate m is strictly positive we are sure that as soon as $t^* > 0$, $x_l(t^*) > 0$ and we can take it as initial condition in the last equation. \square

Migratory birds example.

Thus, in the presence of a dead-end simple path we have a minoration of the growth which is potentially positive even when $m \rightarrow +\infty$. The larger m , the greatest the inflation effect. The possibility of having dead-end paths in a time varying network is not exceptional in natural networks. Consider for instance seasonally migrating species such as storks. It can be idealized by the following model. Let's consider two sites, say $\pi_1 =$ for north, π_2 for south and let's consider two seasons, say winter and summer. Assume that in winter the south is a "source" and the north is a "sink" while in summer the opposite is the case.

On the figure 4, on the left, we indicate a migration from north to south in winter and vice versa in summer which could be called a "migration to the source". The corresponding equations are

$$\text{Winter} \begin{cases} \frac{dx_1}{dt} = (r_1^1 - m)x_1 \\ \frac{dx_2}{dt} = mx_1 + r_2^1x_2 \end{cases} \quad \text{Summer} \begin{cases} \frac{dx_1}{dt} = r_1^2x_1 + mx_2 \\ \frac{dx_2}{dt} = (r_2^2 - m)x_2 \end{cases} \tag{27}$$

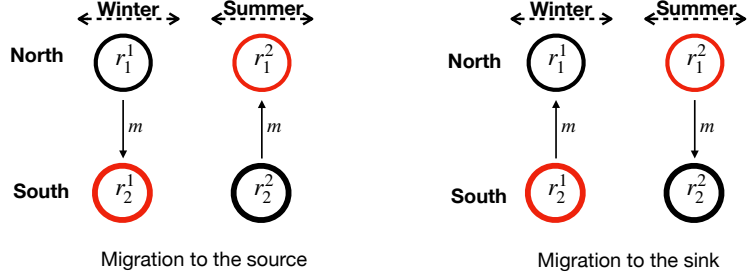


Figure 4: Two possibilities for migration.

where $r_1^1 < 0 < r_2^1$ and $r_2^2 < 0 < r_1^2$. In this example both paths "north" → "south" in winter and "south" → "north" are dead-end paths and $\mathcal{C} = \text{"north" } \rightarrow \text{"south" } \rightarrow \text{"north"}$ is a circuit such that $\chi^{\mathcal{C}} > 0$. From proposition 2 we expect that the whole system is a source with T large enough and m not too small nor too large. But we can say more, since the two "migration to the source" are "dead-end" paths in the sense of the previous remark we can drop the "m not too large" of proposition 2 and claim that as soon as t and m are large enough the system is a source and, moreover, the larger m , the higher the growth rate.

For this very simple system it is possible (using formal calculus software) to compute explicitly the growth. Indeed, let $r_1^1 = r_2^2 = s$, $r_2^1 = r_1^2 = 1$ with $s < 0$, and assume that the two seasons are of equal length $\frac{T}{2}$ and let

$$A^1 = \begin{pmatrix} s-m & 0 \\ m & 1 \end{pmatrix} \quad A^2 = \begin{pmatrix} 1 & m \\ 0 & s-m \end{pmatrix} \quad (28)$$

the matrix of the linear system operating during winter and during summer respectively. After winter the population is given by

$$x(T/2) = e^{\frac{T}{2} \cdot A^1} x(0)$$

and after summer by

$$x(T) = e^{\frac{T}{2} \cdot A^2} x(T/2) = e^{\frac{T}{2} \cdot A^2} e^{\frac{T}{2} \cdot A^1} x(0)$$

The matrix

$$M(m, T) \stackrel{\text{def}}{=} e^{\frac{T}{2} \cdot A^2} e^{\frac{T}{2} \cdot A^1}$$

(called the monodromy matrix of the periodic system) expresses the growth after one period. Let $\lambda(m, T)$ be its dominant eigenvalue (i.e. with the greatest modulus). One knows that the system (27) is a source if $\lambda(m, T) > 1$ and a sink if $\lambda(m, T) < 1$. Moreover one knows that $\frac{\log(\lambda(m, T))}{T}$ is the asymptotic growth rate (i.e. the Lyapunov exponent) of $x_1(t)$ and $x_2(t)$:

$$\frac{\log(\lambda(m, T))}{T} = \lim_{t \rightarrow \infty} \frac{\log(x_1(t))}{T} = \lim_{t \rightarrow \infty} \frac{\log(x_2(t))}{T}$$

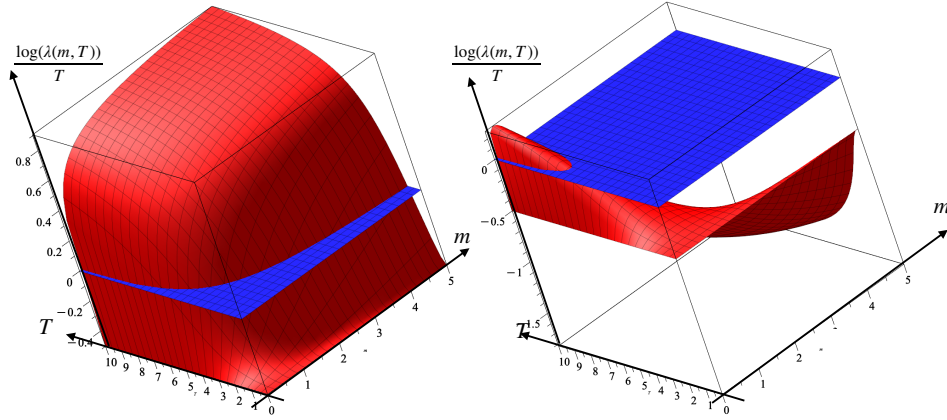


Figure 5: On the left : growth of system (27). On the right growth of system (??).
Parameters : $r_1^1 = r_2^2 = -2$; $r_2^1 = r_1^2 = 1$

In principle it is not difficult to compute $M(m, T)$ and its eigenvalues but it is a bit intricate and it is better to ask to some software (here we used Maple) to compute them for us. Maple says that the dominant eigenvalue is given by

$$\lambda(m, T) = \frac{\left(A + \sqrt{(B + C + D + E)m^2}\right)}{2(m - s + 1)^2}$$

$$A = -4\left(-\frac{s}{2} + m + \frac{1}{2}\right)(s - 1)e^{-\frac{T(-1+m-s)}{2}} + m^2e^T + m^2e^{-T(m-s)}$$

$$B = -8\left(-\frac{s}{2} + m + \frac{1}{2}\right)(s - 1)e^{-\frac{T(-1+3m-3s)}{2}}$$

$$C = \left(-2m^2 + (16s - 16)m - 8(s - 1)^2\right)e^{-T(-1+m-s)}$$

$$D = -8\left(-\frac{s}{2} + m + \frac{1}{2}\right)(s - 1)e^{-\frac{T(m-s-3)}{2}}$$

$$E = (e^{-2T(m-s)} + e^{2T})m^2$$

This is a complicated expression but we can see that when m is large one can neglect all the terms which have e^{-Tm} in factor and it remains only

$$\lambda(m, T) \approx \frac{m^2e^T}{(1 + m - s)^2}$$

which is easily understood. But we can also ask to Maple to plot the exact graph of $(m, T) \mapsto \frac{\log(\lambda(m, T))}{T}$ which is done on figure 5-left. So the faster is the migration from the "sink" to the "source" the better will be the growth.

It is interesting to look now to the same system but with the direction of migrations reversed as it is shown on figure 4-right.

For this system $\mathcal{C} = \text{"north"} \rightarrow \text{"south"} \rightarrow \text{"north"}$ is a circuit such that $\chi^{\mathcal{C}} > 0$ (actually it has the same growth index than previously). Thus, proposition 2 applies, which is somewhat counter intuitive. How is it possible to have growth when the population systematically flees out the "source" site to go to the "sink" site? Like previously we can compute the monodromy matrix of this system and ask to Maple the expression of its dominant eigenvalue $\mu(m, T)$ (that we do not show here) and the graph of $(m, T) \mapsto \frac{\log(\lambda(m, T))}{T}$ which is shown on the right of figure 5.

