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Non-linear population discrete models with two time scales: re-scaling of part of the slow process

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Abstract

In this work we present a reduction result for discrete-time systems with two time scales. In order to be valid, previous results in the field require some strong hypotheses that are difficult to check in practical applications. Roughly speaking, the iterates of a map as well as their differentials must converge uniformly on compact sets. Here, we eliminate the hypothesis of uniform convergence of the differentials at no significant cost in the conclusions of the result. This new result is then used to extend to non-linear cases the reduction of some population discrete models involving processes acting at different time scales. In practical cases, some processes that occur at a fast time scale are often only measured at slow time intervals, notably mortality. For a general class of linear models that include such a kind of processes, it has been shown that a more realistic approach requires the re-scaling of those processes to be considered at the fast time scale. We develop the same type of re-scaling in some non-linear models and prove the corresponding reduction results. We also provide an application to a particular model of a structured population in a two-patch environment.

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1 Introduction

We consider discrete systems in the framework of population dynamics models. The complexity of these models can be treated distinguishing the different time scales at which the different processes involved act. In an idealization of this approach we proposed (see [1] and the references therein) to merge two different processes acting at different time scales in a single model as we describe next. The effect of the fast process during a fast time unit is represented by a general map F, and a general map S describes the slow process in a slow time unit. We choose the latter as the time unit of the common discrete model. If the slow time unit is approximately k times larger than the fast one, we consider that during this interval the fast process acts sequentially k times followed by the slow process acting once. The combined effect of the two processes during a slow time unit is therefore represented by the composition of map S and the kth iterate $F^{(k)}$ of map F. If we let the vector

$X(t)$ represent the population state at time t, the general form of the system is

$$X(t + 1) = S\big(F^{(k)}\big(X(t)\big)\big). \tag{1}$$

The subsequent issue is to take advantage of the existence of time scales to reduce the proposed system. The reduction we are referring to can be considered to be part of the so-called methods of aggregation of variables, which exist in different mathematical settings [2, 3]. It consists of finding a certain number of global variables, which are functions of the state variables, and a reduced system, approximately describing their dynamics, such that it is possible to get information on the asymptotic behavior of the solutions of the original system in terms of this reduced system. This procedure has a direct interpretation in terms of ecological hierarchy theory [4] and the concept of up-scaling through ecological hierarchical levels [5, 6]. In general, aggregation methods are approximate in the sense that quantitatively the dynamics of the original system cannot be described exactly by the dynamics of the reduced one. However, the error incurred decreases when the ratio of time scales increases and, for a large enough value of this ratio, the two systems have the same qualitative dynamics.

In [7] it is proved that system (1) can be reduced if the limit of the iterates of map F exists and can be expressed as the composition of two maps going through a lower dimensional space. With additional hypotheses it is possible to extract information on the asymptotic behavior of the solutions of system (1) by means of the reduced system. To be specific, one can study the existence, stability and basins of attraction of steady states and periodic solutions of the original system by performing the study for the corresponding aggregated system. The additional hypotheses essentially consist in the convergence on compact sets of the F iterates and their differentials. However, the latter assumption is generally too involved, if not impossible, to be proved in particular applications.

The main result in this work proves that the mere convergence on compact sets of the F iterates is enough to obtain almost the same results as in [7]. The downside is that we cannot guarantee the convergence of the system dynamics to the attractor, equilibrium or periodic solution, obtained through the analysis of the reduced system. However, we prove that this dynamics remains as close to the attractor as desired if the ratio of time scales is sufficiently large. Therefore, from the point of view of population dynamics models this last property is good enough to obtain valuable qualitative results.

This reduction result is applied in the context of discrete-time models of structured metapopulations with two time scales. The aim is to extend to the non-linear case certain results obtained in [8] for linear models. In structured metapopulation models that distinguish time scales, biological evidence suggests associating the slow one to the local demography (maturation, survival, reproduction) and the fast one to the movements between patches. When we express this in the form of system (1) we are representing that individuals perform at first a series of k dispersal events between patches followed by a demographic event in the arrival patch. This way of separating slow and fast processes seems acceptable as far as reproduction is concerned, particularly in the case of populations with non-overlapping generations. Nevertheless, it is arguable whether survival should be considered at the slow time scale because deaths may occur at any moment of a slow time interval, i.e., in any of the patches through which individuals pass during this interval. In order to include this issue in the model, and having in mind that survival data may only

exist for slow time units, in [8] it is proposed to move survival from the slow to the fast process by approximating its effect during the fast time unit, i.e., *re-scaling* survival to the fast time scale.

According to this discussion, we present two general discrete-time models of structured metapopulations with two time scales. In the first one we consider the effect of survival in the time step corresponding to the slow process and, in the second one, in that corresponding to the fast process. The main result of this work makes it possible to extend the reduction method to the latter case.

This general framework is used to illustrate the effects of fast dispersals on local demography that emerge at the global metapopulation level. To this end, we extend the non-spatial model presented in [9] to a habitat with two patches between which fast dispersals are considered. The model is structured into three classes: juveniles and two adult stages. Adults that reproduce at the end of an interval of time do not reproduce at the end of the following one. A fraction of those not having reproduced do so at the end of the following interval. Thus, adults are classified into those reproducing at the end of the time interval, active adults, and those who do not, inactive adults. The aim of this consideration is studying the reproductive synchrony of adults. The model in [9] is a discrete-time non-linear matrix model whose inherent projection matrix is imprimitive [10]. This entails that the stability of the extinction equilibrium when R_0 increases through 1 bifurcates either to the stability of a non-extinction equilibrium or of a synchronous 2-cycle. The first option represents adults reproductive asynchrony whereas the second one is associated to reproductive synchrony.

Both metapopulation models, with or without re-scaled survival, and with local dynamics based on the model [9], can be studied through their associated reduced systems. Indeed, these have the same functional form as the system in [9] so that the results therein can be applied.

The main result on systems reduction is developed in Sect. 2. Two general discrete-time models of structured metapopulations with two time scales are presented in Sect. 3. The first one considers the dispersal process to be fast and the local demographic one, including survival, to be slow, whilst in the second one survival is transferred from the slow to the fast process. These two general models are applied in Sect. 4 to the particular case of a population structured into three classes inhabiting in a two-patch environment. With the help of these two particular models we illustrate how the effect of fast dispersals can make emerge at the global level asymptotic properties different from those occurring at the local level. The models are also used to show that the modelling choice regarding survival can imply drastic changes in behavior. A discussion and an Appendix with the proofs of some results complete the work.

2 Reduction of slow-fast discrete systems

The point of departure is Ref. [7] so we recall the presentation therein.

Let $N \in \mathbb{Z}_+$ and let $\Omega_N \subset \mathbb{R}^N$ be a set with non-empty interior. We start by introducing the *original* or *complete* model in the following general form:

$$X_k(t+1) = H_k\big(X_k(t)\big), \tag{2}$$

where $k \in \mathbb{Z}_+$ and $H_k : \Omega_N \longrightarrow \Omega_N, H_k \in \mathcal{C}^1(\Omega_N)$. System (1) is a particular case of system (2) where $H_k = S \circ F^{(k)}$.

In order to carry out the reduction of the model, we assume the following conditions.

Hypothesis 2.1 *The following pointwise limit exists in Ω_N:*

$$\lim_{k \to \infty} H_k(X) =: H(X) \in \mathcal{C}^1(\Omega_N). \tag{3}$$

Hypothesis 2.2 *There exist a subset $\Omega_q \subset \mathbb{R}^q$ with $q < N$ and two maps $G : \Omega_N \to \Omega_q$ and $T : \Omega_q \to \Omega_N$ of class $\mathcal{C}^1$ on their respective domains such that*

$$H = T \circ G. \tag{4}$$

The approximate reduction of system (2) is carried out in two steps. First, we define the auxiliary system

$$X(t + 1) = H\big(X(t)\big). \tag{5}$$

Applying G to both members of the previous expression we have

$$G\big(X(t + 1)\big) = G \circ H\big(X(t)\big) = G \circ T \circ G\big(X(t)\big),$$

and so by defining the global variables

$$Y(t) := G\big(X(t)\big) \in \mathbb{R}^q, \tag{6}$$

we obtain the reduced or aggregated system

$$Y(t + 1) = \bar{H}\big(Y(t)\big), \tag{7}$$

where we have introduced the notation $\bar{H} := G \circ T$.

Note that through this procedure we have constructed an approximation that allows us to reduce a system with N variables to a new system with q variables. In most practical applications, q is much smaller than N.

Reference [7] presents results that allow one to relate the existence of equilibrium points and periodic orbits for systems (2) and (7). More specifically, if certain conditions are met (see below) and the aggregated system has a hyperbolic p-periodic point Y^* ($p \in \mathbb{N}$), then for a large enough value of k the original system has a hyperbolic associated p-periodic point X_k^* that can be approximated in terms of Y^*. Moreover, X_k^* is (locally) asymptotically stable (resp. unstable) if and only if Y^* is (locally) asymptotically stable (resp. unstable) and, in the first case, the basin of attraction of X_k^* can be approximated in terms of that corresponding to Y^*.

For the previous results to hold, in addition to Hypotheses 2.1 and 2.2 one must include two additional conditions.

Hypothesis 2.3 *The limit in* (3) *is uniform on all compact sets of Ω_N.*

The second condition is that $\lim_{k \to \infty} DH_k = DH$ uniformly on compact sets of Ω_N, where DH denotes the differential.

In practice, when applying approximate reduction techniques to population models even in simple settings, the (uniform) convergence of the differentials required in the second condition is difficult to check and involves lengthy reasonings and calculations (see for example the proofs in [11, 12]). In more general situations, proving that the condition holds is completely unfeasible. This shows the need for results that allow one to drop this condition and still offer a relationship between the aggregated and the original model.

Next we present a result of this type where, in the case in which the reduced system (7) has m-periodic hyperbolic points, the local dynamics of the original system (2) can be characterized in terms of them. Roughly speaking, and restricting our attention to the case of equilibrium points, it states that if the aggregated system (7) has a hyperbolic locally asymptotically stable equilibrium point Y^*, then if we choose any sufficiently small neighborhood U of the point $X^* := T(Y^*)$ and the value of k is large enough, there is an equilibrium point X_k^* of system (2) in U and all trajectories starting in U do not leave it. Also, if Y^* is hyperbolic and unstable for (7) then any neighborhood of X^* is unstable [13] provided the value of k is large enough.

Let us first recall the following definition.

Definition 1 Let $\Omega \subset \mathbb{R}^N$ and let $f : \Omega \to \Omega$. We say that a compact set $C \subset \Omega$ is a trapping region for system $X(t + 1) = f(X(t))$ whenever $f(C) \subset \text{int}(C)$ (interior of C).

For each $\delta > 0$ and $X \in \mathbb{R}^N$ let us denote $B(X, \delta) := \{x \in \mathbb{R}^N : \|x - X\| < \delta\}$ where $\| * \|$ denotes the Euclidean norm in $\mathbb{R}^N$ and let $\bar{B}(X, \delta)$ denote the adherence of $B(X, \delta)$. Now we have the following.

