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Dispersal-induced growth or decay in a time-periodic environment.

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Abstract

This paper is a follow-up to a previous work where we considered populations with time-varying growth rates living in patches and irreducible migration matrix between the patches. 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. The migration matrix can be reducible, so that the results apply in the case, important for applications, where there is migration in one direction in one season and in the other direction in another season. We also consider dispersal-induced decay (DID), where each population, when isolated, grows exponentially, while populations die out when dispersal between populations is present.

Keywords: Dispersal-induced growth, Dispersal-induced decay, Periodic linear cooperative systems, Principal Lyapunov exponent, Averaging, Singular perturbations, Perron root, Metzler matrices, Sink, Source

MSC Classification: 92D25 , 34A30 , 34C11 , 34C29 , 34E15 , 34D08 , 37N25

Contents

1 Introduction

We considered in [3] the model of populations of sizes $x_i(t)$ $(1 \le i \le n)$, inhabiting n patches, and subject to time-periodic local growth rates $r_i(t)$ $(1 \le i \le n)$, and migration $m\ell_{ij}(t) \ge 0$, from patch j to patch i, where the parameter $m \ge 0$ measures the strength of migration, and the numbers $\ell_{ij}(t)$, $i \ne j$, encode the topology of the dispersal network and the relative rates of dispersal among different patches: At time t, there is a migration from patch j to patch i if and only if $\ell_{ij}(t) > 0$. We then have the differential equations

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

It is assumed that

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

We proved, see [3, Proposition 1] that in the irreducible migration case (i.e. for any t, any two patches are connected by migration, either directly, or through other patches), if $m > 0$, any solution of (1) with $x_i(0) \ge 0$ for $1 \le i \le n$ and $x(0) \ne 0$, satisfies $x_i(t) > 0$ for all $t > 0$. Moreover, the limits

$$\Lambda[x_i] := \lim_{t\to\infty}\frac{1}{t}\ln(x_i(t)), \tag{2}$$

exist are equal, and they do not depend on the initial condition. Their common value is called the growth rate of the system (1). When this property is satisfied, we say that the system *admits a growth rate*, or *the growth rate exists*.

Let $T > 0$. If we replace the time t by t/T in the right-hand side of (1) we obtain the T-periodic linear system:

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

The common value of the $\Lambda[x_i]$ given by (2) is denoted $\Lambda(m,T)$ to recall its dependence on the parameters m and T. The main results in [3] are on the asymptotic properties of $\Lambda(m,T)$ when $T \to 0$ and $T \to \infty$. In particular, it is proved that

$$\lim_{m\to 0}\lim_{T\to\infty}\Lambda(m,T) = \chi, \text{ where } \chi := \int_0^1 \max_{1\le i\le n} r_i(t)dt. \tag{4}$$

Therefore, if $\chi > 0$, $\Lambda(m,T) > 0$ for suitable values of m and T.

A patch is called a *sink* when, in the absence of dispersion ($m = 0$), the population goes to extinction, i.e. $\bar{r}_i = \int_0^1 r_i(t)dt < 0$. In the case where all patches are sinks, it is sometimes possible to find $m > 0$ and $T > 0$ such that $\Lambda(m,T) > 0$, i.e. the population is exponentially growing on each patch. 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 [8], who considered the case of time independent and symmetric migration (i.e. $\ell_{ij} = \ell_{ji}$) and when the functions $r_i(t)$ are continuous.

This surprising phenomenon of populations that can *persist in an environment consisting of sink habitats only* was first studied by Jansen and Yoshimura [7] and has already been pointed by Holt [5] on particular systems and called *inflation* [6]. For further details and complements on the mathematical modelling of this phenomenon and the biological motivations, the reader is referred to [1, 3, 8] and the references therein.

The matrix $L(t)$ whose off diagonal elements are $\ell_{ij}(t)$, $i \neq j$, and diagonal elements $\ell_{ii}(t)$ are given by $\ell_{ii}(t) = -\sum_{j\neq i} \ell_{ji}(t)$, $1 \leq i \leq n$, is called the migration or dispersal matrix. Using the matrix $L(t)$, the equations (3) can be written as

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

$x = (x_1, \cdots, x_n)^\top$, and $R(\tau) = \operatorname{diag}(r_1(\tau), \cdots, r_n(\tau))$. In addition to the assumptions that $L(\tau)$ has non-negative off diagonal elements, it is assumed in [3] that for all t, $L(t)$ is *irreducible.* 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. The aim of this paper is to relax this condition on the irreducibility of the migration matrix and to replace it by the following assumption.

Hypothesis 2. The average migration matrix $\overline{L} = \int_0^1 L(t)dt$ is irreducible.

A sufficient (but non necessary) condition ensuring that $\overline{L}$ is irreducible is that $L(t)$ is irreducible for some $t \in [0,1]$. Therefore, the results in this paper extend the results of [8] where the migration matrix is assumed to be time-independent and irreducible and the results of [3], where $L(t)$ is assumed to be irreducible for all $t \in [0,1]$.

The results of [8] are based on the strict monotonycity of the function $T \mapsto \Lambda(m,T)$, which is true when the matrix L is time independent and symmetric. Indeed, it is strictly increasing, except in the case where all the r_i's are equals (see [8, Lemma 2]). This result follows from general results of Liu et al. [9] on the principal eigenvalue of a periodic linear system. But, as we have shown in [3], the monotonicity of $T \mapsto \Lambda(m,T)$ is no longer true if $L(\tau)$ is not constant. We conjectured in [3] that this function is strictly increasing in the non symmetric constant case. But this conjecture is not true, as it was shown by Monmarché et al. [10].

To prove the results in [3] we used classical methods of dynamical systems theory: the Perron-Frobenius theorem, the method of averaging and Tikhonov's theorem on singular perturbations. The proofs in the more general context of the present paper use the same tools. For example, the existence of the growth rate $\Lambda(m,T)$ follows from Perron-Frobenius's theorem applied to the monodromy matrix, which is nonnegative and irreducible since $\overline{L}$ is irreducible (see Lemma 1, below). The determination of the limits of $\Lambda(m,T)$ as m tends to 0 or infinity, follows the same steps as the proofs in [3] and makes use of the method of averaging and Tikhonov's theorem on singular perturbations (see Appendix A). We discuss the DIG phenomenon in the more general context, where Hypothesis 2 is satisfied. In this paper, we also consider the case of populations in a set of patches, with dispersal among them, that go to extinction, despite the fact that all these patches are sources. We call this phenomenon *dispersal-induced decay* (DID). We determine a family of migration matrices such that

$$\lim_{m\to\infty} \Lambda(m,T) = \sigma, \ \text{where } \sigma := \int_0^1 \min_{1\leq i\leq n} r_i(t)dt. \tag{6}$$

Therefore if $\sigma < 0$, $\Lambda(m,T) < 0$ for suitable values of m and T, and DID occurs if $\bar{r}_i > 0$ for all i.

The paper is organized as follows. In Section 2 we give our main results on the existence of the growth rate and its limits as m and/or T tend to 0 or infinity (some proofs are postponed to Appendix A). In Section 3 and Appendix C, by means of examples of the cases with 2 and 3 patches and piecewise constants growth rates and migration we illustrate our principal results and show how the needed hypothesis can be verified. In Section 4 we discuss the results in more detail and propose some questions for further research. In Appendix B we provide a statement of the theorem of Tikhonov on singular perturbations which is used to prove the asymptotic behavior of the growth rate when the period is large ($T \to \infty$), or the migration rate is large ($m \to \infty$).

2 Results

Throughout the paper, the following notation is 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. We also 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, $x_i > 0$.

Let $\mathcal{M}$ be the set of Metzler $n \times n$ matrices, i.e. having off diagonal nonnegative entries. Let $A : \mathbb{R} \to \mathcal{M}$, be a 1-periodic function. We consider the linear 1-periodic system of differential equations

$$\frac{dx}{dt} = A(t)x, \tag{7}$$

with initial condition $x(0) > 0$, under the following assumptions:

(i) There exist τ_i, $i = 0 \dots N+1$ with $0 = \tau_0 < \tau_1 < \dots < \tau_N < \tau_{N+1} = 1$, such that for $k = 0 \dots N$, $A|_{[\tau_k,\tau_{k+1})}$ are continuous functions, and $\lim_{\tau \to \tau_{k+1}} A(\tau)$ exist.
(ii) The average matrix $\overline{A} = \int_0^1 A(t)dt$ is irreducible.

Assumption (i) implies that the solutions of (7) are continuous and piecewise $\mathcal{C}^1$ functions satisfying (3) except at the points of discontinuity of the function $A(t)$.

2.1 The growth rate

The aim of this section is to show that under Assumptions (i) and (ii), the system (7) admits a growth rate. Since the system (7) is a periodic system, its study reduces to the study of its fundamental matrix solution $X(t)$, i.e. the solution of the matrix-valued differential equation

$$\frac{dX}{dt} = A(t)X, \qquad X(0) = I, \tag{8}$$

where I is the identity matrix. Since $A(t)$ is Metzler, for all $t > 0$, $X(t)$ has non-negative entries.
Lemma 1. *Under Assumptions (i) and (ii), there exists $t_1 > 0$ such that $X(t)$ has positive entries for all $t \geq t_1$.*

Proof. The proof is similar to the proof of [2, Lemma 6(i)]. First observe that $X(t)$ has positive entries if and only if $e^{Rt}X(t)$ has positive entries, for all $R > 0$. Therefore, replacing $A(\tau)$ by $A(\tau) + RId$ for $R > \|A\|_\infty$,[1] we can assume without loss of generality that $A(\tau)$ has nonnegative entries for all $\tau \in [0, 1]$.

Let $x(t) = X(t)x$ with $x \in \mathbb{R}^n_+ \setminus \{0\}$. Suppose $x_i(0) > 0$. Then $x_i(t) > 0$ because $\dot{x}_i(t) \geq A_{ii}(t)x_i(t) \geq 0$. By irreducibility of $\overline{A}$, for all $j \neq i$, there exists a sequence $i_0 = i, i_1, \dots, i_p = j$ such that $\overline{A}_{i_k i_{k-1}} > 0$ for $k = 1, \dots p$. Since $\tau \mapsto A(\tau)$ is periodic, one has, for any integer $N \geq 1$,

$$\frac{1}{N}\int_0^N A(\tau)d\tau = \overline{A}.$$

Therefore, there exists a sequence $t_1 > t_2 > \dots > t_p$ with

$$A_{i_k i_{k-1}}(t_k) > 0.$$

By right continuity of $\tau \mapsto A(\tau)$, we also have $A_{i_k i_{k-1}}(t) > 0$ for $t_k \leq t \leq t_k + \varepsilon$ for some $\varepsilon > 0$. It follows that $\dot{x}_{i_1}(t) \geq A_{i_1,i}(t)x_1(t) > 0$ for all $t_1 \leq t \leq t_1 + \varepsilon$. Hence $x_{i_1}(t) > 0$ for all $t > t_1$. Similarly $x_{i_2}(t) > 0$ for all $t > t_2$ and, by recursion, $x_j(t) > 0$ for all $t > t_p$. In summary, we have shown that for all $i, j \in \{1, \dots, n\}$ there exists a time t_p depending on i, j, such that for all $t \geq t_p$ $x_j(t) > 0$ whenever $x_i(0) > 0$. Hence, for all t sufficiently large, provided $x_i(0) > 0$, one has $x_j(t) > 0$, which implies that the $i - th$ column of $X(t)$ has positive entries, and conclude the proof. ∎

[1] $\|A\|_\infty = \sup_{\tau \in [0,1]} \|A(\tau)\|$ is finite thanks to Assumption (i).

The matrix $X(1)$ is called the monodromy matrix of the system (7). The previous lemma insures that $X(1)^p = X(p)$ has positive entries for an integer $p \geq t_1$. This implies that $X(1)$ is irreducible; otherwise there exists a permutation matrix P such that

$$X(1) = P \begin{pmatrix} U & Y \\ 0 & V \end{pmatrix} P^\top \Longrightarrow X(1)^p = P \begin{pmatrix} U^p & W \\ 0 & V^p \end{pmatrix} P^\top \text{ has zero entries.}$$

By the Perron-Frobenius theorem for irreducible non negative matrices, $X(1)$ has a dominant eigenvalue (an eigenvalue of maximal modulus, called the *Perron-Frobenius root*), which is positive. We denote it by μ. There exists a unique vector, called *Perron-Frobenius vector*, $\pi \gg 0$, such that $\sum_{i=1}^n \pi_i = 1$ and $X(1)\pi = \mu\pi$.

Let $\Delta := \left\{x \in \mathbb{R}_+^n : \sum_{i=1}^n x_i = 1\right\}$ be the unit $n-1$ simplex of $\mathbb{R}_+^n$. The change of variables $\rho = \sum_{i=1}^n x_i$, $\theta = \frac{x}{\rho}$, transforms the system (7) into

$$\frac{d\rho}{dt} = \langle A(t)\theta, \mathbf{1}\rangle\rho, \tag{9}$$

$$\frac{d\theta}{dt} = A(t)\theta - \langle A(t)\theta, \mathbf{1}\rangle\theta. \tag{10}$$

Here $\mathbf{1} = (1, \ldots, 1)^\top$ and $\langle x, \mathbf{1}\rangle = \sum_{i=1}^n x_i$ is the usual Euclidean scalar product of vectors x and $\mathbf{1}$. The equation (10) is a differential equation on Δ.

Theorem 2. *Let Assumptions (i) and (ii) be satisfied. Let μ be the Perron-Frobenius root of the monodromy matrix $X(1)$ of (7). Let $\pi \in \Delta$, be its Perron-Frobenius vector. Let $\Lambda := \ln(\mu)$. The solution $\theta^*(t)$ of (10), such that $\theta^*(0) = \pi$, is a 1-periodic solution, and is globally asymptotically stable. Moreover, if $x(t)$ is a solution of (7) such that $x(0) > 0$, then $x(t) \gg 0$ for all $t \geq t_1$ (where t_1 is as in Lemma 1) and, for all i,*

$$\lim_{t\to\infty} \frac{1}{t} \ln(x_i(t)) = \int_0^1 \langle A(\tau)\theta^*(\tau), \mathbf{1}\rangle d\tau = \Lambda. \tag{11}$$

Proof. The proof is given in Section A.1. □

Corollary 3. *The following inequalities are true: $\sigma \leq \Lambda \leq \chi$, where*

$$\sigma = \overline{\min_{1\leq i\leq n} \textstyle\sum_{j=1}^n A_{ji}}, \quad \chi = \overline{\max_{1\leq i\leq n} \textstyle\sum_{j=1}^n A_{ji}} \tag{12}$$

Proof. For all $t \geq 0$ and $\theta \in \Delta$,

$$\min_{1\leq i\leq n} \sum_{j=1}^n A_{ji}(t) \leq \langle A(t)\theta, \mathbf{1}\rangle \leq \max_{1\leq i\leq n} \sum_{j=1}^n A_{ji}(t)$$

and the result follows from the integral representation (11) of Λ. □

Let $T > 0$. If we replace the time t by t/T in the right-hand side of (7) we obtain the T-periodic linear system:

$$\frac{dx}{dt} = A(t/T)x, \tag{13}$$

The change of variables

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

transforms (7) and the corresponding matrix-valued equation (8) into the equations

$$\frac{dy}{d\tau} = TA(\tau)y, \qquad \frac{dY}{d\tau} = TA(\tau)Y. \tag{14}$$

These equations are 1-periodic. Therefore, Theorem 2 has the following corollary.

