Fast Dispersal in Semelparous Populations

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Abstract. We consider a model for the dynamics of a semelparous age-structured population where individuals move among different sites. The model consists of a system of difference equations with two time scales. Individual movements are considered to be fast in comparison to demographic processes. We propose a general model with $m + 1$ age classes and n different sites. Demography is described locally by a general density dependent Leslie matrix. Dispersal for each age-class is defined by a stochastic matrix depending on the total numbers of individuals in each class. The $(m + 1) \times n$ dimensional two time scales system is *approximately* reduced to an $m + 1$ dimensional semelparous Leslie model. In the case of 2 age-classes and 2 sites with constant dispersal rates we consider the bifurcation that occurs at the trivial equilibrium using the inherent net reproductive number as the bifurcation parameter. We find that different dispersal strategies can change at the global level the local demographic outcome. This modeling framework can be further used to correctly embed different fast processes in population-level models.

Keywords and phrases: structured population, discrete model, dispersal, time scales

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1. Introduction.

The movement and dispersal of organisms are recognized to be crucial ingredients of ecological interactions and that it is the reason for their inclusion in many mathematical models in ecology and epidemiology [5]. The problems in dispersal, movement and spatial ecology have been of great interest in the past [24] as they presently are [18]. The subject has, on the one hand, raised interesting mathematical problems and, on the other hand, helped to get insights into important applied problems. To put just a couple of examples, in conservation biology those associated with the design of nature reserves [21] and in the field of behavioural ecology how individuals move to optimize foraging [25].

It is usual that models for population dynamics focus on population growth and survival. These are processes describable on a slower time scale than the one associated to processes arising at the individual level [26]. In this work we consider a discrete model of an age-structured population living in a multi-site habitat and assume that dispersal acts at a fast time scale in comparison to demography.

The local dynamics, concerning demography, is defined in terms of a particular case of nonlinear Leslie matrix model, that of a semelparous population, i.e., only the oldest class is reproductive. Nevertheless the construction and reduction of the model performed in section 2 would be also valid in the general case

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of a stage-structured population. There is a considerable literature on semelparous Leslie models, see [10] and the references therein. This is partly motivated by the study of long cyclic outbreaks of periodical insects or, more generally, of temporal synchronization of the population dynamics that can be found in nature [4].

In general matrix models the local stability of the extinction equilibrium $x^* = 0$ is characterized by the inherent reproductive number R_0, the expected number of offspring per individual per lifetime at low density. If $R_0 < 1$ then $x^* = 0$ is locally asymptotically stable and it is unstable if $R_0 > 1$ [6]. If the Jacobian matrix evaluated at $x^* = 0$ is irreducible a branch of positive equilibria bifurcates from $x^* = 0$ at $R_0 = 1$ [16]. This branch exchanges stability with $x^* = 0$. The stability of the positive equilibria near the bifurcation point depends on the direction of the bifurcation. The bifurcation can be either supercritical if density effects are deleterious or subcritical if there exist Allee effects. In the first case positive equilibria are associated to values of $R_0 > 1$ and are stable. In the opposite case, the positive equilibria correspond to $R_0 < 1$ and are unstable [6].

For semelparous Leslie models the bifurcation situation is more complicated since all the eigenvalues of the Jacobian matrix at $x^* = 0$ for $R_0 = 1$ have modulus equal to 1 yielding a non-generic scenario. It is known that still a branch of positive equilibria bifurcates from $x^* = 0$ at $R_0 = 1$ but the equilibria stability is not determined solely by the direction of the bifurcation [6–8]. The boundary of the positive cone is invariant for semelparous Leslie models. Any orbit initially with a number of missing age classes keeps this number at each point in time. This kind of orbits are called synchronized. The extreme case is when only a single age class is present at a time, which is called a single-class orbit. In [7] it is proved that, together with the bifurcating branch of positive equilibria, there exists a continuum of nonnegative single-class cycles that bifurcates from the trivial equilibrium at $R_0 = 1$. These two bifurcating branches represent two different dynamics, one of them tends to equilibrate with all age classes present and the other oscillates with all but one age classes missing. Characterizing the stability of both dynamics is an important and difficult problem.

In [7,11] a complete accounting of the bifurcation at $R_0 = 1$ is presented for two-dimensional semelparous Leslie models, i.e., for semelparous models of biennial populations with a juvenile stage and an adult stage of equal time duration. When both branches of positive equilibria and single-class synchronous two-cycles bifurcate super-critically, one of them is stable and the other one is unstable for R_0 near 1. Roughly speaking, if inter-class competition is stronger than intra-class competition the single-class two-cycles are stable and the dynamics tends to separated age classes, while stronger intra-class competition leads to equilibration with overlapping generations. Extension of these results to dimensions other than 2 can be found in [7–10]. Other studies, not based upon bifurcation, of semelparous models appear in [12,14] for the biennial case and in [15] for the m-dimensional case.

The movements of individuals are defined for each age-class by a stochastic matrix, that in general depends on the total numbers of individuals in each class across all sites. To put together both processes, demography and dispersal, at different time scales we first assume that within a slow time unit the slow process, demography, is represented by map S and, analogously, within a fast time unit the fast process, dispersal, is represented by map F. The combined effect of both processes during a slow time unit is then represented as the composition of map S and the k-th iterate of map F, assuming that the slow time unit is divided into a large number k of fast time units. Denoting by vector X the state variables and t the slow time variable, the general form of the system is: $X(t+1) = S\left(F^{(k)}(X(t))\right)$.

The techniques of reduction of this kind of systems form part of so-called methods of aggregation of variables appeared first in economy and later introduced in mathematical ecology [13,17,20], where they have a direct interpretation in terms of ecological hierarchy theory [19]. The aggregation of a system consists of finding a certain number of global variables, functions of its state variables, and a system describing their dynamics. In general, aggregation methods are *approximate* in the sense that the consistency between the dynamics of the global variables in the initial and the aggregated systems is not exact but improves with increasing time scales ratio. Reviews of aggregation methods in different mathematical settings are presented in [1,2].