This figure compares the Lyapunov exponents for the "migration towards the source" and the "migration towards the sink" for the same parameter value r_j^i . We can see that the two plots are very different. In the case of "migration towards the source", except for the small blue region corresponding to low migration rates or to a short period, the growth rates are positive and increasing with m and T . On the contrary, in the case of "migration towards the sink", the growth rate is essentially negative, which is expected, except for a small region corresponding to very large values of T and very small values of m , which is not intuitive but was predicted by proposition 2.

4.3 Minimizing is not characterizing.

As said in proposition 2, the existence of a circuit with positive growth index is a **sufficient** condition for the existence of DIG. Here we show that this condition is far from being necessary.

4.4 Two examples.

3 sites, 2 seasons.

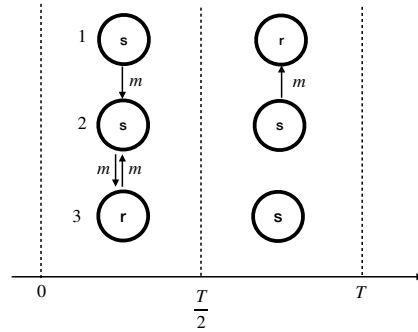
Consider the system Σ defined by the scheme on the right. It is the T-periodic system $\Sigma(r, s, m, T)$ defined by

$$\frac{dx}{dt} = A_1 x \quad \text{if } t \in [0, \frac{T}{2}[$$

$$\frac{dx}{dt} = A_2 x \quad \text{if } t \in [\frac{T}{2}, T[$$

with

$$A_1 = \begin{pmatrix} s-m & 0 & 0 \\ m & s-m & m \\ 0 & m & r-m \end{pmatrix} \quad A_2 = \begin{pmatrix} r & m & 0 \\ 0 & s-m & 0 \\ 0 & 0 & s \end{pmatrix} \quad (29)$$



We assume that $s < -r < 0$. With this condition it is easily seen that, in the absence of migration, each site is a "sink". As one can see easily, the only T-circuit of this system is the circuit $\mathcal{C} = |1 \rightarrow 2| |2 \rightarrow 1|$ whose growth index $\chi^{\mathcal{C}}$ is $\frac{s}{2} + \frac{r}{2} < 0$. so the proposition 2 does not apply and we cannot conclude to the existence of DIG.

However, there are T and m such that the system is growing, as we will now show. Define

$$M(r, s, m, T) = e^{TA_1} e^{TA_2} \quad (30)$$

As we know the solution $x(T)$ of $\Sigma(r, s, m, T)$ at time T , from the initial condition x_0 is given by

$$x(T) = M(r, s, m, T)x_0 \quad (31)$$

Now we ask to Maple to compute the matrix $M(r, s, m, T)$. With our computer Maple is not able to compute the eigenvalues of $M(r, s, m, T)$ but fortunately it is sufficient to consider its entry $[M(r, s, m, T)]_{1,1}$ (first line, first column). Indeed we have $x_1(T) \geq [M(r, s, m, T)]_{1,1}x_1(0)$ and by the way $x_1(mT) \geq [M(r, s, m, T)]_{1,1}^m x_1(0)$. Hence if $[M(r, s, m, T)]_{1,1} > 1$ the system is growing. From Maple we obtain

$$[M(r, s, m, T)]_{1,1} = \frac{A + B + C + D + 2E}{2\Delta(m-s+1)(s-1+\Delta)}$$

with $\Delta = \sqrt{4m^2 + (s-1)^2}$ and

$$A = ((1-s)^2 + (1-s)\Delta + 2m^2) e^{-\frac{T(-3+2m-s+\Delta)}{4}}$$

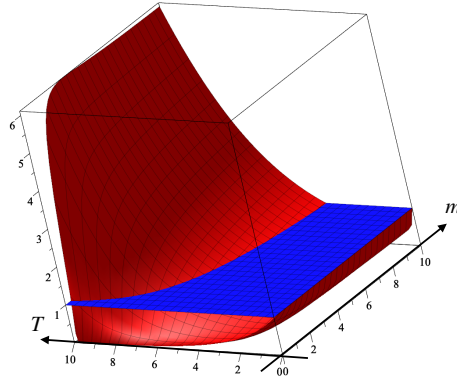
$$B = ((1-s)^2 - (1-s)\Delta + 2m^2) e^{\frac{T(-4m+3s+1+\Delta)}{4}}$$

$$C = (-(1-s)^2 - (1-s)\Delta - 2m^2) e^{-\frac{T(4m-3s-1+\Delta)}{4}}$$

$$D = (-(1-s)^2 + (1-s)\Delta - 2m^2) e^{\frac{T(3-2m+s+\Delta)}{4}}$$

$$E = -\left((m-2s+2)e^{-\frac{T}{2}(m-s-1)} + e^{-T(m-s)}(s-1)\right)\Delta$$

We do not try to simplify nor analyse directly this expression but ask to Maple to draw for us the graph of $(m, T) \mapsto [M(r, s, m, T)]_{1,1}$. On the right, one sees the result in the case $r = 1$ and $s = -2$. As we observe, for sufficiently large values of m and T (for instance $(5, 10)$) the entry $[M(r, s, m, T)]_{1,1}$ is strictly greater than 1. Thus there is DIG which is not predicted by proposition 2.



If one looks carefully to this example one can see that the T-circuit (which is not a simple circuit since it has a loop) $|1 \rightarrow 2 \rightarrow 3 \rightarrow 2||2 \rightarrow 1|$ has an index which is $\frac{r}{2} + \frac{r}{2} = r$ which is strictly positive.

3 sites, 3 seasons

On figure 6 below one sees two periods of the underlying graph of the following T-periodic system given by

$$x \in [0, \frac{T}{3}[\implies \frac{dx}{dt} = A_1 x; x \in [\frac{T}{3}, \frac{2T}{3}[\implies \frac{dx}{dt} = A_2 x; x \in [\frac{2T}{3}, T[\implies \frac{dx}{dt} = A_3 x \quad (32)$$

with

$$\underbrace{\begin{pmatrix} r & 0 & 0 \\ 0 & s-m & m \\ 0 & m & s-m \end{pmatrix}}_{A_1} \quad \underbrace{\begin{pmatrix} s-m & 0 & m \\ 0 & r & 0 \\ m & 0 & s-m \end{pmatrix}}_{A_2} \quad \underbrace{\begin{pmatrix} s-m & m & 0 \\ m & s-m & 0 \\ 0 & 0 & r \end{pmatrix}}_{A_3} \quad (33)$$

It was proved in [4] (see § 4.5.2), thanks to the computation by Maple of the principal eigenvalue of $M = e^{\frac{T}{3}A_3} e^{\frac{T}{3}A_2} e^{\frac{T}{3}A_1}$ that for $r = 1$ and $s = -1$ DIG is not present, while it occurs for $r = 1$ and $s = -0.8$ (see fig. 9 of [4]).

Since, as it is readily seen, there is no T-circuit in this system, our proposition 2 does not apply and thus is unable to predict the presence of DIG for $s = -0.8$.

The next section is devoted to some extensions to Proposition 2 that enable us to deal with these two examples.

4.5 Better sufficient condition for DIG

For simplicity of exposition we have stated and proved a simple growth condition (our proposition 2). But from this we can demonstrate the following more efficient condition which is suggested by the two previous examples.

Let us consider the system (5) with p seasons.

Definition 5

- A **static path** :

$$a_0 \rightarrow a_1 \rightarrow \cdots \rightarrow a_{i-1} \rightarrow a_i \rightarrow \cdots a_{l-1} \rightarrow a_l$$

is a sequence of links connecting sites a_1, \dots, a_p **without requiring**, as in the case of simple paths, that all the sites be different. Unlike a simple path, such a path can have **loops**.

- A **dynamic path** is like previously a sequence of paths which respect the seasons.
- **qT-circuit**. Let q be an integer. A qT -circuit \mathcal{C} is a dynamic path such that

$$a_0 \neq a_p; a_0 \neq a_{2p}; \cdots; a_0 \neq a_{(q-1)p}; a_0 = a_{qp}$$

◦ The **growth index** of a qT -circuit \mathcal{C} is :

$$\chi^{\mathcal{C}} = \frac{1}{q} \sum_{k=1}^{qP} (t_k - t_{k-1}) \max_{\pi_i \in \Gamma^k} r_i^k \quad (34)$$

Proposition 6 Consider the system (5) on the underlying network (12). Let \mathcal{C} be a qT -circuit and its growth index $\chi^{\mathcal{C}}$. Then there exist T^* , constant $C > 0$ and $\mu > 0$ (independent of m) such that

$$T > T^* \implies x_{i^1(0)}(qT) \geq Cm^L e^{qT(\chi^{\mathcal{C}} - \mu \times m)} x_{i^1(0)}(0) \quad (35)$$

where L is the total length of the circuit.