Corollary 4. *Let Assumptions (i) and (ii) be satisfied. Let $\mu(T)$ be the Perron-Frobenius root of the monodromy matrix $X(T)$ of (13). Let $\Lambda(T) := \frac{1}{T}\ln(\mu)$. If $x(t)$ is a solution of (13) such that $x(0) > 0$, then $x(t) \gg 0$ for all t large enough, and, for all i,*

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

Proof. Using Theorem 2, for any solution $y(\tau)$ of (14), such that $y(0) > 0$, $y(\tau) \gg 0$ for all τ large enough and

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

where $\mu(T)$ is the Perron root of the monodromy matrix $Y(1) = X(T)$. Since

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

we deduce that for all i, $\lim_{t\to\infty} \frac{1}{t} \ln(x_i(t)) = \frac{1}{T} \ln(\mu(T)) =: \Lambda(T)$. □

2.2 Fast and slow regimes

The aim of this section is to determine the limits of the growth rate $\Lambda(T) := \frac{1}{T} \ln(\mu(T))$ for small and large T.

Using assumption (ii), by the Perron-Frobenius theorem (applied to $\overline{A} + rI$ for $r > 0$ sufficiently large), the spectral abscissa of $\overline{A}$, i.e. the largest real part of its eigenvalues, is an eigenvalue of $\overline{A}$ and is denoted $\lambda_{max}(\overline{A})$.

Theorem 5. *Let Assumptions (i) and (ii) be satisfied. The growth rate of (14) satisfies*

$$\lim_{T\to 0} \Lambda(T) = \lambda_{max}(\overline{A}). \tag{15}$$

Proof. The proof is given in Section A.2. □

Since the matrix $A(\tau)$ is Metzler, the Perron theorem (applied to $A(\tau) + rI$ for $r > 0$ sufficiently large), the spectral abscissa $\lambda_{max}(A(\tau))$ is an eigenvalue of $A(\tau)$ and it admits a non negative eigenvector $v(\tau) \in \Delta$. Note that in contrast with the case where the matrix $A(\tau)$ is irreducible, considered in [3], $\lambda_{max}(A(\tau))$ is not necessarily simple (i.e. of algebraic multiplicity 1), we do not have $v(\tau) \gg 0$ and there are possibly other nonnegative eigenvectors for $A(\tau)$, corresponding to other eigenvalues. We have the following result:

Lemma 6. *The eigenvector $v(\tau)$ is an equilibrium point of the autonomous differential equation on the simplex Δ*

$$\frac{d\theta}{dt} = F(\tau, \theta), \qquad \text{where } F(\tau, \theta) = A(\tau)\theta - \langle A(\tau)\theta, \mathbf{1}\rangle\theta. \tag{16}$$

In this equation, $\tau \in [0, 1]$ is considered as a parameter.

Proof. Since $A(\tau)v(\tau) = \lambda_{max}(A(\tau))v(\tau)$ and $\langle v(\tau), \mathbf{1}\rangle = 1$,

$$\begin{aligned} F(\tau, v(\tau)) &= A(\tau)v(\tau) - \langle A(\tau)v(\tau), \mathbf{1}\rangle v(\tau) \\ &= \lambda_{max}(A(\tau))v(\tau) - \lambda_{max}(A(\tau))v(\tau) = 0. \end{aligned}$$

Therefore $v(\tau)$ is an equilibrium of (16). □

We make the following assumption.

Hypothesis 3. We assume that $v(\tau)$ is asymptotically stable for the differential equation (16) and has a basin of attraction which is uniform with respect to the parameter $\tau \in [0, 1]$.

More precisely, the condition of uniformity with respect to τ means that for each subdivision interval $[\tau_k, \tau_{k+1})$ on which the system is continuous, $v(\tau)$ is asymptotically stable and has a basin of attraction which is uniform with respect to the parameter $\tau \in [\tau_k, \tau_{k+1})$ and, for $\tau = \tau_k$, the basin of attraction of $v(\tau_k)$ contains the limit at right

$$v(\tau_k - 0) = \lim_{\tau\to\tau_k, \tau<\tau_k} v(\tau).$$

For more information on this hypothesis, we refer the reader to Appendix B. Moreover, in Section 3 and Appendix C, we present several examples of how this assumption can be verified, as well as a case where it is not.

Theorem 7. *Let Assumptions (i) and (ii) be satisfied. Assume that Hypothesis 3 is satisfied. The growth rate of (14) satisfies*

$$\lim_{T\to\infty} \Lambda(T) = \overline{\lambda_{max}(A)} \tag{17}$$

Proof. The proof is given in Section A.3. □

2.3 Low and high migration rate

We now consider the special case of (5), where $A(\tau) = R(\tau) + mL(\tau)$. Note that if Hypotheses 1 and 2 are satisfied, then Assumptions (i) and (ii) are satisfied, so that Theorem 2 applies and asserts that the system (5) has a growth rate given by

$$\Lambda(m,T) = \frac{1}{T}\ln(\mu(m,T)),$$

where $\mu(m,T)$ is the Perron-Frobenius root of the monodromy matrix $X(m,T)$ of (5). The aim of this section is to determine the limits of the growth rate $\Lambda(m,T)$ for small and large m.

For a low migration rate, we have the following result.

Proposition 8. *Assume that Hypotheses 1 and 2 are satisfied. For all $T > 0$, the growth rate $\Lambda(m,T)$ of (5) satisfies*

$$\Lambda(0,T) := \lim_{m\to 0}\Lambda(m,T) = \max_i \overline{r}_i. \tag{18}$$

Proof. The proof is the same as the proof of [3, Eq. (14)]. Indeed, the proof in [3] only uses the continuous dependence of the solutions of (5) on the parameter m. For the details, we refer the reader to [3, Section 5.5]. □

For a high migration rate, we need an additional assumption. We recall that 0 is the spectral abscissa of $L(\tau)$. It is an eigenvalue of $L(\tau)$ and it admits a non negative eigenvector $p(\tau) \in \Delta$. Note that $p(\tau)$ is an equilibrium point of the differential equation on the simplex Δ

$$\frac{d\eta}{ds} = L(\tau)\eta, \tag{19}$$

where $\tau \in [0,1]$ is considered as a parameter.

Hypothesis 4. We assume that $p(\tau)$ is asymptotically stable for the differential equation (19) and has a basin of attraction which is uniform with respect to the parameter $\tau \in [0,1]$.

As in Hypothesis 3, the condition of uniformity with respect to τ means that for each subdivision interval $[\tau_k, \tau_{k+1})$ on which the system is continuous, $p(\tau)$ is asymptotically stable and has a basin of attraction which is uniform with respect to the parameter $\tau \in [\tau_k, \tau_{k+1})$ and, for $\tau = \tau_k$, the basin of attraction of $p(\tau_k$ contains the limit at right

$$p(\tau_k - 0) = \lim_{\tau\to\tau_k, \tau<\tau_k} p(\tau).$$

In Section 3 and Appendix C, we present several examples of how this assumption can be verified, as well as a case where it is not. We have the following result

Theorem 9. *Assume that Hypotheses 1, 2 and 4 are satisfied. Then, for all $T > 0$ the growth rate $\Lambda(m,T)$ of (5) satisfies*

$$\Lambda(\infty,T) := \lim_{m\to\infty}\Lambda(m,T) = \sum_{i=1}^{n}\overline{p_i r_i}. \tag{20}$$

Proof. The proof is given in Section A.4. □

2.4 Double limits

In [8] and [3] the main tool to study the DIG phenomenon is the computation of the double limit (4). Let us prove that this formula is also true in the more general context of this paper. According to Theorem 7, the limit

$$\Lambda(m,\infty) := \lim_{T\to\infty}\Lambda(m,T) = \overline{\lambda_{max}\left(R + mL\right)} \tag{21}$$

exists when Hypotheses 1, 2, and 3 are satisfied.

Proposition 10. *Assume that Hypotheses 1, 2, and 3 are satisfied. Then,*

$$\lim_{m\to 0}\Lambda(m,\infty) = \chi, \tag{22}$$

where $\chi = \overline{\max_{1\le i\le n} r_i}$ is defined by (4).

Proof. The proof is the same as the proof of [3, Eq. (17)]. Indeed, the proof in [3] for $\lim_{m\to 0}\Lambda(m,\infty)$ only uses the continuity of the spectral abscissa. For the details, we refer the reader to [3, Section 5.7]. $\square$

According to Theorem 5, the limit

$$\Lambda(m,0) := \lim_{T\to 0}\Lambda(m,T) = \lambda_{max}\left(\overline{R+mL}\right) \tag{23}$$

exists when Hypotheses 1 and 2 are satisfied. We determine now the limits of $\Lambda(m,0)$ as m tends to 0 or infinity.

Proposition 11. *Assume that Hypotheses 1 and 2 are satisfied. Then,*

$$\lim_{m\to 0}\Lambda(m,0) = \max_i \overline{r}_i, \tag{24}$$

and

$$\lim_{m\to\infty}\Lambda(m,0) = \sum_{i=1}^{n} q_i\overline{r}_i, \tag{25}$$

where $q \gg 0$ in the Perron vector of $\overline{L}$, i.e. $q\in\Delta$ and $\overline{L}q = 0$. Moreover, if $\overline{r}_i = \overline{r}$, for all i, $\Lambda(m,0) = \overline{r}$ for all $m > 0$, and, if the $\overline{r}_i$ are not equal,

$$\frac{d}{dm}\Lambda(m,0) < 0, \quad \frac{d^2}{dm^2}\Lambda(m,0) > 0. \tag{26}$$

Proof. For (24) and (25), the proof is the same as the proof of [3, Eq. (16)]. Indeed, the proof in [3] for $\lim_{m\to 0}\Lambda(m,0)$ only uses the continuity of the spectral abscissa, and the proof in [3] for $\lim_{m\to\infty}\Lambda(m,0)$ only use the fact that $\overline{L}$ is irreducible. Moreover, for (26), the proof is the same as the proof of [3, Eq. (18)]. Indeed, the proof in [3] for the first and second derivatives of $\Lambda(m,0)$ only uses the fact that $\overline{L}$ is irreducible. For the details, we refer the reader to [3, Section 5.7]. $\square$

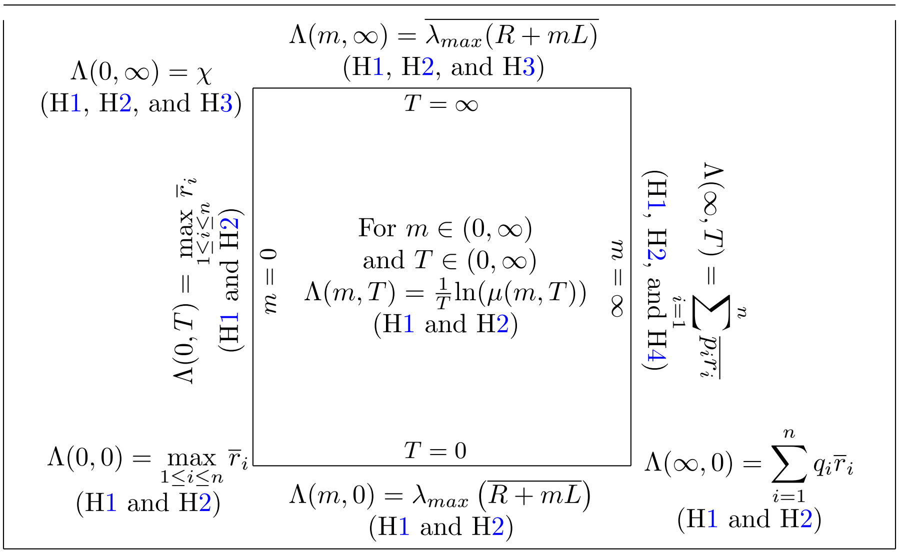

Fig. 1 The hypotheses under which the growth rate exists and its limits can be determined. Compare with [3, Fig. 1], which was obtained under H1 and the assumption that the matrix $L(\tau)$ is irreducible for all $\tau\in[0,1]$.

The results given by (18), (20), (21), (22), (23), (24), and (25) extend the results given [3] and are summarized in Figure 1.

Remark 1. Note that in the special case considered in [3],

$$\Lambda(\infty,\infty) := \lim_{m\to\infty}\Lambda(m,\infty) = \sum_{i=1}^{n}\overline{p_i r_i}, \tag{27}$$

see [3, Eq. (17)]. On the other hand, if $r_i(\tau) = r(\tau)$, for all i, $\Lambda(m,T) = \overline{r}$ for all $m > 0$ and $T > 0$, and, if the growth rates are not equal,

$$\frac{d}{dm}\Lambda(m,\infty) < 0, \quad \frac{d^2}{dm^2}\Lambda(m,\infty) > 0, \tag{28}$$

see [3, Eq. (19)]. However, the proofs of (27) and (28) use the irreducibility of $L(\tau)$, and these results are not always satisfied in the case where only Hypothesis 2 is satisfied.

2.5 Dispersal induced growth

Following [3, 8], we say that dispersal-induced growth (DIG) occurs if all patches are sinks ($\overline{r}_i < 0$ for all i), but $\Lambda(m,T) > 0$ for some values of m and T.

Theorem 12. *Assume that Hypotheses 1 and 2 are satisfied. For all $m > 0$ and $T > 0$, $\sigma \leq \Lambda(m,T) \leq \chi$, where*

$$\sigma = \int_0^1 \min_{1\leq i\leq n} r_i(t)dt, \quad \chi = \int_0^1 \max_{1\leq i\leq n} r_i(t)dt. \tag{29}$$

Proof. Since the ith column of $A(t) = R(t) + mL(t)$ sums to $r_i(t)$, the numbers σ and χ defined by (12) are given by (29) and the result follows from Corollary 3. □

According to Theorem 12, a necessary condition for DIG to occur is $\chi > 0$. In fact, this condition is also sufficient, as shown by the following result.