In the appendix it is summarized the aggregation procedure for $X(t+1) = S\left(F^{(k)}\left(X(t)\right)\right)$. It is assumed that there exists a limit system for k tending to infinity that admits perfect aggregation, i.e., there exist global variables which dynamics is identical both in the initial system and in the reduced one. In mathematical terms the limit of $F^{(k)}$ can be expressed as the composition of two maps going through a less dimensional space. Roughly speaking, the global variables are constants of motion for fast dynamics, and the equilibria attained by fast dynamics depend solely on global variables. In our model the role of global variables is played by the total numbers of individuals in each age class. These total numbers do not change with dispersal. At the same time, dispersal tend to distribute individuals according to certain proportions that depend on these total numbers. In [23] it is shown that assuming the convergence on compact sets of the sequence of maps $F^{(k)}$ and their differentials it is possible to study the existence, stability and basins of attraction of steady states and periodic solutions of the initial system performing the study for the corresponding aggregated system. In [3] can be found a review of aggregation of discrete systems with applications to population dynamics models.

The main general goal of this work consists in showing the influence of fast dispersal on population demography. We first present a general framework of a discrete model for a semelparous age-structured population which individuals moves fast among different spatial sites. The model could be straightforwardly extended to a general stage-structured population. We particularize the general framework to study the case of semelparous biennial populations inhabiting a two-sites environment. The influence of fast dispersal is first studied through the survival of the population as reflected by the zero solution stability. In a second step, once the survival threshold is attained, we analyze how dispersal can change the tendency of the population to either equilibrate with both age classes present or oscillates towards single-class synchronous two-cycles. The influence of fast dispersal is taken into account by comparing the outcomes of local (isolated sites) and global (interconnected sites) dynamics.

The organization of the paper is the following. In Section 2 we specify the mathematical formulation of a general class of two time scales discrete nonlinear dynamical systems coupling a density dependent demographic process associated to a semelparous structured population at the slow time scale with a dispersal process among several different sites at the fast time scale. A reduction process is applied, yielding the so-called aggregated model through which we obtain some information on the asymptotic behaviour of the initial model. Section 3 is devoted to the application of these results to the particular case of a biennial semelparous population living in a two sites habitat. Some conclusions are given in Section 4. To facilitate the reading a summary of the aggregation results for discrete systems is included in the appendix together with the proofs of the theorems of previous sections.

2. Presentation of the model.

In this section we present the model in full generality. It is a discrete model involving two processes acting at different time scales. We first introduce both processes, fast and slow, to follow with the construction of the complete model and its reduction. We use the aggregation method summarized in the appendix A.1.

We consider an age structured population with a semelparous life history inhabiting an environment divided into several different sites. The local demography in each site is described in the form of a semelparous nonlinear Leslie model. We generally assume that the number of age classes of the population is $m+1$. The m first classes corresponding to immature individuals and the last one to adults. Considering n sites we denote $J_i^j(t)$ and $A^j(t)$ the number of immature individuals of age i and adults, respectively, in site j at time t for $i = 1, \ldots, m$ and $j = 1, \ldots, n$.

We also denote $\bar{x}_{J_i} = \text{col}\left(J_i^1, \ldots, J_i^n\right)$ the state vector of individuals of age i and $\bar{x}_A = \text{col}\left(A^1, \ldots, A^n\right)$ the state vector of adults. The population vector is called $X = col\left(\bar{x}_{J_1}, \ldots, \bar{x}_{J_m}, \bar{x}_A\right)$.

Finally, the total numbers of individuals in each class are denoted $J_i = \sum_{j=1}^n J_i^j$ and $A = \sum_{j=1}^n A^j$. We call $Y = col\left(J_1, \ldots, J_m, A\right)$ the vector of these total numbers.

Apart from demography the population is subjected to a dispersal process. In comparison to demography the dispersal process is considered fast.

2.1. Fast process: Dispersal.

We consider that individuals in each class move among patches with dispersal rates that can generally depend on Y, the total numbers of individuals in each class. Dispersal in each class is represented by matrices $M_{J_i}(Y)$, $M_A(Y)$, that we assume to be regular stochastic for all $Y \in \mathbb{R}^n_+$. So, they have 1 as strictly dominant eigenvalue, $\bar{1} = (1, \overset{(n)}{\ldots}, 1)$ is an associated left eigenvector and there exists a column vector, denoted $\bar{\nu}_{J_i}(Y)$, $\bar{\nu}_A(Y)$, representing the corresponding stable probability distribution which is the positive right eigenvector that verifies $\bar{1}\bar{\nu}_{J_i}(Y) = 1$, $\bar{1}\bar{\nu}_A(Y) = 1$.

In the procedure of reduction of the model we need the limit of the fast process that it is readily describable in terms of vectors $\bar{\nu}_{J_i}(Y)$ and $\bar{\nu}_A(Y)$. The Perron-Frobenius theorem implies that

$$\lim_{k \to \infty} (M_{J_i}(Y))^k = \bar{\nu}_{J_i}(Y)\bar{1} \quad \text{and} \quad \lim_{k \to \infty} (M_A(Y))^k = \bar{\nu}_A(Y)\bar{1} \tag{2.1}$$

We denote $M(Y) = \text{diag}\,(M_{J_1}(Y), \ldots, M_{J_m}(Y), M_A(Y))$ the matrix representing dispersal for the whole population. Calling $V(Y) = \text{diag}\,(\bar{\nu}_{J_1}(Y), \ldots, \bar{\nu}_{J_m}(Y), \bar{\nu}_A(Y))$ and $U = \text{diag}\left(\bar{1}, \overset{(n+1)}{\ldots}, \bar{1}\right)$ we can express the limit of the powers of matrix $M(Y)$ in the following form

$$\lim_{k \to \infty} (M(Y))^k = V(Y)U \tag{2.2}$$

Following the notation of the appendix A.1, the fast dynamics in the complete model is represented by the map

$$F(X) = M(Y)X \tag{2.3}$$

where the vector Y of total individuals in each class can be written in terms of X as UX.