Proof . In the appendix B.4 we explain how we can extend the lemma to a path with one loop. From the idea of this extension, it's not difficult to right a proof of the proposition. \square

Let's return to the example of the section 4.4 of 3 sites over 2 seasons and consider the T-circuit with a loop during season 1:

$$\underbrace{|1 \rightarrow 2 \rightarrow 3 \rightarrow 2|}_{\text{season1}} \underbrace{|2 \rightarrow 1|}_{\text{season2}}$$

The growth index of such a circuit, calculated as before by taking the dominant growth rate on consecutive paths, is :

$$\frac{1}{2}r + \frac{1}{2}r = r$$

which is positive and Proposition 6 predicts the growth.

Let's now take the example of 3 sites over 3 seasons given in Section 4.4 and observe a duration of 2 periods as shown in Figure 6. On this figure we can observe the dynamic 2T-circuit

$$|1 \rightarrow 1| |1 \rightarrow 2| |2 \rightarrow 2| |2 \rightarrow 3| |3 \rightarrow 3| |3 \rightarrow 1| \quad (36)$$

and remark that the succession of dominant growth rates on the six successive paths is

$$r || s || r || s || r || s \quad (37)$$

and the growth index is $\frac{1}{2} \left(\frac{1}{3}r + \frac{1}{3}s + \frac{1}{3}r + \frac{1}{3}s + \frac{1}{3}r + \frac{1}{3}s \right) = \frac{r+s}{2}$ which is positive as soon as $r > -s$. Thus proposition 6 predicts, for instance, that

$$r = 1, s > -1 \implies \text{growth for suitable } (m, T)$$

The Lyapunov exponent of system (32) and (33) :

$$\Lambda(m, T) = \frac{\log(\lambda(m, T))}{T} \quad (38)$$

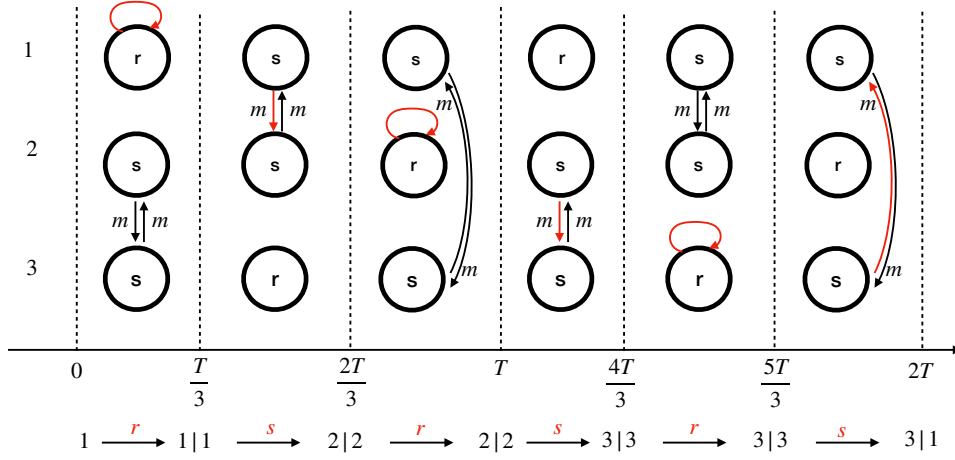


Figure 6: Underlying network of system (32) and (33) on a duration of 2-periods. Below the description of a 2T-circuit.

where $\lambda(m, T)$ is the dominant eigenvalue of $e^{\frac{T}{3}A_3}e^{\frac{T}{3}A_2}e^{\frac{T}{3}A_1}$, gives the asymptotic growth rate of the system. It can be computed by Maple and we show on figure 7 the graph of $T \mapsto \Lambda(0.5, T)$. We see that with $s = -0.9$ there is growth as soon as $T > 20$.

Proposition 6 implies that there is growth as soon as $r > -s$. Actually, it even provides the following lower bound on the Lyapunov exponent of the system:

$$\sup_{(m,T)} \Lambda(m, T) \geq \frac{r+s}{2}.$$

A natural question is whether it is possible to find parameters m and T for which $\Lambda(m, T)$ is strictly greater than $\frac{r+s}{2}$. We have proven in [6, Proposition 18] that this is not the case, and therefore that

$$\sup_{(m,T)} \Lambda(m, T) = \frac{r+s}{2}.$$

In other words, for this example, it is not possible to get a larger upper bound for the growth than using our minimizing methods.

5 Extension to random perturbations of the duration of seasons

In this section, we show that our results remain true if the duration of each season is random, instead of being deterministic. More precisely we consider a succession of "cycles" (or "years") indexed by j composed of a succession of p "seasons" indexed by k of random length $TU^{j,k}$, where $T > 0$ is a parameter and

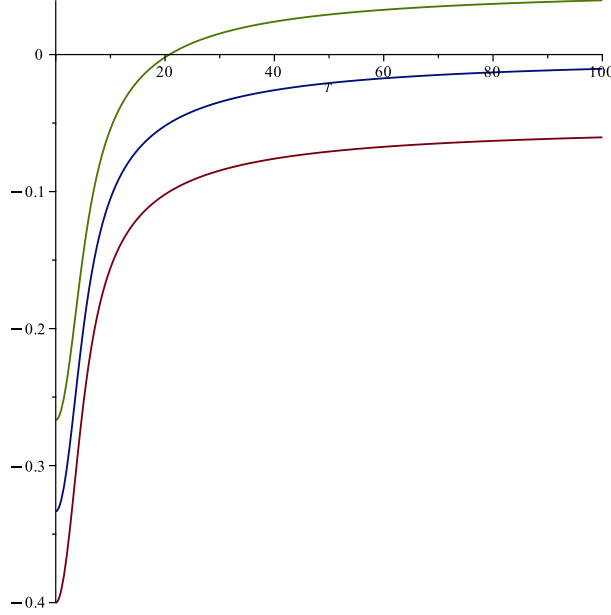


Figure 7: Graph of $T \mapsto \Lambda(0.5, T)$ (see (38)) for $s = -0.9$ (green), $s = -1$ (blue), $s = -1.1$

$\mathbf{U}^j = (U^{j,k})_{1 \leq k \leq p}$ is a random vector with values in \mathbb{R}_+^p . We assume that $(\mathbf{U}^j)_{j \geq 1}$ is a sequence of independent and identically distributed random variables

Remark 2 *The periodic case corresponds to the case where $U^{j,k} = t_k - t_{k-1}$ almost surely, for all $j \geq 1$ and $k = 1, \dots, p$.*

In order to avoid that the duration of a season is 0 or has an infinite mean, we make the following assumption:

Hypothesis 3 *For all $k = 1, \dots, p$, $\mathbb{P}(U^{j,k} = 0) = 0$ and $\mathbb{E}(U^{j,k}) = \mathbb{E}(U^{1,k}) < +\infty$.*

The definition of a simple T-circuit is the same as in the periodic case and we precise the definition of the growth index in that case:

Definition 6 *Growth index of a circuit with random duration* Let

$$\mathcal{C} = a_0 \Gamma^1 a_1 \Gamma^2 a_2 \cdots a_{k-1} \Gamma^k a^k \cdots a_{p-1} \Gamma^p a_p \quad (39)$$

with

$$a_{k-1} \Gamma^k a_k = \left\{ a_{k-1} = \pi_{i^k(0)} \rightarrow \pi_{i^k(1)} \rightarrow \cdots \rightarrow \pi_{i^k(j)} \rightarrow \pi_{i^k(l^k)} = a_k \right\}$$

be a simple T-circuit defined on the underlying time varying network of the system (21). We call random growth index of the j -th cycle of the simple T-circuit \mathcal{C} the

number

$$\chi_{stoc}^{j,\mathcal{C}} = \sum_{k=1}^p U^{j,k} \max_{j=0}^{l^k} r_{i^k(j)}^k \quad (40)$$

and mean growth index the number

$$\chi_{stoc}^{\mathcal{C}} = \sum_{k=1}^p \mathbb{E}(U^{1,k}) \max_{j=0}^{l^k} r_{i^k(j)}^k \quad (41)$$

Using exactly the same proof as for Proposition 3, we can prove:

Proposition 7 Consider the system (21) on the underlying network (12). Consider the simple T -circuit \mathcal{C} defined by (80) and its random growth index $\chi_{stoc}^{\mathcal{C}}$. Then for all $T > 0$,

$$x_{i^1(0)}(T(U^{1,1} + \dots + U^{1,p})) \geq \left(\prod_{k=1}^p C_k(TU^{1,k}) \right) m^L e^{T(\chi_{stoc}^{1,\mathcal{C}} - nm)} x_{i^1(0)}(0) \quad (42)$$

where L is the total length of the circuit, and $C_k(\cdot)$ is the increasing function given by Lemma 1 on the path $\pi_{i^k(0)} \Gamma^k \pi_{i^k(l_k)}$.