Theorem 13. *Assume that $\chi > 0$. For all migration matrices satisfying Hypotheses 1, 2 and 3, there exist $m > 0$ and $T > 0$ such that $\Lambda(m,T) > 0$. Therefore, if $\overline{r}_i < 0$ for all i, DIG occurs if and only if $\chi > 0$.*

Proof. The result follows from

$$\sup_{m>0,T>0} \Lambda(m,T) = \chi,$$

which is an consequence of (22) and Theorem 12 □

Theorem 13 extends the result of [3, Theorem 6] to the case where the irreducibility of the migration matrix is replaced by the weaker Hypotheses 2 and 3 of the present paper.

2.6 Dispersal induced decay

We say that dispersal-induced decay (DID) occurs if all patches are sources ($\overline{r}_i > 0$ for all i), but $\Lambda(m,T) < 0$ for some values of m and T. According to Theorem 12, a necessary condition for DID to occur is $\sigma < 0$.

Remark 2. Theorem 13 follows from the fact that χ, the upper bound of $\Lambda(m,T)$, is in fact its supremum. There is no similar result when $\sigma < 0$, because the lower bound σ of $\Lambda(m,T)$ is far from being its infimum. Indeed, if the migration matrix L is time independent, then from [3, Theorem 10],

$$\inf_{m>0,T>0} \Lambda(m,T) = \sum_1^n q_i\overline{r}_i,$$

where q_i is the Perron vector of $L = \overline{L}$, and, in general, $\sigma < \sum_1^n q_i\overline{r}_i$. In particular, if $\overline{r}_i > 0$ for all i, DID cannot occur if the migration matrix is time independent.

Our aim now is to describe a class of local growth functions $r_i(t)$ satisfying Hypothesis 1, such that there exist migration matrices for which

$$\inf_{m>0,T>0} \Lambda(m,T) = \sigma.$$

Therefore, for this class of growth functions, if $\overline{r}_i > 0$ for all i, and $\sigma < 0$, DID occurs.

We make the following assumption.

Hypothesis 5. Let $[\tau_k, \tau_{k+1}] \subset [0,1]$ be an interval on which the functions $r_i(\tau)$ are continuous. Assume that there exist a finite subdivision of this interval, such that, when t is in an interval of the subdivision, $\min_{1\leq i\leq n} r_i(t)$ is obtained for some index, denoted $i_k(t)$. More precisely, we assume that there exist $\tau_k = t_0^k < \ldots < t_{l_k}^k = \tau_{k+1}$ and a piecewise constant function $i_k : [\tau_k, \tau_{k+1}) \to \{1,\ldots,n\}$, such that,

$$\text{for } j = 0,\ldots,l_k - 1, \text{ we have } t \in [t_j^k, t_{j+1}^k) \Longrightarrow \min_{1\leq i\leq n} r_i(t) = r_{i_k(t)}. \tag{30}$$

This assumptions is satisfied if the growth functions are piecewise constant, and also in the case where there are not rapid oscillations. For example in the two patches case ($n = 2$), the growth functions $r_1(t)$ defined on $[0,1]$ by $r_1(t) = t\sin\left(\frac{2\pi(1-t)}{t}\right)$ and $r_2(t) = 0$ do not satisfy (30). We have the following result.

Theorem 14. *Assume that the $r_i(t)$ satisfy Hypotheses 1 and 5, and $\sigma < 0$. There exist migration matrices satisfying Hypotheses 1 and 2, and there exist $m > 0$ and $T > 0$ such that $\Lambda(m,T) < 0$. Therefore, if $\overline{r}_i > 0$ for all i, and $\sigma < 0$, DID can occur.*

Proof. Let $L(t)$ be the migration matrix for which migration is only to a site that achieves the minimum $r_i(t)$. Using the notations in Hypothesis 5, $L(t) = (\ell_{ij}(t))$ is defined as follows:

$$\text{If } j \neq i \text{ and } t \in [t_j^k, t_{j+1}^k),\ \text{ then } \ell_{ij}(t) = \begin{cases} 1 \text{ if } i = i_k(t) \text{ and } j \neq i, \\ 0 \text{ if } i \neq i_k(t) \text{ and } j \neq i. \end{cases} \tag{31}$$

Two cases must be distinguished.

- Case 1: For any index i, there exist $k = 0 \ldots N$ and $t \in [\tau_k, \tau_{k+1})$ such that $r_i(t)$ is the minimum of the $r_j(t)$, $1 \leq j \leq n$, i.e. $i = i_k(t)$. In this case, the averaged matrix $\overline{L}$ has positive off-diagonal elements, and is therefore irreducible.
- Case 2: There is a subset I of indices that never achieve the minimum of $r_i(t)$. In this case we add to one of the matrices $L(t)$ small migration terms to the sites $i \in I$. More precisely, on the first interval subdivision $[t_0^0, t_1^0)$, with $t_0^0 = 0$, we consider the migration matrix defined as follows:

$$\text{If } j \neq i \text{ and } t \in [t_0^0, t_1^0),\ \text{ then } \ell_{ij}(t) = \begin{cases} 1 \text{ if } i = i_0(t) \text{ and } j \neq i, \\ \varepsilon \text{ if } i \in I \text{ and } j \neq i, \\ 0 \text{ if } i \neq i_0(t), i \notin I \text{ and } j \neq i. \end{cases} \tag{32}$$

  For the other interval subdivision $[t_j^k, t_{j+1}^k)$, with $(j,k) \neq (0,0)$, we define the migration matrix by (31). In this case, the averaged matrix $\overline{L}$ has positive off-diagonal elements, and hence, it is irreducible.

Therefore, the migration matrix $L(t)$ satisfies Hypotheses 1 and 2, and consequently $\Lambda(m,T)$ exists. We can see that this migration matrix also satisfy Hypothesis 4. Indeed, in Case 1, the migration matrix is defined by (31), and its Perron vector is the vector $p(\tau)$ defined by

$$p_i(\tau) = \begin{cases} 1 \text{ if } i = i_k(\tau), \\ 0 \text{ if } i \neq i_k(\tau). \end{cases}$$

Moreover, $p(t)$ is the unique eigenvector in the simplex, and hence, it is GAS for the differential equation (19). Using Theorem 9,

$$\lim_{m\to\infty} \Lambda(m,T) = \sum_{i=1}^{n} \overline{p_i r_i} = \overline{\min_{1\leq j\leq n} r_j} = \sigma.$$

In Case 2, if $(j,k) \neq (0,0)$, the migration matrix is defined by (31) for $t \in [t_j^k, t_{j+1}^k)$. For $t \in [t_0^0, t_1^0)$, it is defined by (32). In this first subdivision interval, its Perron vector is the vector $p(\tau)$ defined by

$$p_i(\tau) = \begin{cases} 1 \text{ if } i = i_0(\tau), \\ \varepsilon \text{ if } i \in I, \\ 0 \text{ if } i \neq i_0(\tau) \text{ and } i \notin I. \end{cases}$$

Moreover, $p(\tau)$ is the unique eigenvector in the simplex, and hence, it is GAS for the differential equation (19). Using Theorem 9,

$$\lim_{m\to\infty} \Lambda(m,T) = \sum_{i=1}^{n} \overline{p_i r_i} = \overline{\min_{1\leq j\leq n} r_j} + \varepsilon \sum_{i\in I} \int_{t_0^0}^{t_1^0} \overline{r_i} = \sigma + \varepsilon \sum_{i\in I} \int_{t_0^0}^{t_1^0} \overline{r_i}.$$

Therefore, if $\sigma < 0$, there exist $m > 0$ and $T > 0$ such that $\Lambda(m,T) < 0$. $\square$

3 Examples

3.1 Two patches case

3.1.1 Unidirectional migration to the most unfavourable patch

Consider the case of two patches, where the growth rates are defined by

$$r_1(\tau) = \begin{cases} a_1 \text{ if } 0 \le \tau < 1/2, \\ b_1 \text{ if } 1/2 \le \tau < 1, \end{cases} \qquad r_2(\tau) = \begin{cases} b_2 \text{ if } 0 \le \tau < 1/2, \\ a_2 \text{ if } 1/2 \le \tau < 1. \end{cases} \tag{33}$$

Hence, $\overline{r}_i = \frac{a_i+b_i}{2}$, $i = 1, 2$. We assume that $a_1 \ge b_1$ and $a_2 \ge b_2$, and we consider an unidirectional migration to the most unfavourable patch, i.e. the patch with growth rate b_i, defined by the matrix

$$L(\tau) = \begin{bmatrix} -1 & 0 \\ 1 & 0 \end{bmatrix} \text{ for } \tau \in [0, 1/2) \quad \text{and} \quad L(\tau) = \begin{bmatrix} 0 & 1 \\ 0 & -1 \end{bmatrix} \text{ for } \tau \in [1/2, 1). \tag{34}$$

Proposition 15. *The system with growth rates (33), where $a_1 \ge b_1$ and $a_2 \ge b_2$, and migration matrix (34), admits a growth rate $\Lambda(m, T)$ and*

$$\begin{aligned} &\Lambda(0, T) = \max(\overline{r}_1, \overline{r}_2), \quad \Lambda(\infty, T) = \tfrac{b_1+b_2}{2}, \\ &\Lambda(m, 0) = \tfrac{1}{2}\left(\overline{r}_1 + \overline{r}_2 - m + \sqrt{(\overline{r}_1 - \overline{r}_2)^2 + m^2}\right), \\ &\Lambda(0, 0) = \max(\overline{r}_1, \overline{r}_2), \quad \Lambda(\infty, 0) = \tfrac{\overline{r}_1+\overline{r}_2}{2}. \end{aligned}$$

Moreover, if $a_1 \ge b_2$ and $a_2 \ge b_1$, then $\sigma = \frac{b_1+b_2}{2}$ and $\chi = \frac{a_1+a_2}{2}$, and

$$\Lambda(m, \infty) = \begin{cases} \chi - m & \text{if } 0 < m < a_1 - b_2, \\ \frac{a_2+b_2-m}{2} & \text{if } a_1 - b_2 \le m \le a_2 - b_1, \\ \sigma & \text{if } m > a_2 - b_1, \end{cases}$$

where we assumed, without loss of generality, that $a_1 - b_2 \le a_2 - b_1$, i.e. $\overline{r}_1 \le \overline{r}_2$.

Proof. Since $\overline{L}$ is irreducible, from Theorem 2 we deduce that $\Lambda(m, T)$ exists. From Proposition 8 we deduce that $\Lambda(0, T) = \max(\overline{r}_1, \overline{r}_2)$.

On the other hand, the Perron-Frobenius vector $p(\tau) = (p_1(\tau), p_2(\tau))$ of $L(\tau)$ is given by

$$p_1(\tau) = \begin{cases} 0 \text{ if } \tau \in [0, 1/2), \\ 1 \text{ if } \tau \in [1/2, 1), \end{cases} \qquad p_2(\tau) = \begin{cases} 1 \text{ if } \tau \in [0, 1/2), \\ 0 \text{ if } \tau \in [1/2, 1). \end{cases}$$

We can see that Hypothesis 4 is satisfied. Indeed the differential system on the simplex, parametrized by $\theta_1 \in [0, 1]$, corresponding to the matrix $L(\tau)$ is

$$\frac{d\theta_1}{dt} = -\theta_1, \quad \text{for } \tau \in [0, 1/2), \quad \frac{d\theta_1}{dt} = 1 - \theta_1, \quad \text{for } \tau \in [1/2, 1),$$

It admits an equilibrium which is GAS in the simplex. This equilibrium is $\theta_1 = 0$, and hence $p(\tau) = (0, 1)$, for $\tau \in [0, 1/2)$. This equilibrium is $\theta_1 = 1$, and hence $p(\tau) = (1, 0)$, for $\tau \in [1/2, 1)$. Using Theorem 9, $\Lambda(\infty, T) = \overline{p_1 r_1 + p_2 r_2} = \frac{b_1+b_2}{2}$.

Now we prove the formulas for $\Lambda(m, 0)$ and its limits when $m \to 0$ and $m \to \infty$. The matrix $A(\tau)$ is defined by

$$A(\tau) = \begin{cases} A_1 \text{ if } 0 \le \tau < 1/2 \\ A_2 \text{ if } 1/2 \le \tau < 1 \end{cases}, \text{ with } A_1 = \begin{bmatrix} a_1 - m & 0 \\ m & b_2 \end{bmatrix}, \; A_2 = \begin{bmatrix} b_1 & m \\ 0 & a_2 - m \end{bmatrix}.$$

The average of $A(\tau)$ is

$$\overline{A} = \begin{bmatrix} \overline{r}_1 - m/2 & m/2 \\ m/2 & \overline{r}_2 - m/2 \end{bmatrix}$$

Using Theorem 5,

$$\Lambda(m, 0) = \lambda_{max}(\overline{A}) = \frac{1}{2}\left(\overline{r}_1 + \overline{r}_2 - m + \sqrt{(\overline{r}_1 - \overline{r}_2)^2 + m^2}\right).$$

The results for the limits of $\Lambda(m,0)$ as $m \to 0$ and $m \to \infty$ can be obtained by taking the limits in this formula. They can also be obtained using Proposition 11. Indeed, the Perron-Frobenius vector q of $\overline{L}$ is given by $q_1 = q_2 = 1/2$. Hence,

$$\Lambda(0,0) = \max\left(\overline{r}_1, \overline{r}_2\right), \quad \Lambda(\infty, 0) = \frac{\overline{r}_1 + \overline{r}_2}{2}.$$

Now we prove the formulas for $\Lambda(m,\infty)$. The eigenvalues of A_1 are $a_1 - m$ and b_2 and those of A_2 are $a_2 - m$ and b_1. Assume that $a_1 \geq b_2$ and $a_2 \geq b_1$. Then,

$$\lambda_{max}(A_1) = \begin{cases} a_1 - m & \text{if } 0 < m < a_1 - b_2, \\ b_2 & \text{if } m \geq a_1 - b_2, \end{cases} \quad \lambda_{max}(A_2) = \begin{cases} a_2 - m & \text{if } 0 < m < a_2 - b_1, \\ b_1 & \text{if } m \geq a_2 - b_1. \end{cases}$$

Without loss of generality, we assumed that $a_1 - b_2 \leq a_2 - b_1$.

