Stochastic matrix metapopulation models with fast migration: Re-scaling survival to the fast scale

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A B S T R A C T

In this work we address the analysis of discrete-time models of structured metapopulations subject to environmental stochasticity. Previous works on these models made use of the fact that migrations between the patches can be considered fast with respect to demography (maturation, survival, reproduction) in the population. It was assumed that, within each time step of the model, there are many fast migration steps followed by one slow demographic event. This assumption allowed one to apply approximate reduction techniques that eased the model analysis. It is however a questionable issue in some cases since, in particular, individuals can die at any moment of the time step. We propose new non-equivalent models in which we re-scale survival to consider its effect on the fast scale. We propose a more general formulation of the approximate reduction techniques so that they also apply to the proposed new models. We prove that the main asymptotic elements in this kind of stochastic models, the Stochastic Growth Rate (SGR)[1] and the Scaled Logarithmic Variance (SLV), can be related between the original and the reduced systems, so that the analysis of the latter allows us to ascertain the population fate in the first. Then we go on to considering some cases where we illustrate the reduction technique and show the differences between both modelling options. In some cases using one option represents exponential growth, whereas the other yields extinction.

1. Introduction

Mathematical models used in ecology, trying to mimic natural systems complexity, are often described by a large number of variables corresponding to various interacting organization levels. The use of reduction and approximation techniques is a common approach in the analysis of the proposed models. Among these techniques we could include the so-called *aggregation of variables* methods (Auger et al., 2008). They are in consonance with the important issue of up-scaling in the framework of ecological hierarchy theory (Lischke et al., 2007).

In this context, we consider stochastic linear discrete systems as population dynamics models. We distinguish time scales to deal with the complexity of these models. Our approach consists in assuming the existence of two different processes acting together at different time scales. Both processes are represented in matrix form, each of them in its associated time scale. We choose as time unit of the common discrete model the characteristic one of the slow process. We suppose that the slow time unit is approximately k times larger than the fast one and, further, that in this large interval the fast process sequentially acts k

times followed by the slow process acting once. Thus, the combined effect of both processes can be described by the product of the slow-process matrix times the k-th power of the fast-process matrix.

The treated models incorporate environmental stochasticity, which refers to unpredictable temporal fluctuations in environmental conditions. A number of different environmental conditions are considered and their variation is characterized by a sequence of random variables corresponding to the different time steps of the discrete system (Tuljapurkar, 1990; Tuljapurkar and Caswell, 1997; Caswell, 2001). Each environment is characterized by its corresponding matrix of vital rates. Given certain hypotheses on the pattern of temporal variation and the vital rates in each environment, the distribution of total population size is asymptotically lognormal, with an expected value and a variance dependent on two parameters. The first one is the *stochastic growth rate* λ_S (SGR), which is the stochastic analogue of the dominant eigenvalue for deterministic systems (we follow Cohen's definition for the SGR (Cohen, 1979) because it allows one to directly compare the stochastic rate of growth with its deterministic analogue, although some authors (Tuljapurkar, 1990; Caswell, 2001) define the SGR as the logarithmic

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[1] Stochastic Growth Rate (SGR). Scaled Logarithmic Variance (SLV).

rate of growth, i.e., $\log\lambda_S$). The second one is the *scaled logarithmic variance* (SLV), which characterizes the asymptotic deviation of the population size from its mean value. The analytical derivation of the SGR and SLV is not feasible in most situations, so it is necessary to resort to computer simulations.

The reduction of two-scale discrete systems for populations subject to environmental stochasticity was introduced in Sanz and Bravo de la Parra (2000), where some results relating the moments of the solutions of original and the reduced systems were provided. In Sanz and Bravo de la Parra (2007) we studied how the SGR of the original system can be approximated by the reduced system SGR for a finite number of environments and a Leslie-type demography. Those results were extended in Alonso and Sanz (2009) to the case of an infinite number of different environmental conditions and the relationship between the SLV of the original and the reduced systems was established.