Theorem 2 *Let us assume Hypotheses* 2.1, 2.2 *and* 2.3. *Let* $m \in \mathbb{N}$, *let* $Y^* \in \mathbb{R}^q$ *be an hyperbolic* m-*periodic point of system* (7) *and let* $X^* := T(Y^*)$.

1. *Assume* Y^* *is locally asymptotically stable and let* $X_0 \in \Omega_N$ *be such that* $Y_0 := G(X_0)$ *satisfies* $\lim_{n \to \infty} \bar{H}^{mn}(Y_0) = Y^*$. *Then we have the following.*

   (1.a) *There exists* $\delta_0 > 0$ *such that, for every* $\delta > 0$ *satisfying* $0 < \delta < \delta_0$, *there exists* $k_\delta \in \mathbb{Z}_+$ *such that, for all* $k \geq k_\delta$, $\bar{B}(X^*, \delta)$ *is a trapping region for mapping* H_k^m *and, moreover,* H_k^m *has at least a fixed point* X_k^* *in* $B(X^*, \delta)$.

   (1.b) *There exists* $\delta_0 > 0$ *such that, for every* $\delta > 0$ *satisfying* $0 < \delta < \delta_0$, *there exist* $n_\delta, k_\delta \in \mathbb{Z}_+$ *such that* $H_k^{mn+1}(X_0) \in B(X^*, \delta)$ *for all* $k \geq k_\delta$ *and* $n \geq n_\delta$.

2. *Assume* Y^* *is unstable. Then there exists* $\delta_0 > 0$ *such that, for every* $\delta > 0$ *satisfying* $0 < \delta < \delta_0$ *and any point* X *such that* $\|X - X^*\| = \delta$, *there exists* $k_\delta \in \mathbb{Z}_+$ *such that* $H_k^m(X) \notin \bar{B}(X^*, \delta)$ *for all* $k \geq k_\delta$. *In particular* $\bar{B}(X^*, \delta)$ *is not a stable set for* $H_k^m(X)$.

Proof In [7] it is proved, using only Hypotheses 2.1 and 2.2, that if Y^* is a m-periodic point of system (7) then $X^* := T(Y^*)$ is a m-periodic point of system (5) and, moreover, $\rho(D\bar{H}^m(Y^*)) = \rho(DH^m(X^*))$, where $\rho(A)$ denotes the spectral radius of matrix A, so that if Y^* is hyperbolic asymptotically stable (resp. hyperbolic unstable) for (7) then X^* is hyperbolic a.s. (resp. hyperbolic u.) for (5).

1.a. Let us assume that Y^* is a hyperbolic a.s. m-periodic point for system (7) and therefore so is X^* for system (5). Let $0 < \gamma < 1$ be such that $\rho(DH^m(X^*)) < \gamma$. Then it is well known that there exist $\delta_0 > 0$ and a consistent matrix norm $\| \cdot \|$ in $\mathbb{R}^{N \times N}$ such that

$\|DH^m(X)\| \leq \gamma$ for every $X \in \bar{B}(X^*, \delta_0)$. Let δ be such that $0 < \delta < \delta_0$. Then, if $X \in \bar{B}(X^*, \delta)$

$$\left\| H^m(X) - X^* \right\| = \left\| H^m(X) - H^m\left(X^*\right) \right\| \leq \gamma \left\| X - X^* \right\| \leq \gamma \delta.$$

From the uniform convergence of H_k to H on compact sets it follows (see Lemma 11 in the Appendix) that there exists $k_\delta \in \mathbb{Z}_+$ such that, for all $k \geq k_\delta$,

$$\sup_{X \in \bar{B}(X^*, \delta)} \left\| H_k^m(X) - H^m(X) \right\| < \delta(1 - \gamma).$$

Then for every $X \in \bar{B}(X^*, \delta)$ and every $k \geq k_\delta$

$$\left\| H_k^m(X) - X^* \right\| \leq \left\| H_k^m(X) - H^m(X) \right\| + \left\| H^m(X) - X^* \right\|$$
$$\leq \sup_{X \in \bar{B}(X^*, \delta)} \left\| H_k^m(X) - H^m(X) \right\| + \left\| H^m(X) - X^* \right\| < \delta(1 - \gamma) + \gamma \delta = \delta,$$

so that $\bar{B}(X^*, \delta)$ is a trapping region for mapping H_k^m as we wanted to prove.

Moreover, since for $k \geq k_\delta$ the set $\bar{B}(X^*, \delta)$ is convex, compact and positively invariant for H_k^m, then Brouwer's fixed point theorem [14] ensures that there exists at least a fixed point X_k^* for H_k^m in $\bar{B}(X^*, \delta)$.

1.b. Let δ_0 be like in (1.a) and let δ be such that $0 < \delta < \delta_0$. Now using (1.a) we know that there exists $k_\delta' \in \mathbb{Z}_+$ such that, for all $k \geq k_\delta'$,

$$H_k^m\left(\bar{B}\left(X^*, \delta\right)\right) \subset B\left(X^*, \delta\right). \tag{8}$$

Let $X_0 \in \Omega_N$ be such that $Y_0 := G(X_0)$ satisfies $\lim_{n \to \infty} \bar{H}^{mn}(Y_0) = Y^*$. Thus, the continuity of T implies $\lim_{n \to \infty} T(\bar{H}^{mn}(Y_0)) = T(Y^*)$. Using that $T \circ \bar{H}^{n-1} \circ G = H^n$ (Proposition 3.3. in [7]) and the fact that $G(X_0) = Y_0$ it follows that

$$\lim_{n \to \infty} H^{mn+1}(X_0) = X^*.$$

Then there exists $n_\delta \in \mathbb{Z}_+$ such that, for all $n \geq n_\delta$,

$$\left\| H^{mn+1}(X_0) - X^* \right\| < \delta/2. \tag{9}$$

The uniform convergence of H_k to H on compact sets of Ω_N implies, using Lemma 11, that $\lim_{k \to \infty} H_k^{mn_\delta+1}(X_0) = H^{mn_\delta+1}(X_0)$. Therefore, there exists $k_\delta'' \in \mathbb{Z}_+$ such that for all $k \geq k_\delta''$

$$\left\| H_k^{mn_\delta+1}(X_0) - H^{mn_\delta+1}(X_0) \right\| < \delta/2. \tag{10}$$

Using now (9) and (10) we have for all $k \geq k_\delta''$

$$\left\| H_k^{mn_\delta+1}(X_0) - X^* \right\| \leq \left\| H_k^{mn_\delta+1}(X_0) - H^{mn_\delta+1}(X_0) \right\|$$
$$+ \left\| H_k^{mn_\delta+1}(X_0) - H^{mn_\delta+1}(X_0) \right\| < \delta/2 + \delta/2 = \delta,$$

that is, $H_k^{mn_\delta+1}(X_0) \in B(X^*, \delta)$. Finally, taking $k_\delta = \max(k'_\delta, k''_\delta)$ and using (8) we have, for all $k \geq k_\delta$, and all $n \geq n_\delta$, $H_k^{mn+1}(X_0) \in B(X^*, \delta)$ and so the result is proved.

2. Let $\| * \|$ be any norm in $\mathbb{R}^N$. Let λ be an eigenvalue λ of $DH^m(X^*)$ such that $|\lambda| > 1$ and let u be an unit vector belonging to the corresponding eigenspace. Now let $\mu > 0$ be such that $\gamma := |\lambda| - \mu$ is larger than 1.

We know that

$$H^m(X) = X^* + DH^m(X^*)(X - X^*) + \|X - X^*\|G(X),$$

where G is continuous in a neighborhood of X^*, so that there exists $\delta_0 > 0$ such that for all X satisfying $\|X - X^*\| < \delta_0$ we have $\|G(X)\| < \mu$.

Now let δ be such that $0 < \delta < \delta_0$ and let $X := X^* + \delta u \in \bar{B}(X^*, \delta)$. Then

$$\begin{aligned}
\|H^m(X) - X^*\| &= \|H^m(X^* + \delta u) - X^*\| = \|\delta DH^m(X^*)u + \|\delta u\|G(X^* + \delta u)\| \\
&\geq \delta\|DH^m(X^*)u\| - \|\delta u\|\|G(X^* + \delta u)\| \\
&= \delta|\lambda|\|u\| - \delta\|G(X^* + \delta u)\| > \delta|\lambda| - \delta\mu = \gamma\delta.
\end{aligned}$$

From the uniform convergence of H_k^m to H^m on compact sets (Lemma 11 in the Appendix) it follows that there exists $k_\delta \in \mathbb{Z}_+$ such that, for all $k \geq k_\delta$,

$$\sup_{X \in \bar{B}(X^*, \delta)} \|H_k^m(X) - H^m(X)\| < \delta(\gamma - 1).$$

Then if X is such that $\|X - X^*\| = \delta$ we have for all $k \geq k_\delta$

$$\begin{aligned}
\|H_k^m(X) - X^*\| &\geq \|H^m(X) - X^*\| - \|H_k^m(X) - H^m(X)\| \\
&\geq \|H^m(X) - X^*\| - \sup_{X \in \bar{B}(X^*, \delta)} \|H_k^m(X) - H^m(X)\| > \gamma\delta - \delta(\gamma - 1) = \delta,
\end{aligned}$$

as we wanted to prove.   □

Remark 3 For fixed $k \geq k_\delta$ it is not possible to claim that X_k^* is attracting or stable. However, Theorem 2 provides information about the original system which is, for all practical purposes, as valuable as that provided by the results of [7], and has the advantage of dropping the above-mentioned stringent condition on the convergence of the differentials.

3 Two time scales structured metapopulations models: re-scaling survival to the fast time unit

In this section we present two density-dependent discrete population models whose dynamics is driven by two processes, slow and fast. The population is considered structured into q stages and inhabiting an environment divided into r patches. In the first general model that we propose, the fast process includes the movements of the individuals between patches and the slow process consists in all demographic issues. After this, we propose a new model where we carry out the re-scaling of the death process to the fast time unit.

We consider the dispersal between patches to be fast with respect to demography and we denote by k the ratio between the characteristic time scales of the two processes.

The state of the population at time t is represented by the vector

$$X(t) := \left(X_1(t), \ldots, X_q(t)\right)^\mathsf{T} \in \mathbb{R}_+^{qr},$$

where $X_i(t) := (x_i^1(t), \ldots, x_i^r(t)) \in \mathbb{R}_+^r$ and $x_i^\alpha(t)$ denotes the population density in stage i and patch α at time t.