If $0 < m < a_1 - b_2$, then $\lambda_{max}(A_1) = a_1 - m$, $\lambda_{max}(A_2) = a_2 - m$, and their corresponding Perron-Frobenius vectors are given by

$$v_1 = \left(\frac{a_1 - b_2 - m}{a_1 - b_2}, \frac{m}{a_1 - b_2}\right), \quad v_2 = \left(\frac{m}{a_2 - b_1}, \frac{a_2 - b_1 m}{a_2 - b_1}\right), \tag{35}$$

respectively. Let us prove that Hypothesis 3 is satisfied. Indeed the differential system on the simplex (parametrized by $\theta_2 \in [0,1]$), corresponding to the matrix A_1, is

$$\frac{d\theta_2}{dt} = (1 - \theta_2)(m - (a_1 - b_2)\theta_2). \tag{36}$$

Since $0 < m < a_1 - b_2$, it admits $\theta_2 = 1$ and $\theta_2 = \frac{m}{a_1 - b_2} \in (0,1)$ as equilibria, the first being unstable and the second being globally asymptotically stable in the interior of the simplex. Therefore, v_1 is GAS in the interior of the simplex. Similarly, the differential system on the simplex (parametrized by $\theta_1 \in [0,1]$), corresponding to the matrices A_2, is

$$\frac{d\theta_1}{dt} = (1 - \theta_1)(m - (a_2 - b_1)\theta_1). \tag{37}$$

Since $0 < m < a_2 - b_1$, it admits $\theta_1 = 1$ and $\theta_1 = \frac{m}{a_2 - b_1} \in (0,1)$ as equilibria, the first being unstable and the second being globally asymptotically stable in the interior of the simplex. Therefore, v_2 is GAS in the interior of the simplex. Using Theorem 7,

$$\Lambda(m,\infty) = \frac{\lambda_{max}(A_1) + \lambda_{max}(A_2)}{2} = \frac{a_1 - m + a_2 - m}{2} = \chi - m.$$

If $a_1 - b_2 < m < a_2 - b_1$, then $\lambda_{max}(A_1) = b_2$, $\lambda_{max}(A_2) = a_2 - m$, and their corresponding Perron-Frobenius vectors are given by $v_1 = (0,1)$ and v_2 given by (35), respectively. We have already seen that v_2 is GAS for the differential equation (37). Since $m > a_1 - b_2$, the differential equation (36) admits only $\theta_2 = 1$ as a GAS equilibrium. Therefore, $v_1 = (0,1)$ is GAS in the interior of the simplex. Using Theorem 7,

$$\Lambda(m,\infty) = \frac{\lambda_{max}(A_1) + \lambda_{max}(A_2)}{2} = \frac{b_2 + a_2 - m}{2}.$$

Finally, if $m > a_2 - b_1$, then $\lambda_{max}(A_1) = b_2$, $\lambda_{max}(A_2) = b_1$, and their corresponding Perron-Frobenius vectors are given by $v_1 = (0,1)$ and $v_2 = (1,0)$, respectively. We have already seen that v_1 is GAS for the differential equation (36). Since $m > a_2 - b_1$, the differential equation (37) admits only $\theta_1 = 1$ as a GAS equilibrium. Therefore, $v_2 = (1,0)$ is GAS in the interior of the simplex. Using Theorem 7,

$$\Lambda(m,\infty) = \frac{\lambda_{max}(A_1) + \lambda_{max}(A_2)}{2} = \frac{b_2 + b_1}{2} = \sigma.$$

This ends the proof for the formulas giving $\Lambda(m,\infty)$. □

3.1.2 Unidirectional migration to the most favourable patch

In the previous example the migration is unidirectional from the patch where the local growth rate is a_i to the patch where it is $b_i \leq a_i$. Let us consider the opposite situation where the migration is unidirectional to the patch where the local growth rate is a_i. For this purpose we use the migration matrix

$$L(\tau) = \begin{bmatrix} 0 & 1 \\ 0 & -1 \end{bmatrix} \text{ for } \tau \in [0, 1/2) \quad \text{and} \quad L(\tau) = \begin{bmatrix} -1 & 0 \\ 1 & 0 \end{bmatrix} \text{ for } \tau \in [1/2, 1). \tag{38}$$

We have the following result whose proof is similar to the proof of Proposition 15.

Proposition 16. *The system with growth rates (33), where $a_1 \geq b_1$ and $a_2 \geq b_2$, and migration matrix (38) admits a growth rate $\Lambda(m,T)$ and we have the same formulas for $\Lambda(0,T)$ and $\Lambda(m,0)$ as in Proposition 15, while the limit $\Lambda(\infty,T)$ is now given by $\Lambda(\infty,T) = \frac{a_1+a_2}{2}$. Moreover, if $a_1 \geq b_2$ and $a_2 \geq b_1$, then $\sigma = \frac{b_1+b_2}{2}$ and $\chi = \frac{a_1+a_2}{2}$, and, $\Lambda(m,\infty) = \chi$.*

Remark 3. The limit $\Lambda(0,\infty) = \chi$ can be obtained directly from the formulas in Propositions 15 and 16, giving $\Lambda(m,\infty)$ or by using Proposition 10.

Remark 4. Note that from the formulas for $\Lambda(m,\infty)$ in Propositions 15 and 16, we deduce that $\Lambda(\infty,\infty) = \overline{p_1 r_1 + p_2 r_2} = \Lambda(\infty,T)$, a formula which is always true in the case where $L(\tau)$ is irreducible for all τ, see Remark 1. However the strict convexity stated in (28) is note true, since $\Lambda(m,\infty)$ is piecewise linear or constant.

3.1.3 Dispersal induced growth or decay

For the systems considered in Propositions 15 and 16, $\Lambda(0,\infty) = \chi$. Therefore, using Theorem 13, if $\overline{r}_1 < 0$, $\overline{r}_2 < 0$ and $\chi > 0$, then the patches are sinks and DIG occurs. This result rigorously establishes the conclusions made numerically in [3, Section 4.5.1].

The systems considered in Proposition 15 provides examples for which DID can occur. Indeed since $\Lambda(\infty,T) = \sigma$, the lower bound σ of $\Lambda(m,T)$ is its infimum. Hence, if $\overline{r}_1 > 0$, $\overline{r}_2 > 0$ and $\sigma < 0$, then the patches are sources and DID occurs. These systems give an illustration for Theorem 14. To prove this theorem, we have shown that for the migration matrix, which consists at each instant in migrating to the most unfavourable patch, the σ is the limit of $\Lambda(m,T)$ when m tends to infinity. Therefore, if $\sigma < 0$ and m is large enough, $\Lambda(m,T) < 0$.

It should be noted that, for DID to occur, migration need not be to the worst-case patch only. To see this, consider again example (33) with $a_1 = a_2 = a > 0$ and $b_1 = b_2 = b < 0$, such that $a + b > 0$, for which both patches are sources and $\sigma = b < 0$. Consider the migration matrix defined by

$$L(\tau) = \begin{bmatrix} -1 & \varepsilon \\ 1 & -\varepsilon \end{bmatrix} \text{ for } \tau \in [0, 1/2) \quad \text{and} \quad L(\tau) = \begin{bmatrix} -\varepsilon & 1 \\ \varepsilon & -1 \end{bmatrix} \text{ for } \tau \in [1/2, 1),$$

where $\varepsilon > 0$. The Perron-Frobenius vector $p(\tau) = (p_1(\tau), p_2(\tau))$ of $L(\tau)$ is given by

$$p_1(\tau) = \begin{cases} \frac{\varepsilon}{1+\varepsilon} & \text{if } \tau \in [0,1/2), \\ \frac{1}{1+\varepsilon} & \text{if } \tau \in [1/2,1), \end{cases} \qquad p_2(\tau) = \begin{cases} \frac{1}{1+\varepsilon} & \text{if } \tau \in [0,1/2), \\ \frac{\varepsilon}{1+\varepsilon} & \text{if } \tau \in [1/2,1). \end{cases}$$

Using Theorem 9 (or [3, Eq. (15)] since the migration matrix is irreducible),

$$\Lambda(\infty,T) = \overline{p_1 r_1 + p_2 r_2} = \frac{b + \varepsilon a}{1+\varepsilon}.$$

Hence, if $b + \varepsilon a < 0$, DID occurs. This condition means that $\varepsilon < -b/a < 1$. Thus, ε, which represents the migration rate from the unfavourable patch to the favourable patch, is smaller than 1, which represents the migration rate from the favourable patch to the unfavourable patch.

3.2 Three patches case

3.2.1 The threshold χ is positive, but DIG does not occur

We consider the three-patch model described in Fig. 2, which is [3, Fig. 8]. The migration is symmetric and is only between the patches where the growth rate is b.

Proposition 17. *The system defined in Fig. 2 admits a growth rate Λ and*

$$\Lambda(0,T) = \Lambda(m,0) = \frac{a+2b}{3}.$$

Moreover, Hypotheses 3 and 4 are not satisfied and we cannot use Theorems 7 and 9 to determine $\Lambda(m,\infty)$ *and* $\Lambda(\infty,T)$*.*

Proof. The matrix $A(\tau)$ is given by

$$A(\tau) = A_1 := \begin{bmatrix} b-m & m & 0 \\ m & b-m & 0 \\ 0 & 0 & a \end{bmatrix} \text{ for } \tau \in [0,1/3),$$

and similar formulas for $\tau \in [1/3,2/3)$ and $\tau \in [2/3,1)$. The average of the migration matrix is

$$\overline{L} = \begin{bmatrix} -2/3 & 1/3 & 1/3 \\ 1/3 & -2/3 & 1/3 \\ 1/3 & 1/3 & -2/3 \end{bmatrix}$$

It is irreducible. Therefore, the growth rate exists. Using Proposition 8,

$$\Lambda(0,T) = \max\left(\overline{r}_1, \overline{r}_2, \overline{r}_3\right) = \frac{a+2b}{3}.$$

Moreover, the eigenvalues of $\overline{A}$ are $\frac{a+2b}{3}$, $\frac{a+2b}{3} - m$ and $\frac{a+2b}{3} - m$. Using Theorem 5,

$$\Lambda(m,0) = \lambda_{max}\left(\overline{A}\right) = \frac{a+2b}{3}.$$

Let us look at why our Hypothesis 3 is not satisfied. The eigenvalues of A_1 are a, b, and $b-2m$. Since $a \geq b$, the spectral abscissa of A_1 is

$$\lambda_{max}(A_1) = a.$$

The corresponding Perron-Frobenius vector is $v_1 = (0,0,1)$. Note that the matrix has another nonnegative eigenvector, corresponding to its eigenvalue b, and given by $w_1 = (1/2,1/2,0)$. The differential system associated to the matrix A_1 on the simplex Δ, parametrized by θ_1 and θ_2, is

$$\begin{aligned} \tfrac{d\theta_1}{dt} &= m(\theta_2 - \theta_1) + (a-b)(\theta_1+\theta_2-1)\theta_1, \\ \tfrac{d\theta_2}{dt} &= m(\theta_1 - \theta_2) + (a-b)(\theta_1+\theta_2-1)\theta_2. \end{aligned}$$

It admits v_1 and w_1 as equilibria, the first being stable and the second unstable (a saddle point), see

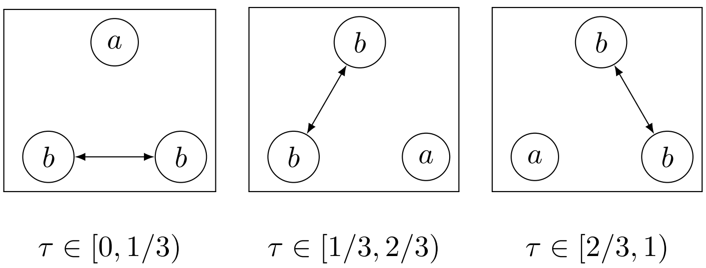

Fig. 2 The three-patch model, where the migration is symmetrical between the worst patches with growth rates $b \leq a$.

Figure 3. Note that the lines $\theta_3 = 0$ and $\theta_1 = \theta_2$ are invariant by the flow. The basin of attraction of v_1 is the subset $\theta_3 > 0$ of the simplex.

When $\tau \in [1/3,2/3)$, we prove that, the differential equation on the simplex admits $v_2 = (0,1,0)$ and $w_2 = (1/2,0,1/2)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is the subset $\theta_2 > 0$ of the simplex. Similarly, when $\tau \in [2/3,1)$, we prove that, the differential equation on the simplex admits $v_3 = (1,0,0)$ and $w_3 = (0,1/2,1/2)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is the subset $\theta_1 > 0$ of the simplex. Note that $v_3 = v(0-0)$ does not belong to the basin of attraction of $v_1 = v(0)$.

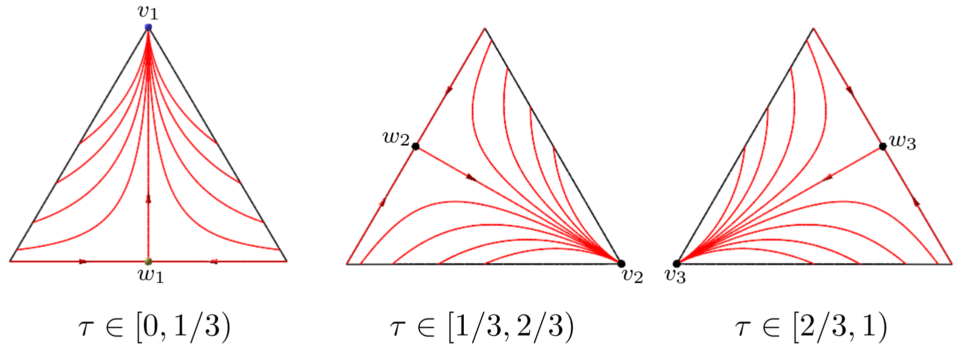

Fig. 3 The flow on the simplex for the system described in Fig. 2. Note that v_3 does not belong to the basin of attraction of v_1, v_1 does not belong to the basin of attraction of v_2 and v_2 does not belong to the basin of attraction of v_3.

Indeed, it is attracted by w_1. Similarly, $v_3 = v(1/3 - 0)$ does not belong to the basin of attraction of $v_2 = v(1/3)$ and $v_2 = v(2/3 - 0)$ does not belong to the basin of attraction of $v_3 = v(2/3)$. Therefore, Hypothesis 3 is not satisfied and Theorem 7 cannot be used to determine the limit $\Lambda(m, \infty)$.