In this work, we focus on the analysis of discrete-time models of structured metapopulations with environmental stochasticity and two time scales. Its purpose is extending to the stochastic case the study performed in Nguyen-Huu et al. (2011) for deterministic models. In the aforementioned way of separating the slow and the fast process one includes in the former all mechanisms having to do with local demography (maturation, survival, reproduction) and in the fast one the migration between patches. In Nguyen-Huu et al. (2011) it is argued that this way of separating the slow and the fast process might be unrealistic in some ecological situations. Indeed, this approach can be seen as assuming that individuals perform at first a series of k migration events followed by a demographic event in the arrival patch. The assumption sounds realistic for reproduction when discrete models describe populations with separated generations, but not so much for processes like survival, since deaths can happen in any moment of the slow time step. To reflect this point in the model we propose to alternatively include survival in the fast process approximating its effect during the fast time unit, and we refer to it as the *re-scaling* of survival to the fast time scale.

The aim of this work is to adapt the method of re-scaling to the proposed stochastic models and to compare the asymptotic behaviour of the models with and without re-scaled survival. In order to do so, we use the aforementioned reduction techniques, that need to be extended (see Appendix B) so that they also apply to the new model with re-scaled survival.

The re-scaling procedure, described here for survival in the context of structured metapopulations models, might be generalized to a much larger setting. Nevertheless, we consider that it is more accessible to present it in this particular yet still meaningful case.

The structure of the paper is as follows:

In Section 2.1 we present two different metapopulation models for a structured population subject to environmental stochasticity. The migration among the different patches is assumed fast with respect to demography in the first of these models. In the second one, part of demography, survival, is re-scaled to the fast scale. With the help of the results in Appendix B, we propose in Section 2.2 a reduction technique of both models to simplify their analysis and comparison.

The results of Section 2 are applied in Section 3. In Section 3.1 we treat the case of an unstructured population in a multipatch environment where, with the help of the reduction technique, we obtain approximate closed expressions of the parameters defining the long term behaviour of the solutions in both models. In Section 3.2 some results for two classes model are established. Finally, in Section 3.3, with the help of a particular simple case, the relationships between both modeling approaches are discussed.

Following a discussion, two appendices are included. Appendix A briefly introduces the basic form of matrix models with environmental stochasticity and the result on the distribution of population size when the environmental variation is a homogeneous Markov chain. Appendix B includes the presentation of a general reducible linear discrete system with environmental stochasticity, defined by means of sequences of

matrices with limits suitable for reduction, together with the construction of its reduced system and the relationship between their corresponding asymptotic elements.

2. Methods

2.1. Two-scale structured metapopulations models with environmental stochasticity

In this section, we present a stochastic discrete population model whose dynamics is driven by two processes, slow and fast, whose corresponding characteristic time scales are very different from each other. The population is considered structured into q classes and inhabiting an environment divided into r patches. We first assume that the fast process has to do with the movements of the individuals between patches whereas the slow process encompasses all the demographic issues: births, deaths and transitions between classes. In a second step, we will undertake the re-scaling to the fast scale of the death process.

We represent the state of the population at time t by vector

$$\boldsymbol{x}(t) := (\boldsymbol{x}^1(t), ..., \boldsymbol{x}^q(t))^{\mathrm{T}} \in \mathbb{R}_+^{\mathrm{qr}},$$

where $\boldsymbol{x}^i(t) := (x^{i1}(t), ..., x^{ir}(t)) \in \mathbb{R}_+^r$ and $x^{i\alpha}(t)$ denotes the population density of class i in patch α.

We choose as the projection interval of our model the one corresponding to the slow dynamics, i.e., the time elapsed between times t and $t + 1$, and we denote it by Δ_t.

We assume that the population can be subject to n different environmental conditions that we consider indexed by the set $\mathcal{I} = \{1, ..., n\}$. The environmental variation is characterized by a sequence of random variables τ_t, $t = 0, a, b, ..$. defined on a certain probability space $(\Omega, \mathcal{F}, p)$ (Billingsley, 2012) over the state space $\mathcal{I}$. For each realization $\omega \in \Omega$ of the process, the population is subject to environmental conditions $\tau_{t+1}(\omega)$ between times t and $t + 1$.

For each environment $\eta \in \mathcal{I}$, the slow process is defined by a nonnegative projection matrix $\mathbf{D}_\eta = [\boldsymbol{D}_\eta^{\mathrm{ij}}]_{1 \leq i,j \leq q} \in \mathbb{R}_+^{\mathrm{qr} \times \mathrm{qr}}$, divided into blocks $\boldsymbol{D}_\eta^{\mathrm{ij}} = \mathrm{diag}(d_\eta^{\mathrm{ij},\alpha})_{\alpha = 1, ..., r} \in \mathbb{R}_+^{r \times r}$, where $d_\eta^{\mathrm{ij},\alpha}$ represents the rate of individual's transition from class j to class i in patch α during the slow time interval in environment $\eta \in \mathcal{I}$.