2.2. Slow process: Demography.

Demography represents the slow dynamics in the model. It is considered a local process and thus, for each site $j = 1, \ldots, n$, depending on the local variables $X^j := \left(J_1^j, \ldots, J_m^j, A^j\right)$ and described by the nonlinear Leslie-like matrix model for a semelparous population which matrix reads as follows

$$\begin{pmatrix} 0 & 0 & 0 \cdots & 0 & f^j \varphi^j(X^j) \\ s_1^j \sigma_1^j(X^j) & 0 & 0 \cdots & 0 & 0 \\ 0 & s_2^j \sigma_2^j(X^j) & 0 \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 \cdots & 0 & 0 \\ 0 & 0 & 0 \cdots & s_m^j \sigma_m^j(X^j) & 0 \end{pmatrix} \tag{2.4}$$

For $i = 1, \ldots, m$, $s_i^j \sigma_i^j(X^j)$ represents the fraction of individuals in age class i that survive to age class $i+1$. We assume that s_i^j and $\sigma_i^j(X^j)$ are positive constants and functions verifying $s_i^j \sigma_i^j(X^j) \leq 1$ for all nonnegative X^j. f^j and $\varphi^j(X^j)$ are also assumed to be positive and $f^j \varphi^j(X^j)$ is the adult fertility rate. In order that s_i^j and f^j represent the inherent vital rates in each site j we also assume that $\sigma_i^j(\bar{0}) = 1$ and $\varphi^j(\bar{0}) = 1$.

To define the demography for the whole population, having in mind the order of the variables in vector X, we need to write a block Leslie matrix

$$L(X) = \begin{pmatrix} 0 & 0 & 0 \cdots & 0 & \Phi(X) \\ \Sigma_1(X) & 0 & 0 \cdots & 0 & 0 \\ 0 & \Sigma_2(X) & 0 \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 \cdots & 0 & 0 \\ 0 & 0 & 0 \cdots & \Sigma_m(X) & 0 \end{pmatrix}$$

where, for $i = 1, \ldots, m$,

$$\Sigma_i(X) = \text{diag}\left(s_i^1 \sigma_i^1(X^1), \ldots, s_i^n \sigma_i^n(X^n)\right)$$

and

$$\Phi(X) = \text{diag}\left(f^1 \varphi^1(X^1), \ldots, f^n \varphi^n(X^n)\right).$$

The slow dynamics, demography, of the complete model is thus defined by the map

$$S(X) = L(X) X \tag{2.5}$$

2.3. The complete model.

We build up the complete model combining the two processes, (2.3) and (2.5), presented in subsections 2.1 and 2.2. This discrete system uses the unit of time associated to demography. Compared to the demographic process dispersal is much more frequent so that we consider them acting at different time scales. To represent this we use a positive integer k measuring the time scales ratio. We suppose that, on average, k dispersal processes, as describe by map F in (2.3), take place within each unit of time. By reasoning sequentially we let F act k times, $F^{(k)}$, followed by S, obtaining the following system of difference equations

$$X(t+1) = S\left(F^{(k)}(X(t))\right) = L\left((M(Y(t)))^k X(t)\right) (M(Y(t)))^k X(t), \tag{2.6}$$

that it is of the form of system (A.1) in the appendix.

2.4. The aggregated model.

We use the method described in the appendix A.1 to reduce the system (2.6).

To apply the aggregation method we first need to calculate the map $\bar{F}$ limit of the iterates of the map F. Having in mind that $UF(X) = UX$, that is, Y is invariant for F, we obtain from (2.2) and (2.3) that

$$\bar{F}(X) = \lim_{k \to \infty} F^{(k)}(X) = \lim_{k \to \infty} (M(Y))^k X = V(Y)UX = V(Y)Y. \tag{2.7}$$

$\bar{F}$ can be decomposed as required in hypothesis (H2) in the appendix A.1:

$$\bar{F}(X) = (E \circ G)(X) = V(UX)UX \tag{2.8}$$

where $G : \mathbb{R}^{(m+1) \times n} \longrightarrow \mathbb{R}^{m+1}$, $G(X) = UX = Y$, and $E : \mathbb{R}^{m+1} \longrightarrow \mathbb{R}^{(m+1) \times n}$, $E(Y) = V(Y)Y$.

The global variables $G(X)$, the variables of the reduced system, are the total number of individuals in each age class. $E(Y)$ represents the equilibrium that the fast dynamics attains for each given value Y of the global variables.

The aggregated system for the global variables, (A.3), associated to system (2.6) is

$$Y(t+1) = (G \circ S \circ E)(Y(t)) = \bar{S}(Y(t)) = U L\left(V(Y(t))Y(t)\right) V(Y(t)) Y(t). \tag{2.9}$$

Under simple regularity conditions for the coefficients in system (2.6) theorem A.1 in the appendix applies, [22], and thus it is possible to study the existence, stability and basins of attraction of steady states and periodic solutions of the initial system (2.6) performing the study for the aggregated system (2.9).

3. Two ages and two sites model with constant dispersal rates.

In this section we consider the simplified case of a population where we distinguish just two age classes: juvenile (immature) and adult (mature) individuals. The structured population is further assumed to be composed of two local populations coupled by dispersal.

Following notations in section 2, dropping the unnecessary subscript i of immature age classes, we denote J^j and A^j, respectively, the numbers of juveniles and adults in patch $j = 1, 2$. The population vector is thus $X = \mathrm{col}\left(J^1, J^2, A^1, A^2\right)$. The total number of juveniles and adults individuals are $J = J^1 + J^2$ and $A = A^1 + A^2$, and the vector with these global variables is $Y = (J, A)$.

Juvenile and adult dispersal rates are supposed to be constant and represented by the stochastic matrices M_J and M_A:

$$M_J = \begin{pmatrix} 1 - p_J & q_J \\ p_J & 1 - q_J \end{pmatrix}, \quad M_A = \begin{pmatrix} 1 - p_A & q_A \\ p_A & 1 - q_A \end{pmatrix}$$

where $0 < p_J, q_J, p_A, q_A < 1$, so that both matrices are regular. $M = \mathrm{diag}\left(M_J, M_A\right)$. Fast dynamics is represented by the map

$$F\left(X\right) = MX \tag{3.1}$$

Its k-iterate is

$$F^{(k)}\left(X\right) = M^k X = \mathrm{diag}\left(M_J^k, M_A^k\right) X$$

and its limit $\bar{F}$ can be decomposed in the following form

$$\bar{F}\left(X\right) = \lim_{k \to \infty} F^{(k)}\left(X\right) = \begin{pmatrix} \nu_J & \nu_J & 0 & 0 \\ 1 - \nu_J & 1 - \nu_J & 0 & 0 \\ 0 & 0 & \nu_A & \nu_A \\ 0 & 0 & 1 - \nu_A & 1 - \nu_A \end{pmatrix} X = \begin{pmatrix} \nu_J & 0 \\ 1 - \nu_J & 0 \\ 0 & \nu_A \\ 0 & 1 - \nu_A \end{pmatrix} \begin{pmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{pmatrix} X$$

where $\nu_J = q_J/(p_J + q_J)$ and $\nu_A = q_A/(p_A + q_A)$ represent the stable fractions of juveniles and adults in site 1. Thus, we have in this case the following values for matrices V and U:

$$V = \begin{pmatrix} \nu_J & 0 \\ 1 - \nu_J & 0 \\ 0 & \nu_A \\ 0 & 1 - \nu_A \end{pmatrix}, \quad U = \begin{pmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{pmatrix}$$