For each stage i, we represent dispersal by a projection matrix which is a primitive probability matrix $M_i(Y) \in \mathbb{R}_+^{r \times r}$ possibly depending on the total number of individuals in each stage, that is, on the vector

$$Y := (y_1, \ldots, y_q)^\mathsf{T},$$

where $y_i := \sum_{\alpha=1}^r x_i^\alpha = \mathbf{1} X_i$ is the total population in stage i and we are denoting $\mathbf{1} := (1, \overset{(r)}{\ldots}, 1)$. Vector Y will play the role of global variables (6) in the reduced system. If we denote $\mathbf{U} := \mathrm{diag}(\mathbf{1}, \ldots, \mathbf{1}) \in \mathbb{R}_+^{q \times qr}$ we can express Y in terms of X in the following way:

$$G(X) := Y = \mathbf{U}X.$$

Finally, we define $\mathbf{M}(Y) := \mathrm{diag}(M_1(Y), \ldots, M_q(Y))$ and thus the map F defining the fast process, i.e., dispersal, is

$$F(X) := \mathbf{M}(Y)X = \mathbf{M}(\mathbf{U}X)X.$$

The fact that vector $\mathbf{1}$ is a left eigenvector of matrices M_i associated to eigenvalue 1 implies that $\mathbf{U}\mathbf{M}(\mathbf{U}X) = \mathbf{U}$, so $\mathbf{U}\mathbf{M}(\mathbf{U}X)X = \mathbf{U}X$ and

$$F^{(k)}(X) = \mathbf{M}(\mathbf{U}X)^k X,$$

that is, we can express the kth iterate of map F in terms of the power k of matrix $\mathbf{M}(\mathbf{U}X)$.

In the sequel we assume that all the vital rates, and therefore the resulting vital rate matrices, are C^1 functions of their corresponding variables.

To represent the slow process, associated to demography, we define a non-negative projection matrix that can depend on the state variables

$$\mathbf{D}(X) = \left[D_{ij}(X)\right]_{1 \le i,j \le q} \in \mathbb{R}^{qr \times qr},$$

and is divided into blocks $D_{ij}(X) = \mathrm{diag}(d_{ij}^\alpha(X)) \in \mathbb{R}^{r \times r}$ where $d_{ij}^\alpha(X)$ represents the rate of individual transition from stage j to stage i in patch α during a slow time interval when the state of the population is represented by the vector X. Thus, the map defining the slow process is

$$S(X) := \mathbf{D}(X)X.$$

With the maps F and S we propose a first two time scales model in the form of system (1):

$$X(t+1) = S\left(F^{(k)}\left(X(t)\right)\right) = \mathbf{D}\left(\mathbf{M}\left(\mathbf{U}X(t)\right)^k X(t)\right)\mathbf{M}\left(\mathbf{U}X(t)\right)^k X(t). \tag{11}$$

In this model individuals first perform a series of k dispersal events followed by a demographic update that occurs in the arrival patch. This assumption is realistic concerning reproduction specially in the case of populations with separated generations. However, the situation might be different for a process like mortality, for individuals may die at any time during the dispersal process. Now we show how to take this into account by proposing a new model, based on the previous one, in which mortality acts at the fast time scale, i.e., we re-scale survival to the fast time scale.

Let $s_i^\alpha > 0$ be the stage and patch specific survival rate for stage i and patch α, that is, the fraction of individuals in stage i ($i = 1, \ldots, q$) alive at time t that survive to time $t + 1$ in patch α ($\alpha = 1, \ldots, r$). We assume that s_i^α possibly depends on Y, i.e., $s_i^\alpha = s_i^\alpha(Y)$.

We first factor out every coefficient $d_{ij}^\alpha(X)$ in matrix $\mathbf{D}(X)$ in order to make the survival rate appear explicitly, i.e., we define

$$\tilde{d}_{ij}^\alpha(X) := d_{ij}^\alpha(X)/s_j^\alpha(Y).$$

This factorization can be extended to matrix $\mathbf{D}(X)$. Indeed, we define

$$\tilde{D}_{ij}(X) = \mathrm{diag}\big(\tilde{d}_{ij}^\alpha(X)\big)_{\alpha=1,\ldots,r}, \qquad \tilde{\mathbf{D}}(X) = \big[\tilde{D}_{ij}(X)\big]_{1\le i,j\le q},$$
$$S_j(Y) = \mathrm{diag}\big(s_j^\alpha(Y)\big)_{\alpha=1,\ldots,r} \quad \text{and} \quad \mathbf{S}(Y) = \mathrm{diag}\big(S_j(Y)\big)_{j=1,\ldots,q},$$

so that $D_{ij}(X) = \tilde{D}_{ij}(X)S_j(Y)$ and

$$\mathbf{D}(X) = \tilde{\mathbf{D}}(X)\mathbf{S}(Y).$$

We can now write $\mathbf{S}(Y) = \mathbf{S}_k(Y)^k$, i.e., $\mathbf{S}(Y)$ is the kth power of the matrix $\mathbf{S}_k(Y)$ given by

$$\mathbf{S}_k(Y) = \mathrm{diag}\big(S_{j,k}(Y)\big)_{j=1,\ldots,q} \quad \text{and} \quad S_{j,k}(Y) = \mathrm{diag}\big(s_j^\alpha(Y)^{1/k}\big)_{\alpha=1,\ldots,r}.$$

We consider the matrix $\mathbf{S}_k(Y)$ to describe the effect of survival at the fast time scale, and based on it we propose a second two time scales model with re-scaled survival:

$$X(t + 1) = \tilde{\mathbf{D}}\big(\big(\mathbf{S}_k\big(\mathbf{U}X(t)\big)\mathbf{M}\big(\mathbf{U}X(t)\big)\big)^k X(t)\big)\big(\mathbf{S}_k\big(\mathbf{U}X(t)\big)\mathbf{M}\big(\mathbf{U}X(t)\big)\big)^k X(t). \tag{12}$$

In this model individuals first perform a series of k dispersal events in which mortality is taken into account in each of them through corresponding survival rate. The rest of the demographic process follows at the slow time scale.

3.1 Reduction of models (11) and (12)

To reduce (11) we show how the corresponding sequence of maps

$$H_k(X) = \mathbf{D}\big(\mathbf{M}(\mathbf{U}X)^k X\big)\mathbf{M}(\mathbf{U}X)^k X$$

satisfies Hypotheses 2.1, 2.2, and 2.3.

The key point is to find the limit of the powers of matrix $\mathbf{M}(\mathbf{U}X)$. We use the fact that the $M_i(\mathbf{U}X)$ are primitive probability matrices. Therefore their dominant eigenvalue is 1,

vector $\mathbf{1}$ is an associated left eigenvector and there exists, for each $i = 1, \ldots, q$ and $\mathbf{U}X \in \mathbb{R}_+^q$, a unique column positive right eigenvector $V_i(\mathbf{U}X) \in \mathbb{R}^r$ such that $\mathbf{1}V_i(\mathbf{U}X) = 1$. The Perron–Frobenius theorem yields

$$\lim_{k \to \infty} M_i(\mathbf{U}X)^k = V_i(\mathbf{U}X))\mathbf{1}.$$

Calling $\mathbf{V}(\mathbf{U}X) := \mathrm{diag}(V_i(\mathbf{U}X)))_{i=1,\ldots,q} \in \mathbb{R}_+^{qr \times q}$ we have

$$\lim_{k \to \infty} \mathbf{M}(\mathbf{U}X)^k = \mathbf{V}(\mathbf{U}X)\mathbf{U}$$

and thus

$$\lim_{k \to \infty} H_k(X) = \mathbf{D}\big(\mathbf{V}(\mathbf{U}X)\mathbf{U}X\big)\mathbf{V}(\mathbf{U}X)\mathbf{U}X,$$

and so the limit in Hypothesis 2.1 exists. The decomposition of this limit required in Hypothesis 2.2 is obtained by defining $G(X) = \mathbf{U}X$ and $T(Y) = \mathbf{D}(\mathbf{V}(Y)Y)\mathbf{V}(Y)Y$. The rest of the technical details involved in proving that Hypotheses 2.1 and 2.3 hold can be found in [12].

The reduced system associated to (11) is

$$Y(t + 1) = \bar{H}\big(Y(t)\big) = G\big(T\big(Y(t)\big)\big) = \mathbf{U}\mathbf{D}\big(\mathbf{V}\big(Y(t)\big)Y(t)\big)\mathbf{V}\big(Y(t)\big)Y(t). \tag{13}$$

Theorem 2 can be applied to systems (11) and (13) so that we can obtain information on the asymptotic behavior of solutions to system (11) by performing the analysis in the reduced system (13).

We now proceed to the reduction of system (12), for which we have

$$H_k(X) = \tilde{\mathbf{D}}\big(\big(\mathbf{S}_k(\mathbf{U}X)\mathbf{M}(\mathbf{U}X)\big)^k X\big)\big(\mathbf{S}_k(\mathbf{U}X)\mathbf{M}(\mathbf{U}X)\big)^k X.$$

In this occasion we have to calculate the limit of the kth power of matrix $\mathbf{S}_k(\mathbf{U}X)\mathbf{M}(\mathbf{U}X)$.

A straightforward application of Proposition 12 in the Appendix to each of the diagonal blocks of matrix $\mathbf{S}_k(\mathbf{U}X)\mathbf{M}(\mathbf{U}X)$ yields the result. For every $i = 1, \ldots, q$ let $Z_i(\mathbf{U}X) = (\log(s_i^1(\mathbf{U}X)), \ldots, \log(s_i^r(\mathbf{U}X))) \in \mathbb{R}^r$ be a row vector and define the scalar $\gamma_i(\mathbf{U}X) := \exp(Z_i(\mathbf{U}X)V_i(\mathbf{U}X))$. Denoting

$$\tilde{\mathbf{V}} := \mathrm{diag}\big(\gamma_i(\mathbf{U}X)V_i(\mathbf{U}X)\big)_{i=1,\ldots,q} \in \mathbb{R}_+^{q \times qr},$$

we obtain

$$\lim_{k \to \infty} \big(\mathbf{S}_k(\mathbf{U}X)\mathbf{M}(\mathbf{U}X)\big)^k = \tilde{\mathbf{V}}(\mathbf{U}X)\mathbf{U}.$$

Therefore,

$$\lim_{k \to \infty} H_k(X) = \tilde{\mathbf{D}}\big(\tilde{\mathbf{V}}(\mathbf{U}X)\mathbf{U}X\big)\tilde{\mathbf{V}}(\mathbf{U}X)\mathbf{U}X.$$
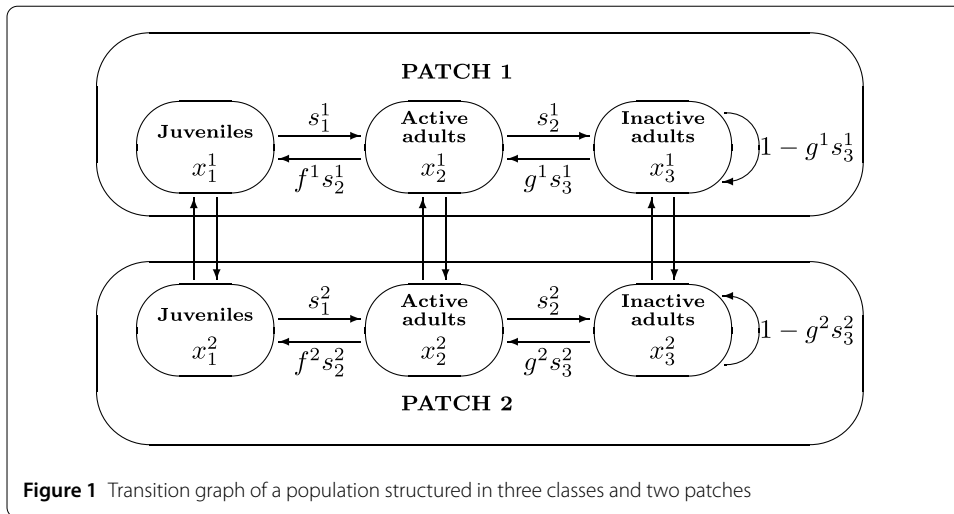
Figure 1 Transition graph of a population structured in three classes and two patches

Defining $G(X) = \mathbf{U}X$ and $\tilde{T}(Y) = \tilde{\mathbf{D}}(\tilde{\mathbf{V}}(Y)Y)\tilde{\mathbf{V}}(Y)Y$, Hypotheses 2.1, 2.2 and 2.3 are met and the reduced system associated to (12) is

$$Y(t+1) = \tilde{H}(Y(t)) = G(\tilde{T}(Y)) = \mathbf{U}\tilde{\mathbf{D}}(\tilde{\mathbf{V}}(Y(t))Y(t))\tilde{\mathbf{V}}(Y(t))Y(t). \tag{14}$$

4 Models (11) and (12) in a three-stage, two-patch case

We propose the model of a population inhabiting a two-patch environment. Following the model presented in [9], locally the population is considered structured into three classes corresponding to juveniles and two adult stages. Adults that reproduce at the end of an interval of time do not reproduce at the end of the following one. A fraction of those not having reproduced do so at the end of the following interval. Thus, adults are classified into those reproducing at the end of the time interval, active adults, and those adults who do not, inactive adults. The aim of this consideration is analyzing the reproductive synchrony of adults.