Moreover, the migration matrix corresponding to A_1 is

$$L_1 := \begin{bmatrix} -1 & 1 & 0 \\ 1 & -1 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Its eigenvalues are 0, 0, and -2. Therefore its spectral abscissa 0 is not a simple eigenvalue and Hypothesis 4 is not satisfied. □

We assume that $a > 0 > b$ and $a + 2b < 0$. Therefore $\overline{r}_1 = \overline{r}_2 = \overline{r}_3 = \frac{a+2b}{3} < 0$ and $\chi = a > 0$. Does the DIG phenomenon occurs for this system ? We saw in [3, Section 4.5.2], by numerical simulation, that DIG occurs for $a = 1$, $b = -0.8$, but does not occur when $a = 1$, $b = -1$. In fact, DIG does not occur when $a + b \leq 0$.

Proposition 18. *For all $m > 0$ and $T > 0$,*

$$\Lambda(m, T) \leq \frac{a+b}{2}, \text{ and } \Lambda(\infty, T) := \lim_{m\to\infty} \Lambda(m, T) = \frac{a+b}{2}.$$

Therefore, DIG occurs if and only if $a + b > 0$.

Proof. The proof is given in Section A.5. □

Determining the limit $\Lambda(m, \infty)$ is an open problem. Numerical simulations suggest that $\Lambda(m, \infty) = \frac{a+b}{2}$. It is proved in [4] that

$$\Lambda(0, \infty) := \lim_{m\to 0} \lim_{T\to\infty} \Lambda(m, T) = \frac{a+b}{2},$$

which also proves that DIG occurs if and only if $a + b > 0$, in agreement with simulations presented in [3, Fig. 9]. The system defined in Fig. 2 is an example where $\chi = a > 0$ and DIG does not occur when $a + b \leq 0$.

3.2.2 DIG occurs if and only if $\chi > 0$

We consider the three-patch model described in Fig. 4, where the migration is symmetric and between the patches where the growth rate are a and b, with $a > b$.

Proposition 19. *The system defined in Fig. 4 admits a growth rate Λ and*

$$\Lambda(0, T) = \Lambda(m, 0) = \tfrac{a+2b}{3},$$
$$\Lambda(m, \infty) = \tfrac{1}{2}\left(a + b - 2m + \sqrt{(a-b)^2 + 4m^2}\right), \quad \Lambda(0, \infty) = a.$$

Moreover, Hypothesis 4 is not satisfied and we cannot use Theorem 9 to determine $\Lambda(\infty, T)$.

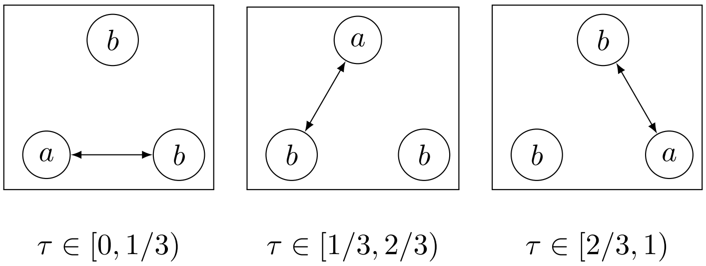

Fig. 4 The three-patch model, where the migration is symmetrical between patches with growth rates $a > b$.

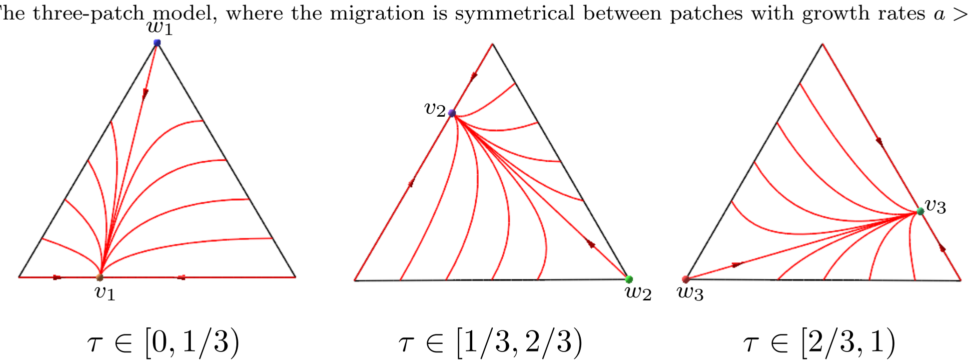

Fig. 5 The flow on the simplex for the system described in Fig. 4. Note that v_3 belongs to the basin of attraction of v_1, v_1 belongs to the basin of attraction of v_2 and v_2 belongs to the basin of attraction of v_3.

Proof. The matrix $A(\tau)$ is given by

$$A(\tau) = A_1 := \begin{bmatrix} a-m & m & 0 \\ m & b-m & 0 \\ 0 & 0 & b \end{bmatrix} \text{ for } \tau \in [0, 1/3),$$

and similar formulas for $\tau \in [1/3, 2/3)$ and $\tau \in [2/3, 1)$. The average of the migration matrix is irreducible. Therefore, the growth rate exists. The proofs for the formulas $\Lambda(0, T)$ and $\Lambda(m, 0)$ are the same as in the proofs of Proposition 17.

The eigenvalues of A_1 are b and $\frac{a+b-2m\pm\sqrt{c}}{2}$, where $c = (a-b)^2 + 4m^2$. We assume that $a > b$. The spectral abscissa of A_1 is

$$\lambda_{max}(A_1) = \frac{a+b-2m+\sqrt{(a-b)^2+4m^2}}{2}.$$

The corresponding Perron-Frobenius vector is $v_1 = (\theta, 1-\theta, 0)$, where

$$\theta = \frac{a-b+2m-\sqrt{(a-b)^2+4m^2}}{2(a-b)}.$$

Note that the matrix has another nonnegative eigenvector, corresponding to its eigenvalue b, and given by $w_1 = (0, 0, 1)$. The differential system associated to the matrix A_1 on the simplex Δ, parametrized by θ_1 and θ_2, is

$$\begin{aligned} \tfrac{d\theta_1}{dt} &= m(\theta_2 - \theta_1) + (a-b)\theta_1(1-\theta_1), \\ \tfrac{d\theta_2}{dt} &= m(\theta_1 - \theta_2) - (a-b)\theta_1\theta_2. \end{aligned}$$

It admits v_1 and w_1 as equilibria, the first being stable and the second unstable (a saddle point), see Figure 5. Note that the line $\theta_3 = 0$ is invariant by the flow. The basin of attraction of v_1 is $\Delta \setminus \{w_1\}$.

When $\tau \in [1/3, 2/3)$, we prove that, the differential equation on the simplex admits $v_2 = (1 - \theta, 0, \theta)$ and $w_2 = (0, 1, 0)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is $\Delta \setminus \{w_2\}$. Similarly, when $\tau \in [2/3, 1)$, we prove that, the differential equation on the simplex admits $v_3 = (0, \theta, 1-\theta)$ and $w_3 = (1, 0, 0)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is $\Delta \setminus \{w_3\}$. Note that $v_3 = v(0-0)$ belongs to the basin of attraction of $v_1 = v(0)$. Similarly, $v_1 = v(1/3 - 0)$ belongs to the basin of attraction of $v_2 = v(1/3)$ and $v_2 = v(2/3-0)$ belongs to the basin of attraction of $v_3 = v(2/3)$. Therefore, Hypothesis 3 is satisfied and according to Theorem A.4, we obtain the formula for

$$\Lambda(m,\infty) = \frac{\lambda_{max}(A_1)+\lambda_{max}(A_2)+\lambda_{max}(A_3)}{3} = \frac{a+b-2m+\sqrt{(a-b)^2+4m^2}}{2}.$$

The formula $\Lambda(0,\infty) = a$ can be obtained by taking the limit $m \to 0$ in this formula or by applying and Proposition 10. The proof that Hypothesis 4 is not satisfied, is the same as in the proof in Proposition 17. $\square$

From the formula giving $\Lambda(m,\infty)$ we deduce that $\Lambda(\infty,\infty) = \frac{a+b}{2}$. This example shows that the formula (27) is not true in general. Actually, the Perron vector $p(\tau)$ is not defined in this case since 0 is not a simple eigenvalue of the migration matrix. Determining the limit $\Lambda(\infty,T)$ is an open problem. Numerical simulations suggest that for all $T>0$, $\Lambda(\infty,T) = \frac{a+b}{2}$.

4 Discussion

We have considered the T-periodic piecewise continuous linear differential system

$$\frac{dx_i}{dt} = r_i(t/T)x_i + m\sum_{j\neq i}\left(\ell_{ij}(t/T)x_j - \ell_{ij}(t/T)x_i\right), \quad 1\leq i\leq n. \tag{39}$$

representing n populations of sizes $x_i(t)$, inhabiting n patches, and subject to T-periodic piecewise continuous local growth rates $r_i(t)$ $(1\leq i\leq n)$, and migration rates $m\ell_{ij}(t)\geq 0$, from patch j to patch i, where the parameter $m\geq 0$ measures the strength of migration, and the numbers $\ell_{ij}(t)\geq 0$, $i\neq j$, encode the relative rates of dispersal among different patches. We extended the results in [3], obtained in the case where the migration matrix $L(t) = (\ell_{ij}(t)$ is irreducible for all t, to the more general case where only the averaged matrix $\overline{L}$ is assumed to be irreducible.

We proved that, as soon as m is positive,

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

where $\mu(m,T)$ is the Perron-Frobenius root of the monodromy matrix associated to (39). Indeed, the irreducibility of $\overline{L}$ implies that this matrix has non negative entries and is irreducible. Hence the growth rate is the same on every patch.

We considered the surprising *dispersal induced growth (DIG)* phenomenon, where the populations persist and grow exponentially, despite the fact that all patches are sinks (i.e. $\overline{r}_i<0$, for all i) when there is no dispersal between them. We also considered the surprising *dispersal induced decay (DID)* phenomenon, where the populations decay exponentially, despite the fact that all patches are sources (i.e. $\overline{r}_i>0$, for all i) when there is no dispersal between them. For this purpose we considered the numbers

$$\sigma = \int_0^1 \min_{1\leq i\leq n} r_i(t)dt, \quad \chi = \int_0^1 \max_{1\leq i\leq n} r_i(t)dt.$$

Consider the idealized habitat, called the *ideal best habitat*, whose growth rate at any time is that of the habitat with maximal growth at this time. Hence, χ is the average growth rate in this idealized habitat. If the population does not grow exponentially in the idealized best habitat (i.e. if $\chi\leq 0$), then from Theorem 12 we deduce that DIG does not occur. Moreover, thanks to Theorem 13 the population can survive if and only it would survive in the idealized best habitat.

Similarly, consider the idealized habitat, called the *ideal worst habitat*, whose growth rate at any time is that of the habitat with minimal growth at this time. Hence, σ, is the average growth rate in this idealized habitat. If the population does not extinct in the idealized worst habitat (i.e. if $\sigma\geq 0$), then from Theorem 12 we deduce that DID does not occur. Moreover, thanks to Theorem 14, if the population is extinct in the idealized worst habitat, then there exist migration matrices for which it is extinct in the real environment with dispersion.

Following [3], our proofs rely mostly on the reduction of the system on the simplex Δ. Instead of considering the size x_i of the population on each patch we consider the total population $\rho = \sum_{i=1}^n x_i$ and the proportion $\theta_i = x_i/\rho$ on each patch. In these new variables (ρ,θ) the system has nice properties. It turns out that the system of θ variables is non linear, but independent of ρ. We prove then that it has a globally asymptotically stable periodic solution θ^* from which we deduce the existence of the growth rate $\Lambda(m,T)$, and an integral expression of it, using the periodic function θ^*. Moreover, on this θ system we can apply averaging, from which we can deduce our small T asymptotics of $\Lambda(m,T)$, and Tikhonov's theorem from which we deduce our large m or T asymptotics of $\Lambda(m,T)$.

In the case considered in [3], the the irreducibility of the matrix $L(\tau)$ implies that of $A(\tau) = R(\tau)+mL(\tau)$ and therefore the existence of its spectral abscissa $\lambda_{max}(A(\tau))$, and the fact that the corresponding Perron-Frobenius vector $v(\tau)$ is a GAS equilibrium of the differential equation (16) on the simplex. In the more general case of this paper, this property is not always satisfied and we must add Hypothesis 3, saying that $v(\tau)$ exists and is a an asymptotically stable equilibrium of the differential equation (16) and has a basin of attraction which is uniform with respect to the parameter $\tau \in [0,1]$. We then derive formula (21) giving the limit $\Lambda(m,\infty)$ of $\Lambda(m,T)$ when T tends to infinity and the formula (27) giving the limit of $\Lambda(m,\infty)$ when m tends to 0.

In the case considered in [3], the irreducibility of the matrix $L(\tau)$ implies the existence of its Perron-Frobenius vector $p(\tau)$ and the fact that $p(\tau)$ is a GAS equilibrium of the differential equation (19) on the simplex. In the more general case of this paper, this property is not always satisfied and we must add Hypothesis 4, saying that $p(\tau)$ exists and is a an asymptotically stable equilibrium of the differential equation (19) and admits a basin of attraction which is uniform in $\tau \in [0,1]$. We then derive formula (20) giving the limit of $\Lambda(m,T)$ when m tends to infinity.

The formula (22) plays a major role in the study of the DIG phenomenon. Indeed, this formula shows that the number χ is the supremum of $\Lambda(m,T)$ and explain why DIG occurs if and only if χ is positive. Also, the formula (20) plays a major role in the study of the DID phenomenon. Indeed, this formula shows that for a class of migration matrices, the number σ is the infimum of $\Lambda(m,T)$ and explain why DID occurs if and only if σ is negative.

The possibility that $L(\tau)$ is not irreducible for all τ is not a simple desire for mathematical generality. Indeed, the assumption that the migration matrix is irreducible is certainly not realized in many real systems. Our study recovers in particular the case of two patches with two seasons and, during the first season, there is migration from patch one to patch two and conversely from patch two to one during season two, like migrating birds do between places in north or south. In this case the migration matrix $L(\tau)$ is not irreducible but DIG or DID can be observed as we have shown in Section 3. The formulas formula (22) and (20), which plays a major role in the study of the DIG and DID phenomenon need to add Hypotheses 3 and 4. We presented in Section 3 several examples of how these hypotheses can be verified, as well as a case where they are not. The study of the asymptotics of $\Lambda(m,T)$ when T is large or m is large, in the case where the assumptions 3 or 4 are not satisfied is a major open question that will be investigated in future work.