Note that, for each environment η, matrix $[d_\eta^{\mathrm{ij},\alpha}]_{1 \leq i,j \leq q} \in \mathbb{R}_+^{q \times q}$ represents demography in patch α. This matrix does not appear as such in our formulation due to the chosen ordering of the state variables.

Concerning the fast process, let $p_\eta^{i,\alpha\beta}$ represent the rate of migration from patch β to patch α for individuals of class i. Therefore $\boldsymbol{P}_\eta^i = [p_\eta^{i,\alpha\beta}]_{1 \leq \alpha,\beta \leq r} \in \mathbb{R}_+^{r \times r}$ is a column-stochastic matrix that we assume primitive, meaning the ability of individuals initially present in every patch to eventually reach any other patch. Finally, the matrix representing the fast process for the whole population and each η is $\mathbf{P}_\eta = \mathrm{diag}(\boldsymbol{P}_\eta^i)_{i=1, ..., q} \in \mathbb{R}_+^{\mathrm{qr} \times \mathrm{qr}}$

We now introduce the first way of modeling the fast-slow system. Since the time step of the complete model is the one corresponding to the slow dynamics, we need to approximate the effect of the fast process over this time interval. In order to do so, we assume that the fast process acts k times before the slow process does, where k might take a large value. Let τ_{t+1} be the environmental process that selects the environment to which the population is subjected during interval Δ_t. Then, the complete system reads as follows

$$\boldsymbol{x}_k(t + 1) = \mathbf{D}_{\tau_{t+1}}(\mathbf{P}_{\tau_{t+1}})^k \boldsymbol{x}_k(t), \tag{1}$$

where $(\mathbf{A})^k$ denotes the k-power of matrix $\mathbf{A}$.

Model (1) can be interpreted as making individuals first perform a series of k dispersal events followed by the demographic process that occurs in the patch of arrival. This assumption might be realistic in some aspects, such as reproduction, because discrete models are mainly used for species having offspring once every time unit. However, the situation is different in the case of mortality since individuals may die at any time.

Therefore, we propose next a new version of model (1) in which mortality acts at the fast time scale, and we call this re-scaling of survival to the fast time scale.

Let $s_\eta^{j,\alpha} > 0$ be the survival rate of class j in patch α and environment η. First, we factor every demographic coefficient in order to make $s_\eta^{j,\alpha}$ appear explicitly, i.e., we define $\tilde{d}_\eta^{ij,\alpha}$ through

$$d_\eta^{ij,\alpha} = \tilde{d}_\eta^{ij,\alpha} s_\eta^{j,\alpha}.$$

Defining $\tilde{\boldsymbol{D}}_\eta^{ij} = \mathrm{diag}(\tilde{d}_\eta^{ij,\alpha})_{\alpha=1,\dots,r}$ and $\boldsymbol{S}_\eta^j = \mathrm{diag}(s_\eta^{j,\alpha})_{\alpha=1,\dots,r}$ we have

$$\boldsymbol{D}_\eta^{ij} = \tilde{\boldsymbol{D}}_\eta^{ij} \boldsymbol{S}_\eta^j.$$

Similarly, denoting $\tilde{\boldsymbol{D}}_\eta = [\tilde{\boldsymbol{D}}_\eta^{ij}]_{1 \le i,j \le q}$ and $\mathbf{S}_\eta = \mathrm{diag}(\boldsymbol{S}_\eta^j)_{j=1,\dots,q}$ we have

$$\mathbf{D}_\eta = \tilde{\mathbf{D}}_\eta \mathbf{S}_\eta.$$

Now, we make power k appear explicitly in the survival rates by defining matrices $\boldsymbol{S}_{k,\eta}^j = \mathrm{diag}((s_\eta^{j,\alpha})^{1/k})_{\alpha=1,\dots,r}$, and $\mathbf{S}_{k,\eta} = \mathrm{diag}(\boldsymbol{S}_{k,\eta}^j)_{j=1,\dots,q}$, that verify $(\boldsymbol{S}_{k,\eta}^j)^k = \boldsymbol{S}_\eta^j$ and $(\mathbf{S}_{k,\eta})^k = \mathbf{S}_\eta$.