From this proposition, we can prove that the DIG threshold is exponentially small with respect to the parameter T :

Proposition 8 Assume that $\mathbb{E}(|\log(U^{j,k})|) < +\infty$ and that there exists a circuit \mathcal{C} with $\chi_{stoc}^{\mathcal{C}} > 0$. Then, for all $\varepsilon > 0$, there exists $T^* > 0$ such that for all $T \geq T^*$, one has

$$m^*(T) \leq e^{\frac{1}{L}(1-\varepsilon)T\chi_{stoc}^{\mathcal{C}}}$$

Proof. Without loss of generality, we assume that $i_1(0) = 1$. Set $X_0 = x_1(0)$ and for all $j \geq 1$,

$$X^j = x_1 \left(T \sum_{j=1}^n \sum_{k=1}^p U^{j,k} \right).$$

Then, Proposition 7 implies that

$$X_j \geq \prod_{j=1}^n Y^j X_0,$$

where

$$Y^j = \left(\prod_{k=1}^p C_k(TU^{j,k}) \right) m^L e^{T(\chi_{stoc}^{j,\mathcal{C}} - nm)}$$

Note that Y^j is a sequence of i.i.d. random variables, such that $\mathbb{E}(|\log Y^j|) < +\infty$. Hence, the strong law of large numbers implies that, almost surely,

$$\lim_{j \rightarrow \infty} \frac{1}{j} \sum_{j=1}^n \log(Y^j) = \mathbb{E}(\log Y^1).$$

Therefore,

$$\limsup_{j \rightarrow \infty} \frac{1}{j} \log(X_j) \geq \mathbb{E}(\log Y^1),$$

and the system is growing provided $\mathbb{E}(\log Y^1) > 0$. Let

$$\tilde{C}(T) = \sum_{k=1}^p \mathbb{E} \left(\log C_k(TU^{1,k}) \right),$$

then

$$\mathbb{E}(\log Y^1) = \tilde{C}(T) + L \log(m) + T(\chi_{stoc}^{\mathcal{C}} - nm)$$

Let $\varepsilon > 0$. We can assume that $m < \frac{\varepsilon \chi_{stoc}^{\mathcal{C}}}{2n-1}$, so that

$$\mathbb{E}(\log Y_1) \geq \tilde{C}(T) + L \log(m) + T \left(1 - \frac{\varepsilon}{2}\right) \chi_{stoc}^{\mathcal{C}}$$

Now, it is easily seen that for all $k = 1, \dots, p$, $\log(C_k(TU^{1,k}))$ converges monotonically to a finite limit as T goes to infinity. Hence, by monotone convergence, $\frac{1}{T} \tilde{C}(T) \rightarrow 0$ as T goes to infinity. Therefore, for some $T^* > 0$ and all $T \geq T^*$, we have $\tilde{C}(T) \geq -\frac{\varepsilon}{2} T \chi_{stoc}^{\mathcal{C}}$, and thus

$$\mathbb{E}(\log Y_1) \geq L \log(m) + T(1 - \varepsilon) \chi_{stoc}^{\mathcal{C}}$$

6 Discussion

In this article, we considered the evolution of populations at different sites linked by migration paths. Environmental conditions vary periodically over time, as do migration rates between each site. The models are continuous time models. We wanted to highlight how the evolution of the structure of the migration network influences total population growth. But rather than give precise growth results for a given model, we have sought to identify a method for minimizing growth, based on certain properties of the dynamic graph underlying the dynamic system.

To do this, we defined the growth index $\chi^{\mathcal{C}}$ of a simple T-circuit \mathcal{C} . A simple T-circuit is a route from site to site that respects the migration links existing during a given season and returning to the starting point. Our main result, proposition 3 is that *if there is a simple T-circuit with a strictly positive growth index, then the total population is growing for some values of m and T* . Following [24] we called this the DIG (Dispersal Induced Growth) effect.

Perhaps the most important point that we can emphasize here is that we do not make the assumption that migration matrices are irreducible, which allows us to cover realistic cases such as seasonal population migrations from one site to another.

To keep things mathematically as simple as possible - we're only using very elementary mathematical results from undergraduate courses - we've chosen to consider only periodic systems which coefficients are piecewise constant. There is

little doubt that they are still true in the piecewise continuous case but this deserves further investigations.

One of the advantages of the "piecewise constant" hypothesis is that it can be immediately extended to systems where the length of the seasons is no longer a fixed quantity but a random one, which is obviously much more realistic. As an example of what can be done, in section 5 we define a stochastic version of the growth index along a circuit and demonstrate that the growth threshold is exponentially small with respect to the parameter T .

We studied the growth phenomenon as a function of two parameters, m which measures the intensity of the migration, and T which measures the duration of the cycles. In the observation of real phenomena, this latter parameter is not always relevant, especially when cycles are years, months or other cyclic phenomena determined by astronomical revolutions.

In models of population dynamics forced by a periodic environment, the period is often fixed, e.g. year, month, and it is not very relevant, apart from mathematical considerations, to take, as we did, the period as a parameter. A statement like "If the duration of the year is long enough, then..." doesn't make much sense. For instance, a model of the form

$$\Sigma(r_i(\cdot), \ell_{i,j}(\cdot), m, S) \quad \frac{dx_i(t)}{dt} = (r_i(t) + S\sigma_i(t))x_i(t) + m \sum_{j=1}^n \ell_{i,j}(t)x_j$$

with $r(\cdot)$, $\sigma_i(\cdot)$, $\ell_{i,j}(\cdot)$ have a fixed period 1, where $S\sigma_i(\cdot)$ is a fluctuation around some average value r_i is more relevant to express modification of environmental parameters as a function of altitude, or latitude. There is no doubt that our method of minorization along paths also works for $\Sigma(r_i(\cdot), \ell_{i,j}(\cdot), m, S)$.

One area where our approach seems promising is that of epidemiology. Indeed, [20, 21] have shown that the phenomenon of inflation plays a negative role in the persistence of infected subjects. Network models are also well developed in this field and the analysis of the T-circuits as defined here could be useful by detecting where suppressing contact between infected and susceptible people is most effective.

There is a large body of literature (see [32] and its bibliography for a recent example) on the question of inflation in discrete-time models. Insofar as in a discrete-time model it is possible to transfer the entire population instantaneously from one site to another, which is not possible for continuous-time models, the questions that arise in the two cases are not exactly the same and, as a result, the comparison of results is not immediate. This could be the subject of further work.

Finally, we must make the following observation. On examples with few sites like the ones we've looked at, it's not difficult to determine the circuits and therefore calculate the associated growth indices. But what about systems with a large number of sites? This is a question of graph theory that we have not yet addressed.

A Linear differential equations.

For the convenience of the reader we recall some elementary facts regarding linear differential equations and systems that can be found in elementary textbooks.

A.1 Closed form solutions for non autonomous linear differential equations .

Let $t \mapsto a(t)$ and $t \mapsto b(t)$ be two integrable functions.

Proposition 9 *Let $x(t, x_0)$ be the solution of the initial value problem*

$$\frac{dx}{dt} = a(t)x + b(t) \quad x(0) = x_0 \quad (43)$$

If one denotes $m(t) = \int_0^t a(\tau) d\tau$ one has

$$x(t, x_0) = e^{m(t)} \left(x_0 + \int_0^t e^{-m(s)} b(s) ds \right) \quad (44)$$

If $a(t)$ is just a constant (44) reads

$$x(t, x_0) = e^{ta} x_0 + \int_0^t e^{-sa} b(s) ds \quad (45)$$

A.2 Linear systems.