A Proofs

The proofs in the more general context of this paper follow the same steps as the proofs in [3]. The main tool in [3] was Perron's theorem applied to the monodromy matrix, which is positive because, in [3], $A(t)$ was assumed to be irreducible for all $t \in [0,1]$. In the more general context of this paper where this assumption is replaced by the irreducibility of the average matrix $\overline{A}$, the main tool is Perron-Frobenius's theorem applied to the monodromy matrix, which is nonnegative and irreducible according to Lemma 1. For the sake of completeness, we give a sketch of the proofs, and we refer the reader to [3] for the details.

A.1 Proof of Theorem 2

Recall that the solution $x(t,x_0)$ to (5) such that $x(0,x_0)=x_0$ writes

$$x(t,x_0) = X(t)x_0 \tag{40}$$

where $X(t)$ is the solution to the matrix valued differential equation (8). The flow (40) of (5) induces a flow on Δ, given by

$$\Psi(t,\theta) = \frac{X(t)\theta}{\langle X(t)\theta, \mathbf{1}\rangle}. \tag{41}$$

Let $\Phi := X(1)$ be the monodromy matrix, μ its Perron-Frobenius root and π the corresponding Perron-Frobenius vector. Using $\Phi\pi = \mu\pi$, $\langle \pi, \mathbf{1}\rangle = 1$, and (41),

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

Therefore π is a fixed point of $\Psi(1,\theta)$, so that $\Psi(t,\pi)$ is a 1-periodic orbit in Δ. The global stability of this orbit follows from the Perron-Frobenius projector formula

$$\lim_{k\to\infty}\frac{\Phi^k x}{\langle \Phi^k x, \mathbf{1}\rangle} = \pi, \tag{42}$$

For any $\theta_0 \in \Delta$, the solution $\theta(t)$ of (10) with initial condition $\theta(0) = \theta_0$ is given by $\theta(t,\theta_0) = \Psi(t,\theta_0)$, where Ψ is given by (41). Using (9), and $x = \rho\theta$,

$$x(t,x_0) = \theta\left(t, x_0/\rho_0\right)\rho_0 e^{\int_0^t \langle A(s)\theta(s,x_0/\rho_0),\mathbf{1}\rangle ds}, \tag{43}$$

where $\rho_0 = \langle x_0, \mathbf{1}\rangle$. Using (43), the Lyapunov exponent of the components of any solution $x(t,x_0)$ 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 $U(s) = \langle A(s)\theta\left(s,x_0/\rho_0\right),\mathbf{1}\rangle$. Using the global asymptotic stability of the periodic orbit $\theta^*(t) := \Psi(t,\pi)$,

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

For the details, we refer the reader to the proof of [3, Theorem 25]. This proves the first equality in (11). Let $x(t) = X(t)\pi$ be the solution of (5), such that $x(0) = \pi$. Since $x(1) = \Phi\pi = \mu\pi$, we have $x(k) = \Phi^k\pi = \mu^k\pi$. Hence

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

which proves the second equality in (11).

A.2 Proof of Theorem 5

The proof is the same as the proof in [3, Eq. (12)]. Indeed, the proof in [3] only uses the averaging theorem, see [3, Theorem 17], and the fact the matrix $\overline{A}$ is irreducible.

Since the matrix $\overline{A}$ is irreducible, its Perron-Frobenius vector $w = (w_1,\cdots,w_n)^\top$, corresponding to its spectral abscissa $\lambda_{max}(\overline{A})$, is a globally asymptotically stable equilibrium of the averaged equation of (10) on the simplex Δ

$$\tfrac{d\theta}{dt} = \overline{A}\theta - \langle\overline{A}\theta,\mathbf{1}\rangle\theta.$$

Using the averaging theorem, we deduce that, as $T \to 0$, the T-periodic solution $\theta^*(t,T)$ of (10) converges toward w. Hence, using (11), as $T \to 0$,

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

For the details, we refer the reader to [3, Section 5.3]. This proves (15).

A.3 Proof of Theorem 7

The proof follows the same steps as the proof of [3, Eq. (13)]. Indeed, the result in [3] only uses Tikhonov's theorem on singular perturbations, see [3, Proposition 27], and the fact that the Perron-Frobenius vector $v(\tau)$ of $A(\tau)$ is globally asymptotically stable for (16). Note that, in the case where $A(\tau)$ is irreducible for all $\tau \in [0,1]$, we have $v(\tau) \gg 0$, and its global asymptotic stability in the simplex Δ is guaranteed, see [3, Proposition 24]. In the more general case where only the average matrix $\overline{A}$ is assumed to be irreducible, we need to introduce Hypothesis 3.

We use the change of variable $\tau = t/T$ and $\eta(\tau) = \theta(T\tau)$. The equation (10) becomes

$$\frac{1}{T}\frac{d\eta}{d\tau} = A(\tau)\eta - \langle A(\tau)\eta, 1\rangle\eta \tag{44}$$

Using Remark 5 in Appendix B, for any $\nu > 0$, as small as we want, as $T \to \infty$, the unique T-periodic solution $\eta^*(t,T)$ of (10) satisfies

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

where $\tau_0 = 0$ and τ_k, $1 \le k \le p$, are the discontinuity points of $A(\tau) = R(\tau) + mL(\tau)$. 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 (11),

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

For the details, we refer the reader to [3, Section 5.4]. This proves (17).

A.4 Proof of Theorem 9

The proof follows the same steps as the proof of [3, Eq. (15)]. Indeed, the result in [3] only uses Tikhonov's theorem and the fact that the Perron-Frobenius vector $p(\tau)$ of $L(\tau)$ is globally asymptotically stable for (19). Note that, in the case where $L(\tau)$ is irreducible for all $\tau \in [0,1]$, we have $p(\tau) \gg 0$, and its global asymptotic stability in the simplex Δ is guaranteed, see [3, Proposition 24]. In the more general case where only the average matrix $\overline{A}$ is assumed to be irreducible, we need to introduce Hypothesis 4.

Using the decomposition $A(\tau) = R(\tau) + mL(\tau)$, the equation (10) on the simplex Δ is

$$\frac{d\theta}{dt} = R(t/T)\theta + mL(t/T)\theta - \langle R(t/T)\theta, \mathbf{1}\rangle\theta - m\langle L(t/T)\theta, \mathbf{1}\rangle\theta, \tag{45}$$

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

$$\frac{1}{m}\frac{d\eta}{d\tau} = TL(\tau)\eta + \frac{1}{m}\left[TR(\tau)\eta - T\langle R(\tau)\eta, \mathbf{1}\rangle\eta\right]. \tag{46}$$

Using Remark 6 in Appendix B, for any $\nu > 0$, as small as we want, as $T \to \infty$, the unique T-periodic solution $\theta^*(t,T)$ of (45) satisfies

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

where $\tau_0 = 0$ and τ_k, $1 \le k \le p$, are the discontinuity points of $A(\tau) = R(\tau) + mL(\tau)$. From (11), $\Lambda(m,T) = \int_0^1 \langle R(\tau)\theta^*(T\tau, T), \mathbf{1}\rangle d\tau$. Since ν can be chosen as small as we want, as $m \to \infty$,

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

For the details, we refer the reader to [3, Section 5.6]. This proves (20).

A.5 Proof of Proposition 18

Consider the system

$$t \in [0, T/3) \Rightarrow \tfrac{dx}{dt} = A_1 x,\ t \in [T/3, 2T/3) \Rightarrow \tfrac{dx}{dt} = A_2 x,\ t \in [2T/3, 1) \Rightarrow \tfrac{dx}{dt} = A_2 x, \tag{47}$$

with

$$A_1 = \begin{pmatrix} a & 0 & 0 \\ 0 & b-m & m \\ 0 & m & b-m \end{pmatrix}, \; A_2 = \begin{pmatrix} b-m & 0 & m \\ 0 & a & 0 \\ m & 0 & b-m \end{pmatrix}, \; A_3 = \begin{pmatrix} b-m & m & 0 \\ m & b-m & 0 \\ 0 & 0 & a \end{pmatrix}.$$

Consider the permutation matrix

$$P = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{pmatrix},$$

and note that $PA_1P^{-1} = A_3$, $PA_2P^{-1} = A_1$ and $PA_3P^{-1} = A_2$. For $x \in \mathbb{R}^3_+$, set $f(x) = x^\intercal Px$ and $U(t) = f(x(t))$ where $x(t)$ is solution to (47). Then

$$\begin{aligned} \frac{dU(t)}{dt} &= (A_t x(t))^\intercal Px(t) + x(t)^\intercal PA_t x(t) \\ &= x(t)^\intercal (A_t^\intercal + PA_tP^{-1})Px(t) \end{aligned}$$

Since A_i is symmetric and P orthogonal, the matrix $A_i + PA_iP^{-1}$ is symmetric. Thus, for all x, y, we get

$$x^\intercal (A_i + PA_iP^{-1})y \le \lambda_{\max}(A_i + PA_iP^{-1})x^\intercal y,$$

which leads to

$$\frac{dU(t)}{dt} \le \lambda_{\max}(A_t + PA_tP^{-1})U_t$$

and thus,if $U_0 \neq 0$,

$$U(t) \le U_0 \exp\left(\int_0^t \lambda_{\max}(A_s + PA_sP^{-1})ds \right).$$

It is easily seen that $\lambda_{\max}(A_{i+2} + A_i)$ does not depend on i. Hence,

$$U(t) \le U_0 \exp\left(\lambda_{\max}(A_3 + A_1)t \right)$$

We have

$$A_3 + A_1 = \begin{pmatrix} a+b-m & m & 0 \\ m & 2(b-m) & m \\ 0 & m & a+b+m \end{pmatrix}$$

Due to Perron-Frobenius theory, $\lambda_{\max}(A_3+A_1) \le \max_i R_i$, where R_i it the sum of the coefficients on the i-th raw. Here, we have $R_1 = R_3 = a+b$, while $R_2 = 2b < R_1$. Therefore, $\lambda_{\max}(A_3+A_1) \le a+b$, and we end up with

$$U(t) \le U_0 \exp\left((a+b)t \right).$$

Recall that $U(t) = f(x(t)) = x_1(t)x_2(t) + x_2(t)x_3(t) + x_3(t)x_1(t)$. From Theorem 2, we have for all i

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

Therefore, for some initial condition $(x_1(0), x_2(0), x_3(0)) \neq 0$, for all $\varepsilon > 0$, there exists t_0 such that for all $t \ge t_0$,

$$U_0 \exp\left((a+b)t \right) \ge U(t) \ge 3e^{2(\Lambda(m,T)-\varepsilon)t}.$$

Since this is true for all $t \ge t_0$, we deduce that $2(\Lambda(m,T) - \varepsilon)$ has to be smaller that $a+b$. Finally, since ε was arbitrary, it implies as announced that for all $m > 0$ and $T > 0$, $\Lambda(m,T) \le \frac{a+b}{2}$.

We can easily compute the limit $\lim_{T\to\infty} \Lambda(m,T)$. Indeed, we have explicitly

$$e^{TA_1} = \begin{pmatrix} e^{aT} & 0 & 0 \\ 0 & f_m(T)e^{bT} & g_m(T)e^{bT} \\ 0 & g_m(T)e^{bT} & f_m(T)e^{bT} \end{pmatrix}$$

where $f_m(T) = \frac{1}{2}(1 + e^{-2mT})$ and $g_m(T) = \frac{1}{2}(1 - e^{-2mT})$ are bounded and converge to 1 when T goes to infinity for each fixed $m > 0$. From this, we deduce that

$$X(T) = e^{\frac{T}{3}A_3} e^{\frac{T}{3}A_2} e^{\frac{T}{3}A_1} = e^{\frac{(a+2b)T}{3}} B(T) + o(e^{-\gamma T})$$

for some $\gamma > 2m - 3b$ and where

$$B(T) = \begin{pmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ e^{\frac{(a-b)T}{3}} & 1 & 1 \end{pmatrix}.$$

We can check that

$$\lambda_{\max}(B(T)) = \frac{\sqrt{4e^{\frac{(a-b)T}{3}}+5}+3}{2} = e^{\frac{(a-b)T}{6}}\left(1+o(e^{-(a-b)\frac{T}{6}})\right),$$

so that

$$\frac{1}{T}\log(\mu(T)) = \frac{(a+2b)}{3} + \frac{(a-b)}{6} + o(1) = \frac{a+b}{2} + o(1).$$

Therefore, as $m \to \infty$, $\Lambda(m,T) = \frac{a+b}{2} + o(1)$.

B Singular perturbations

Consider the singularly perturbed differential equation

$$\varepsilon\frac{d\eta}{d\tau} = f(\tau,\eta,\varepsilon), \tag{48}$$

where $f : [0,1]\times\mathbb{R}^n\times(0,\infty)\to\mathbb{R}^n$ is a function, verifying the conditions $(SP1)$ and $(SP2)$ that will be specified below.

When $\varepsilon \to 0$, (48) is a singularly perturbed equation with n fast variables η and one slow variable τ. Using the fast time $s = \tau/\varepsilon$, this equation can be rewritten

$$\begin{aligned} \tfrac{d\eta}{ds} &= f(\tau,\eta,\varepsilon), \\ \tfrac{d\tau}{ds} &= \varepsilon. \end{aligned} \tag{49}$$

The slow curve of (49) is given by $\eta = \xi(\tau)$, where $\xi(\tau)$ is the equilibrium of the fast equation

$$\frac{d\eta}{ds} = f(\tau,\eta,0), \tag{50}$$

obtained by letting $\varepsilon = 0$ in (49). Therefore, in the fast equation (50), τ is considered as a constant parameter. We make the following assumptions.

(SP1) There is a finite set $D = \{\tau_k, 1\le k\le p : 0<\tau_1<\cdots<\tau_p<1\}$, such that f is continuous on $([0,1]\setminus D)\times\mathbb{R}^n\times(0,\infty)$, differentiable with respect of η, and has right and left limits at the discontinuity points $\tau_k \in (0,1)$, $k = 1,\ldots,p$.
(SP2) The equilibrium $\eta = \xi(\tau)$ of the fast equation (50) is asymptotically stable with a basin of attraction which is uniform. This means that for each subdivision interval $[\tau_k,\tau_{k+1})$ on which the f is continuous, $\xi(\tau)$ is an asymptotically stable equilibrium of the fast equation (50) and has a basin of attraction which is uniform with respect to the parameter $\tau\in[\tau_k,\tau_{k+1})$ and, for $\tau = \tau_k$, the basin of attraction of $\xi(\tau_k)$ contains the limit at right $\xi(\tau_k - 0) := \lim_{\tau\to\tau_k,\tau<\tau_k}\xi(\tau)$.