Finally we obtain the following expression for matrix $\mathbf{D}_\eta$

$$\mathbf{D}_\eta = \tilde{\mathbf{D}}_\eta (\mathbf{S}_{k,\eta})^k.$$

This expression suggests the next complete model, not equivalent to model (1), in which it is considered that mortality acts as the fast time scale:

$$\tilde{\boldsymbol{x}}_k(t + 1) = \tilde{\mathbf{D}}_{\tau_{t+1}}(\mathbf{S}_{k,\tau_{t+1}} \mathbf{P}_{\tau_{t+1}})^k \tilde{\boldsymbol{x}}_k(t). \tag{2}$$

This model can be interpreted as follows: individuals first perform a series of k dispersal events in which in each of them we consider mortality by taking into account the survival rate in the patch of arrival. This is followed by the rest of the demographic process, that occurs at the slow time scale.

2.2. Reduction of systems (1) and (2)

Following Appendix B, for system (1) we can take

$$\boldsymbol{H}_{k,\eta} = \mathbf{D}_\eta (\mathbf{P}_\eta)^k,$$

and now we must express its limit when k tends to infinity in the appropriate form so that Hypotheses 1 and 2 are met.

The fact that matrix $\boldsymbol{P}_\eta^i$ is column-stochastic and primitive implies that 1 is its dominant eigenvalue, the row vector $\bar{\boldsymbol{I}} = (1, \dots, 1) \in \mathbb{R}^r$ is an associated left eigenvector and there exists a unique positive right eigenvector $\boldsymbol{v}_\eta^i \in \mathbb{R}^r$ such that $\bar{\boldsymbol{I}} \boldsymbol{v}_\eta^i = 1$. The Perron–Frobenius theorem yields that

$$\lim_{k \to \infty} (\boldsymbol{P}_\eta^i)^k = \boldsymbol{v}_\eta^i \bar{\boldsymbol{I}}.$$

Calling $\mathbf{V}_\eta := \mathrm{diag}(\boldsymbol{v}_\eta^i)_{i=1,\dots,q} \in \mathbb{R}_+^{qr \times q}$ and $\mathbf{G} := \mathrm{diag}(\bar{\boldsymbol{I}})_{i=1,\dots,q} \in \mathbb{R}_+^{q \times qr}$, we have that

$$\lim_{k \to \infty} (\mathbf{P}_\eta)^k = \mathbf{V}_\eta \mathbf{G} \quad \text{and so} \quad \lim_{k \to \infty} \mathbf{D}_\eta (\mathbf{P}_\eta)^k = \mathbf{D}_\eta \mathbf{V}_\eta \mathbf{G}.$$

Thus, matrix $\mathbf{D}_\eta \mathbf{V}_\eta$ plays the role of matrix $\boldsymbol{D}_\eta$ in (23). We can now write the reduced system (27) for the global variables $\boldsymbol{y}(t) = \mathbf{G}\boldsymbol{x}(t)$, the total number of individuals in each class associated to system (1), in the following form:

$$\boldsymbol{y}(t + 1) = \mathbf{G} \mathbf{D}_{\tau_{t+1}} \mathbf{V}_{\tau_{t+1}} \boldsymbol{y}(t) = \hat{\boldsymbol{H}}_{\tau_{t+1}} \boldsymbol{y}(t). \tag{3}$$

Let us now proceed to the reduction of system (2), for which we have, still following Appendix B,

$$\boldsymbol{H}_{k,\eta} = \tilde{\mathbf{D}}_\eta (\mathbf{S}_{k,\eta} \mathbf{P}_\eta)^k.$$

To show that Hypotheses 1 and 2 also hold for system (2), we use Theorem A.1. in Nguyen-Huu et al. (2011) to express in a suitable form the limit of matrix $\boldsymbol{H}_{k,\eta}$ when k tends to infinity. For every $i = 1, \dots, q$ and $\eta \in \mathcal{I}$, let $\boldsymbol{w}_\eta^i = (\log(s_\eta^{i,1}), \dots, \log(s_\eta^{i,r})) \in \mathbb{R}^r$ be a row vector and

define the scalar $\gamma_\eta^i = \exp(\boldsymbol{w}_\eta^i \boldsymbol{v}_\eta^i)$ then, (Nguyen-Huu et al., 2011),

$$\lim_{k \to \infty} (\boldsymbol{S}_{k,\eta} \boldsymbol{P}_\eta^i)^k = \gamma_\eta^i \boldsymbol{v}_\eta^i \bar{\boldsymbol{I}}.$$