Notations

We use the following notations : for $x, y \in \mathbb{R}^N$, $x \geq y$ means that for all i , $x_i \geq y_i$; $x > y$ means that $x_i \geq y_i$ and $x \neq y$; and $x \gg y$ means that for all i , $x_i > y_i$. We use the same notations for $n \times p$ matrices considered as elements of $\mathbb{R}^{n \times p}$. Given the system of differential equation in \mathbb{R}^n

$$\Sigma \quad \begin{cases} \frac{dx}{dt} = f(x, t) \end{cases}$$

we denote $x(t, (x_0, t_0))$ its solution with initial condition $x(t_0) = x_0$. We say that Σ is positive ($\Sigma \geq 0$) if $x_0 \geq 0 \implies x(t, (x_0, t_0)) \geq 0$ and given two positive systems

$$\Sigma_1 \quad \begin{cases} \frac{dx_1}{dt} = f(x_1, t) \end{cases} \quad \Sigma_2 \quad \begin{cases} \frac{dx_2}{dt} = f(x_2, t) \end{cases}$$

we say that Σ_1 minorizes Σ_2 (denoted $\Sigma_1 \leq \Sigma_2$) if

$$0 \leq x_{1_0} \leq x_{2_0} \implies x_1(t, (x_{1_0}, t_0)) \leq x_2(t, (x_{2_0}, t_0))$$

Exponential of a matrix.

The exponential of a matrix allows to extend formula (45) to linear systems. Let $x = (x_1, \dots, x_i, \dots, x_n)$ be a vector of \mathbb{R}^n and A an $n \times n$ matrix.

The matrix

$$\text{Id} + tA + \frac{t^2}{2!}A^2 + \dots + \frac{t^k}{k!}A^k + \dots = \sum_{k=0}^{\infty} \frac{t^k}{k!}A^k$$

where Id is the identity matrix, is well defined (the sum is convergent) for every values (positive or negative) of t and is denoted e^{tA} . It has the following properties:

- $t \mapsto e^{tA}x_0$ is the solution of the differential equation

$$\frac{dx}{dt} = Ax \quad x(0) = x_0$$

- For every t_1 and every t_2 one has $e^{t_1A}e^{t_2A} = e^{(t_1+t_2)A}$
- For every t the matrix e^{tA} is invertible and $(e^{tA})^{-1} = e^{-tA}$
- If $t \mapsto b(t)$ is an integrable mapping from \mathbb{R} to \mathbb{R}^n the solution of

$$\frac{dx}{dt} = Ax + b(t) \quad x(0) = x_0 \quad (46)$$

is given by

$$x(t) = e^{tA}x_0 + \int_0^t e^{(t-\tau)A}b(\tau)d\tau \quad (47)$$

Proposition 10 Let $x_0 \neq 0$. Then, for every t one has $e^{tA}x_0 \neq 0$

Proof. This follows from the fact that e^{tA} is invertible. \square

Invariance of the positive orthant for Metzler systems.

A matrix $M = (m_{ij})$ is a Metzler matrix if $i \neq j \implies m_{ij} \geq 0$.

Proposition 11 If M is a Metzler matrix then for every $x_0 \geq 0$ and every $t \geq 0$ one has $x(t) = e^{tM}x_0 \geq 0$.

Proof. If $x_0 = 0$ one has $e^{tM}x_0 \equiv 0$ and the proposition is proved. We assume $x_0 \neq 0$.

First step. We assume that

$$\forall i \ x_{i0} > 0 \text{ and } \forall i \ \forall j : i \neq j \implies m_{ij} > 0 \quad (48)$$

and suppose that $e^{tM}x_0$ is not positive for every $t > 0$. From proposition 10 it is not possible that all the components $x_i(t)$ vanish at the same time and thus, if all the components $x_i(t)$ are not always strictly positive, there must exist $t^* > 0$ (the instant when a component vanishes for the first time) with the following properties:

1. There exists i such that $x_i(t^*) = 0$ and $0 \leq t < t^* \implies x_i(t) > 0$
2. There exist at least one $j \neq i$ such that $x_j > 0$

Since $x(t)$ is a solution of $\frac{dx}{dt} = Mx$ one has $\frac{dx_i}{dt} = m_{ii}x_i(t) + \sum_{j \neq i} m_{ij}x_j(t)$ and, from 2) above, for $t = t^*$

$$\frac{dx_i}{dt}(t^*) = m_{ii}x_i(t^*) + \sum_{j \neq i} m_{ij}x_j(t^*) = \sum_{j \neq i} m_{ij}x_j(t^*) > 0$$

which contradicts point 1). As a consequence such a t^* cannot exist and we have proved that under hypothesis (48)

$$\forall t, \forall i \quad x_i(t) > 0 \quad (49)$$

Second step. Let M be a Metzler matrix and $x_0 \geq 0$. Let

$$M_k = M + \frac{1}{k} \begin{pmatrix} 0 & 1 & 1 & \cdots & 1 \\ 1 & 0 & 1 & \cdots & 1 \\ \cdot & \cdot & \cdot & \cdots & \cdot \\ 1 & \cdots & 1 & 0 & 1 \\ 1 & \cdots & 1 & 1 & 0 \end{pmatrix} \quad x_k = x_0 + \frac{1}{k} \begin{pmatrix} 1 \\ 1 \\ \cdots \\ 1 \\ 1 \end{pmatrix}$$

We know that for every $t \geq 0$ one has

$$\lim_{k \rightarrow \infty} e^{tM_k} x_k = e^{tM} x_0$$

Since M_k, x_k satisfy (48), each component $x_{ik}(t)$ is strictly positive and its limit is positive or equal to 0, which proves the proposition. \square .

Comparison of solutions

We prove the following proposition which is about the comparison of solutions of Metzler systems.

Proposition 12 *Let $M = (m_{ij})$ and $N = (n_{ij})$ be two Metzler matrices such that :*

$$\forall i \forall j \quad m_{ij} \leq n_{ij} \quad (\text{which we denote by } M \leq N \text{ or } N - M \geq 0)$$

Denote $x(t, x_0) = e^{tM} x_0$ and $y(t, y_0) = e^{tN} y_0$ then

$$\forall x_0 \forall y_0 \forall t \geq 0 \quad 0 \leq x_0 \leq y_0 \implies x(t, x_0) \leq y(t, y_0)$$

Proof. Let $z(t) = y(t, y_0) - x(t, x_0)$. We have

$$\frac{dz}{dt} = Ny(t, y_0) - Mx(t, x_0) = N(y(t, y_0) - x(t, x_0)) + (N - M)x(t, x_0)$$

$$\frac{dz}{dt} = Nz(t) + (N - M)x(t, x_0)$$

and from (46) and (47) we have

$$z(t) = e^{tN}z(0) + \int_0^t e^{(t-\tau)N}u(\tau)d\tau \quad (50)$$

with $u(\tau) = (N - M)x(\tau, x_0)$. Since $x_0 \leq y_0$ we have $z(0) \geq 0$ and since N is Metzler, from proposition 11 we have $e^{tN}z(0) \geq 0$.

Let us look now to the second term of (50). Since M is Metzler and $x_0 \geq 0$ we have $x(\tau, x_0) \geq 0$ and from the hypothesis $N - M \geq 0$ we have $(N - M)x(\tau, x_0) = u(\tau) \geq 0$. Since N is Metzler, again from proposition 11 we have

$$\forall \tau \leq t \quad e^{(t-\tau)N}u(\tau) \geq 0$$

which implies

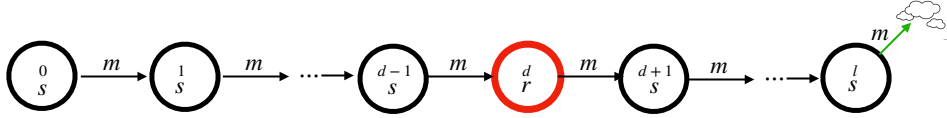
$$\int_0^t e^{(t-\tau)N}u(\tau)d\tau \geq 0$$

and achieves the proof of the proposition. \square

B Proof of proposition 3

B.1 Integration along a path.