Let x_1^α, x_2^α and x_3^α be the number of juveniles, active adults and inactive adults, respectively, in patch $\alpha = 1, 2$. The demographic vector is then

$$X = (x_1^1, x_1^2, x_2^1, x_2^2, x_3^1, x_3^2)^\top \in \mathbb{R}_+^6.$$

The unit of time of the discrete model that we are proposing coincides with the juvenile maturation period. For $i = 1, 2, 3$ and $\alpha = 1, 2$, we denote by $s_i^\alpha \in (0, 1)$ the corresponding survival probabilities, by $f^\alpha > 0$ the adult per capita fecundity rates and by $g^\alpha \in [0, 1]$ the fractions of reproductively inactive adults becoming active at the next time unit. Figure 1 shows a transition graph for the population.

The projection matrix, $\mathbf{D}$, associated to demography, is

$$\mathbf{D} = \begin{pmatrix} 0 & 0 & f^1 s_2^1 & 0 & 0 & 0 \\ 0 & 0 & 0 & f^2 s_2^2 & 0 & 0 \\ s_1^1 & 0 & 0 & 0 & g^1 s_3^1 & 0 \\ 0 & s_1^2 & 0 & 0 & 0 & g^2 s_3^2 \\ 0 & 0 & s_2^1 & 0 & (1-g^1)s_3^1 & 0 \\ 0 & 0 & 0 & s_2^2 & 0 & (1-g^2)s_3^2 \end{pmatrix},$$

which can also be written as

$$\mathbf{D} = \tilde{\mathbf{D}}\mathbf{S} = \begin{pmatrix} 0 & 0 & f^1 & 0 & 0 & 0 \\ 0 & 0 & 0 & f^2 & 0 & 0 \\ 1 & 0 & 0 & 0 & g^1 & 0 \\ 0 & 1 & 0 & 0 & 0 & g^2 \\ 0 & 0 & 1 & 0 & 1-g^1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 1-g^2 \end{pmatrix} \begin{pmatrix} s_1^1 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_1^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_2^1 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_2^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_3^1 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_3^2 \end{pmatrix}.$$

Migrations are represented by primitive probability matrices $M_i \in \mathbb{R}_+^{2\times2}$ ($i = 1, 2, 3$), which are the diagonal blocks of

$$\mathbf{M} = \mathrm{diag}(M_1, M_2, M_3).$$

According to the framework of models (11) and (12), fecundities and transitions from reproductive inactivity may depend on the state variables, whereas the survival and dispersal coefficients could possibly depend on the total number of individuals in each stage

$$Y := (y_1, y_2, y_3)^\top,$$

where $y_i = x_i^1 + x_i^2 = \mathbf{1}X_i$, with $\mathbf{1} = (1, 1)$, is the total population in stage i. We recall that in the present case $\mathbf{U} = \mathrm{diag}(\mathbf{1}, \mathbf{1}, \mathbf{1}) \in \mathbb{R}_+^{3\times6}$, and we have $Y = \mathbf{U}X$.

The model with survival acting at the slow time scale is

$$X(t + 1) = \mathbf{D}\big(\mathbf{M}\big(Y(t)\big)^k X(t)\big)\mathbf{M}\big(Y(t)\big)^k X(t), \tag{15}$$

whereas the model with survival acting at the fast time scale is

$$X(t + 1) = \tilde{\mathbf{D}}\big(\big(\mathbf{S}_k\big(Y(t)\big)\mathbf{M}\big(Y(t)\big)\big)^k X(t)\big)\big(\mathbf{S}_k\big(Y(t)\big)\mathbf{M}\big(Y(t)\big)\big)^k X(t), \tag{16}$$

where $\mathbf{S}_k = \mathrm{diag}(S_{k1}, S_{k2}, S_{k3})$ with $S_{ki} = \mathrm{diag}((s_i^1)^{1/k}, (s_i^2)^{1/k})$ for $i = 1, 2, 3$.

To simplify the calculations we first assume that the dispersal rates are constant.

For $i = 1, 2, 3$ let $V_i = (v_i^1, v_i^2)^\top$ be the unique column positive right eigenvector of matrix M_i associated to eigenvalue 1 such that $\mathbf{1}V_i = 1$. We are using the matrix

$$\mathbf{V} = \mathrm{diag}(V_1, V_2, V_3),$$

to obtain the reduced systems (13) and (14) associated to systems (11) and (12).

We also assume, following the example in Sect. 2 of [9], that the survival rates are constant and fecundities and transitions from reproductive inactivity are locally dependent on the number of active adults. Specifically, we set

$$f^\alpha\big(x_2^\alpha\big) := \frac{\phi^\alpha}{1 + c^\alpha x_2^\alpha} \quad \text{and} \quad g^\alpha\big(x_2^\alpha\big) := \frac{1}{1 + d^\alpha x_2^\alpha}, \quad \alpha = 1, 2,$$

where $\phi^\alpha > 0$ are the inherent fertility rates and parameters c^α and d^α are positive.

To obtain the reduced system associated to system (11) we apply the procedure described in Sect. 3.1. The result is the next 3-dimensional system:

$$Y(t+1) = \begin{pmatrix} 0 & \bar{b}\bar{h}_1(y_2(t)) & 0 \\ \bar{s}_1 & 0 & \bar{s}_3\bar{h}_2(y_2(t)) \\ 0 & \bar{s}_2 & \bar{s}_3(1-\bar{h}_2(y_2(t))) \end{pmatrix} Y(t) = \bar{H}\big(Y(t)\big)Y(t), \tag{17}$$

where

$$\bar{s}_i := s_i^1 v_i^1 + s_i^2 v_i^2 \quad (i=1,2,3), \qquad \bar{b} := \phi^1 s_2^1 v_2^1 + \phi^2 s_2^2 v_2^2,$$

$$\bar{h}_1(y_2) := \frac{\phi^1 s_2^1 v_2^1/\bar{b}}{1+c^1 v_2^1 y_2} + \frac{\phi^2 s_2^2 v_2^2/\bar{b}}{1+c^2 v_2^2 y_2} \quad \text{and} \quad \bar{h}_2(y_2) := \frac{s_3^1 v_3^1/\bar{s}_3}{1+d^1 v_2^1 y_2} + \frac{s_3^2 v_3^2/\bar{s}_3}{1+d^2 v_2^2 y_2}.$$

Associated to system (12) we obtain the following reduced system:

$$Y(t+1) = \begin{pmatrix} 0 & \tilde{b}\tilde{h}_1(y_2(t)) & 0 \\ \tilde{s}_1 & 0 & \tilde{s}_3\tilde{h}_2(y_2(t)) \\ 0 & \tilde{s}_2 & \tilde{s}_3(1-\tilde{h}_2(y_2(t))) \end{pmatrix} Y(t) = \tilde{H}\big(Y(t)\big)Y(t), \tag{18}$$

where

$$\tilde{s}_i := \big(s_i^1\big)^{v_i^1}\big(s_i^2\big)^{v_i^2} \quad (i=1,2,3), \qquad \tilde{b} := \tilde{s}_2\big(\phi^1 v_2^1 + \phi^2 v_2^2\big),$$

$$\tilde{h}_1(y_2) := \frac{\phi^1 \tilde{s}_2 v_2^1/\tilde{b}}{1+c^1\tilde{s}_2 v_2^1 y_2} + \frac{\phi^2\tilde{s}_2 v_2^2/\tilde{b}}{1+c^2\tilde{s}_2 v_2^2 y_2} \quad \text{and} \quad \tilde{h}_2(y_2) := \frac{v_3^1}{1+d^1\tilde{s}_2 v_2^1 y_2} + \frac{v_3^2}{1+d^2\tilde{s}_2 v_2^2 y_2}.$$

The projection matrices, $\bar{H}(Y)$ and $\tilde{H}(Y)$, of systems (17) and (18) verify the hypotheses H1 and H2 of projection matrix P in Sect. 3 of [9], so Theorems 1–3 therein apply to both systems.

We now proceed to adapt the results in Sect. 3 of [9] to systems (17) and (18). Thus, definitions, notation and propositions are directly inspired from it.

In the first place we define the *inherent net reproduction number R_0* associated to a nonlinear system as the net reproduction number (NRN) [15] of the projection matrix of the system in the absence of density dependence, i.e., when the population vector is zero. In this way, the inherent NRNs, $\bar{R}_0$ and $\tilde{R}_0$, of matrices $\bar{H}(Y)$ and $\tilde{H}(Y)$ are

$$\bar{R}_0 = \frac{\bar{b}\bar{s}_1}{1-\bar{s}_2\bar{s}_3} \quad \text{and} \quad \tilde{R}_0 = \frac{\tilde{b}\tilde{s}_1}{1-\tilde{s}_2\tilde{s}_3}. \tag{19}$$

The first result states that the inherent NRN characterizes the stability of the extinction equilibrium of the system as well as its uniform persistence.

Proposition 4 *For system* (17) *(resp.* (18)*) the extinction equilibrium $Y_0^* = \bar{0} = (0,0,0)^\top$ is locally asymptotically stable if $\bar{R}_0 < 1$ (resp. $\tilde{R}_0 < 1$) and unstable if $\bar{R}_0 > 1$ (resp. $\tilde{R}_0 > 1$). Furthermore, if $\bar{R}_0 > 1$ (resp. $\tilde{R}_0 > 1$) then the system* (17) *(resp.* (18)*) is uniformly persistent with respect to Y_0^*.*

Proof The result is a direct consequence of Theorem 1 in [9]. □

In the sequel we concentrate on system (17) and we develop some asymptotic results when $\bar{R}_0$ increases through 1. That entails, as shown in Proposition 4, the destabilization of the extinction equilibrium $Y_0^* = \bar{0}$. The fact that the matrix $\bar{H}(\bar{0})$ is not primitive gives rise to the simultaneous bifurcation of positive equilibria and non-negative 2-cycles [10].

