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Dispersal-induced growth in a time-periodic environment of sink habitats ^{*}

Michel Benaim [†] C. Lobry [‡] T. Sari [§] E. Strickler [¶]

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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 phenomenon, in the context of a deterministic model with periodic variation of growth rates and migration.

Keywords Dispersal-induced growth - Periodic linear cooperative systems - Principal Lyapunov exponent - Perron root - Metzler matrices - Sinks.

Mathematics Subject Classification (2010) 92D25 - 34A30 - 34D08.

1 Introduction

Many plant and animal populations live in separate patches, that are connected by dispersal. The study of the interaction between organism dispersal and environmental heterogeneity, to determine population growth is a central theme of ecological theory [1, 5]. A patch is called a *sink* when, in the absence of dispersion, the environmental conditions lead to the extinction of the population. A surprising phenomenon is that of populations that can *persist in an environment consisting of sink habitats only* as announced in the title of [8]. In fact, this somewhat paradoxical effect of dispersal has already been pointed by Holt [6] on particular systems and called *inflation* [7]. 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 [9]. This author considered the model of populations inhabiting patches, and subject to time-periodic exponential growth rates in each patch and symmetric time-independent dispersal between the patches. The aim of this paper is to present some of the results obtained in our previous work [4] in the deterministic case, where we generalized most of the results of [9] to non symmetric and time-dependent dispersal. Note that the results on the DIG phenomenon remain also valid in a stochastic environment [2, 3, 4]. For further details and complements on the mathematical modelling of the DIG phenomenon and the biological motivations, the reader is referred to [2, 6, 7, 8, 9] and the references therein.

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2 Results

We consider 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 functions, so that $r_i(t/T)$ are periodic with period $T > 0$. The dispersal from patch j to patch i ($i \neq j$) is at rate $m\ell_{ij}(t/T)$ where the parameter $m \geq 0$ measures the strength, and $\ell_{ij}(\tau)$, $i \neq j$, are 1-periodic functions, that encode the topology of the dispersal network and the relative rates of dispersal among different patches: If $\ell_{ij}(\tau) = 0$, there is no migration from patch j to patch i at time τ , if $\ell_{ij}(\tau) > 0$, there is a migration. We then have the differential equations

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

This model extends the model considered by [9] where the migration is time-independent and symmetric. The matrix $L(\tau)$ whose off diagonal elements are $\ell_{ij}(\tau)$, $i \neq j$, and diagonal elements $\ell_{ii}(\tau)$ are given by $\ell_{ii}(\tau) = -\sum_{j \neq i} \ell_{ji}(\tau)$, $1 \leq i \leq n$, is called the migration or dispersal matrix. Using the matrix $L(\tau)$, (1) can be written as

$$\frac{dx}{dt} = A(t/T)x, \quad A(\tau) = R(\tau) + mL(\tau) \quad (2)$$

where $x = (x_1, \dots, x_n)^T$ and $R(\tau) = \text{diag}(r_1(\tau), \dots, r_n(\tau))$. We assume that the functions $\tau \mapsto r_i(\tau)$ and $\tau \mapsto \ell_{ij}(\tau)$ are piecewise continuous 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 (1) are continuous and piecewise C^1 functions satisfying (1) except at the points of discontinuity of the functions r_i and ℓ_{ij} . We also assume that for all $\tau \in [0, 1]$, the matrix $L(\tau)$ is *irreducible*. This assumption means that at each time, every patch is reachable from every other patch, either directly or through other patches.

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 , $x_i > 0$. Since the system (2) is a periodic system, its study reduces to the study of its monodromy matrix $\Phi(T)$, where $\Phi(t)$ is the fundamental matrix solution, i.e. the solution of the matrix-valued differential equation $\frac{dX}{dt} = A(t/T)X$, 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*), and is irreducible for all τ , the monodromy matrix $\Phi(T)$ has positive entries. Therefore, by the Perron theorem, it has a dominant eigenvalue (an eigenvalue of maximal modulus, called the *Perron root*), which is positive. We denote it by $\mu(m, T)$, to emphasize its dependence on m and T . We have the following result [4, Proposition 1].