One considers the system defined on the network



by the equations

$$\Sigma(r, s, l, dm, T) \left\{ \begin{array}{l} j = 0 \cdots d-1 \\ j = d \\ j = d+1 \cdots l \end{array} \right. \left\{ \begin{array}{l} \frac{dy_0}{dt} = (s-m)y_0 \\ \frac{dy_j}{dt} = my_{j-1} + (s-m)y_j \\ \frac{dy_{d-1}}{dt} = my_{d-2} + (s-m)y_{d-1} \\ \frac{dy_d}{dt} = my_{d-1} + (r-m)y_d \\ \frac{dy_{d+1}}{dt} = my_d + (s-m)y_{d+1} \\ \frac{dy_j}{dt} = my_{j-1} + (s-m)y_j \\ \frac{dy_l}{dt} = my_{l-1} + (s-m)y_l \end{array} \right. \quad (51)$$

with $r > s$ and the initial condition $(y_0(t_0) > 0, 0 \cdots, 0, \cdots, 0)$.

Lemma 1 *There exists an increasing function $\theta \mapsto C(\theta)$ such that :*

$$t \geq \theta \implies y_l(t+t_0) \geq C(\theta)m^l e^{t(r-m)}y_0(t_0) \quad (52)$$

Moreover one has

$$C(\theta) = v_{r,s,d} \left(\frac{\theta}{l-d+1} \right) \left(w_{r,s} \left(\frac{\theta}{l-d+1} \right) \right)^{l-d} \quad (53)$$

with

$$v_{r,s,d}(t) = \int_0^t e^{-\tau(r-s)} \frac{\tau^{d-1}}{(d-1)!} d\tau \quad w_{r,s}(t) = \frac{1}{r-s} \left(1 - e^{-t(r-s)} \right) \quad (54)$$

which means that $C(\theta)$ is independent of m .

Proof.

Assume that $t_0 = 0$. In the vector form one has

$$\frac{dy}{dt} = Ay$$

with

$$A = \begin{bmatrix} s-m & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 & 0 \\ m & s-m & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 \\ 0 & m & s-m & 0 & \dots & \dots & \dots & \dots & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & \dots & m & s-m & \dots & \dots & \dots & \dots & 0 \\ 0 & \dots & \dots & \dots & m & r-m & 0 & \dots & \dots & 0 \\ 0 & \dots & \dots & \dots & \dots & m & s-m & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & m & s-m & 0 \\ 0 & \dots & \dots & \dots & \dots & \dots & \dots & \dots & m & s-m \end{bmatrix} \quad (55)$$

One sees immediately that

$$x(t) = e^{-t(s-m)}y(t)$$

is solution of :

$$\frac{dx}{dt} = Bx$$

with

$$B = \begin{bmatrix} 0 & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 & 0 \\ m & 0 & 0 & \dots & \dots & \dots & \dots & \dots & \dots & 0 \\ 0 & m & 0 & 0 & \dots & \dots & \dots & \dots & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & \dots & m & 0 & \dots & \dots & \dots & \dots & 0 \\ 0 & \dots & \dots & \dots & m & r-s & 0 & \dots & \dots & 0 \\ 0 & \dots & \dots & \dots & \dots & m & 0 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & m & 0 & 0 \\ 0 & \dots & \dots & \dots & \dots & \dots & \dots & \dots & m & 0 \end{bmatrix} \quad (56)$$

and the initial condition $x(0) = (x_0(0) = y_0(0) > 0, 0 \cdots, 0, \cdots, 0)$.
From site 0 to site $d - 1$. By successive integrations one has

$$x_{d-1}(t) = m^{d-1} \frac{t^{d-1}}{(d-1)!} x_0(0) \quad (57)$$

On the site d .

From proposition (9) the integration of the differential equation

$$\frac{dx_d}{dt} = mx_{d-1} + (r-s)x_d \quad x_d(0) = 0$$

gives

$$x_d(t) = e^{t(r-s)} \int_0^t e^{-\tau(r-s)} m x_{d-1}(\tau) d\tau = e^{t(r-s)} \int_0^t e^{-\tau(r-s)} m^d \frac{\tau^{d-1}}{(d-1)!} x_0 d\tau$$

Set

$$v_{r,s,d}(t) = \int_0^t e^{-\tau(r-s)} \frac{\tau^{d-1}}{(d-1)!} d\tau \quad (58)$$

We have

$$x_d(t) = e^{t(r-s)} m^d x_0(0) v_{r,s,d}(t)$$

and, since $v_{r,s,d}(t)$ is an increasing function of t one has for every $\theta > 0$ and every integer p

$$t \geq \frac{\theta}{p} \implies x_d(t) \geq e^{t(r-s)} m^d x_0(0) v_{r,s,d} \left(\frac{\theta}{p} \right) \quad (59)$$

where the parameter p will be specified later.

On the site $d + 1$.

One has

$$x_{d+1}(t) = m \int_0^t x_d(\tau) d\tau$$

and from (59) one has

$$t \geq \frac{\theta}{p} \implies x_{d+1}(t) \geq m \int_{\frac{\theta}{p}}^t e^{\tau(r-s)} m^d x_0(0) v_{r,s,d} \left(\frac{\theta}{p} \right) d\tau = m^{d+1} x_0(0) v_{r,s,d} \left(\frac{\theta}{p} \right) \int_{\frac{\theta}{p}}^t e^{\tau(r-s)} m^d d\tau$$

One has

$$\int_{\frac{\theta}{p}}^t e^{\tau(r-s)} m^d d\tau = \frac{1}{r-s} \left(e^{t(r-s)} - e^{\frac{\theta}{p}(r-s)} \right) = \frac{1}{r-s} e^{t(r-s)} \left(1 - e^{-\frac{\theta}{p}(r-s)} \right)$$

And now, since $r - s > 0$, we have

$$t \geq 2 \frac{\theta}{p} \implies \int_{\frac{\theta}{p}}^t e^{\tau(r-s)} m^d d\tau \geq \frac{1}{r-s} e^{t(r-s)} \left(1 - e^{-\frac{\theta}{p}(r-s)} \right) \quad (60)$$

If we denote

$$\boxed{w_{r,s}(t) = \frac{1}{r-s} \left(1 - e^{-t(r-s)}\right)} \quad (61)$$

it follows

$$t \geq \frac{\theta}{p} + 1 \times \frac{\theta}{p} \implies x_{d+1}(t) \geq m^{d+1} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right) w_{r,s} \left(\frac{\theta}{p}\right) e^{t(r-s)}$$

$$\boxed{t \geq 2 \frac{\theta}{p} \implies x_{d+1}(t) \geq e^{t(r-s)} w_{r,s} \left(\frac{\theta}{p}\right) m^{d+1} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right)} \quad (62)$$

On the site $d+2$.

One has

$$x_{d+2}(t) = m \int_0^t x_{d+1}(\tau) d\tau$$

and from (62)

$$t \geq 2 \frac{\theta}{p} \implies x_{d+2} \geq w_{r,s} \left(\frac{\theta}{p}\right) m^{d+2} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right) \int_{\frac{\theta}{p} + 1 \times \frac{\theta}{p}}^t e^{\tau(r-s)} d\tau$$

and like previously

$$t \geq 3 \frac{\theta}{p} \implies x_{d+2} \geq w_{r,s} \left(\frac{\theta}{p}\right) m^{d+2} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right) w_{r,s} \left(\frac{\theta}{p}\right) e^{t(r-s)}$$

$$\boxed{t \geq 3 \frac{\theta}{p} \implies x_{d+2} \geq e^{t(r-s)} \left(w_{r,s} \left(\frac{\theta}{p}\right)\right)^2 m^{d+2} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right)} \quad (63)$$

Iterating the process up to k we have on the site $d+k$.

$$\boxed{t \geq (k+1) \frac{\theta}{p} \implies x_{d+k} \geq e^{t(r-s)} \left(w_{r,s} \left(\frac{\theta}{p}\right)\right)^k m^{d+k} x_0(0) v_{r,s,d} \left(\frac{\theta}{p}\right)} \quad (64)$$

On the site $l = d+k$.