We say that $(\bar{R}_0, \bar{Y}) \in \mathbf{R}_+ \times \mathbf{R}_+^3$ is an equilibrium pair for system (17) when $\bar{Y}$ is an equilibrium for the system and the inherent NRN is $\bar{R}_0$. Clearly $(\bar{R}_0, \bar{0})$ is an equilibrium pair for all values of $\bar{R}_0$.

Clearly, system (17) has periodic orbits on the boundary of the positive cone of the following form:

$$\bar{Y}_2 = (0, y_2, 0)^{\mathrm{T}}, \qquad \bar{Y}_{1,3} = (y_1, 0, y_3)^{\mathrm{T}}$$

for certain values of $y_1, y_2, y_3 > 0$. They are called synchronous 2-cycles and are represented by their two points $(\bar{Y}_2, \bar{Y}_{1,3})$. We call $(\bar{R}_0, (\bar{Y}_2, \bar{Y}_{1,3}))$ a synchronous 2-cycle pair of system (17) if $(\bar{Y}_2, \bar{Y}_{1,3})$ is a synchronous 2-cycle for the associated value of $\bar{R}_0$.

The declared aim of the model in [9] is analyzing the reproductive synchrony of adults. Concerning that, the synchronous 2-cycles represent reproductive synchrony, i.e., all adults reproduce simultaneously in only one of the two points of the cycle, whereas the positive equilibria represent reproductive asynchrony, i.e., there are reproducing adults at each point of time. Through models (15) and (16) we can study how dispersal affect reproductive synchrony. At the same time, we are interested in analyzing whether choosing one model versus the other could result in different outcomes.

In the next result, conditions for the existence and stability of equilibrium and synchronous 2-cycle pairs are obtained. To do so, we define the following four quantities:

$$\bar{c}_w := (1 - \bar{s}_2 \bar{s}_3) \bar{s}_1 \bar{h}_1'(0), \qquad \bar{c}_b := \bar{s}_1 \bar{s}_2 \bar{s}_3 (1 - \bar{s}_3) \bar{h}_2'(0), \tag{20}$$

and

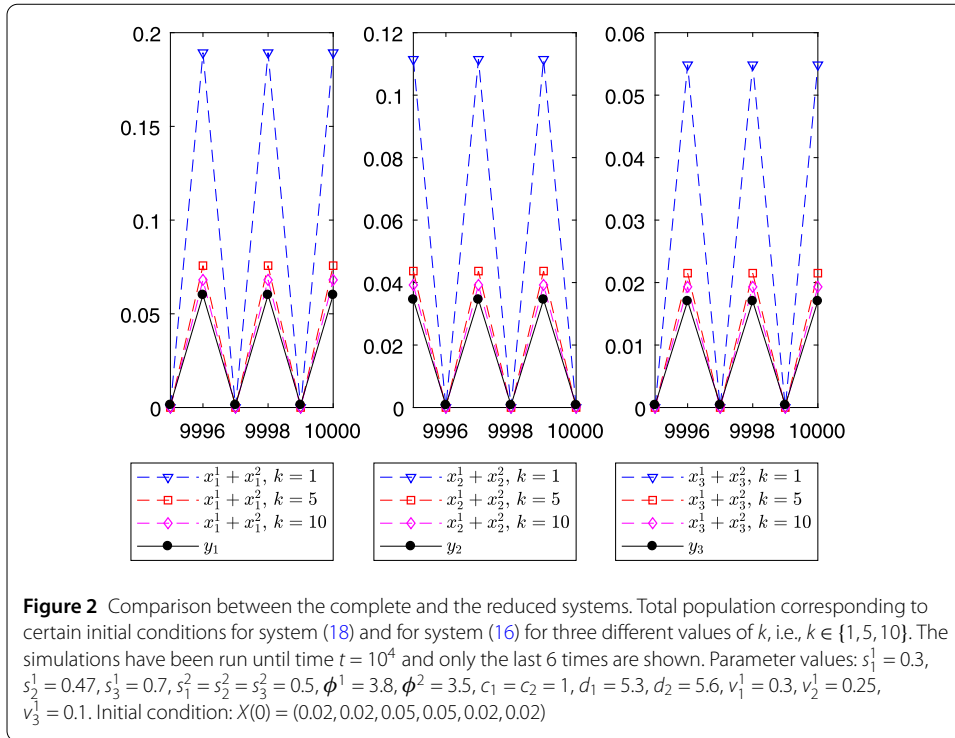$$\bar{a}_+ := \bar{c}_w + \bar{c}_b, \qquad \bar{a}_- := \bar{c}_w - \bar{c}_b. \tag{21}$$

Proposition 5 *For system* (17):

1. *A continuum $\bar{C}_e$ of positive equilibrium pairs bifurcates from the extinction equilibrium pair $(\bar{R}_0, \bar{Y}) = (1, \bar{0})$. In a neighborhood of $(1, \bar{0})$, the positive equilibrium pairs $(\bar{R}_0, \bar{Y}) \in \bar{C}_e$ have, for $0 < \varepsilon \ll 1$, the parameterizations*

$$\bar{R}_0(\varepsilon) = 1 - \frac{\bar{a}_+}{1 - \bar{s}_2 \bar{s}_3} \varepsilon + O(\varepsilon^2), \qquad \bar{Y}(\varepsilon) = \begin{pmatrix} 1 - \bar{s}_2 \bar{s}_3 \\ \bar{s}_1 \\ \bar{s}_1 \bar{s}_2 \end{pmatrix} \varepsilon + O(\varepsilon^2).$$

2. *A continuum $\bar{C}_2$ of synchronous 2-cycles pairs bifurcates from the extinction equilibrium pair $(\bar{R}_0, \bar{Y}) = (1, \bar{0})$. In a neighborhood of $(1, \bar{0})$, the synchronous 2-cycles pairs $(\bar{R}_0, (\bar{Y}_2, \bar{Y}_{1,3})) \in \bar{C}_2$ have, for $0 < \varepsilon \ll 1$, the parameterizations*

$$\bar{R}_0(\varepsilon) = 1 - \frac{\bar{c}_w}{1 - \bar{s}_2 \bar{s}_3} \varepsilon + O(\varepsilon^2),$$

Figure 2 Comparison between the complete and the reduced systems. Total population corresponding to certain initial conditions for system (18) and for system (16) for three different values of k, i.e., $k \in \{1, 5, 10\}$. The simulations have been run until time $t = 10^4$ and only the last 6 times are shown. Parameter values: $s_1^1 = 0.3$, $s_2^1 = 0.47$, $s_3^1 = 0.7$, $s_1^2 = s_2^2 = s_3^2 = 0.5$, $\phi^1 = 3.8$, $\phi^2 = 3.5$, $c_1 = c_2 = 1$, $d_1 = 5.3$, $d_2 = 5.6$, $v_1^1 = 0.3$, $v_2^1 = 0.25$, $v_3^1 = 0.1$. Initial condition: $X(0) = (0.02, 0.02, 0.05, 0.05, 0.02, 0.02)$

$$\bar{Y}_2(\varepsilon) = \begin{pmatrix} 0 \\ \bar{s}_1 \\ 0 \end{pmatrix} \varepsilon + O(\varepsilon^2), \qquad \bar{Y}_{1,3}(\varepsilon) = \begin{pmatrix} 1 - \bar{s}_2\bar{s}_3 \\ 0 \\ \bar{s}_1\bar{s}_2 \end{pmatrix} \varepsilon + O(\varepsilon^2).$$

3. (a) If $\bar{a}_- < 0$ *the equilibria of the pairs in $\bar{C}_e$ are locally asymptotically stable and the* *2-cycles of the pairs in $\bar{C}_2$ are unstable.*
   (b) If $\bar{a}_- > 0$ *the equilibria of the pairs in $\bar{C}_e$ are unstable and the 2-cycles of the pairs* *in $\bar{C}_2$ are locally asymptotically stable.*

Proof It is a direct consequence of Theorems 2 and 3 in [9]. □

The previous result refers to system (17). Since systems (17) and (18) have the same functional form, an analogous result holds for the latter. In particular, it is the sign of the quantity

$$\tilde{a}_- := (1 - \tilde{s}_2\tilde{s}_3)\tilde{s}_1\tilde{h}_1'(0) - \tilde{s}_1\tilde{s}_2\tilde{s}_3(1 - \tilde{s}_3)\tilde{h}_2'(0), \tag{22}$$

which decides the asymptotic stability of either the equilibria of the pairs in $\tilde{C}_e = (\tilde{R}_0, \tilde{Y})$ ($\tilde{a}_- < 0$) or the synchronous 2-cycles of the pairs in $\tilde{C}_2 = (\tilde{R}_0, (\tilde{Y}_2, \tilde{Y}_{1,3}))$ ($\tilde{a}_- > 0$) that bifurcate from the extinction equilibrium pair $(\tilde{R}_0, \tilde{Y}) = (1, \bar{0})$.

The results in Sects. 2 and 3 justify that the previous results regarding the reduced systems (17) and (18) can be used to obtain information about the local dynamics of the original two time scales models (15) and (16).

In Fig. 2, a simulation regarding the relationship between systems (18) and (16) is shown, illustrating the fact that, for large enough values of k, the reduced system (18) is a good approximation of the complete system (16). Starting from the same initial condition we

have simulated system (18) and system (16) for three different values of k. The reduced system (18) presents a 2-cycle and so does the complete system (16) for the three values of k. For $k = 10$, the orbit of the complete system is approximated very closely by that corresponding to the reduced system.

4.1 The effect of fast dispersal

The effect of dispersal in populations and in particular its effect at a global level when local isolated populations are connected, has considerable biological interest and has been addressed in a number of different contexts (see [16–18] among others). In this section we deal with models (15) and (16) and present some results that show how dispersal can change the two main asymptotic issues regarding the dynamics of the population. The first one is the survival of the population as reflected by the extinction equilibrium stability. Then, once the survival threshold is attained, we address the second issue, i.e., the tendency of the population towards either reproductive synchrony or asynchrony, represented by the stability of synchronous 2-cycles or positive equilibria, respectively.

We compare the outcomes of local (isolated sites) and global (dispersal interconnected sites) population dynamics. The reduction procedure applied to systems (15) and (16) allows us to use the corresponding reduced systems (17) and (18) to study their asymptotic behavior. So, we use quantities $\bar{R}_0$ (resp. $\tilde{R}_0$) and $\bar{a}_-$ (resp. $\tilde{a}_-$) to characterize, respectively, survival and reproductive synchrony at the global level in the two systems. The influence of fast dispersal in the population dynamics is reflected through the values v_i^α that appear in the coefficients of matrices $\bar{H}(Y)$ (17) and $\tilde{H}(Y)$ (18). We recall that $V_i = (v_i^1, v_i^2)^\mathsf{T}$ $(i = 1, 2, 3)$ is the dominant probability normed eigenvector of matrix M_i and therefore its components represent the equilibrium distribution of dispersal for individuals of class i, i.e., v_i^j is the proportion of individuals of class i present in patch j after dispersal has reached equilibrium. Their value is

$$v_i^1 = \frac{q_i}{p_i + q_i}, \qquad v_i^2 = \frac{p_i}{p_i + q_i}, \quad i = 1, 2, 3,$$

where p_i (resp. q_i) is the migration rate from patch one to patch two (resp. from patch two to patch one) for individuals of class i.