Recall that an equilibrium is asymptotically stable if it is stable and attractive. The basin of attraction $B(\xi(\tau))$ is the set of initial conditions which are attracted by the equilibrium $\xi(\tau)$. The basin of attraction is said to be uniform with respect of the parameter $\tau\in[\tau_k,\tau_{k+1})$ if there exists $\delta>0$ such that for all $\tau\in[\tau_k,\tau_{k+1})$, the ball of center $\xi(\tau)$ and radius δ is contained in the basin of attraction $B(\xi(\tau))$.

Using the Tikhonov's theorem on singular perturbations we have the following result.

Proposition 20. *Assume that the conditions (SP1) and (SP2) are satisfied. Assume that η_0 belongs to the basin of attraction of $\xi(0)$. Let $\nu>0$. For ε small enough, the solution $\eta(\tau,\varepsilon)$ of (48) with initial condition $\eta(0,\varepsilon)=\eta_0$, is defined on $[0,1]$ and, as $\varepsilon\to 0$,*

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

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

Proof. The result is a particular case of [3, Proposition 27]. □

Remark 5. Theorem 20 applies to the equation (44) which can then be written, noting $\varepsilon = 1/T$, as

$$\varepsilon\frac{d\eta}{d\tau} = A(\tau)\eta - \langle A(\tau)\eta,1\rangle\eta$$

Using the fast time $t = m\tau$, the fast equation is the equation (16), where $\tau \in [0,1]$ is considered as a parameter. Using Hypothesis 3, the fast equation admits the Perron-Frobenius vector $v(\tau)$ of $A(\tau)$ as an equilibrium which has a basin of attraction which is uniform. Therefore, the conditions (SP1) and (SP2) are satisfied. Hence, $\eta(\tau,\varepsilon)$ is approximated by the slow curve $v(\tau)$ excepted on the set $\bigcup_{k=0}^{p}[\tau_k, \tau_k+\nu]$, where ν is as small as we want.

Remark 6. Theorem 20 applies to the equation (46), which can be written, noting $\varepsilon = 1/m$, as

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

Using the fast time $s = m\tau$, the fast equation is the equation (19), where τ is considered as a parameter. Using Hypothesis 4, the Perron-Frobenius vector $p(\tau)$ of $L(\tau)$, is asymptotically stable for (19) and has a basin of attraction which is uniform. Therefore, the conditions (SP1) and (SP2) are satisfied. Hence, $\eta(\tau,\varepsilon)$ is approximated by the slow curve $p(\tau)$ excepted on the set $\bigcup_{k=0}^{p}[\tau_k, \tau_k+\nu]$, where ν is as small as we want.

C Supplementary examples

The aim of this section is to illustrate Theorem 7, which calculates the limit $\Lambda(m,\infty)$, with various examples. Our aim is to see how to verify Hypothesis 3. For this purpose we consider the models defined in Fig. 6, 8, 10, 12, 14, and 16. In all these figures, there are three patches, two with a growth rate equal to b and the third with the growth rate equal to $a > b$. The growth rate is indicated in the patch. Patch 1 is at bottom left, patch 2 at bottom right and patch 3 at top. There are 3 seasons. There is only one migration per season. Migration is always in the positive direction (counter-clockwise).

Proposition 21. *For the models defined in Fig. 6, 8, 10, 12, 14, and 16 the growth rate exits and satisfies*

$$\Lambda(0,T) = \Lambda(m,0) = \frac{a+2b}{3}.$$

Moreover, Hypothesis 4 is not satisfied and we cannot use Theorem 9 to determine $\Lambda(\infty,T)$.

Proof. The average of the migration matrix is

$$\overline{L} = \frac{1}{3}\begin{bmatrix} -1 & 0 & 1 \\ 1 & -1 & 0 \\ 0 & 1 & -1 \end{bmatrix}$$

It is irreducible. Therefore, the growth rate exists and

$$\Lambda(0,T) = \max\left(\overline{r}_1, \overline{r}_2, \overline{r}_3\right) = \frac{a+2b}{3}.$$

The average of the matrix A is

$$\overline{A} = \frac{1}{3}\begin{bmatrix} a+2b-m & 0 & m \\ m & a+2b & 0 \\ 0 & m & a+2b-m \end{bmatrix}$$

The spectral abscissa of $\overline{A}$ is $\frac{a+2b}{3}$. Therefore,

$$\Lambda(m,0) = \lambda_{max}\left(\overline{A}\right) = \frac{a+2b}{3}.$$

Moreover, in each season the migration matrix has eigenvalues 0, 0, and -1. Therefore its spectral abscissa 0 is not a simple eigenvalue and Hypothesis 4 is not satisfied. □

C.1 Migration from a b-patch to a b-patch

We distinguish the cases shown in Figures 6 and 8.

Proposition 22. *For the systems defined in Figs. 6 and 8 Hypothesis 3 is not satisfied and we cannot use Theorem 7 to determine* $\Lambda(m,\infty)$.

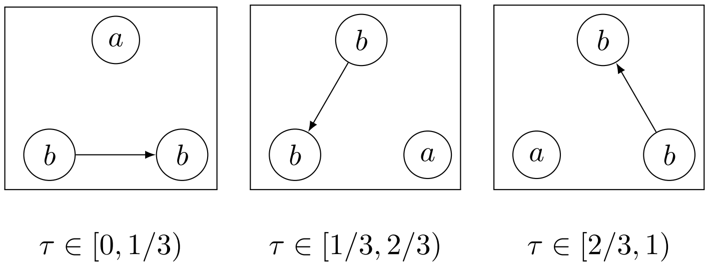

Fig. 6 The migration is from a b-patch to a b-patch (Case 1).

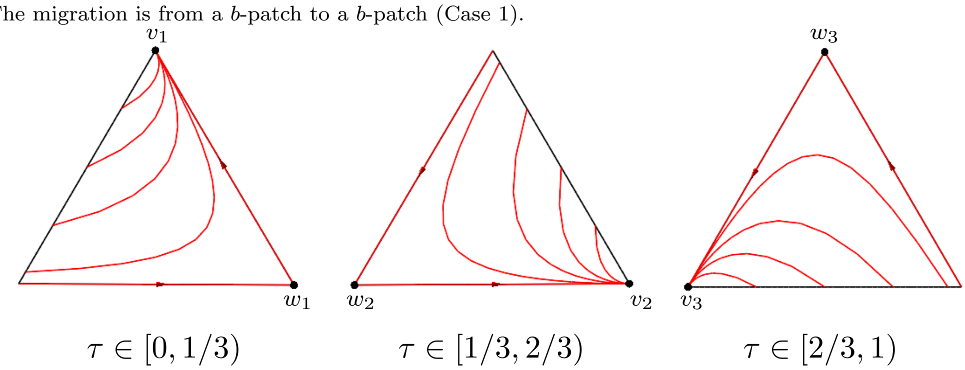

Fig. 7 The flow on the simplex for the system described in Fig. 6. Hypothesis H3 is not satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, does not belong to the basin of attraction of v_2, the stable equilibrium of the system, during season 2, since it is attracted by w_2. Similarly, at the end of season 2, v_2 does not belong to the basin of attraction of v_3, and, at the end of season 3, v_3 does not belong to the basin of attraction of v_1.

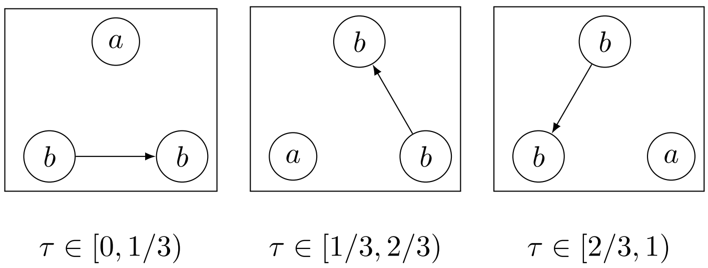

Fig. 8 The migration is from a b-patch to a b-patch (Case 2). This case is obtained from Case 1 in Fig. 6 by swapping seasons 2 and 3.

Proof. The matrix $A(\tau)$ is given by

$$A(\tau) = A_1 := \begin{bmatrix} b-m & & 0 \\ m & b & 0 \\ 0 & 0 & a \end{bmatrix} \text{ for } \tau \in [0, 1/3),$$

and similar formulas for $\tau \in [1/3, 2/3)$ and $\tau \in [2/3, 1)$. Let us look at why our Hypothesis 3 is not satisfied. The eigenvalues of A_1 are a, b, and $b - 2m$. Since $a > b$, the spectral abscissa of A_1 is

$$\lambda_{max}(A_1) = a.$$

The corresponding Perron-Frobenius vector is $v_1 = (0, 0, 1)$. Note that the matrix has another non-negative eigenvector, corresponding to its eigenvalue b, and given by $w_1 = (0, 1, 0)$. The differential system associated to the matrix A_1 on the simplex Δ, parametrized by θ_1 and θ_3, is

$$\begin{aligned} \tfrac{d\theta_1}{dt} &= -\theta_1(m + (a-b)\theta_3), \\ \tfrac{d\theta_3}{dt} &= -\theta_3(\theta_3 - 1)(a-b). \end{aligned}$$

It admits v_1 and w_1 as equilibria, the first being stable and the second unstable (a saddle point), see Figure 7. The basin of attraction of v_1 is the subset $\theta_3 > 0$ of the simplex.

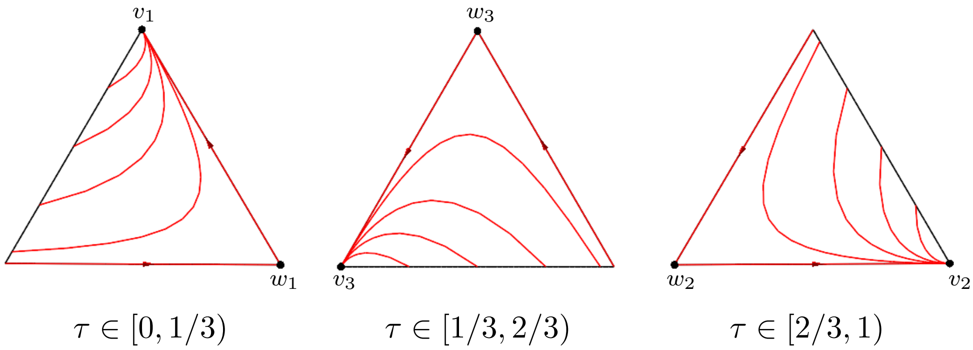

Fig. 9 The flow on the simplex for the system described in Fig. 8. Hypothesis 3 is not satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, does not belong to the basin of attraction of v_3, the stable equilibrium of the system, during season 2, since it is the equilibrium w_3. Similarly, at the end of season 2, v_3 does not belong to the basin of attraction of v_2, and, at the end of season 3, v_2 does not belong to the basin of attraction of v_1.

When $\tau \in [1/3, 2/3)$, we prove that, the differential equation on the simplex admits $v_2 = (0, 1, 0)$ and $w_2 = (1, 0, 0)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is the subset $\theta_2 > 0$ of the simplex. Similarly, when $\tau \in [2/3, 1)$, we prove that, the differential equation on the simplex admits $v_3 = (1, 0, 0)$ and $w_3 = (0, 0, 1)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is the subset $\theta_1 > 0$ of the simplex.

Note that $v_3 = v(0-0)$ does not belong to the basin of attraction of $v_1 = v(0)$. Indeed, it is attracted by w_1. Similarly, $v_1 = v(1/3-0)$ does not belong to the basin of attraction of $v_2 = v(1/3)$ and $v_2 = v(2/3-0)$ does not belong to the basin of attraction of $v_3 = v(2/3)$. Therefore, Hypothesis 3 is not satisfied and Theorem 7 cannot be used to determine the limit $\Lambda(m, \infty)$.

For the system defined in Fig. 8, seasons 2 and 3 are swapped. The flow on the simplex is shown in Fig. 9. Hypothesis 3 is not satisfied. Indeed $v_2 = v(0-0)$ does not belong to the basin of attraction of $v_1 = v(0)$, since it coincides with w_1. Similarly, $v_1 = v(1/3 - 0)$ does not belong to the basin of attraction of $v_3 = v(1/3)$ and $v_3 = v(2/3 - 0)$ does not belong to the basin of attraction of $v_2 = v(2/3)$. Therefore, Theorem 7 cannot be used to determine the limit $\Lambda(m, \infty)$. □

C.2 Migration from a *b* patch to an *a*-patch

We distinguish the cases shown in Figures 10 and 12.

Proposition 23. *For the system defined in Fig. 10 Hypothesis 3 is not satisfied and we cannot use Theorem 7 to determine $\Lambda(m, \infty)$. For the system defined in Fig. 12 Hypothesis 3 is satisfied and for all $m > 0$,*

$$\Lambda(m, \infty) = a.$$

Proof. The matrix $A(\tau)$ is given by

$$A(\tau) = A_1 := \begin{bmatrix} b - m & & 0 \\ m & a & 0 \\ 0 & 0 & b \end{bmatrix} \text{ for } \tau \in [0, 1/3),$$

and similar formulas for $\tau \in [1/3, 2/3)$ and $\tau \in [2/3, 1)$.

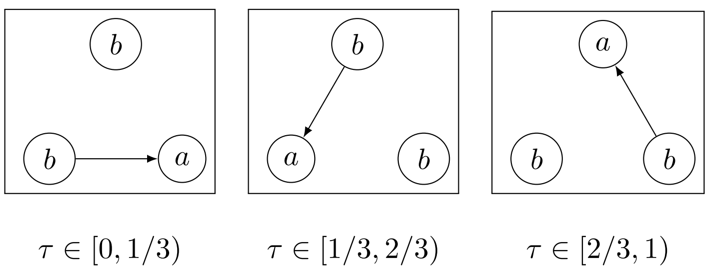

Fig. 10 The migration is from a b-patch to and a-patch (Case 1).