If we apply (64) with $k = l - d$ and $p = l - d + 1$ we get

$$\boxed{t \geq \theta \implies x_l \geq e^{t(r-s)} \left(w_{r,s} \left(\frac{\theta}{l-d+1}\right)\right)^{l-d} m^l x_0(0) v_{r,s,d} \left(\frac{\theta}{l-d+1}\right)} \quad (65)$$

and if we put $C(\theta) = \left(w_{r,s} \left(\frac{\theta}{l-d+1}\right)\right)^{l-d} v_{r,s,d} \left(\frac{\theta}{l-d+1}\right)$

$$\boxed{t \geq \theta \implies x_l(t) \geq C(\theta) e^{t(r-s)} m^l x_0(0)} \quad (66)$$

Now, if we turn back to $y_l(t) = e^{t(s-m)} x_l(t)$

$$t > \theta \implies y_l(t) > C(\theta) m^l e^{t(r-m)} y_0(0) \quad (67)$$

and, since the matrix A does not depend on t , for any initial condition $y_0(t_0)$

$$t > \theta \implies y_l(t+t_0) > C(\theta) m^l e^{t(r-m)} y_0(t_0) \quad (68)$$

which ends the proof of the lemma. \square

B.2 Minorization through a path

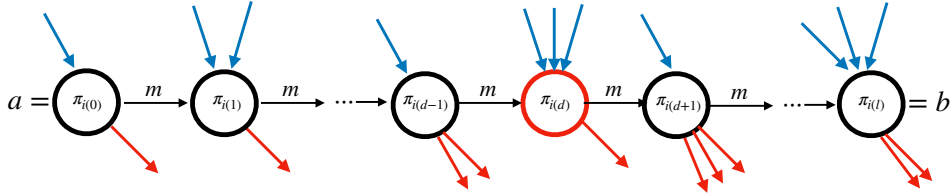
Let $\Pi = \{\pi_1, \dots, \pi_i, \dots, \pi_n\}$ be a set of n sites. In this subsection we consider the system

$$\Sigma(r_i, \ell_{ij}, m, T) \quad \begin{cases} \frac{dx_i}{dt} = r_i x_i + m \sum_{j=1}^n \ell_{ij} x_j & i = 1, \dots, n \end{cases} \quad (69)$$

where r_i are constant and $\ell_{ij} \in \{0, 1\}$ are associated to the static network \mathcal{N}

$$\pi_i \rightarrow \pi_j \in \mathcal{N} \iff \ell_{ji} = 1$$

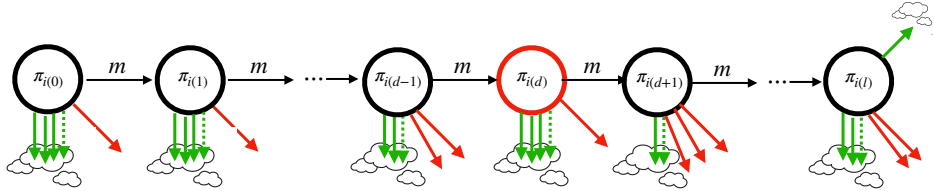
Consider an arbitrary simple path $a\Gamma b$ of \mathcal{N} like the following one



For each site $\pi_{i(j)}$ we have represented in blue the incoming links (from any site of the network) in the site, in black the link that connects to the next site in the path, and finally, in red, the links that leave the site to some other site of the network. Notice that there is no "black arrow" leaving the last site.

Our aim in this subsection is to minorize $x_{i(l)}(t)$ given an initial condition such that $x_{i(0)}(t_0) > 0$.

Compare the following picture to the previous one :



- We have cut all the blue links.
- The number of links leaving each site (red+black) is smaller than $n - 1$. We have added links (in green) to the "clouds" in a number such that the total links leaving the site is just the maximum total number $n - 1$ of possible links leaving a site.

From this picture we define a new system on \mathcal{N} in the following manner :

$$\Sigma(r_i, a\Gamma b, m, T) \left\{ \begin{array}{l} \pi_i \notin a\Gamma b \implies \frac{d\xi_i}{dt} = (r_i - \alpha - m)\xi_i \\ i = i(0) \implies \frac{d\xi_{i(0)}}{dt} = (r_{i(0)} - \alpha - m)\xi_{i(0)} \\ 0 < j \leq l \implies \frac{d\xi_{i(j)}}{dt} = m\xi_{i(j-1)} + (r_{i(j)} - \alpha - m)\xi_{i(j)} \\ i = i(l) \implies \frac{d\xi_{i(l)}}{dt} = m\xi_{i(l-1)} + (r_{i(l)} - \alpha - m)\xi_{i(l)} \end{array} \right. \quad (70)$$

where $\alpha = (n-2) \times m$. By construction it is evident that the system $\Sigma(r_i, a\Gamma b, m, T)$ minorizes the system $\Sigma(r_i, \ell_{ij}, m, T)$

$$\Sigma(r_i, a\Gamma b, m, T) \leq \Sigma(r_i, \ell_{ij}, m, T)$$

and that its restriction to $a\Gamma b$, also denoted by $\Sigma(r_i, a\Gamma b, m, T)$, is independent of the $\xi_i(t)$ for $\pi_i \notin a\Gamma b$.

Now define a **"dominant" site** $i(d)$ as a site such that for every $j = 0 \cdots l$ one has $r_{i(d)} \geq r_{i(j)}$; let $\sigma = \min_{j=0 \cdots l} r_{i(j)} - 1$. The "-1" in the definition of σ is there to ensure that $\sigma < r_{i(d)}$. For $j \neq d$ replace in $\Sigma(r_i, a\Gamma b, m, T)$, the term $r_i - \alpha - m$ by $s - m$ and $r_{i(d)} - m$ by $r - m$. We obtain

$$\Sigma(r, s, l, d, m, T) \left\{ \begin{array}{l} j = 0 \cdots d-1 \left\{ \begin{array}{l} \frac{dy_0}{dt} = (s-m)y_0 \\ \frac{dy_j}{dt} = my_{j-1} + (s-m)y_j \\ \frac{dy_{d-1}}{dt} = my_{d-2} + (s-m)y_{d-1} \end{array} \right. \\ j = d \left\{ \begin{array}{l} \frac{dy_d}{dt} = my_{d-1} + (r-m)y_d \\ \frac{dy_{d+1}}{dt} = my_d + (s-m)y_{d+1} \end{array} \right. \\ j = d+1 \cdots l \left\{ \begin{array}{l} \frac{dy_j}{dt} = my_{j-1} + (s-m)y_j \\ \frac{dy_l}{dt} = my_{l-1} + (s-m)y_l \end{array} \right. \end{array} \right. \quad (71)$$

Again, by construction

$$\Sigma(r, s, l, d, m, T) \leq \Sigma(r_i, \ell_{ij}, m, T) \quad (72)$$

The system $\Sigma(r, s, ld, m, T)$ is exactly the system (51) of the lemma 1 and by the way (52) applies

$$t \geq \theta \implies y_l(t + \theta) \geq C(\theta) m^l e^{t(r-m)} y_0(t_0) = C(\theta) m^l e^{t(r_{i(d)} - \alpha - m)} y_0(t_0) \quad (73)$$

with

$$C(\theta) = v_{r,s,d} \left(\frac{\theta}{l-d+1} \right) \left(w_{r,s} \left(\frac{\theta}{l-d+1} \right) \right)^{l-d} \quad (74)$$

and

$$v_{r,st,d}(t) = \int_0^t e^{-\tau(r-s)} \frac{\tau^{d-1}}{(d-1)!} d\tau \quad w_{r,s}(t) = \frac{1}{r-s} \left(1 - e^{-t(r-s)} \right) \quad (75)$$

Replacing r and s by their definition one has $r-s = r_{i(d)} - \sigma$ which gives

$$v_{r,st,d}(t) = \int_0^t e^{-\tau(r_{i(d)}-\sigma)} \frac{\tau^{d-1}}{(d-1)!} d\tau \quad w_{r,s}(t) = \frac{1}{r_{i(d)}-\sigma} \left(1 - e^{-t(r_{i(d)}-\sigma)} \right) \quad (76)$$

which is independent of m . We have proved the proposition

Proposition 13 Consider the system $\Sigma(r_i, \ell_{ij}, m, T)$

$$\Sigma(r_i, \ell_{ij}, m, T) \quad \left\{ \frac{dx_i}{dt} = r_i x_i + m \sum_{j=1}^n \ell_{ij} x_j \quad i = 1, \dots, n \right. \quad (77)$$

defined on some static network \mathcal{N} and a simple path

$$a\Gamma b = \{a = \pi_{i(0)} \rightarrow \pi_{i(1)} \rightarrow \dots \rightarrow \pi_{i(j)} \rightarrow \dots \rightarrow \pi_{i(l)} = b\} \quad (78)$$

on it. Let $r_{i(d)} = \max_{j=0..l} r_{i(j)}$ $\sigma = \min_{j=0..l} r_{i(j)} - 1$. Then there exist θ , $C(\theta) > 0$ and $\mu > 0$ such that :

$$t \geq \theta \implies x_l(t+t_0) \geq C(\theta) m^l e^{t(r_{i(d)}-\mu \times m)} x_0(t_0) \quad (79)$$

(take $\mu = n - 1$ and $C(\theta)$ given by (74) and (76)).