At the local level, i.e., if patches $\alpha = 1, 2$ are considered isolated, the matrix representing the population dynamics in each of them is

$$\mathbf{D}^\alpha(Y) = \begin{pmatrix} 0 & s_2^\alpha \phi^\alpha \frac{1}{1+c^\alpha y_2^\alpha} & 0 \\ s_1^\alpha & 0 & s_3^\alpha \frac{1}{1+d^\alpha y_2^\alpha} \\ 0 & s_2^\alpha & s_3^\alpha (1 - \frac{1}{1+d^\alpha y_2^\alpha}) \end{pmatrix}. \tag{23}$$

Effect of dispersal on extinction. The stability of the extinction equilibrium is locally determined by the corresponding inherent NRN,

$$R_0^\alpha := \frac{\phi^\alpha s_1^\alpha s_2^\alpha}{1 - s_2^\alpha s_3^\alpha}, \quad \alpha = 1, 2, \tag{24}$$

and the tendency towards reproductive synchrony or asynchrony by

$$a_-^\alpha := -\left(1 - s_2^\alpha s_3^\alpha\right) s_1^\alpha c^\alpha + s_1^\alpha s_2^\alpha s_3^\alpha \left(1 - s_3^\alpha\right) d^\alpha, \quad \alpha = 1, 2. \tag{25}$$

If we consider homogeneous sites concerning survival and fertility, i.e., $s_i^1 = s_i^2 =: s_i$ for $i = 1, 2, 3$ and $\phi^1 = \phi^2 =: \phi$, we obtain

$$R_0^1 = R_0^2 = \bar{R}_0 = \tilde{R}_0 = \frac{\phi s_1 s_2}{1 - s_2 s_3}, \tag{26}$$

so that, in particular, the population survives or gets extinct locally if and only if it does globally.

On the other hand, differences in local parameters, i.e., s_1^1 vs. s_1^2 and ϕ^1 vs. ϕ^2, can result in different survival outcomes at the local and the global levels provided appropriate dispersal rates are chosen. In the next result we show that under certain conditions, adequate dispersal strategies can transform the local population extinction in isolated patches into global survival.

Proposition 6 *Let us assume $s_i^1 = s_i^2 =: s_i$ for $i = 2, 3$, $R_0^1 < 1$ and $R_0^2 < 1$. If $\max\{s_1^1 \phi^2, s_1^2 \phi^1\} > (1 - s_2 s_3)/s_2$ then there exist intervals $I_1, I_2 \subseteq [0, 1]$ (resp. $\tilde{I}_1, \tilde{I}_2 \subseteq [0, 1]$) such that $\bar{R}_0 > 1$ (resp. $\tilde{R}_0 > 1$) for $v_1^1 \in I_1$ and $v_2^1 \in I_2$ (resp. $v_1^1 \in \tilde{I}_1$ and $v_2^1 \in \tilde{I}_2$).*

Proof Let us assume, without loss of generality, that $s_1^1 \phi^2 \geq s_1^2 \phi^1$ and use $v_i^2 = 1 - v_i^1$ for $i = 1, 2, 3$ to obtain

$$\bar{R}_0 = \frac{s_2}{1 - s_2 s_3} \left(v_1^1 s_1^1 + \left(1 - v_1^1\right) s_1^2 \right) \left(v_2^1 \phi^1 + \left(1 - v_2^1\right) \phi^2 \right)$$

$$> \frac{s_2}{1 - s_2 s_3} v_1^1 \left(1 - v_2^1\right) s_1^1 \phi^2.$$

This last expression, considered as a function of variables v_1^1 and v_2^1, is continuous and takes the value $s_1^1 \phi^2 s_2/(1 - s_2 s_3) > 1$ for $v_1^1 = 1$ and $v_2^1 = 0$. This yields the existence of the intervals $I_1, I_2 \subseteq [0, 1]$ that ensure $\bar{R}_0 > 1$ for $(v_1^1, v_2^1) \in I_1 \times I_2$.

The proof for $\tilde{R}_0 > 1$ is analogous. □

The previous result says that, given certain (common) adult survival rates, if the juvenile survival rate in one of the patches together with the fertility rate in the other are large enough to sustain the population, then there exist appropriate dispersal rates to compensate poor local survival conditions.

The opposite result also holds. Adequately chosen dispersal rates, under appropriate conditions, can make two isolated viable populations go extinct when they are connected.

Proposition 7 *Let us assume $s_i^1 = s_i^2 = s_i$ for $i = 2, 3$, $R_0^1 > 1$ and $R_0^2 > 1$. If $\min\{s_1^1 \phi^2, s_1^2 \phi^1\} < (1 - s_2 s_3)/s_2$ then there exist intervals $I_1, I_2 \subseteq [0, 1]$ (resp. $\tilde{I}_1, \tilde{I}_2 \subseteq [0, 1]$) such that $\bar{R}_0 < 1$ (resp. $\tilde{R}_0 < 1$) for $v_1^1 \in I_1$ and $v_2^1 \in I_2$ (resp. $v_1^1 \in \tilde{I}_1$ and $v_2^1 \in \tilde{I}_2$).*

Proof Analogous to the proof of Proposition 6. □

Effect of dispersal on reproductive synchrony. We now illustrate the influence of fast dispersal on the population's reproductive synchrony. We do so in the particular case of homogeneous patches, i.e., when all demographic parameters are the same in both patches:

$$s_i^1 = s_i^2 =: s_i \quad \text{for } i = 1, 2, 3; \qquad \phi^1 = \phi^2 =: \phi; \qquad c^1 = c^2 =: c; \qquad d^1 = d^2 =: d. \tag{27}$$

Thus, the demographic local matrices coincide

$$\mathbf{D}^1(Y) = \mathbf{D}^2(Y) = \begin{pmatrix} 0 & s_2\phi\frac{1}{1+cy_2} & 0 \\ s_1 & 0 & s_3\frac{1}{1+dy_2} \\ 0 & s_2 & s_3(1-\frac{1}{1+dy_2}) \end{pmatrix}, \tag{28}$$

but, due to the dispersal rates, are different from the demographic global matrices for systems (17) and (18),

$$\bar{H}(Y) = \begin{pmatrix} 0 & s_2\phi(\frac{v_2^1}{1+cv_2^1y_2} + \frac{v_2^2}{1+cv_2^2y_2}) & 0 \\ s_1 & 0 & s_3(\frac{v_3^1}{1+dv_2^1y_2} + \frac{v_3^2}{1+dv_2^2y_2}) \\ 0 & s_2 & s_3(1-(\frac{v_3^1}{1+dv_2^1y_2} + \frac{v_3^2}{1+dv_2^2y_2})) \end{pmatrix} \tag{29}$$

and

$$\tilde{H}(Y) = \begin{pmatrix} 0 & s_2\phi(\frac{v_2^1}{1+cs_2v_2^1y_2} + \frac{v_2^2}{1+cs_2v_2^2y_2}) & 0 \\ s_1 & 0 & s_3(\frac{v_3^1}{1+ds_2v_2^1y_2} + \frac{v_3^2}{1+ds_2v_2^2y_2}) \\ 0 & s_2 & s_3(1-(\frac{v_3^1}{1+ds_2v_2^1y_2} + \frac{v_3^2}{1+ds_2v_2^2y_2})) \end{pmatrix}.$$

As we pointed out in (26), these four matrices have the same inherent NRNs, $R_0^1 = R_0^2 = \bar{R}_0 = \tilde{R}_0 = \phi s_1 s_2/(1-s_2 s_3)$, which we assume to be larger than 1. Then the local reproductive synchrony at both patches is determined by the sign of (24)

$$a_- = s_1 s_2 s_3 (1-s_3)d - (1-s_2 s_3)s_1 c, \tag{30}$$

the global reproductive synchrony in the case of system (15) by the sign of $\bar{a}_-$ in (21)

$$\bar{a}_- = s_1 s_2 s_3 (1-s_3)d(v_2^1 v_3^1 + (1-v_2^1)(1-v_3^1)) - (1-s_2 s_3)s_1 c((v_2^1)^2 + (1-v_2^1)^2), \tag{31}$$
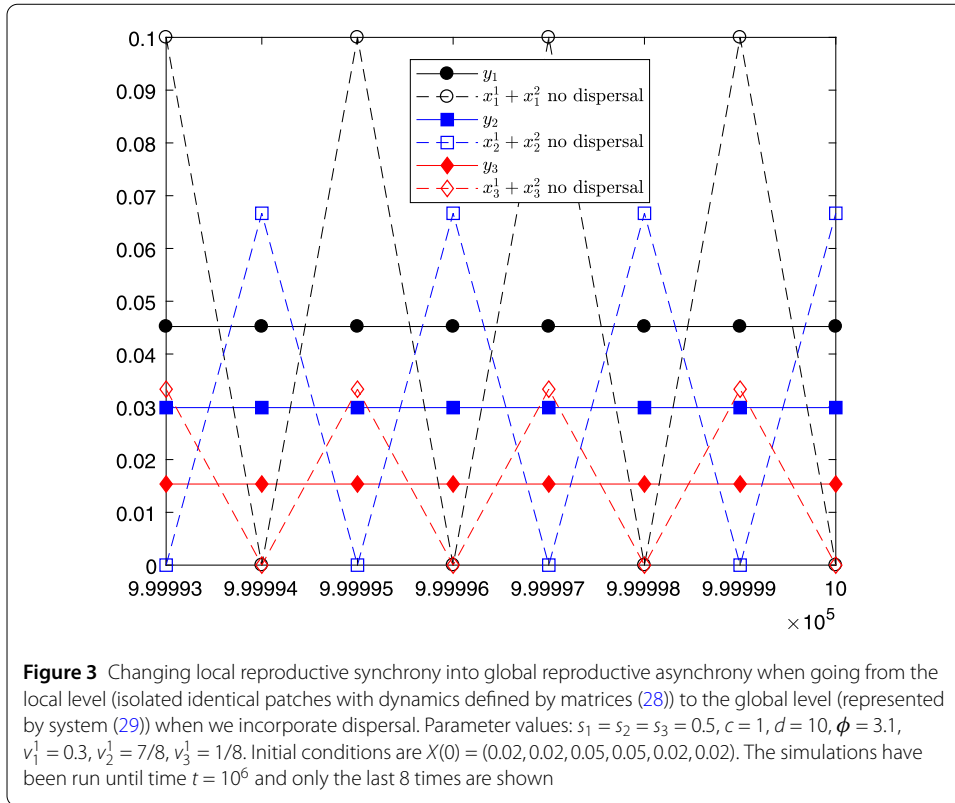
and, in the case of system (16), by the sign of $\tilde{a}_-$ (22). Note that $\tilde{a}_- = s_2\bar{a}$ and so the sign of $\tilde{a}_-$ coincides with that of $\bar{a}_-$, so that we will concentrate on the sign of $\bar{a}_-$.

