

A Time Discrete Linear Model of Population Structured by Age and the Time of Residence: Non-autonomous case

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Abstract. The model we propose is a generalization of the linear discrete model to the case of time varying environment. We present a time discrete time varying model of the dynamics of a population structured by the age and the time spent in one of the two patches it lives in. Migration takes place between the two patches, birth is allowed in each patch, we which to allow the parameters of the model to be time dependent and are a function of age and the time spent in a given area.

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1. INTRODUCTION

In this work we extend our model in the linear case to account for the case of a time varying environment. In particular, we will deal with the cases of cyclically varying environment and of an environment in process of stabilization.

Periodic environment models are relevant because of the pronounced seasonal periodicities in many environments[6, 7]. If environmental differences

between years are negligible in comparison with difference between seasons, projection models with a time step shorter than the annual cycle naturally appear to vary in a period fashion [14, 15, 22]. The literature offers different approaches to the study of these models. The classical one (Skellam see, [20]), which is the one we will follow, is based in transforming the original system into a time invariant one considering the length of a cycle as the projection interval.

The case of environmental variation tending to stabilization has not been addressed with profusion in literature, but it responds to important biological considerations. Indeed, environments do not constantly maintain its characteristics, but are frequently subjected to perturbations caused by different incidental climatological conditions such as prolonged drought or rains, extreme temperatures, etc., which induce perturbations in the vital rates of the population. If we suppose that these perturbations do not alter the equilibrium, we might wonder whether, in the long run, the system is independent of those incidental perturbations and depends only of the equilibrium vital rates. Because of the resemblance with the time invariant case, we could also think that under certain conditions the system is strongly ergodic, i.e., it has a fixed asymptotic population structure independent of initial conditions, and its growth is asymptotically exponential. Moreover, we could like to know when that population structure and asymptotic exponential growth are those corresponding to the case when the environment constantly has the equilibrium characteristics. Most of the mathematical results behind this subject are proposed by Senata [20].

Section 2 proposes a linear time discrete model in the general case of varying environment, We build a model with age structure which contains a simple count of the sort of migration effects widely observed in bio-populations such as fish and bird population, we classify individuals by spatial patch, age and time spent in a given patch. This idea has been mainly inspired from the work by O.Arino and W.V.Smith [3]. These authors presented a linear continuous model for age structured populations which migrate between several locations, taking into consideration the time spent in a given area. they illustrate how this model may be applied to a certain fishery problem by considering the species *pollachius virens*. This fish is better known as the *saithe*.

Section 3 presents an introduction to the general treatment for cyclical linear system. We show that under wide conditions, the asymptotic population structure of system is cyclical.

Section 4 has the same structure as section 3, but in this occasion we address the case of an stabilizing environment. We give sufficient conditions for a general system to exhibit strong ergodicity (tendency towards a fixed population structure independent of the initial conditions) and an exponential asymptotic growth.

2. SPATIAL-MODEL CONSTRUCTION

The model we propose is a generalization of the linear discrete model considering in [19] in which we want to allow the parameters of the model to be time dependent.

We consider a population of N (≥ 2) individuals divided among two patches. Patches may be thought of as distinct but spatial overlap is not excluded in general. Population segments are further distinguished in terms of migration status. For the modeled fish population, the annual cycle of reproduction and overwintering is indexed by t . In this sense, we classify individuals by spatial patch they are in, the age and the time spent in the patch, and we allow migration, survival and fertility rates to depend on these three factors. The models include two processes, demography determines the moments of birth of each individual as well as the transition between different age groups, while migration characterizes the change of spatial patch. Migration is supposed to take place after growth, thus, the only changes in the overall number of individuals take place during the growth phase (no individual can be lost during the dispersal phase). We assume that the length of time spent in each age class is the same is equal to the interval between two measurements of population. We will denote by:

$X_{t,i}^{a,b}$: the number of individuals at time t in patch i with age in the interval $[a-1, a[$ which are migrants from the other patches, having lived in patch i for time b , $a = 1, \dots, q$, $b = 1, \dots, a-1$, $i = 1, 2$, $t = 0, 1, 2, \dots$

$X_{t,i}^{a,a}$: the number of those individuals who were born at time t in patch i and have remained up to age class a in the patch. $a = 1, \dots, q$, $t = 0, 1, 2, \dots$, $i = 1, 2$.