Calling $\tilde{\mathbf{V}}_\eta := \mathrm{diag}(\gamma_\eta^i \boldsymbol{v}_\eta^i)_{i=1,\dots,q}$ it follows that

$$\lim_{k \to \infty} \tilde{\mathbf{D}}_\eta (\mathbf{S}_{k,\eta} \mathbf{P}_\eta)^k = \tilde{\mathbf{D}}_\eta \tilde{\mathbf{V}}_\eta \mathbf{G},$$

and, therefore, the reduced system (27) associated to system (2) for the same global variables $\tilde{\boldsymbol{y}}(t) = \mathbf{G}\tilde{\boldsymbol{x}}(t)$, is

$$\tilde{\boldsymbol{y}}(t + 1) = \mathbf{G} \tilde{\mathbf{D}}_{\tau_{t+1}} \tilde{\mathbf{V}}_{\tau_{t+1}} \tilde{\boldsymbol{y}}(t) = \tilde{\boldsymbol{H}}_{\tau_{t+1}} \tilde{\boldsymbol{y}}(t). \tag{4}$$

The interest of the proposed reduction method is that it is possible to obtain asymptotic results for systems (1) and (2) through the analysis of the reduced systems (3) and (4).

We need to impose some conditions so that the systems involved have indeed good asymptotic properties. Theorem Appendix 1 in A presents sufficient hypotheses so that the total population size of a matrix model with environmental stochasticity is asymptotically lognormal and describable in terms of a couple of constants, the stochastic growth rate (SGR) and the scaled logarithmic variance (SLV). In Appendix B the reduction of matrix models with environmental stochasticity is presented in a general setting. In particular, it is proved that under suitable hypotheses for both the complete and the reduced systems, the total population size is asymptotically lognormal. Moreover, the SGR and the SLV of the complete system can be approximated by those corresponding to the reduced system.

Assume that the following two conditions are met:

- The environmental variation τ_t is a homogeneous irreducible and aperiodic Markov chain, i.e., its matrix of transition probabilities is primitive. We denote its (unique and positive) stationary probability distribution by $\pi = (\pi_1, \dots, \pi_n)$.
- The sets $\{\hat{\boldsymbol{H}}_1, \dots, \hat{\boldsymbol{H}}_n\}$ and $\{\tilde{\boldsymbol{H}}_1, \dots, \tilde{\boldsymbol{H}}_n\}$ are ergodic, i.e., for each of them there exists a positive integer g such that any product of g matrices (with repetitions allowed) drawn from the set is a positive matrix. It is easy to check that for each $\eta \in \mathcal{I}$, the incidence matrix of $\tilde{\boldsymbol{H}}_\eta$ coincides with that of $\hat{\boldsymbol{H}}_\eta$ and, therefore, if one of the previous sets is ergodic so is the other.

Now we apply Proposition 2 and Theorem 3 in Appendix B and obtain that systems (3) and (4), and for k large enough also systems (1) and (2), verify that the total population size is asymptotically lognormal. Moreover, denoting their corresponding SGR and SLV by $\hat{\lambda}_S$, $\tilde{\lambda}_S$, $\hat{\lambda}_{S,k}$, $\tilde{\lambda}_{S,k}$ and $\hat{\sigma}^2$, $\tilde{\sigma}^2$, σ_k^2, $\tilde{\sigma}_k^2$ respectively we have

$$
\begin{aligned}
\lim_{k \to \infty} \lambda_{S,k} &= \hat{\lambda}_S, & \lim_{k \to \infty} \sigma_k &= \hat{\sigma}, \\
\lim_{k \to \infty} \tilde{\lambda}_{S,k} &= \tilde{\lambda}_S, & \lim_{k \to \infty} \tilde{\sigma}_k &= \tilde{\sigma}.
\end{aligned}
\tag{5}
$$

Thus, the lognormal asymptotic distribution for the complete system (1) can be approximated through the constants $\hat{\lambda}_S$ and $\hat{\sigma}$ associated to the reduced system (3). The same happens to system (2) using the constants $\tilde{\lambda}_S$ and $\tilde{\sigma}$ associated to (4). Therefore, in order to establish a comparison between systems (1) and (2), we can compare the SGR and the SLV of their corresponding simpler aggregated systems.