Slow dynamics, associated to demography, is defined locally by the nonlinear Leslie matrix for $j = 1, 2$

$$L^j\left(J^j, A^j\right) = \begin{pmatrix} 0 & f^j \varphi^j(J^j, A^j) \\ s^j \sigma^j(J^j, A^j) & 0 \end{pmatrix}. \tag{3.2}$$

and for the whole population by the map

$$S\left(X\right) = L\left(X\right) X \tag{3.3}$$

where the density-dependent Leslie matrix reads as follows

$$L\left(X\right) = \begin{pmatrix} 0 & 0 & f^1 \varphi^1(J^1, A^1) & 0 \\ 0 & 0 & 0 & f^2 \varphi^2(J^2, A^2) \\ s^1 \sigma^1(J^1, A^1) & 0 & 0 & 0 \\ 0 & s^2 \sigma^2(J^2, A^2) & 0 & 0 \end{pmatrix}.$$

The entries of matrix $L(X)$ verify the following hypothesis:

H: For $j = 1, 2$, $s^j > 0$, $f^j > 0$, $\sigma^j(J^j, A^j)$ and $\varphi^j(J^j, A^j)$ are functions C^2 on an open neighbourhood of the positive cone and positive on the positive cone, $\sigma^j(0,0) = 1$ and $\varphi^j(0,0) = 1$, and $s^j \sigma^j(J^j, A^j) \leq 1$ on the positive cone.

R. Bravo de la Parra, M. Marvá, F. Sansegundo   Fast Dispersal in Semelparous Populations

The complete model (2.6) becomes

$$X(t+1) = L\left(M^k X(t)\right) M^k X(t) \tag{3.4}$$

and the aggregated model (2.9)

$$Y(t+1) = \bar{S}(Y(t)) = \bar{L}(Y(t))Y(t) = \begin{pmatrix} 0 & \hat{\varphi}(VY(t)) \\ \hat{\sigma}(VY(t)) & 0 \end{pmatrix} Y(t) \tag{3.5}$$

where

$$\hat{\sigma}(VY) = \nu_J s^1 \sigma^1(\nu_J J, \nu_A A) + (1-\nu_J)s^2\sigma^2((1-\nu_J)J, (1-\nu_A)A)$$

and

$$\hat{\varphi}(VY) = \nu_A f^1 \varphi^1(\nu_J J, \nu_A A) + (1-\nu_A)f^2\varphi^2((1-\nu_J)J, (1-\nu_A)A).$$

Calling the global inherent vital rates

$$\bar{s} = \hat{\sigma}(\bar{0}) = \nu_J s^1 + (1-\nu_J)s^2 \qquad \text{and} \qquad \bar{f} = \hat{\varphi}(\bar{0}) = \nu_A f^1 + (1-\nu_A)f^2$$

and defining

$$\bar{\sigma}(J,A) := \hat{\sigma}(VY)/\hat{\sigma}(\bar{0}) \qquad \text{and} \qquad \bar{\varphi}(J,A) := \hat{\varphi}(VY)/\hat{\varphi}(\bar{0})$$

we notice that the nonlinear Leslie matrix $\bar{L}$ in system (3.5)

$$\bar{L}(J,A) = \begin{pmatrix} 0 & \bar{f}\,\bar{\varphi}(J,A) \\ \bar{s}\,\bar{\sigma}(J,A) & 0 \end{pmatrix}. \tag{3.6}$$

has the same form as the matrix L^j (3.2) that defines the local demography. Its coefficients verify hypothesis H too.

As mentioned at the end of section 2 theorem A.1 in the appendix applies to system (3.4) and so we study the existence and stability of its steady states and periodic solutions with the help of the reduced system (3.5).

It turns out that system (3.5) as well as the local Leslie model defined by matrices (3.2) are of the form of system (10) in [7]. We use in particular Theorem 4.1 in [7] to compare the local demographic behaviour in the initial model (considering isolated sites) and the global demographic behaviour as reflected in the aggregated model (3.5) where dispersal is taken into account.

3.1. Stability of bifurcating equilibria and single class 2-cycles.

In this section we recall the main results established in [7] for semelparous biennial populations that apply to both the isolated local dynamics and the global dynamics as described by matrices (3.2) and (3.6), respectively. We denote any of them in the following form

$$Y(t+1) = \mathcal{L}(Y(t))Y(t) = \begin{pmatrix} 0 & f\,\varphi(Y(t)) \\ s\,\sigma(Y(t)) & 0 \end{pmatrix} Y(t) \tag{3.7}$$

where the coefficients of matrix $\mathcal{L}$ verify hypothesis H.

The bifurcation results in [7] start by identifying the bifurcation parameter which is

$$R_0 := s \cdot f \tag{3.8}$$

called the *inherent net reproductive value*, the expected number of offspring per individual per lifetime at low density. Then it is defined a branch (also known as continuum) of trivial solutions from which other equilibrium states bifurcate. The set $\mathcal{C}_0 := (\bar{0}, R_0) \in \{\bar{0}\} \times [0, +\infty)$ consisting of the zero solution of system (3.5) together with all possible values of R_0 is known as the branch of trivial solutions. In the next result the stability of the zero solution is readily characterized in terms of R_0.

Theorem 3.1. *Let us assume that hypothesis H holds for the semelparous Leslie model* (3.7). *Then, the extinction equilibrium $\bar{0}$ is (locally asymptotically) stable if $R_0 < 1$ and is unstable if $R_0 > 1$.*

Proof.- It follows from linearization. ∎

Using R_0 as bifurcation parameter, Theorem 3.1 establishes that $\mathcal{C}_0$ looses its stability as R_0 crosses the threshold value 1.