Individuals are assumed to have a maximum possible age class q .

2.1. The total population. The total population in patch i is given by:

$$P_i(t) = \sum_{a=1}^q \sum_{b=1}^a X_{t,i}^{a,b} \quad i = 1, 2$$

2.2. The dynamics of migrants. Using $S_i^{a,a}(t)$ the survival rate for natives in patch i during interval $[t, t+1[$ and $S_i^{a,b}(t)$ the survival rate for migrants in patch i during interval $[t, t+1[$, possibly different from that of natives in patch i , $i = 1, 2$.

For the migration rate, we use the migration rate during interval $[t, t+1[$ (from patch j to patch i for individuals of age class a and having lived in patch j for time b), $p_{ij}^{a,b}(t) \geq 0$, $t, j = 1, 2$.

$$\left\{ \begin{array}{l} X_{t+1,1}^{a+1,1} = \sum_{b=1}^a p_{12}^{a+1,b+1}(t) S_2^{a,b}(t) X_{t,2}^{a,b} \\ \\ X_{t+1,2}^{a+1,1} = \sum_{b=1}^a p_{21}^{a+1,b+1}(t) S_1^{a,b}(t) X_{t,1}^{a,b} \\ \\ X_{t+1,i}^{a+1,b+1} = p_{ii}^{a+1,b+1}(t) S_i^{a,b}(t) X_{t,i}^{a,b} \end{array} \right. \begin{array}{l} a = 1, \dots, q - 1, \\ \\ a = 1, \dots, q - 1, \\ \\ i = 1, 2 \quad , \quad a = 1, \dots, q - 1, \quad b = 1, \dots, a \end{array}$$

2.3. **The production of eggs.** We denote by: $f_i^{a,a}(t)$ the fertility coefficients for natives of patch i during interval $[t, t + 1[$, while $f_i^{a,b}(t)$ is the possibly different fertility rate for migrants of patch i during interval $[t, t + 1[$, $i = 1, 2$.

The abundance of the young of the year at time $t + 1$ is:

$$X_{t+1,i}^{1,1} = \sum_{j=1}^2 \sum_{a=1}^q \sum_{b=1}^a p_{ij}^{11}(t) f_j^{a,b}(t) X_{t,j}^{a,b} \quad i = 1, 2$$

To simplify the presentation of the system, we introduce some notations (as usual, A^T means the transpose of A). The variables corresponding to age a and time spent b are given by vector $X_t^{a,b} = (X_{t,1}^{a,b}, X_{t,2}^{a,b})^T$ and therefore, the composition of the population in age a is described by the column vector $X_t^a = (X_t^{a,1}, X_t^{a,2}, \dots, X_t^{a,a})^T$ with $2a$ components, and the whole population is described by the column vector $X_t = (X_t^1, X_t^2, \dots, X_t^q)^T$ which therefore has $q^2 + q$ components.

The demography for the whole population will be given by a generalized Leslie matrix

$$M(t) = \begin{pmatrix} f^1(t) & f^2(t) & f^3(t) & \dots & f^q(t) \\ s^1(t) & 0 & 0 & \dots & 0 \\ 0 & s^2(t) & 0 & \ddots & \vdots \\ \vdots & 0 & \ddots & 0 & 0 \\ 0 & \dots & 0 & s^{q-1}(t) & 0 \end{pmatrix}$$