3. Results

In this section we present some results comparing the two modelling options represented by systems (1) and (2). Specifically, we carry out this comparison through their respective SGRs and SLVs.

In most ecological models, the exact derivation of the SGR and the SLV is not feasible. This is due to the fact that there is not an explicit expression for the stationary distribution of the population structure. Therefore, it is necessary to approximate those parameters by computer simulations or appropriate perturbation techniques (Tuljapurkar and Caswell, 1997). The results presented in Section 2.2 justify using the

simpler aggregated systems to carry out these simulations. Moreover, there are particular cases in which our reduction procedure transforms a complex model into a reduced one for which we can obtain the SGR and the SLV exactly.

We proceed to introduce two such cases.

3.1. Unstructured models

We first consider the models of Section 2.1 when $q = 1$, i.e., there is no structure in the population.

We represent the state of the population at time t by vector

$$\boldsymbol{x}(t) := (x^1(t), ..., x^r(t)) \in \mathbb{R}_+^r,$$

where $x^\alpha(t)$ denotes the population density in patch α. For each environment $\eta \in \mathcal{I}$, the slow process is defined by the nonnegative matrix $\mathbf{D}_\eta = \text{diag}(d_\eta^\alpha)_{\alpha=1,...,r}$, where d_η^α, that we assume positive, represents the growth rate of the population in patch α during a slow time interval. Regarding the fast process, we represent migrations between patches under environment η by a column-stochastic primitive matrix $\mathbf{P}_\eta \in \mathbb{R}_+^{r \times r}$. We denote $\boldsymbol{v}_\eta = (v_\eta^1, ..., v_\eta^r)$ the unique (positive) right eigenvector of matrix $\mathbf{P}_\eta$ associated to eigenvalue 1 whose entries sum up to 1.

In this case model (1) reads

$$\boldsymbol{x}_k(t + 1) = \mathbf{D}_{\tau_{t+1}} \left(\mathbf{P}_{\tau_{t+1}} \right)^k \boldsymbol{x}_k(t). \tag{6}$$

Regarding model (2), let $s_\eta^\alpha > 0$ be the survival rate in patch α and environment η. Then we define $\tilde{d}_\eta^\alpha > 0$ through $\tilde{d}_\eta^\alpha = s_\eta^\alpha / d_\eta^\alpha$, and denote $\tilde{\mathbf{D}}_\eta = \text{diag}(\tilde{d}_\eta^\alpha)_{\alpha=1,...,r}$ and $\mathbf{S}_{k,\eta} = \text{diag}((s_\eta^\alpha)^{1/k})_{\alpha=1,...,r}$ to obtain

$$\tilde{\boldsymbol{x}}_k(t + 1) = \tilde{\mathbf{D}}_{\tau_{t+1}} \left(\mathbf{S}_{k,\tau_{t+1}} \mathbf{P}_{\tau_{t+1}} \right)^k \tilde{\boldsymbol{x}}_k(t). \tag{7}$$

In both cases, the reduced system is a scalar system in which the only variable is the total population size.

For system (6) the reduced system is

$$y(t + 1) = \hat{h}_{\tau_{t+1}} y(t), \tag{8}$$

with

$$\hat{h}_\eta = \sum_{\alpha=1}^r v_\eta^\alpha d_\eta^\alpha, \quad \eta \in \mathcal{I}. \tag{9}$$

In the case of system (7), the reduced system becomes

$$\tilde{y}(t + 1) = \tilde{h}_{\tau_{t+1}} \tilde{y}(t), \tag{10}$$

where in this case

$$\tilde{h}_\eta = \exp\left(\sum_{\alpha=1}^r v_\eta^\alpha \log(s_\eta^\alpha) \right) \sum_{\alpha=1}^r v_\eta^\alpha \tilde{d}_\eta^\alpha, \quad \eta \in \mathcal{I}. \tag{11}$$

Since (8) and (10) are scalar, we are able to find analytical expressions for their SGRs, $\hat{\lambda}_S$ and $\tilde{\lambda}_S$, and their SLVs, $\hat{\sigma}^2$ and $\tilde{\sigma}^2$.