Obviously, apart from the zero solution and its stability, the existence and stability of other attractor sets is of interest. In [7] it is shown that, under appropriate conditions, two different positive branches bifurcate from the trivial branch $\mathcal{C}_0$ at $R_0 = 1$. One of these branches, denoted $\mathcal{C}_e$, consists of positive equilibrium points. The other positive branch, denoted $\mathcal{C}_2$, consists of single-class 2-cycles. The existence of single-class orbits is a particular feature of the system (3.7). Any single-class vector, i.e., one with just one non-zero component, is mapped into another single-class vector with a different non-zero component. Thus, a single-class initial vector yields a single-class orbit alternating the non-zero age-class at a time.

Let us recall that if matrix $\mathcal{L}(\bar{0})$ were primitive the direction of bifurcation would decide whether the bifurcating branch of positive equilibrium points is stable (supercritical) or unstable (subcritical). As matrix $\mathcal{L}(\bar{0})$ is not primitive the stability of this branch is not only decided by the direction of the bifurcation, the simultaneous existence of a branch of single-class 2-cycles also plays a role. See [7,10] for further details.

The conditions to be hold such that the non-trivial branches of equilibria and single-class 2-cycles bifurcate to the left or to the right and are stable or unstable depend on the following two quantities [7]:

$$\delta_1 := \partial_1^0 \sigma + s\partial_2^0 \varphi \qquad\qquad \delta_2 := s\partial_2^0 \sigma + \partial_1^0 \varphi \qquad\qquad (3.9)$$

where σ and φ are those of system (3.7) and ∂_j^0 denotes partial differentiation with respect to the j-th variable and evaluation at $\bar{0}$. Quantities δ_1 and δ_2 admit a simple interpretation in terms of intra and inter-class competition. As pointed out in [7], a density regulation effect in the survivorship term σ or in the fecundity term φ means that these terms are decreasing in the corresponding variable, J or A, i.e., $\partial_i^0 \sigma < 0$ or $\partial_i^0 \varphi < 0$ with $i = 1$ or $i = 2$. The opposite inequality indicates the existence of an Allee effect in the term with respect to the involved variable. Therefore, the terms δ_1 and δ_2 can be interpreted as measures, respectively, of the intra-class and the inter-class competition at low densities. Even if the terms involved in δ_k may have different signs, the sign of δ_k, for $k = 1, 2$, indicates whether the effect of intra-class ($k = 1$) or inter-class ($k = 2$) competition leads to either the Allee effect (positive sign) or the density regulation effect (negative sign).

In the following theorem we state the conditions, given in [7] Theorem 4.1, ensuring the stability of the bifurcating branches $\mathcal{C}_e$ and $\mathcal{C}_2$ in terms of the intra-class and inter-class competition parameters δ_1 and δ_2.

Theorem 3.2. *Consider the nonlinear Leslie model* (3.7) *and assume that hypothesis H holds. Assume also that $\delta_1 < 0$, $\delta_1 + \delta_2 < 0$ and let $\mathcal{C}_e$ and $\mathcal{C}_2$ be the branches of positive equilibrium points and single class 2-cycles bifurcating from the trivial branch at $R_0 = 1$. Then $\mathcal{C}_e$ and $\mathcal{C}_2$ bifurcate supercritically and*

1. If $\delta_1 < \delta_2$ then $\mathcal{C}_e$ is stable and $\mathcal{C}_2$ unstable.
2. If $\delta_1 > \delta_2$ then $\mathcal{C}_e$ is unstable and $\mathcal{C}_2$ stable.

We notice that the stability of any of the two branches is found when both bifurcate supercritically [7]. In this case there is a dichotomy between both branches, for $\delta_1 < \delta_2$, stronger intra-class competition, $\mathcal{C}_e$ is stable and $\mathcal{C}_2$ unstable and for $\delta_1 > \delta_2$, stronger inter-class competition, $\mathcal{C}_e$ is unstable and $\mathcal{C}_2$ stable.

3.2. The effect of fast dispersal.

We address in this section the main goal of this work. It consist in showing the influence of fast dispersal on population demography. We focus first on the survival of the population as reflected by the zero

solution stability. Secondly, once the survival threshold is attained, we pay attention to the tendency of the population towards either stable equilibration or periodic oscillations with just one age-class present at a time. This last aspect is defined by which of the bifurcating branches, $\mathcal{C}_e$ of equilibria or $\mathcal{C}_2$ of single-class 2-cycles, is stable.

The influence of fast dispersal is analyzed by comparing the outcomes of local (isolated sites) and global (interconnected sites) dynamics. Taking into account that systems associated to the local dynamics (matrices (3.2)) and to the global dynamics (matrix (3.6)) have the same form (3.7) we use local and global versions of the parameters R_0, δ_1 and δ_2 to compare, with the help of theorems 3.1 and 3.2, the asymptotic behaviour of the population in both cases. Thus, we call $\bar{R}_0 = \bar{s}\bar{f}$ the global net inherent reproductive number, and $R_0^1 = s^1 f^1$ and $R_0^2 = s^2 f^2$ the net inherent reproductive number in patch $j = 1, 2$, respectively. Similarly, using (3.9), we define $\bar{\delta}_1$, the global intra-class competition coefficient, and $\bar{\delta}_2$, the global inter-class competition coefficient, and the corresponding local ones δ_1^j and δ_2^j for the isolated patch $j = 1, 2$.

It is important to keep in mind that the global parameters $\bar{R}_0$, $\bar{\delta}_1$ and $\bar{\delta}_2$ incorporate information about the asymptotic spatial distribution of individuals of each age class as a result of fast dispersal. Coefficients ν_J and ν_A (see the definition of matrix $\bar{L}$ (3.6)) represent the stable fractions of juvenile and adult individuals living in site 1.

It is straightforward to see that a certain homogeneity concerning sites, to be specific $s^1 = s^2 = s$ and $f^1 = f^2 = f$, prevents survivorship changes at the global level. In fact, $\bar{s} = s$ and $\bar{f} = f$. Thus, $\bar{R}_0 = R_0^1 = R_0^2 = sf$. The population gets extinct (survives) locally if and only if it does globally.

On the other hand, differences in local parameters s^1 and s^2, and f^1 and f^2 allow drastic changes of the local outcome at the global level depending on dispersal rates. In the following theorem we show conditions yielding extinction of the local populations for isolated sites together with dispersal strategies enabling the population to survive.

Theorem 3.3. *Consider system* (3.5) *and assume that hypothesis H holds as well as that* $s^j f^j < 1$ *for* $j = 1, 2$. *If* $\max\{s^1 f^2, s^2 f^1\} > 1$ *then there exist intervals* $I_1, I_2 \subseteq [0,1]$ *such that* $\bar{R}_0 > 1$ *for* $(\nu_J, \nu_A) \in I_1 \times I_2$.