where we have for $a = 1, \dots, q$ and $b = 1, \dots, a$

$$\begin{aligned}
 f^a(t) &= (f^{a,1}(t), f^{a,2}(t), \dots, f^{a,a}(t)) \in R^{2 \times 2a} \\
 f^{a,b}(t) &= \text{diag}(f_1^{a,b}(t), f_2^{a,b}(t)) \in R^{2 \times 2} \\
 s^a(t) &= (0, \dots, 0, c^a(t))^T \in R^{2(a+1) \times 2a} \\
 c^a(t) &= \text{diag}(c^{a,1}(t), \dots, c^{a,a}(t)) \in R^{2a \times 2a} \\
 c^{a,b}(t) &= \text{diag}(S_1^{a,b}(t), S_2^{a,b}(t)) \in R^{2 \times 2}
 \end{aligned}$$

$$P^{a,1}(t) = \begin{pmatrix} p_{11}^{a,1}(t) & p_{12}^{a,1}(t) \\ p_{21}^{a,1}(t) & p_{22}^{a,1}(t) \end{pmatrix} \in R^{2 \times 2}$$

for $a = 2, \dots, q$ and $b = 2, \dots, a$

$$P^{a,b}(t) = \begin{pmatrix} 0 & p_{12}^{a,b}(t) \\ p_{21}^{a,b}(t) & 0 \end{pmatrix} \in R^{2 \times 2}$$

$$L^{a,b}(t) = \begin{pmatrix} p_{11}^{a,b}(t) & 0 \\ 0 & p_{22}^{a,b}(t) \end{pmatrix} \in R^{2 \times 2}$$

Therefore, if we consider a fixed projection interval, the migratory process for group a will be represented, during the time interval $[t, t + 1[$, by a regular stochastic matrix (i.e., a primitive stochastic matrix) [2, 4, 5, 8, 9, 10, 11, 12, 13, 16, 21] of dimension $2a \times 2a$

$$P^a(t) = \begin{pmatrix} P^{a,1}(t) & P^{a,2}(t) & P^{a,3}(t) & \dots & \dots & P^{a,a}(t) \\ 0 & L^{a,2}(t) & 0 & \dots & \dots & 0 \\ 0 & 0 & L^{a,3}(t) & 0 & \dots & \vdots \\ \vdots & \vdots & 0 & \ddots & 0 & \vdots \\ \vdots & \vdots & \vdots & 0 & \ddots & 0 \\ 0 & 0 & 0 & 0 & 0 & L^{a,a}(t) \end{pmatrix}$$

The matrix $P(t)$ which represents the migration for the whole population during that interval is then

$$P(t) = \begin{pmatrix} P^{1,1}(t) & 0 & \dots & \dots & 0 \\ 0 & P^2(t) & 0 & \dots & 0 \\ \vdots & 0 & P^3(t) & \ddots & \vdots \\ \vdots & \dots & \ddots & \ddots & 0 \\ 0 & \dots & \dots & 0 & P^q(t) \end{pmatrix}$$

The global model describing the rate of change for the whole population X consists of the following system of $q^2 + q$ difference equations

$$\begin{aligned}
 X_{t+1} &= P(t)M(t)X_t \\
 (2.1) \qquad &= L(t)X_t
 \end{aligned}$$

where $L(t)$ is given by

$$L(t) = \begin{pmatrix} F^1(t) & F^2(t) & F^3(t) & \dots & F^q(t) \\ G^1(t) & 0 & 0 & \dots & 0 \\ 0 & G^2(t) & 0 & \ddots & \vdots \\ \vdots & 0 & \ddots & 0 & 0 \\ 0 & \dots & 0 & G^{q-1}(t) & 0 \end{pmatrix}$$

and

$$\begin{aligned}
 F^i(t) &= P^{1,1}(t) f^i(t) & i = 1, \dots, q \\
 G^i(t) &= P^i(t) s^{i-1}(t) & i = 2, \dots, q
 \end{aligned}$$

3. ALL RATES INDEPENDENT ON THE TIME OF RESIDENCE

In this section, we will suppose that the migration, survival and fertility rates depend only on the spatial patch and the age of the individuals (i.e.: $f_i^{a,b}(t) = f_i^a(t)$, $S_i^{a,b}(t) = S_i^a(t)$, $p_i^{a,b}(t) = p_i^a(t)$ $a = 1, \dots, q$, $b = 1, \dots, a$, $i = 1, 2$, $t = 1, 2, \dots$). Under these conditions, the model is similar to classical models for which we may refer for example to [17, 18].