We recall that we assume condition C1, and so the Markov chain τ_t has a stationary probability distribution $\pi = (\pi_1, \pi_2, ..., \pi_n)$. Since the d_η^α and the $\tilde{d}_\eta^\alpha$ are positive and so are vectors $\boldsymbol{v}_\eta$, then the $\hat{h}_\eta$ and $\tilde{h}_\eta$ are also positive and as a consequence the sets $\{\hat{h}_1, ..., \hat{h}_n\}$ and $\{\tilde{h}_1, ..., \tilde{h}_n\}$ are ergodic, so Condition C2 holds. Thus, for large enough k all four systems (6), (7), (8) and (10) meet the sufficient hypotheses for the existence of an asymptotic lognormal distribution for population size.

Using (21) we can obtain explicitly the SGR and the SLV that characterize the asymptotic distribution for systems (8) and (10), the reason being that in these cases the normalized population $y(t)/||y(t)||$ is trivial (equal to 1 with probability one), and so the stationary distribution of the chain $(\tau_t, y(t)/||y(t)||)$ is simply that of τ_t. Then it is immediate to obtain that

$$\log \hat{\lambda}_S = \sum_{\eta=1}^n \pi_\eta \log \hat{h}_\eta = \sum_{\eta=1}^n \pi_\eta \log\left(\sum_{\alpha=1}^r v_\eta^\alpha d_\eta^\alpha \right), \log \tilde{\lambda}_S = \sum_{\eta=1}^n \pi_\eta \log \tilde{h}_\eta$$

$$= \sum_{\eta=1}^n \pi_\eta \left(\sum_{\alpha=1}^r v_\eta^\alpha \log(s_\eta^\alpha) + \log\left(\sum_{\alpha=1}^r v_\eta^\alpha \tilde{d}_\eta^\alpha \right) \right).$$

Regarding the SLV, for the sake of simplicity in the mathematical expressions we will only consider the IID case, i.e., the case with no serial correlation in τ_t (the general expressions can be found in Alonso and Sanz (2009)). In that case it is immediate to conclude that

$$\hat{\sigma}^2 = \sum_{\eta=1}^n \pi_\eta (\log \hat{h}_\eta)^2 - \left(\sum_{\eta=1}^n \pi_\eta \log \hat{h}_\eta \right)^2,$$

$$\tilde{\sigma}^2 = \sum_{\eta=1}^n \pi_\eta (\log \tilde{h}_\eta)^2 - \left(\sum_{\eta=1}^n \pi_\eta \log \tilde{h}_\eta \right)^2.$$

3.2. Two-stage models

We consider a population structured into two stage-specific classes: non-reproductive juveniles (class 1) and reproductive adults (class 2). The demography, which governs the transition between the different classes, is defined by the survival rates of juveniles and adults, the maturation rates of juveniles and the fertility rates of adults.

We represent the state of the population at time t by vector

$$\boldsymbol{x}(t) := (\boldsymbol{x}^1(t), \boldsymbol{x}^2(t))^{\mathrm{T}} \in \mathbb{R}_+^{2r},$$

where $\boldsymbol{x}^i(t) := (x^{i1}(t), ..., x^{ir}(t)) \in \mathbb{R}_+^r$ and $x^{i\alpha}(t)$ denotes the population density of class i in patch α.

Let $\alpha \in \{1, ..., r\}$, $j \in \{1, 2\}$ and $\eta \in \mathcal{I}$. For each patch α and each environment η, let $s_\eta^{j,\alpha}$ be the fraction of individuals of class j alive at time n that survive to time $n + 1$. Also, let m_η^α be the fraction of the surviving juveniles that mature and become adults. Finally, supposing that reproduction happens at the end of each period of time $[t, t + 1)$, let f_η^α be the number of juveniles produced by an adult individual in patch α that has survived to time $t + 1$.