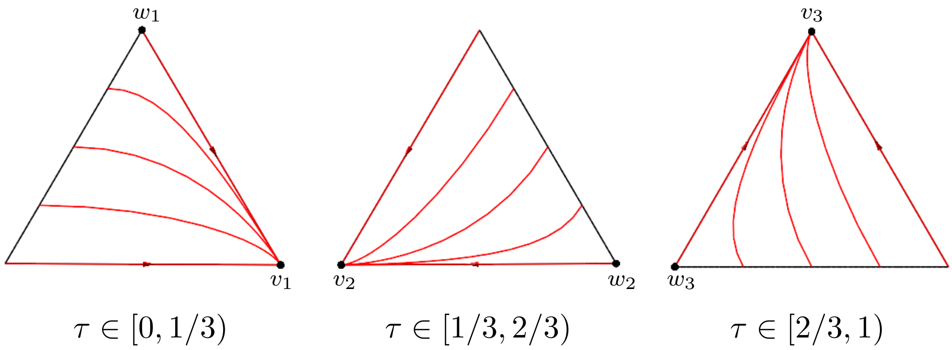

Fig. 11 The flow on the simplex for the system described in Fig. 10. Hypothesis 3 is not satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, does not belong to the basin of attraction of v_2, the stable equilibrium of the system, during season 2, since it is the equilibrium w_2. Similarly, at the end of season 2, v_2 does not belong to the basin of attraction of v_3, and, at the end of season 3, v_3 does not belong to the basin of attraction of v_1.

Let us look at why our Hypothesis 3 is not satisfied. The eigenvalues of A_1 are a, b, and $b-m$. Since $a > b$, the spectral abscissa of A_1 is

$$\lambda_{max}(A_1) = a.$$

The corresponding Perron-Frobenius vector is $v_1 = (0, 1, 0)$. Note that the matrix has another non-negative eigenvector, corresponding to its eigenvalue b, and given by $w_1 = (0, 0, 1)$. The differential system associated to the matrix A_1 on the simplex Δ, parametrized by θ_1 and θ_3, is

$$\begin{aligned}\tfrac{d\theta_1}{dt} &= \theta_1((a-b)(\theta_1+\theta_3-1)-m),\\ \tfrac{d\theta_3}{dt} &= \theta_3(\theta_1+\theta_3-1)(a-b).\end{aligned}$$

It admits v_1 and w_1 as equilibria, the first being stable and the second unstable (a saddle point), see Figure 11. The basin of attraction of v_1 is $\Delta \setminus \{w_1\}$.

When $\tau \in [1/3, 2/3)$, we prove that, the differential equation on the simplex admits $v_2 = (1, 0, 0)$ and $w_2 = (0, 1, 0)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is $\Delta \setminus \{w_2\}$. Similarly, when $\tau \in [2/3, 1)$, we prove that, the differential equation on the simplex admits $v_3 = (0, 0, 1)$ and $w_3 = (1, 0, 0)$ as equilibria. The second one is a saddle point. The first one is stable and its basin of attraction is $\Delta \setminus \{w_3\}$.

Note that $v_3 = v(0-0)$ does not belong to the basin of attraction of $v_1 = v(0)$. Indeed, it coincides with w_1. Similarly, $v_1 = v(1/3-0)$ does not belong to the basin of attraction of $v_2 = v(1/3)$ and $v_2 = v(2/3-0)$ does not belong to the basin of attraction of $v_3 = v(2/3)$. Therefore, Hypothesis H3 is not satisfied and Theorem 7 cannot be used to determine the limit $\Lambda(m, \infty)$.

For the system defined in Fig. 12, seasons 2 and 3 are swapped. The flow on the simplex is shown in Fig. 13. Hypothesis 3 is satisfied. Indeed, $v_2 = v(0-0)$ belongs to the basin of attraction of $v_1 = v(0)$, $v_1 = v(1/3-0)$ belongs to the basin of attraction of $v_3 = v(1/3)$ and $v_3 = v(2/3-0)$ belongs to the basin of attraction of $v_2 = v(2/3)$. Therefore, using Theorem 7,

$$\Lambda(m, \infty) = \frac{\lambda_{max}(A_1) + \lambda_{max}(A_2) + \lambda_{max}(A_3)}{3} = \frac{a+a+a}{3} = a.$$

This ends the proof. □

C.3 Migration from an *a*-patch to a *b*-patch

We distinguish the cases shown in Figures 14 and 16.

Proposition 24. *For the system defined in Fig. 14 Hypothesis 3 is not satisfied and we cannot use Theorem 7 to determine $\Lambda(m, \infty)$. For the system defined in Fig. 16 Hypothesis 3 is satisfied and for $m \in (0, b-a)$,*

$$\Lambda(m, \infty) = a - m.$$

For $m > b - a$, Hypothesis 3 is not satisfied and we cannot use Theorem 7 to determine $\Lambda(m, \infty)$.

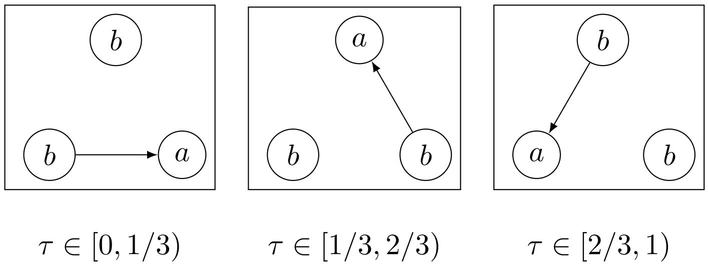

Fig. 12 The migration is from a b-patch to an a-patch (Case 2). This case is obtained from Case 1 in Fig. 10 by swapping seasons 2 and 3.

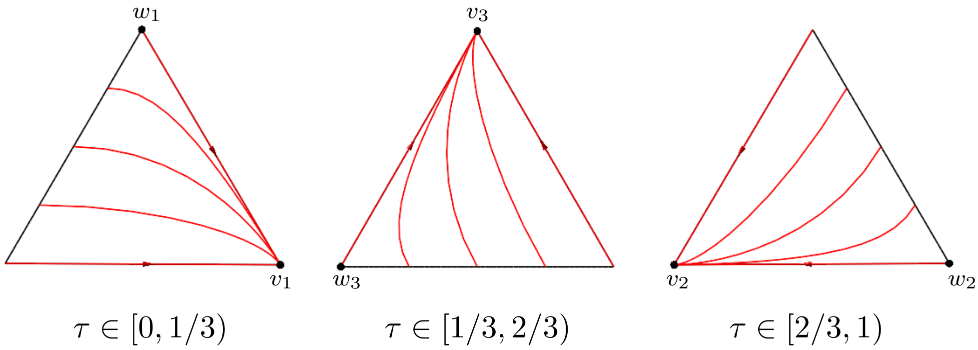

Fig. 13 The flow on the simplex for the system described in Fig. 12. Hypothesis 3 is satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, belongs to the basin of attraction of v_3, the stable equilibrium of the system, during season 2. Similarly, at the end of season 2, v_3 belongs to the basin of attraction of v_2, and, at the end of season 3, v_2 belongs to the basin of attraction of v_1.

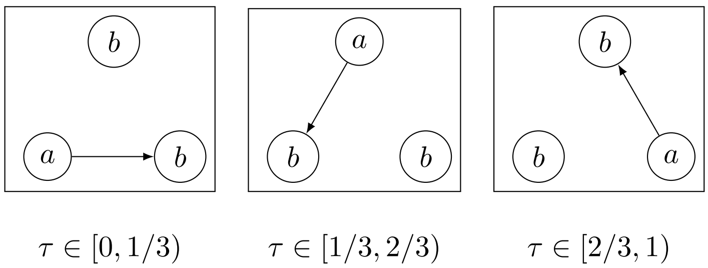

Fig. 14 The migration is from an a-patch to a b-patch (Case 1).

Proof. The matrix $A(\tau)$ is given by

$$A(\tau) = A_1 := \begin{bmatrix} a-m & & 0 \\ m & b & 0 \\ 0 & 0 & b \end{bmatrix} \text{ for } \tau \in [0, 1/3),$$

and similar formulas for $\tau \in [1/3, 2/3)$ and $\tau \in [2/3, 1)$. Let us look at why our Hypothesis 3 is not satisfied. The eigenvalues of A_1 are $a - m$, b, and b. The spectral abscissa of A_1 is

$$\lambda_{max}(A_1) = \begin{cases} a - m & \text{if } 0 < m < a - b, \\ b & \text{if } m > a - b. \end{cases}$$

Let us first consider the case $m < a - b$. The corresponding Perron-Frobenius vector is $v_1 = \left(\frac{a-b-m}{a-b}, \frac{m}{a-b}, 0\right)$. Note that the the eigenvalue b admits $(0, 0, 1)$ and $(0, 1, 0)$ as eigenvectors. The differential system associated to the matrix A_1 on the simplex Δ, parametrized by θ_1 and θ_2, is

$$\begin{aligned} \tfrac{d\theta_1}{dt} &= -\theta_1((a-b)(\theta_1 - 1) + m), \\ \tfrac{d\theta_3}{dt} &= -\theta_1((a-b)\theta_2 - m). \end{aligned}$$

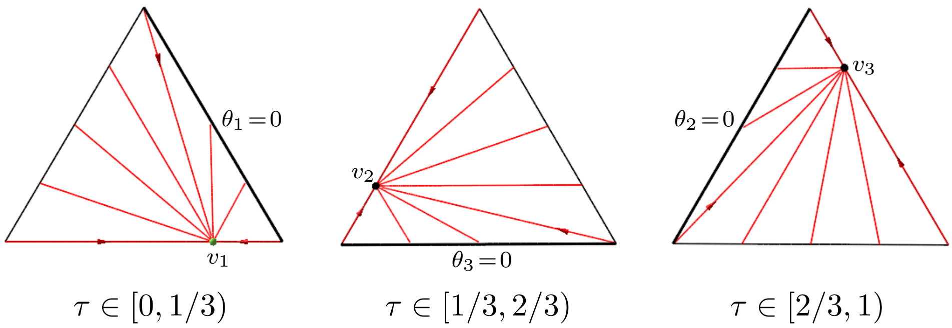

Fig. 15 The flow on the simplex for the system described in Fig. 14. Hypothesis 3 is not satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, does not belong to the basin of attraction of v_2, the stable equilibrium of the system, during season 2, since it belongs to the invariant set $\theta_3 = 0$. Similarly, at the end of season 2, v_2 does not belong to the basin of attraction of v_3, and, at the end of season 3, v_3 does not belong to the basin of attraction of v_1.

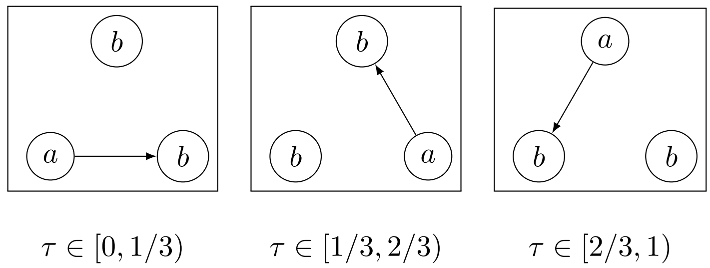

Fig. 16 The migration is from an a-patch to a b-patch (Case 2). This case is obtained from Case 1 in Fig. 14 by swapping seasons 2 and 3.

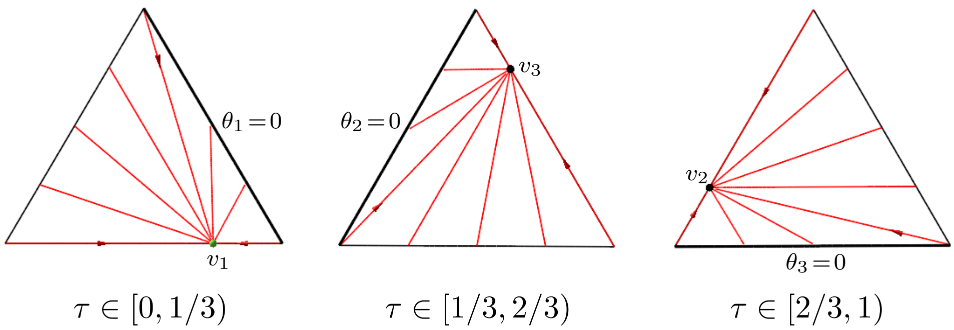

Fig. 17 The flow on the simplex for the system described in Fig. 16. Hypothesis 3 is satisfied. Indeed, at the end of season 1, v_1, which is the stable equilibrium of the system, belongs to the basin of attraction of v_3, the stable equilibrium of the system, during season 2. Similarly, at the end of season 2, v_3 belongs to the basin of attraction of v_2, and, at the end of season 3, v_2 belongs to the basin of attraction of v_1.

It admits v_1 as a stable equilibrium. It also admits the continuous set $\theta_1 = 0$ of non isolated equilibria, corresponding to the eigenvectors corresponding to the eigenvalues b, see Figure 15. The basin of attraction of v_1 is the subset $\theta_1 > 0$ of Δ.

When $\tau \in [1/3, 2/3)$, we prove that, the differential equation on the simplex has a continuous set of non-isolated equilibria, given by $\theta_3 = 0$ and the stable equilibrium $v_2 = \left(\frac{m}{a-b}, 0, \frac{a-b-m}{a-b}\right)$, whose basin of attraction is is the subset $\theta_3 > 0$ of Δ. Similarly, when $\tau \in [2/3, 1)$, we prove that, the differential equation on the simplex admits has a continuous set of non-isolated equilibria, given by $\theta_2 = 0$ and the stable equilibrium $v_2 = \left(0, \frac{m}{a-b}, \frac{a-b-m}{a-b}\right)$, whose basin of attraction is is the subset $\theta_2 > 0$ of Δ.

Note that $v_3 = v(0-0)$ does not belong to the basin of attraction of $v_1 = v(0)$. Indeed, it belongs to the invariant set $\theta_1 = 0$. Similarly, $v_1 = v(1/3-0)$ does not belong to the basin of attraction of $v_2 = v(1/3)$ and $v_2 = v(2/3-0)$ does not belong to the basin of attraction of $v_3 = v(2/3)$. Therefore, Hypothesis H3 is not satisfied and Theorem 7 cannot be used to determine the limit $\Lambda(m, \infty)$.

For the system defined in Fig. 16, seasons 2 and 3 are swapped. The flow on the simplex is shown in Fig. 17. Hypothesis 3 satisfied. Indeed, $v_2 = v(0-0)$ belongs to the basin of attraction of $v_1 = v(0)$, $v_1 = v(1/3-0)$ belongs to the basin of attraction of $v_3 = v(1/3)$ and $v_3 = v(2/3-0)$

belongs to the basin of attraction of $v_2 = v(2/3)$. Therefore, using Theorem 7,

$$\Lambda(m, \infty) = \frac{\lambda_{max}(A_1) + \lambda_{max}(A_2) + \lambda_{max}(A_3)}{3} = \frac{a - m + a - m + a - m}{3} = a - m.$$

If $m > a - b$ the spectral abscissa is not a simple eigenvalue of A_1 and hence, Hypothesis 3 is not satisfied. □

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