We denote by

$$y_{t,i}^a = \sum_{b=1}^a X_{t,i}^{a,b} \qquad i = 1, 2$$

then; for $i = 1, 2$

$$\begin{aligned}
 y_{t+1,i}^1 &= X_{t+1,i}^{1,1} \\
 &= \sum_{j=1}^2 \sum_{a=1}^q \sum_{b=1}^a p_{ij}^1(t) f_j^a(t) X_{t,j}^{a,b} \\
 &= \sum_{j=1}^2 p_{ij}^1(t) \sum_{a=1}^q f_j^a(t) \sum_{b=1}^a X_{t,j}^{a,b} \\
 &= \sum_{j=1}^2 p_{ij}^1(t) \sum_{a=1}^q f_j^a(t) y_{t,j}^a
 \end{aligned}$$

for $a = 1, \dots, q - 1$

$$\begin{aligned}
 y_{t+1,i}^{a+1} &= \sum_{b=1}^{a+1} X_{t+1,i}^{a+1,b} \\
 &= X_{t+1,i}^{a+1,1} + \sum_{b=1}^a X_{t+1,i}^{a+1,b+1} \\
 &= \sum_{\substack{j=1 \\ j \neq i}}^2 p_{ij}^{a+1}(t) \sum_{b=1}^a S_j^a(t) X_{t,j}^{a,b} + \sum_{b=1}^a p_{ii}^{a+1}(t) S_i^a(t) X_{t,i}^{a,b} \\
 &= \sum_{\substack{j=1 \\ j \neq i}}^2 p_{ij}^{a+1}(t) S_j^a(t) \sum_{b=1}^a X_{t,j}^{a,b} + p_{ii}^{a+1}(t) S_i^a(t) \sum_{b=1}^a X_{t,i}^{a,b} \\
 &= \sum_{j=1}^2 p_{ij}^{a+1}(t) S_j^a(t) y_{t,j}^a
 \end{aligned}$$

For $a = 1, \dots, q$ we define

$$\begin{aligned}
 P_a(t) &= \begin{pmatrix} p_{11}^a(t) & p_{12}^a(t) \\ p_{21}^a(t) & p_{22}^a(t) \end{pmatrix} \\
 S_a(t) &= \text{diag}(S_1^a(t), S_2^a(t)) \\
 F_a(t) &= \text{diag}(f_1^a(t), f_2^a(t)) \\
 y_t^a &= (y_{t,1}^a, y_{t,2}^a)^T \\
 y_t &= (y_t^1, y_t^2, \dots, y_t^q)^T
 \end{aligned}$$

the matrix characterizing the migration is

$$D(t) = \begin{pmatrix} P_1(t) & 0 & 0 & \dots & 0 \\ 0 & P_2(t) & 0 & \ddots & \vdots \\ 0 & 0 & P_3(t) & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & 0 & \dots & 0 & P_q(t) \end{pmatrix}$$

and the demography for the whole population is modeled for each interval $[t, t + 1[$ by the following generalized Leslie matrix

$$G(t) = \begin{pmatrix} F_1(t) & F_2(t) & F_3(t) & \cdots & F_q(t) \\ S_1(t) & 0 & 0 & \cdots & 0 \\ 0 & S_2(t) & 0 & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & S_{q-1}(t) & 0 \end{pmatrix}$$

The general system consists of the following system of $2q$ difference equations

$$y_{t+1} = D(t)G(t)y_t$$

Thus, when assuming that the matrix does not depend on the time of residence, one can aggregate the state vector in such a way that only the age-structure remains. This is, indeed, the most usual type of model that can be encountered in the literature.