Proof.- See appendix A.2.

In words, the condition $sf > 1$ means that the survival rate s and the fecundity rate f are, together, large enough to sustain the population. Thus, appropriate dispersal rates allow the population to locate juvenile individuals mostly in the patch with the largest survival rate and adult individuals mostly in the patch with the largest fecundity rate. In this way, the dispersal strategy compensates poor local survivorship conditions represented by $s^j f^j < 1$ ($j = 1, 2$).

The opposite result can also be found. Under appropriate conditions, two isolated viable populations may get extinct when connected with the adequate dispersal rates.

Theorem 3.4. *Consider system* (3.5) *and assume that hypothesis H holds as well as that* $s^j f^j > 1$ *for* $j = 1, 2$. *If* $\min\{s^1 f^2, s^2 f^1\} < 1$ *then there exist intervals* $I_1, I_2 \subseteq [0,1]$ *such that* $\bar{R}_0 < 1$ *for* $(\nu_J, \nu_A) \in I_1 \times I_2$.

Proof.- See appendix A.2.

We now present two results showing that adequate dispersal rates can exchange the tendency to equilibration or periodic oscillations between the local and global levels, when the inherent net reproductive value goes through 1.

Assuming periodic oscillations at each site and density regulation effect in both the survivorship and the fecundity terms, we can find dispersal rates resulting at the global level in equilibration and also dispersal rates maintaining periodic oscillations.

Theorem 3.5. *Consider system* (3.5) *and assume that hypothesis H holds. Let us assume also that* $\partial_i^0 \sigma^j < 0$ *and* $\partial_i^0 \varphi^j < 0$, *for* $i, j = 1, 2$ *and*

$$\delta_1^j > \delta_2^j \qquad for\ j = 1, 2,$$

Then there exist intervals $I_1, I_2 \subseteq [0, 1]$ *such that*

$$\bar{\delta}_1 > \bar{\delta}_2 \qquad for\ all\ (\nu_J, \nu_A) \in I_1 \times I_2$$

and also there exist intervals $I_3, I_4 \subseteq [0, 1]$ *such that*

$$\bar{\delta}_1 < \bar{\delta}_2 \qquad for\ all\ (\nu_J, \nu_A) \in I_3 \times I_4.$$

Proof.- See appendix A.2.

On the one hand, if in one of the sites $\delta_1^j > \delta_2^j$, that is, there is a stronger inter-class competition, yielding periodic oscillations (theorem 3.2), then the same happens globally provided that dispersal tends to move most of the population to this site. On the other hand, in spite of having stronger inter-class competition in both sites when isolated, if dispersal distributes most of the juvenile individuals in one site and most of the adult individuals in the other site then the global inter-class competition is much reduced and equilibration can be the outcome at the global level.

It is not so easy to imagine how to change from equilibration at the local level, $\delta_1^j < \delta_2^j$, to periodic oscillations at the global level, $\bar{\delta}_1 > \bar{\delta}_2$, but surprisingly enough this can be the case even with homogenous sites. Let us assume that demographic coefficients in both sites are identical:

$$s^1 = s^2 = s,\ f^1 = f^2 = f,\ \sigma^1(J, A) = \sigma^2(J, A) = \sigma(J, A)\ and\ \varphi^1(J, A) = \varphi^2(J, A) = \varphi(J, A). \quad (3.10)$$

The following result finds sufficient conditions so that stronger local intra-class competition is transformed into stronger global inter-class competition in an environment with homogeneous sites.

Theorem 3.6. *Consider system* (3.5) *with homogeneous sites* (3.10). *Assume hypothesis H*, $\partial_i^0 \sigma < 0$ *and* $\partial_i^0 \varphi < 0$ *for* $i = 1, 2$, *and*

$$\delta_1 < \delta_2$$

If $\partial_1^0 \sigma \neq s \partial_2^0 \varphi$ *then there exist values of* ν_J *and* ν_A *such that*

$$\bar{\delta}_1 > (\nu_J \nu_A + (1 - \nu_J)(1 - \nu_A))\,\delta_1,$$

and in this case $\delta_2 < \bar{\delta}_1 / (\nu_J \nu_A + (1 - \nu_J)(1 - \nu_A))$ *implies*

$$\bar{\delta}_1 > \bar{\delta}_2.$$

Proof.- See appendix A.2.

The first assertion of the theorem holds under very general conditions and the last one needs an assumption that it is independent of the previous ones because it just involves $\partial_2^0 \sigma$ and $\partial_1^0 \varphi$. So, the conditions to find this sort of global destabilization of a locally stabilized system are not so scarce.

4. Discussion.

In this work we illustrate the importance of dispersal in population dynamics through a relatively simple model that nevertheless capture some important features of this fundamental subject in ecology.

We consider a discrete model of a structured population. The demography corresponds to that of a semelparous age-structured population. The influence of dispersal is studied through two aspects of the long term behaviour of the population. The first one is the viability or extinction of the population.

The second one has to do with the tendency to either equilibration with all age classes present, which is represented by positive equilibria, or oscillations with missing, possibly all but one, age classes. The performed analysis of the influence of individuals movements on changing between these alternative behaviours gives some insights on the general ecological problem.

Spatial heterogeneity is introduced by considering a patchy environment. We assume the habitat of the population divided into different sites with individuals moving among them. We compare the *local* population dynamics for isolated sites with the *global* population dynamics when patches are connected and therefore the local populations interrelated. Dispersal is considered an individual-level process that should be embedded in the population-level demography previously described [26]. We use time scales to do it correctly. We propose local demographic models by means of projection matrices (density dependent Leslie matrices) for the specific unit of time associated to this population-level process. Dispersal is also defined through projection matrices (density dependent stochastic matrices), one for each age class. The unit of time associated to dispersal matrices is considered, as related to an individual level process, much smaller than the demographic one. The model including both processes is a discrete system which time unit is the slow one, i.e., the one associated to demography. The combined effect of both processes during a slow time unit is represented by projecting a number k of times the dispersal process followed by a projection of the demographic process, assuming that the slow time unit is divided into a large number k of fast time units. An approximate reduction of this complete model gives a simpler system for the total number of individuals in each age class. It shows a good population-level description of an individual-level process, what represents a significant example of up-scaling [19].