Remark. In our proof we have added red links "to the clouds" in number such that the total outgoing links is $n - 1$ but it would has been enough in order to use the lemma to add a number of links such that the number outgoing links is just a constant and have a better minorization. This is why we prefer in the statement of the proposition to be not explicit in the definition of μ .

B.3 Minorization through a T-circuit.

We come now to the proof of the proposition 3.

Consider the system $\Sigma(r_i^k, \ell_{i,j}^k, m, T)$ on the underlying network (12). Consider the T -circuit \mathcal{C} defined by

$$\mathcal{C} = a_0 \Gamma^1 a_1 \Gamma^2 a_2 \dots a_{k-1} \Gamma^k a^k \dots a_{p-1} \Gamma^p a_0 \quad (80)$$

with

$$a_{k-1} \Gamma^k a_k = \left\{ a_{k-1} = \pi_{i^k(0)} \rightarrow \pi_{i^k(1)} \rightarrow \dots \pi_{i^k(j)} \rightarrow \pi_{i^k(l^k)} = a_k \right\}$$

and its growth index $\chi^{\mathcal{C}}$.

We have to prove that there exist T^* and constants $C > 0$, $\mu > 0$ (independent of m) such that

$$T > T^* \implies x_{i^1(0)}(T) \geq C m^L e^{T(\chi^{\mathcal{C}} - \mu \times m)} x_{i^1(0)}(0) \quad (81)$$

where L is the total length of the circuit.

Let d^k be a dominant site of the path $a_{k-1}\Gamma^k a_k$ and $r_{d^k}^k$ the corresponding dominant rate.

Consider the first simple path $\pi_1\Gamma^1\pi_{i^1(l^1)}$. Let $\theta > 0$ and let $C^1 = C^{\Gamma^1}(\theta)$ where $C^{\Gamma^1}(\theta)$ is the function of proposition 13 applied to the first path. From (74) and (75) we know that $C^1(\theta) > 0$. Let $T^{*1} \geq \frac{\theta}{t_1}$. From prop 13 we know that

$$T > T^{*1} \implies x_{i^1(l^1)}(T t_1) > C^1 m^{l^1} e^{T t_1 (r_{d^1}^1 - \mu \times m)} x_{i^1(0)}(0) \quad (82)$$

On the interval $[T t_1, T t_2]$ the proposition 13 applies again to the simple path $(\pi_{i^1(l^1)} = \pi_{i^2(0)})\Gamma^2\pi_{i^2(l^2)}$ and thus if we put $C^2 = C^{\Gamma^2}(\theta)$ and $T^{*2} \geq \frac{\theta}{t_2 - t_1}$

$$T > T^{*2} \implies x_{i^2(l^2)}(T t_2) > C^2 m^{l^2} e^{T(t_2 - t_1)(r_{d^2}^2 - \mu \times m)} x_{i^1(l^1)}(T t_1) \quad (83)$$

Combining the two inequalities (82) and (83) we obtain that

$$T > \max\{T^{*1}, T^{*2}\} \implies x_{i^2(l^2)}(T t_2) \geq C^1 C^2 m^{l^1 + l^2} e^{T((r_{d^1}^1 - \mu \times m)t_1 + (r_{d^2}^2 - \mu \times m)(t_2 - t_1))} x_{i^1(0)}(0).$$

If we iterate this application of proposition 13 to the successive simple paths of the circuit up to the last one we get

$$T > \max\{T^{*1} \dots T^{*p}\} \implies x_{i^p(l^p)}(T t_p) \geq C^1 \dots C^p m^{\sum_k l^k} e^{T(\sum_{k=1}^p r_{d^k}^k (t_k - t_{k-1}) - \mu \times m)} x_{i^1(0)}(0)$$

Since $x_{i^p(l^p)}(T t_p) = x_1(T)$ and by definition of $\chi^{\mathcal{C}}$ one has

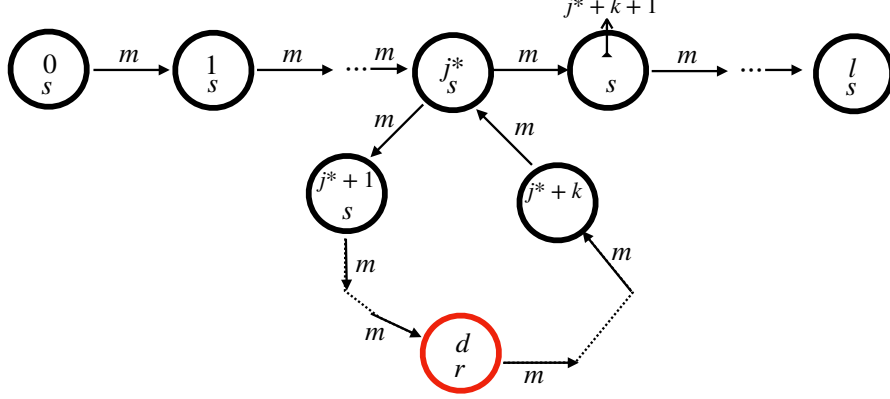
$$T > \max\{T^{*1} \dots T^{*p}\} \implies x_1(T) \geq C^1 \dots C^p m^{\sum_k l^k} e^{T(\chi^{\mathcal{C}} - \mu \times m)} x_{i^1(0)}(0)$$

which proves the proposition.

B.4 Possible extensions

The lemma 1 assumes that the path has no loop. We now give an extension of this lemma in the case of a network with a single simple loop where the dominant site is in the loop.

Consider the system defined by the network :



and we leave it to the reader to write down the equations.

Proposition 14 For the above network, we have for all $\theta > 0$ and all $\beta \in (0, 1)$,

$$t \geq \theta \implies y_l(t + t_0) \geq C(\beta\theta)C((1-\beta)\theta)m^{l+1}e^{t(r-2m)}y_0(t_0) \quad (84)$$

Proof.

Assume that $t_0 = 0$. The idea is to cut the loop into two simple paths, to each of which we apply Proposition 13. First, consider in the above network the simple path

$$0\Gamma d = \{0 \rightarrow 1 \rightarrow \dots \rightarrow j^* \rightarrow j^* + 1 \rightarrow \dots \rightarrow d\}$$

Since the maximal number of links leaving a site is 2 (on site j^*), we deduce from Proposition 13 that for all $\beta \in (0, 1)$ and $\theta > 0$, one has

$$t \geq \beta\theta \implies y_d(t) \geq C(\beta\theta)m^d e^{t(r-2m)}y_0(0) \quad (85)$$

Next, consider the simple path (of length $l - d + 1$ and maximal index r)

$$d\Gamma l = \{d \rightarrow d + 1 \rightarrow \dots \rightarrow j^* \rightarrow j^* + k + 1 \rightarrow j^* + k + l^* = l\}$$

Once again, the maximal number of links leaving a site is 2, so that for all $\beta \in (0, 1)$, for all $t'_0 \geq 0$, for all $\theta > 0$, we have

$$t' \geq (1-\beta)\theta \implies y_l(t' + t'_0) \geq C((1-\beta)\theta)m^{l-d+1}e^{t'(r-2m)}y_d(t'_0). \quad (86)$$

Taking $t = \beta\theta$ in Equation (85), and $t'_0 = \beta\theta$ in Equation (86) yields

$$t' \geq (1-\beta)\theta \implies y_l(t' + \beta\theta) \geq C((1-\beta)\theta)C(\beta\theta)m^{l+1}e^{(t'+\beta\theta)(r-2m)}y_0(0)$$

Noting that $t \geq \theta$ is equivalent to $t' = t - \beta\theta \geq (1-\beta)\theta$, we finally end up with

$$t \geq \theta \implies y_l(t) \geq C((1-\beta)\theta)C(\beta\theta)m^{l+1}e^{t(r-2m)}y_0(0).$$

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