4. CYCLICALLY VARYING ENVIRONMENT

In this section, we study the system proposed in the case of cyclical varying environment, that is, in the case where we have matrices $P(t)$ and $M(t)$ verifying $P(t+\tau) = P(t)$ and $M(t+\tau) = M(t)$ for all t where τ is the periodic of cyclical variation.

4.1. The General Approach. The literature offers several techniques for the study of discrete models

$$(4.1) \quad z_{t+1} = A_t z_t.$$

with cyclical variability, the classical approach [20] which is to study the system at times separated by τ units considering products of matrices of length τ .

From Skellam [20], for each $s \in \{0, 1, \dots, \tau - 1\}$ and all $m = 1, 2, \dots$ we have from system 2

$$(4.2) \quad z_{s+(m+1)\tau} = A_{s+\tau-1} \cdots A_{s+1} A_s z_{s+m\tau}$$

and, if we define $B_s = A_{s+\tau-1} \cdots A_{s+1} A_s$, is

$$(4.3) \quad z_{s+(m+1)\tau} = B_s z_{s+m\tau}$$

so we can study the population at times $s, s + \tau, s + 2\tau \dots$ considering matrix B_s , which is independent of m , making use of the time invariant theory. therefore, if we assume B_s has strictly dominant eigenvalue μ_s , then μ_s gives the asymptotic growth rate per τ time steps of the population (and so $(\mu_s)^{\frac{1}{\tau}}$ is the asymptotic growth rate per time step). For this analysis to be consistent, it must be μ_s (and the rest of the eigenvalues of B_s) independent of the

observation points, that is, $\mu_0 = \dots = \mu_{\tau-1} = \mu$ independent of s . Concerning the stable population vectors, if w_s is a probability normed eigenvector of B_s associated to μ the population at times $s + m\tau$ is asymptotically given by w_s . then for any s' (let say $s' > s$) $w_{s'} = A_{s'-1} \dots A_{s+1} A_s w_s$ is eigenvector of $B_{s'}$ associad to μ and consequently, the population at time $s' + m\tau$ asymptotically has the direction of $w_{s'}$. Notice that it is $w_{s+\tau} = \mu w_s$ so we have that the population structure is asymptotically cyclic with a period not greader than τ .

It is important to take into account that even though B_0, B_1, \dots, B_{s-1} have the same eigenvalues including multiplicities, the irreducibility or the primitivity of one of the B_s does not imply the irreducibility or primitivity of the rest.

As a result of the above discussions we can study system (3) without loss of generality by just choosing $s \in \{0, 1, \dots, \tau - 1\}$ (for example $s = 0$) and then dealing with system (4).

4.2. Cyclically varying demography and migration. We will now apply the above technique to treat our system constructed in the last section for the case of a cyclically varing environment.

We have then as an starting assumption:

H1: Matrices $P(t)$ and $M(t)$ are periodic with period τ .

In the first place we will set out the equations that govern these systems taking as time step that corresponding to a cycle.

Let us consider $s = 0$ (for any other s the treatment would be absolutely analogous).

The system (1) can be put in the form:

$$X_{(m+1)\tau} = CX_{m\tau}$$

Where C is given by

$$(4.4) \quad C = P_{\tau-1}M_{\tau-1} \dots P_1M_1P_0M_0$$

$$C = L_{\tau-1} \dots L_1L_0$$

where

$$(4.5) \quad P_t = P(t) , \quad M_t = M(t) \text{ and } L_t = P_t M_t \text{ for all } t = 0, 1, 2, \dots$$

The purpose for this construction is to chacterize the asymptotic behavior of the system 1 at times multiple of τ (i.e., at times of the form $m\tau$ with m asymptotically large).

For our study we make the following assymption:

H2: C has a simple and strictly dominant eigenvalues μ (necessarily positive), with associated right and left eigenvectors v and w , respectively.