Section 3 uses the general framework developed in section 2 to study the influence of dispersal on the population dynamics in a simplified case: two age classes two sites model. The slow unit of time is taken as the maturation period and it is assumed that no adults survives longer than one time unit (semelparous population). The local model is known as Ebenman's model [11]. The dispersal rates are considered to be constant so that the fast dynamics tends to distribute juvenile and adult individuals between the two sites according to constant proportions. Thus, these constant proportions represent the dispersal strategies of both age classes. The first results show that there exist dispersal strategies capable of reversing the local viability of the population. Local populations tending to extinction can globally persist when connected with adequate dispersal rates provided that the largest local inherent survivorship and fertility rates yield an inherent net reproductive value R_0 bigger than 1. The opposite case can also be found. If the lowest local inherent vital rates yield an $R_0 < 1$ then viable local populations can globally get extinct for particular dispersal strategies.

A second step in analyzing the influence of dispersal on the population dynamics is focusing on the tendency to either equilibrate or oscillate. In the case with density regulation effect in the vital rates, when R_0 gets through the value 1 there is a dichotomy between two different population behaviours. On the one hand, the population can tend to equilibrate with overlapping generations, that is, both age-classes are simultaneously present. The mathematical evidence of this fact is the existence of a bifurcating branch of stable positive equilibrium points, C_e. On the other hand, the population can also tend to oscillate with separated generations, that is, both age-classes alternate with just one of them being non-zero at a time. This latter case is a consequence of the existence of a bifurcating branch of stable 2-cycles, C_2. These two different behaviours can be interpreted in terms of intra-class and inter-class competition intensities. More intense intra-class competition yields equilibration and more intense inter-class competition yields oscillation. We show that these two different behaviours can be exchanged between the local, isolated sites, and the global, dispersal connected sites, levels. A first result shows that for locally isolated populations tending to separated generations there always exist dispersal rates reversing the outcome when both populations are connected. Dispersal rates allow to reduce inter-class competition resulting in equilibration with both age-classes present. It is also possible to find conditions such that dispersal provokes changing the local tendency to equilibrate with overlapping generations. Even considering homogeneous sites, appropriately choosing the dispersal rates may, with some conditions

holding, transform local populations with overlapping generations into a global metapopulation with separated generations.

The results obtained can be extended to semelparous populations with a number m of age classes and density dependent dispersal. It suffices to use the reduction method presented in section 2 and the results on stability of equilibria and cycles for semelparous age structured populations found in [7–10].

Appendices

A.1. Reduction procedure

We briefly describe in this section the approximate aggregation procedure presented in [23] where details can be found.

We suppose a population generally divided into groups, and each of these groups divided into several subgroups. The state at time t of the population with q groups is represented by a vector $X(t) := (\mathbf{x}^1(t), \ldots, \mathbf{x}^q(t))^{\mathsf{T}} \in \mathbb{R}^N$, where every vector $\mathbf{x}^i(t) := (x^{i1}(t), \ldots, x^{iN^i}(t))^{\mathsf{T}} \in \mathbb{R}_+^{N^i}$, $i = 1, \ldots, q$, represents the state of the i group which is divided into N^i subgroups, with $N = N^1 + \cdots + N^q$.

The evolution of the population is driven by two processes which characteristic time scales are very different from each other. These two processes, fast and slow, are defined by two maps

$$F, S : \Omega_N \longrightarrow \Omega_N \quad ; \quad F, S \in C^1(\Omega_N),$$

where $\Omega_N \subset \mathbb{R}^N$ is a nonempty open set.

We use as the time unit of the system coupling both processes that corresponding to the slow process. We approximate the effect of the fast dynamics over a time interval much longer than its own by means of the k-th iterate of map F, $F^{(k)}$, where k represents the time scales ratio. Thus, the complete system is defined by

$$X_k(t + 1) = S(F^{(k)}(X_k(t))) := H_k(X_k(t)), \tag{A.1}$$

In order to proceed to the approximate reduction of the system (A.1) we assume the following two hypotheses on F:

Hypothesis (H1):

The sequence of iterates of F, $\{F^{(k)}\}_{k \in \mathbb{N}}$, converges pointwise on Ω_N to a map $\bar{F} : \Omega_N \to \Omega_N$, such that $\bar{F} \in C^1(\Omega_N)$.

Hypothesis (H2):

There exist a non-empty open subset $\Omega_q \subset \mathbb{R}^q$ with $q < N$ and two maps $G : \Omega_N \longrightarrow \Omega_q$ and $E : \Omega_q \longrightarrow \Omega_N$ with $G \in C^1(\Omega_N)$, $E \in C^1(\Omega_q)$, such that the map $\bar{F}$ of hypothesis H1 can be expressed as $\bar{F} = E \circ G$.

We first define the auxiliary system which approximates (A.1) when $k \to \infty$, i.e., when the fast process has attained its equilibrium. Denoting its vector state at time t by X_t, this auxiliary system is

$$X(t + 1) = S(\bar{F}(X(t))) = (S \circ E \circ G)(X(t)), \tag{A.2}$$

second, we define the global variables through

$$Y := G(X) \in \mathbb{R}^q.$$

and applying G to both sides in (A.2) we obtain the so-called aggregated system associated to system (A.1)

$$Y(t + 1) = (G \circ S \circ E)(Y(t)) := \bar{S}(Y(t)). \tag{A.3}$$

The next theorem relates the asymptotic behavior of systems (A.1) and (A.3) for big enough values of parameter k.

Theorem A.1. *Let us assume that F verify Hypotheses H1 and H2, and that*

$$\lim_{k \longrightarrow \infty} F^{(k)} = \bar{F} \ \ and \ \ \lim_{k \longrightarrow \infty} DF^{(k)} = D\bar{F} \tag{A.4}$$

uniformly on any compact set $K \subset \Omega_N$.

Let $Y^* \in \mathbb{R}^q$ *be a hyperbolic equilibrium point of (A.3). Then there exists $k_0 \in \mathbb{N}$ such that for each $k \geq k_0$ there exists a hyperbolic equilibrium point X_k^* of (A.1) satisfying*

$$\lim_{k \to \infty} X_k^* = X^*$$

where $X^* = E(Y^*)$. Moreover,

1. *If Y^* is asymptotically stable then X_k^* is asymptotically stable for each $k \geq k_0$, and if $X_0 \in \mathbb{R}^N$ is such that $\lim\limits_{n \longrightarrow \infty} \bar{S}^{(n)}(Y_0) = Y^*$, where $Y_0 = G(X_0)$, then*

$$\lim_{n \longrightarrow \infty} H_k^{(n)}(X_0) = X_k^*.$$

2. *If Y^* is unstable then X_k^* is unstable, for each $k \geq k_0$.*

An analogous result can be stated for periodic solutions, see [23].