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

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln(x_i(t)) = \Lambda(m, T),$$

where $\Lambda(m, T) := \frac{1}{T} \ln(\mu(m, T))$. The function Λ is analytic in m and T .

In fact $\Lambda(m, T)$ is the maximal Lyapunov exponent of the system. We call it the growth rate of the system (2). Following [9], we say that *dispersal-induced growth* (DIG) occurs if all patches are sinks ($\bar{r}_i := \int_0^1 r_i(\tau) d\tau < 0$ for all i), 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. We have the following result [4, Theorem 2].

Theorem 2. *For $m > 0$, $T > 0$ we have $\Lambda(m, T) \leq \chi$, where $\chi := \int_0^1 \max_{1 \leq i \leq n} r_i(\tau) d\tau$.*

Consider an idealized habitat whose growth rate at time τ , is $\max_{1 \leq i \leq n} r_i(\tau)$, i.e. that of the habitat with maximal growth at this time. Hence χ is the average growth rate in this idealized habitat. If the population

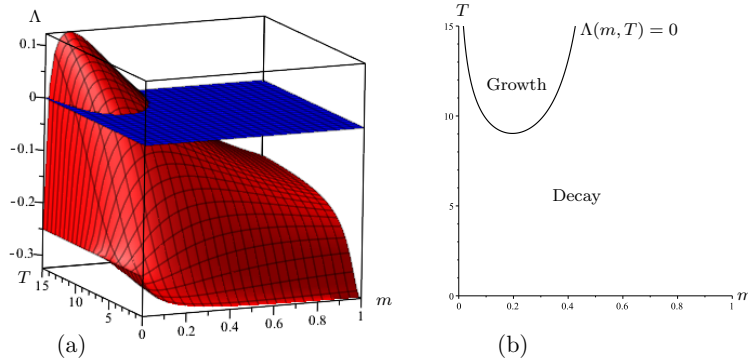


Figure 1: (a) The graph of the function $(m, T) \mapsto \Lambda(m, T)$. (b) The set $\Lambda(m, T) = 0$.

does not grow exponentially in this idealized habitat (i.e. if $\chi \leq 0$), then from Theorem 2 we deduce that DIG does not occur. One of our main results is that the condition $\chi > 0$ which is necessary for DIG to occur is also sufficient. This result follows from the asymptotic behavior of $\Lambda(m, T)$ for large T and small m [4]. We show that $\lim_{m \rightarrow 0} \lim_{T \rightarrow \infty} \Lambda(m, T) = \chi$ so that we have the following result [4, Theorem 6].

Theorem 3. *We have $\sup_{m, T} \Lambda(m, T) = \chi$.*

Therefore, if $\bar{r}_i < 0$ for all i , DIG occurs if and only if $\chi > 0$: a population spreading across sink habitats can grow exponentially (for some values of m and T) if and only if it would survive in the idealized habitat whose growth rate at any time is that of the habitat with maximal growth at this time.

We illustrate this behaviour in Fig. 1 for the two-patch case with time-independent migration given by $\ell_{12} = 2$ and $\ell_{21} = 1$ and growth rates

$$r_1(\tau) = \begin{cases} 1/2 & \text{if } 0 \leq \tau < 1/2 \\ -1 & \text{if } 1/2 \leq \tau < 1 \end{cases}, \quad r_2(\tau) = \begin{cases} -3/2 & \text{if } 0 \leq \tau < 1/2 \\ 1/2 & \text{if } 1/2 \leq \tau < 1 \end{cases}.$$

We have $\chi = 1/2$, $\bar{r}_1 = -1/4$ and $\bar{r}_2 = -1/2$. Therefore, DIG occurs.

3 Discussion

When migration is time-dependent, it is important to see what are the results that remain valid without the assumption of the irreducibility of the matrix migration $L(\tau)$ for all τ . Indeed, this assumption is certainly not realized in many real systems. For instance on a two-patches system with two seasons, if there is migration in one direction in one season and in the other direction in another season, then the matrix $L(\tau)$ would not be irreducible for the times at which migration is in one direction only. What are conditions for DIG when $L(\tau)$ is not irreducible? This question is the subject of future work.

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