Recall that the incidence matrix of a non-negative matrix A is a matrix $F(A)$ of the same dimensions as A given by [20]

$$F(A)_{ij} = \begin{cases} 1 & \text{if } A_{ij} > 0 \\ 0 & \text{if } A_{ij} = 0 \end{cases}$$

Two non-negative matrices A and B of the same dimensions are then said to have the same incidence matrix (and we will denote it $A \sim B$) when both matrices have their non-zero elements in corresponding positions. The properties of irreducibility, reducibility, primitivity, etc., of a non-negative matrix A are functions only of the incidence matrix of A and not of the actual values of its non-zero elements.

Of course, a sufficient condition for C to meet H2 is that C is primitive. In the frequent case that all P_t and all M_t have the same incidence matrix (i.e., $P_t \sim P_{t'}$ and $M_t \sim M_{t'}$ for all t and t'), a necessary and sufficient condition for C to be primitive is then any $P_t M_t$ is primitive.

Then, if the system (1) has a non-negative initial condition X_0 , its asymptotic behavior at times multiple of τ will be given by

$$\lim_{m \rightarrow \infty} \frac{X_{m\tau}}{\mu^m} = \lim_{m \rightarrow \infty} \left(\frac{C}{\mu} \right)^m X_0 = \frac{\langle w, X_0 \rangle}{\langle w, v \rangle} v$$

Where v and w are respectively, right and left eigenvectors of C associated to dominant eigenvalues μ .

For simplicity we make the following assumptions that, as it is immediate to check, will be sufficient conditions for H2 to hold:

1) The incidence matrix for the demography and the migration is constant through time, i.e., $M_t \sim M_{t'}$, $P_t \sim P_{t'}$ for all t and t' . Therefore, if a vital rate is non-zero initially it remains non-zero subsequently.

2) There is at least a non-zero coefficient in the last age class, that is $F_q(t) \neq 0$ for all t and, besides, there exists j such that $\text{g.c.d.}(j, q) = 1$ and there is at least a non-zero fertility coefficient in age class j ($F_j(t) \neq 0$ for all t).

3) For all age classes there is at least a non-zero survival coefficient, i.e., $S_i(t) \neq 0$ for all $i = 1, \dots, q-1$ and all t .

Thus, the results developed in this section are valid for our age and patch structured model. therefore, the model will have an asymptotic cyclical behavior with periode τ . Then the asymptotic growth rate for a cyclic in the model is μ and that the population structure at times $m\tau$ (with m large) is given by the direction of vector v .

5. STABILIZING ENVIRONMENT

This section deals with the treatment of the systems (1) in the case which the environment has a temporal variation that tends to stabilization.

We have then as a starting assumption that P_t and M_t evolve in the way that there exist matrices P and M such that

$$\lim_{t \rightarrow \infty} P_t = P ; \lim_{t \rightarrow \infty} M_t = M$$

Obviously, matrices P and M would represent the migration and demography matrices in the stabilized environment, that is, for asymptotically large time.

5.1. The general approach. Let us consider a general system of the kind

$$(5.1) \quad z_{t+1} = A_t z_t.$$

where $z_t \in R^N$, ($t = 0, 1, 2, \dots$) and $A_t \in R^{N \times N}$ is a sequence of non-negative (not necessarily converging) $N \times N$ matrices. if $z_p \neq 0$ is the population vector at time $p \geq 0$, we obviously have for all $t \geq p$, $z_t = A_{t-1} \dots A_{p+1} A_p z_p$, and, therefore, in order to study the asymptotic behavior of (8) we have to deal with infinite backwards products of non-negative matrices,

Let us denote by $\|*\|$ the l_1 norm in R^N , that is, if $z = (z_1, z_2, \dots, z_N)^T$ we have $\|z\| = \sum_{i=1}^N |z^i|$. Then the total population of system (8) at time t is $\|z_t\|$ and the population structure at time t will be given by $\frac{z_t}{\|z_t\|}$.