Conditions (A.4) are in general difficult to check in practical applications, particularly the uniform convergence of the differentials. For the kind of systems with fast dynamics depending on global variables, as system (2.6), in [22] it is proved that conditions (A.4) are met and therefore that theorem A.1 applies.

A.2. Results on the effect of fast dispersal (section 3.2)

Proof of theorem 3.3.- Assume, for instance, that $s^1 f^2 > 1$. In the extreme case that $\nu_J = 1$ and $\nu_A = 0$, the corresponding global net inherent reproductive value $\bar{R}_0$ reduces to $s^1 f^2 > 1$. Taking into account that $\bar{R}_0$ varies continuously with ν_J and ν_A, there exists $\varepsilon_1, \varepsilon_2 > 0$ such that

$$\bar{R}_0(\nu_J, \nu_A) > 1$$

for all $(\nu_J, \nu_A)) \in (\varepsilon_1, 1] \times [0, \varepsilon_2) \in [0, 1] \times [0, 1]$. ∎

Proof of theorem 3.4.- Analogous to the proof of Theorem 3.3. ∎

Proof of theorem 3.5.- Straightforward calculations done from the coefficients in matrix (3.6) allow to express $\bar{\delta}_1$ and $\bar{\delta}_2$ as continuous functions of ν_J and ν_A in the following way

$$\bar{\delta}_1(\nu_J, \nu_A) = \frac{s^1}{\bar{s}}(\nu_J)^2 \partial_1^0 \sigma^1 + \frac{s^2}{\bar{s}}(1 - \nu_J)^2 \partial_1^0 \sigma^2 + \bar{s}\left(\frac{f^1}{\bar{f}}(\nu_A)^2 \partial_2^0 \varphi^1 + \frac{f^2}{\bar{f}}(1 - \nu_A)^2 \partial_2^0 \varphi^2\right) \tag{A.5}$$

and

$$\bar{\delta}_2(\nu_J, \nu_A) = s^1 \nu_J \nu_A \partial_2^0 \sigma^1 + s^2(1 - \nu_J)(1 - \nu_A)\partial_2^0 \sigma^2 + \frac{f^1}{\bar{f}}\nu_J \nu_A \partial_1^0 \varphi^1 + \frac{f^2}{\bar{f}}(1 - \nu_J)(1 - \nu_A)\partial_1^0 \varphi^2. \tag{A.6}$$

Thus, $\bar{\delta}_k(1, 1) = \delta_k^1$ for $k = 1, 2$. Then, $\delta_1^1 > \delta_2^1$ implies that $\bar{\delta}_1(1, 1) > \bar{\delta}_2(1, 1)$ and together with the continuity of the functions $\bar{\delta}_i(\nu_J, \nu_A)$ yield the existence of intervals I_1 and I_2.

Analogous arguments give the existence of intervals I_3 and I_4 having in mind that $\bar{\delta}_1(1, 0) = \partial_1^0 \sigma^1 + s^1 \partial_2^0 \varphi^2 < 0$ and $\bar{\delta}_2(1, 0) = 0$. ∎

Proof of theorem 3.6.- The coefficients in the aggregated system (2.9) in the case of homogeneous sites (3.10) are:

$$\bar{s} = s, \ \bar{f} = f,$$
$$\bar{\sigma}(J, A) = \nu_J \sigma\left(\nu_J J, \nu_A A\right) + (1 - \nu_J)\sigma\left((1 - \nu_J)J, (1 - \nu_A)A\right), \tag{A.7}$$
$$\bar{\varphi}(J, A) = \nu_A \varphi\left(\nu_J J, \nu_A A\right) + (1 - \nu_A)\varphi\left((1 - \nu_J)J, (1 - \nu_A)A\right).$$

Thus the global intra and inter-class competition coefficients reduce to:

$$\bar{\delta}_1\left(\nu_J, \nu_A\right) = \left((\nu_J)^2 + (1 - \nu_J)^2\right)\partial_1^0\sigma + \left((\nu_A)^2 + (1 - \nu_A)^2\right) s\, \partial_2^0\varphi \tag{A.8}$$

and

$$\bar{\delta}_2\left(\nu_J, \nu_A\right) = \left(\nu_J\nu_A + (1 - \nu_J)(1 - \nu_A)\right)\left(s\, \partial_2^0\sigma + \partial_1^0\varphi\right). \tag{A.9}$$

Now inequality $\bar{\delta}_1 > \left(\nu_J\nu_A + (1 - \nu_J)(1 - \nu_A)\right)\delta_1$ can be rewritten as

$$\left(\nu_J - \nu_A\right)\left(\nu_J - 1/2\right)\partial_1^0\sigma + \left(\nu_A - \nu_J\right)\left(\nu_A - 1/2\right)s\partial_2^0\varphi > 0. \tag{A.10}$$

This inequality for $\nu_J > \nu_A$ reduces to

$$\nu_A > \frac{1}{2} + \frac{\partial_1^0\sigma}{s\partial_2^0\varphi}\left(\nu_J - \frac{1}{2}\right)$$

and for $\nu_J < \nu_A$ to

$$\nu_A < \frac{1}{2} + \frac{\partial_1^0\sigma}{s\partial_2^0\varphi}\left(\nu_J - \frac{1}{2}\right).$$

In the first case it has solutions with $1/2 < \nu_A < \nu_J < 1$ if $\partial_1^0\sigma/(s\partial_2^0\varphi) < 1$ and with $0 < \nu_A < \nu_J < 1/2$ if $\partial_1^0\sigma/(s\partial_2^0\varphi) > 1$. In the second case the inequality can be solved with $0 < \nu_J < \nu_A < 1/2$ if $\partial_1^0\sigma/(s\partial_2^0\varphi) < 1$ and with $1/2 < \nu_J < \nu_A < 1$ if $\partial_1^0\sigma/(s\partial_2^0\varphi) > 1$.

The last assertion is straightforward from (A.9). ∎

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R. Bravo de la Parra, M. Marvá, F. Sansegundo   Fast Dispersal in Semelparous Populations

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