Therefore, in order to illustrate the influence of fast dispersal on reproductive synchrony for both systems (17) and (18), we have to find conditions on v_2^1 and v_3^1 (note that v_1^1 plays no role whatsoever) such that a_- and $\bar{a}_-$ have different signs. In that way we show that adequately chosen adult dispersal rates can alter the tendency to reproductive synchrony or asynchrony of isolated populations.

A first result shows that it is always possible to find adult dispersal rates such that there exists global reproductive asynchrony, $\bar{a}_- < 0$, independently of the local tendency.

Proposition 8 *Let the model coefficients verify conditions (27). Then there exist intervals $I_2, I_3 \subseteq [0,1]$ such that $\bar{a}_- < 0$ for $v_2^1 \in I_2$ and $v_3^1 \in I_3$.*

Proof Equation (31) of $\bar{a}_-$ taken as a function of v_2^1 and v_3^1, $\bar{a}_-(v_2^1, v_3^1)$, is continuous and satisfies $\bar{a}_-(1,0) = -(1-s_2 s_3)s_1 c < 0$, what implies the existence of the intervals I_2 and I_3 meeting the required conditions. □

Figure 3 Changing local reproductive synchrony into global reproductive asynchrony when going from the local level (isolated identical patches with dynamics defined by matrices (28)) to the global level (represented by system (29)) when we incorporate dispersal. Parameter values: $s_1 = s_2 = s_3 = 0.5$, $c = 1$, $d = 10$, $\phi = 3.1$, $v_1^1 = 0.3$, $v_2^1 = 7/8$, $v_3^1 = 1/8$. Initial conditions are $X(0) = (0.02, 0.02, 0.05, 0.05, 0.02, 0.02)$. The simulations have been run until time $t = 10^6$ and only the last 8 times are shown

This result proves that the local reproductive synchrony, $a_- > 0$, can always be changed into global reproductive asynchrony, $\bar{a}_- < 0$, through the appropriate adult dispersal rates. This fact is illustrated in Fig. 3.

In the opposite sense we present the next result in which we provide sufficient conditions so that the local reproductive asynchrony, $a_- < 0$, can be changed into global reproductive synchrony, $\bar{a}_- > 0$, if adult dispersal is adequately chosen.

Proposition 9 *Let the model coefficients verify conditions* (27) *and* $a_- < 0$. *Then there exist intervals* $I_2, I_3 \subseteq [0, 1]$ *such that* $\bar{a}_- > 0$ *for* $v_2^1 \in I_2$, $v_3^1 \in I_3$ *if and only if*

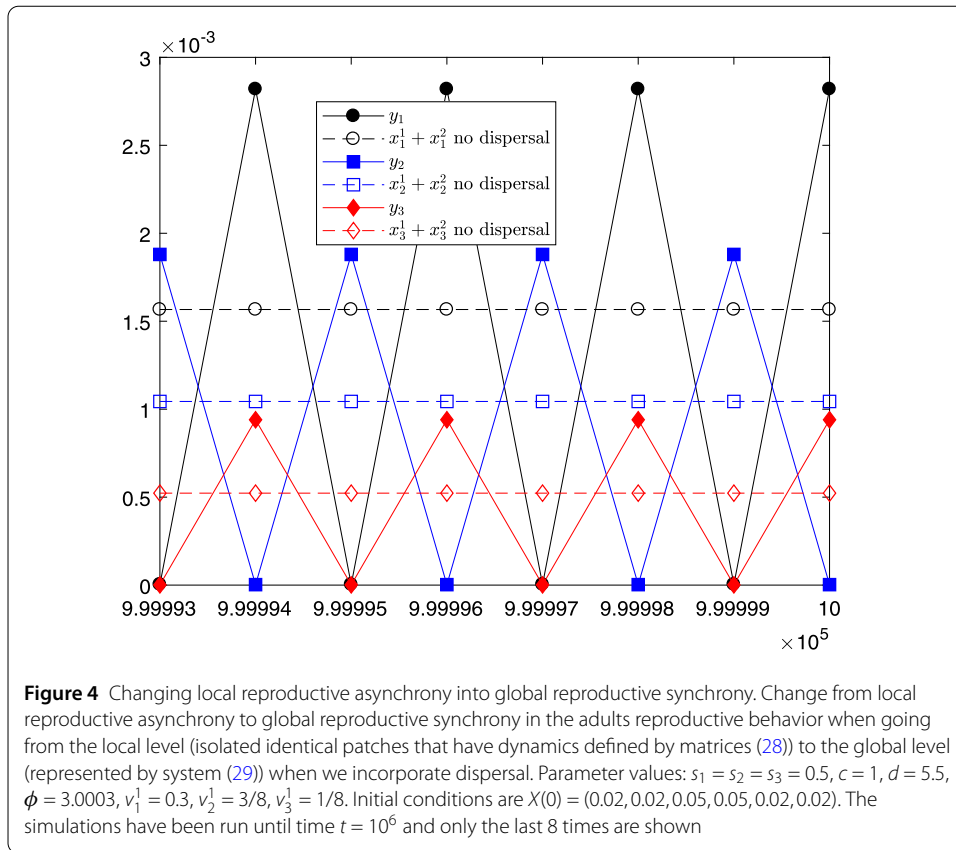$$(1 - s_2 s_3)s_1 c < \frac{1 + \sqrt{2}}{2} s_1 s_2 s_3 (1 - s_3) d.$$

Proof Equation (31) of $\bar{a}_-$ taken as a function of v_2^1 and v_3^1, $\bar{a}_-(v_2^1, v_3^1)$, is continuous and satisfies

$$\bar{a}_-\left(1 - \frac{\sqrt{2}}{2}, 0\right) = s_1 s_2 s_3 (1 - s_3) d \frac{\sqrt{2}}{2} - (1 - s_2 s_3)s_1 c(4 - 2\sqrt{2})$$

$$= (4 - 2\sqrt{2})\left(s_1 s_2 s_3 d \frac{1 + \sqrt{2}}{2} - (1 - s_2 s_3)s_1 c\right) > 0,$$

what implies the existence of the intervals I_2 and I_3 meeting the required conditions.

In the opposite sense, if we assume, by contradiction, that

$$(1 - s_2 s_3)s_1 c \geq \frac{1 + \sqrt{2}}{2} s_1 s_2 s_3 (1 - s_3) d$$

Figure 4 Changing local reproductive asynchrony into global reproductive synchrony. Change from local reproductive asynchrony to global reproductive synchrony in the adults reproductive behavior when going from the local level (isolated identical patches that have dynamics defined by matrices (28)) to the global level (represented by system (29)) when we incorporate dispersal. Parameter values: $s_1 = s_2 = s_3 = 0.5$, $c = 1$, $d = 5.5$, $\phi = 3.0003$, $v_1^1 = 0.3$, $v_2^1 = 3/8$, $v_3^1 = 1/8$. Initial conditions are $X(0) = (0.02, 0.02, 0.05, 0.05, 0.02, 0.02)$. The simulations have been run until time $t = 10^6$ and only the last 8 times are shown

and $\bar{a}_- > 0$ then

$$\frac{1 + \sqrt{2}}{2} \leq \frac{(1 - s_2 s_3) s_1 c}{s_1 s_2 s_3 (1 - s_3) d} < \frac{v_2^1 v_3^1 + (1 - v_2^1)(1 - v_3^1)}{(v_2^1)^2 + (1 - v_2^1)^2}$$

but there are no $v_2^1, v_3^1 \in [0, 1]$ satisfying the previous inequality since the maximum of the function $f(x, y) = (xy + (1 - x)(1 - y))/(x^2 + (1 - x)^2)$ on $[0, 1] \times [0, 1]$ is $(1 + \sqrt{2})/2$.　　□

This change from local reproductive asynchrony to global reproductive synchrony in the adults reproductive behavior for adequate dispersal parameters is illustrated in Fig. 4.

The preceding behavior, in which if appropriate adult dispersal rates are chosen, the existence of a positive locally asymptotically stable equilibrium locally in each site can be transformed globally into the existence of a stable 2-cycle and vice versa, is analogous to the one found in [19] for a semelparous population structured in juveniles and adults, spread out in two patches between which they can migrate.

4.2 Differences between models (15) and (16)
In this section we propose some particular simple settings in which the asymptotic outcomes of systems (15) and (16) differ, thus showing that the decision of placing mortality at the slow or the fast time scale can have crucial consequences.

There is a simple case in which the inherent NRNs $\bar{R}_0$ and $\tilde{R}_0$, associated to systems (15) and (16), coincide. Indeed, if $s_i^1 = s_i^2 =: s_i$, for $i = 1, 2, 3$, then

$$\tilde{R}_0 = \frac{s_1 s_2 (\phi^1 v_2^1 + \phi^2 v_2^2)}{1 - s_2 s_3} = \bar{R}_0.$$

In the next result we show that equal fertilities, $\phi^1 = \phi^2$, imply that $\bar{R}_0$ is larger than $\tilde{R}_0$.

Proposition 10 *In systems* (15) *and* (16)*, if* $\phi^1 = \phi^2 =: \phi$ *then*

$$\tilde{R}_0 < \bar{R}_0.$$

Moreover, there is an interval $I \in \mathbb{R}_+$ such that if $\phi \in I$ then

$$\tilde{R}_0 < 1 < \bar{R}_0. \tag{32}$$

Proof If we use the fact that, for $i = 1, 2, 3$, we have $v_i^1, v_i^2 \in (0, 1)$ and $v_i^1 + v_i^2 = 1$, the inequality relating the weighted arithmetic mean and the weighted geometric mean implies that the survival rates in (17) and (18) verify

$$\tilde{s}_i = \left(s_i^1\right)^{v_i^1} \left(s_i^2\right)^{v_i^2} < s_i^1 v_i^1 + s_i^2 v_i^2 = \bar{s}_i,$$

and the fertility coefficients

$$\tilde{b} = \tilde{s}_2 \left(\phi v_2^1 + \phi v_2^2\right) = \tilde{s}_2 \phi < \bar{s}_2 \phi = \phi s_2^1 v_2^1 + \phi s_2^2 v_2^2 = \bar{b}.$$

Now, it is straightforward that

$$\tilde{R}_0 = \frac{\tilde{b}\tilde{s}_1}{1 - \tilde{s}_2 \tilde{s}_3} < \frac{\bar{b}\bar{s}_1}{1 - \bar{s}_2 \bar{s}_3} = \bar{R}_0.$$

Inequality (32) is a direct consequence of both $\tilde{R}_0$ and $\bar{R}_0$ depending linearly on ϕ.   □

We stress that choosing one of models (15) and (16) over the other can represent the difference between population survival or extinction.

We now present a situation in which the inequalities in Proposition 10 are reversed. We assume that $s_1^1 = s_1^2 = s_1$, $s_1^2 = 0.7$, $s_2^2 = 0.5$, $s_3^1 = s_3^2 = 0.8$, $v_1^1 = v_2^2 = 0.5$, $\phi^1 = \phi$ and $\phi^2 = \alpha\phi$. Straightforward calculations yield

$$\tilde{R}_0 - \bar{R}_0 = s_1 \phi \left(\left(\frac{5\sqrt{35}}{100 - 8\sqrt{35}} - \frac{25}{52} \right) \alpha + \frac{5\sqrt{35}}{100 - 8\sqrt{35}} - \frac{35}{52} \right),$$

therefore, for $\alpha > \frac{65\sqrt{35}+14}{289}$ we have $\bar{R}_0 < \tilde{R}_0$. As this holds for any values of $s_1 \in (0, 1)$ and $\phi > 0$, there are some of them for which

$$\bar{R}_0 < 1 < \tilde{R}_0,$$

which represents the difference between population survival or extinction but exchanging the associated models in Proposition 10.