Let us define a mesure of asymptotic growth rate for system (8). in the time invariant case with constant matrix A (where we suppose that A is primitive) we use as mesure of growth rate the dominant eigenvalue λ of A , since we have for that for any non-zero initial condition z_0 is $\lim_{t \rightarrow \infty} \frac{\|z_{t+1}\|}{\|z_t\|} = \lim_{t \rightarrow \infty} \|z_t\|^{\frac{1}{t}} = \lambda$. Similarly, in the time varing case we might wonder whether there exists a positive number μ such that for all $z_0 \neq 0$ is $\lim_{t \rightarrow \infty} \|z_t\|^{\frac{1}{t}} = \mu$ and then define the asymptotic growth rate as μ .

Another interesting situation appears when the environment tends to stabilization, i.e. there exists a matrix A which represents the environment at equilibrium, such that $\lim_{t \rightarrow \infty} A_t = A$. in that case it can be shown that under some very general conditions, the system behaves asymptotically as if the environment were constant and defined by matrix A . In particular, the population grows asymptotically in an exponential fashion and the population structure converges to a certain vector which is independent of initial condition, i.e. for all $z(0) \neq 0$, $z(0) \geq 0$, it follows $\lim_{t \rightarrow \infty} \frac{z_t}{\|z_t\|} = v$ for certain v . Moreover, we could think that (8) might asymptotically behave as the following system

$$(5.2) \quad z_{t+1} = A z_t$$

i.e., (8) would asymptotically behave as if the environment were constant and equal to the equilibrium environment and so we could ignore the deviations from this equilibrium. In that case, if we suppose that A is primitive with dominant eigenvalue λ and probability normed associated eigenvector v , system (8) would have, for any non-zero population vector at time p an asymptotic growth rate and population structure given by λ and v respectively.

Notice that besides convergence, some restrictions on A_t are easily seen to be necessary for the above results to hold. Indeed, if sequence A_t were such that at some time t_0 the population vector became zeros, it would remain to be zero for all subsequent times, not being therefore independent of the sequence A_t .

As a matter of fact, we shall show that if sequence A_t is such that,

- a) independently of the initial time p and the initial condition z_p , the population vector can never become zero and
- b) matrix A is primitive.

Then all of the above conjectures are true.

The property by which the structure of solutions of (8) tend to approach a constant vector independently of the initial time and the (non-zero) initial condition, is referred to as strong ergodicity.

The study of asymptotic growth rates in variable environments has been addressed to by many authors in the context of stochastic environments (see for example [23]). The case of deterministic varying environments has been investigated by Artzrouni (see [1]) for age structured populations and not necessarily converging vital rates.

Let us introduce some concepts that will be useful to deal with strong ergodicity. A non-negative matrix A is said to be column-allowable (row-allowable) if it has at least a non-zero element in each one of its columns (rows) [20]. Notice that an irreducible matrix is both row and column allowable. It is easy to verify the validity of the following propositions:

- a) A is column -allowable if and only if for all non-negative $x \neq 0$ is $Ax \neq 0$.
- b) for all $p \geq 0$ and all $t \geq p$ is $A_t \dots A_{p+1}A_p$ column -allowable if and only if for all $t \geq 0$ is A_t column allowable.

These propositions can be interpreted in the following way. It is a necessary and sufficient condition for the population of (8) to be always different from zero (independently of the initial time p and the non-zero population vector z_p at time p) that all the matrices A_t be column- allowable. Therefore, in the following we restrict our attention to sequences of environmental conditions represented by column -allowable matrices.

We are ready to introduce in the next theorem the two main results that characterize the asymptotic behavior of (8). The first is due to Seneta (1981)[20] and deals with the strong ergodicity of (8), while the second, which follows as a corollary of the first, characterizes the asymptotic growth rate of (8).

Theorem 1. [20] *let A_n $n \geq 0$ be a sequence of $N \times N$ non-negative and column-allowable matrices that converge to a primitive matrix A with dominant eigenvalue λ and associated probability normed eigenvector v . then for all $p \neq 0$ and all $z_p \neq 0$ is $\|z_n\| \neq 0$ and*

$$\lim_{t \rightarrow \infty} \frac{z_t}{\|z_t\|} = \frac{A_t \cdots A_{p+1} A_p z_p}{\|A_t \cdots A_{p+1} A_p X_p\|} = v$$

$$\lim_{t \rightarrow \infty} \frac{\|z_{t+1}\|}{\|z_t\|} = \lim_{n \rightarrow \infty} \|z_t\|^{\frac{1}{n}} = \lim_{t \rightarrow \infty} \frac{\|A_{t+1} A_t \cdots A_{p+1} A_p z_p\|}{\|A_t \cdots A_{p+1} A_p z_p\|} = \lambda$$

Proof. see [20]. ■

5.2. Stabilizing demography and migration. In the remaining of this section we study the property of strong ergodicity and the asymptotic growth rate for the systems (1) defined in the preceding sections.

Our general assumptions for this section are:

H2. For each $i = 1, \dots, q$, the sequence of matrices $M(t)$ corresponding to the demography converge to a certain matrix M .

H3. For each $i = 1, \dots, q$, the sequence of matrices $P_i(t)$ corresponding to the migration of group i converges to a stochastic matrix P_i .

The above results guarantee that the sequence of matrices $L(t)$ converges to matrix L , which obviously can be interpreted as the matrix that describes the system for the stabilized environment.

We now introduce two hypothesis that will guarantee that the system meets the conditions of theorem 1 and is therefore strongly ergodic.

H4. matrix L is primitive. let λ be the (algebraically simple) dominant eigenvalue of L and let v be the probability normed right eigenvector associated to λ .

H5. For all t , $L(t)$ is column-allowable. We have that this condition is equivalent to the following one: For each t , the transition from any group j to at least another group (possibly also group j), recall that H5 assures population never becomes zero if it is not initially zero.

It is easy to check that sufficient conditions for H4-H5 to be verified are:

H6. For all times, and also in the limit, the internal survival coefficients for all patches and all ages and all time spent are non-zero, i.e., $S_i^{a,b}(t) \neq 0$ and $S_i^{a,b} \neq 0$ for all t, a, b, i, j .

H7. For all times, and also in the limit, the internal survival coefficients for all patches for the last age group are non-zero, i.e., $f_i^{a,b}(t) \neq 0$ and $f_i^{a,b} \neq 0$ for all t, a, b, i, j .

H6. Asymptotically there exists at least a non-zero fertility coefficient for an age i (i.e., $F_i \neq 0$) such that $g.c.d(i, q) = 1$.

The above assumption guarantee that all the results developed in this section are valid for our demography-migration model. Then, independently of the initial time $p \geq 0$ where we consider our biological system starting to evolve and independently of the the non-zero initial population vector $X(p)$, the asymptotic behavior of the system is given by the following proposition.

Proposition 2. [20] *let suppose hypothesis H1 to H6, then for each non-zero condition X_p at time p , we have for the system (1)*

$$\lim_{t \rightarrow \infty} \frac{X_t}{\|X_t\|} = v$$

$$\lim_{t \rightarrow \infty} \frac{\|X_{n+1}\|}{\|X_n\|} = \lim_{t \rightarrow \infty} \|X_t\|^{\frac{1}{t}} = \lambda$$

where λ is the (algebraically simple) dominant eigenvalue of L and v is the probability normed right eigenvector associated to λ

6. CONCLUSION

In this paper we extend our model in time discrete linear models to the case of time varying environment, much of the theory of time-varying matrix models is relatively new. The models presented here is a time varying system, in the case of cyclical and stabilizing temporal variation explored, it only takes into consideration the time of residence in a given area. Under some general conditions, it has been shown that the population verifies the ergodic property: all class tend to represent a strictly positive fixed fraction of the total population.

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