It can be shown that, similarly to what happens regarding survival, there exist situations where models (15) and (16) have different outputs regarding the population reproductive synchrony. Nevertheless, we skip this analysis since we consider that the previous results illustrate clearly our main point here: the choice of model should be as accurate as possible because the results can drastically differ.

5 Discussion

In this work we have extended the results on reduction of two time scales non-linear discrete systems presented in [7]. The new result avoids the need to check a difficult hypothesis, specifically the uniform convergence on compacts sets of the differentials of the iterates of a map. Dropping this hypothesis has an effect on the results that can be given regarding the relationships between the original and the reduced model, but nonetheless can be viewed as a minor effect with regard to the practical study of population dynamics models.

This new result has opened the door to extending to the non-linear case the work on re-scaling developed in [8]. When there are two processes acting at different time scales that must be gathered in a single discrete model, the easiest choice of its time unit is that associated to the slow one. The structure of the model then reflects that the fast process acts a number of times, approximately equal to the ratio between the two time scales, followed by one action of the slow process. It is not always easy to decide if a process occurs at the slow or the fast time scale. Here we have focused on the re-scaling of survival, which is a process usually measured at the slow time scale associated to the rest of the demographic processes. Nevertheless, in a context of fast movements of individuals between patches with different associated survival rates, it can be argued that it should be rather considered as occurring at the fast time scale. Systems (15) and (16) represent general discrete-time models of structured metapopulations with two time scales; in the first one survival acts at the slow time scale and in the second one the re-scaled survival acts at the fast time scale. The reduction results developed in Sects. 2 and 3 associated to these two models yield two aggregated models, (17) and (18), which contain the asymptotic information of the original models. They summarize the global emergent properties [2, 20] that fast dispersal induce out of local demography.

To illustrate this influence of fast dispersal on local demographic dynamics and the relevance of the choice of time scale for the different processes involved in a model, we have proposed a particular case of systems (15) and (16). It is based in the model in [9] and it has three population stages and two patches. The comparison of the local models and the two global models is done through their respective inherent net reproduction numbers, which decide on the survival or extinction of the population, and the coefficients a_- that rule, for viable populations, the tendency to either reproductive synchrony or asynchrony. Even in simple cases it can be shown that viable local populations can get globally extinct for adequate dispersal rates and, the other way round, non-viable local populations can globally survive if migrating appropriately. Along the same lines, different scenarios are presented reversing the outcome of reproductive synchrony/asynchrony between local and global dynamics.

Finally, it is shown that there are some cases where changing from system (15) to (16) (or vice versa) can represent changing the global outcome from survival to extinction or

the other way round. This fact stresses the importance of the choice of time scale (slow ar fast) in which survival is included in the model.

It must be stressed that the result in Theorem 2 can be applied to much more general systems than the specific structured metapopulation models presented in Sect. 3. Also, the convergence results in Proposition 12 have a more general application than the survival re-scaling proposed in this work. We have chosen the context of the work trying to keep at reasonable levels both simplicity and modelling relevance.

An interesting extension of the treated metapopulation models would also include an epidemic disease dynamics together with the demographic and spatial issues. These more general models would encompass time scales too. A relevant issue at this point would be to decide whether the epidemic process must be considered as acting as at the fast or the slow time scale. In the case that it be considered as a slow process together with demography, the reduction of the corresponding two time scales system would not differ much from what has been developed in this work since it mainly depends on the fast process. On the other hand, a general assumption in basic epidemic models is that disease evolution can be considered almost instantaneous with respect to demography and therefore the latter is considered negligible. A different approach to this last assumption is considering in the same model both disease and demographic dynamics at different time scales. The obtained two-time scale systems would be susceptible of reduction. The inclusion of disease dynamics in the fast part of the system would render the reduction procedure more involved, and Theorem 2 should be a tool helping in this task.

Appendix

Lemma 11 *Let Hypotheses* 2.1 *and* 2.3 *hold. Then for any* $m \in \mathbb{N}$ *we have* $\lim_{k \to \infty} H_k^m = H^m$ *uniformly on compact sets of* Ω_N.

Proof It is easy to realize that it suffices with proving the result for $m = 2$.

Let $M \subset \Omega_n$ be a compact set. Since $\lim_{k \to \infty} H_k = H$ uniformly on M, we can find another compact set $C \subset \Omega_n$ and $k^* \in \mathbb{N}$ such that $H(M) \subset C$ and $H_k(M) \subset C$ for all $k \geq k^*$.

Let us now show that $\lim_{k \to \infty} H_k^2 = H^2$ uniformly on K.

The uniform convergence $\lim_{k \to \infty} H_k = H$ on C ensures the existence of a real sequence $\{\alpha_k\}_{k \in \mathbb{N}}$, $\alpha_k > 0$, with $\lim_{k \to \infty} \alpha_k = 0$ and such that $\sup_{X \in C} \|H_k(X) - H(X)\| \leq \alpha_k$. Since

$$\left\| H_k^2(X) - H^2(X) \right\| \leq \left\| H_k\big(H_k(X)\big) - H\big(H_k(X)\big) \right\| + \left\| H\big(H_k(X)\big) - H\big(H(X)\big) \right\|,$$

we have, for $k \geq k^*$,

$$\sup_{X \in M} \left\| H_k^2(X) - H^2(X) \right\| \leq \sup_{Z \in C} \left\| H_k(Z) - H(Z) \right\| + \sup_{\substack{Z_k, Z \in C \\ \|Z_k - Z\| \leq \alpha_k}} \left\| H(Z_k) - H(Z) \right\|.$$

When $k \to \infty$, the first term on the right-hand side converges to zero due to the uniform convergence of H_k to H on C and the second term converges to zero since H is uniformly continuous on C. Therefore the result is proved. □

Proposition 12 *Let* $I, J \in \mathbb{Z}_+$ *and let* $\Omega \subset \mathbb{R}^I$ *be an open set. Let* $M : \Omega \to \mathbb{R}^{J \times J}$ *and* $S : \Omega \to \mathbb{R}^{J \times J}$ *be continuous maps such that*:

a. *For all $Y \in \Omega$, $M(Y)$ is a primitive probability matrix. Let $v(Y)$ be its column Perron right eigenvector normalized so that $\mathbf{1}v(Y) = 1$.*
b. *There exists a continuous map $S' : \Omega \to \mathbb{R}^{J \times J}$ such that $\exp(S'(Y)) = S(Y)$ for all $Y \in \Omega$.*

Let us define, for $Y \in \Omega$, $S_k(Y) := \exp(\frac{1}{k}S'(Y))$, $\bar{M}(Y) := v(Y)\mathbf{1}$ and $\gamma(Y) := \exp(\mathbf{1}S'(Y)v(Y))$. Then we have

$$\lim_{k \to \infty} \left(S_k(Y)M(Y)\right)^k = \lim_{k \to \infty} \left(M(Y)S_k(Y)\right)^k = \gamma(Y)\bar{M}(Y), \tag{33}$$

where the limit is uniform on any compact set of Ω.

Proof Given a fixed $Y \in \Omega$, matrix $M(Y)$ is primitive, its (strictly) dominant eigenvalue is 1 and its associated left eigenvector $u(Y)$, normalized so that $u(Y)^T v(Y) = 1$, is $u(Y) = \mathbf{1}$. Then the existence of the pointwise limit (33) follows as a particular case of Theorem A1 in [8]. Therefore, all we need to prove is that the limit (33) is uniform on compact sets of Ω.

We only need to adjust some details at the beginning of the proof of Theorem A1 in [8] to make it work in the present case via standard compactness arguments. Let $\|\!|\cdot|\!\|$ be the 1-norm in $\mathbb{R}^{J \times J}$. In the first place, since the $M(Y)$ are probability matrices one has

$$\|\!|M(Y)|\!\| = 1 \tag{34}$$

for all $Y \in \Omega$. Now let $K \subset \Omega$ be any compact set. For any $Y' \in K$ there exists $r_{Y'} < 1$ such that $\|\!|M(Y') - \bar{M}(Y')|\!\| < r_{Y'}$. The continuity of M and of the norm imply that if $\bar{r}_{Y'}$ satisfies $r_{Y'} < \bar{r}_{Y'} < 1$, there exists an open neighborhood of Y' in Ω, $\mathcal{U}_{Y'}$, such that

$$\|\!|M(Y) - \bar{M}(Y)|\!\| < \bar{r}_{Y'} \quad \text{for all } Y \in \mathcal{U}_{Y'}. \tag{35}$$

Let $\delta > 0$ and let us denote

$$\left(\delta S(Y)\right)' := S'(Y) + \log \delta I,$$

$$\left(\delta S(Y)\right)_k := \exp\left(\frac{1}{k}\left(\delta S(Y)\right)'\right), \qquad \gamma_{\delta S}(Y) := \exp\left(\mathbf{1}\left(\delta S(Y)\right)'v(Y)\right).$$

It is immediate to check that $(\delta S(Y))_k = \delta^{\frac{1}{k}}S_k(Y)$ and $\gamma_{\delta S}(Y) = \delta\gamma(Y)$. Therefore

$$\left(\left(\delta S(Y)\right)_k M(Y)\right)^k - \gamma_{\delta S}(Y) = \delta\left(S_k(Y)M(Y) - \gamma(Y)\right)^k$$

so that the limit (33) is uniform in K if and only if there exists $\delta > 0$ such that the limit $\lim_{k \to \infty}((\delta S(Y))_k M(Y))^k = \gamma_{\delta S}(Y)$ is uniform in K. Now let $\delta := \min_{Y \in \bar{\mathcal{U}}_{Y'}} \exp(-\|\!|S'(Y)|\!\|) > 0$. Then

$$\|\!|\left(\delta S(Y)\right)_k|\!\| = \delta^{\frac{1}{k}}\left\|\!\left|\exp\left(\frac{1}{k}S'(Y)\right)\right|\!\right\| \leq 1$$

and so we can assume, without loss of generality, that $\|\!|S_k(Y)|\!\| \leq 1$ for all $Y \in \mathcal{U}_{Y'}$ and all $k = 1, 2, \ldots$, from which it follows that

$$\|\!|\left(M(Y)S_k(Y)\right)^i|\!\| \leq \|\!|M(Y)|\!\|^i \|\!|S_k(Y)|\!\|^i = \|\!|S_k(Y)|\!\|^i \leq 1 \tag{36}$$

for all $Y \in \mathcal{U}_{Y'}$ and $i, k \in \mathbb{N}$. Thus, from (34), (35) and (36) the rest of the proof of Theorem A1 in [8] is valid (in the particular case of working with the 1-matrix norm) and shows that the limit (33) is uniform on $\mathcal{U}_{Y'}$. A standard compactness argument ensures the uniform convergence on K and completes the proof. □

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors have equally made contributions. All authors read and approved the final manuscript.

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