Let us define matrices

$$\boldsymbol{S}_\eta^i := \text{diag}(s_\eta^{i,1}, ..., s_\eta^{i,r}), \quad \boldsymbol{M}_\eta := \text{diag}(m_\eta^1, ..., m_\eta^r), \quad \boldsymbol{F}_\eta := \text{diag}(f_\eta^1, ..., f_\eta^r).$$

Then, the projection matrix $\mathbf{D}_\eta$ corresponding to demography for environment η consistent with the ordering of variables in $\boldsymbol{x}(t)$ is

$$\mathbf{D}_\eta = \begin{pmatrix} \boldsymbol{S}_\eta^1 (\boldsymbol{I} - \boldsymbol{M}_\eta) & \boldsymbol{S}_\eta^2 \boldsymbol{F}_\eta \\ \boldsymbol{S}_\eta^1 \boldsymbol{M}_\eta & \boldsymbol{S}_\eta^2 \end{pmatrix} \in \mathbb{R}^{2r \times 2r}.$$

Regarding the fast process, for each environment η and each class i, we represent migrations between patches by a column-stochastic primitive matrix $\boldsymbol{P}_\eta^i \in \mathbb{R}_+^{r \times r}$. We denote $\boldsymbol{v}_\eta^i = (v_\eta^{i,1}, ..., v_\eta^{i,r})$ the unique positive right eigenvector of matrix $\boldsymbol{P}_\eta^i$ associated to eigenvalue 1 whose entries sum up to 1. The matrix representing migration for the whole population is $\mathbf{P}_\eta = \text{diag}(\boldsymbol{P}_\eta^1, \boldsymbol{P}_\eta^2)$.

Therefore, in this setting model (1) has the form

$$\boldsymbol{x}_k(t + 1) = \mathbf{D}_{\tau_{t+1}} (\mathbf{P}_{\tau_{t+1}})^k \boldsymbol{x}_k(t). \tag{12}$$

Following the procedure outlined in Section 2.2, its corresponding reduced system is

$$\boldsymbol{y}(t + 1) = \hat{\boldsymbol{H}}_{\tau_{t+1}} \boldsymbol{y}(t), \tag{13}$$

where

$$\hat{\boldsymbol{H}}_\eta := \begin{pmatrix} \sum_{\alpha=1}^r s_\eta^{1,\alpha} (1 - m_\eta^\alpha) v_\eta^{1,\alpha} & \sum_{\alpha=1}^r s_\eta^{2,\alpha} \phi_\eta^\alpha v_\eta^{2,\alpha} \\ \sum_{\alpha=1}^r s_\eta^{1,\alpha} m_\eta^\alpha v_\eta^{1,\alpha} & \sum_{\alpha=1}^r s_\eta^{2,\alpha} v_\eta^{2,\alpha} \end{pmatrix} \in \mathbb{R}^{2 \times 2}, \quad \eta \in \mathcal{I}. \tag{14}$$

We now turn our attention to model (2), i.e., the model in the case we re-scale survival to the fast scale. In this case, following the

proposed technique we define

$$\tilde{\mathbf{D}}_\eta := \begin{pmatrix} \mathbf{I} - \mathbf{M}_\eta & \mathbf{F}_\eta \\ \mathbf{M}_\eta & \mathbf{I} \end{pmatrix} \in \mathbb{R}^{2r \times 2r},$$

$$\mathbf{S}^i_{k,\eta} := \text{diag}((s^{i,1}_\eta)^{1/k}, ..., (s^{i,r}_\eta)^{1/k}) \in \mathbb{R}^{r \times r}, \quad \mathbf{S}_{k,\eta} := \text{diag}(\mathbf{S}^1_{k,\eta}, \mathbf{S}^2_{k,\eta}) \in \mathbb{R}^{2r \times 2r},$$

and the resulting system has the form

$$\tilde{x}_k(t+1) = \tilde{\mathbf{D}}_{\tau_{t+1}} (\mathbf{S}_{k,\tau_{t+1}} \mathbf{P}_{\tau_{t+1}})^k \tilde{x}_k(t). \tag{15}$$

To obtain the corresponding reduced system we define $\gamma^i_\eta := \exp(\sum_{\alpha=1}^r v^{i,\alpha}_\eta \log s^{i,\alpha}_\eta)$ and then in this setting system (4) takes the form

$$\tilde{y}(t+1) = \tilde{\mathbf{H}}_{\tau_{t+1}} \tilde{y}(t), \tag{16}$$

where

$$\tilde{\mathbf{H}}_\eta := \begin{pmatrix} \gamma^1_\eta \sum_{\alpha=1}^r (1 - m^\alpha_\eta) v^{1,\alpha}_\eta & \gamma^2_\eta \sum_{\alpha=1}^r \phi^\alpha_\eta v^{2,\alpha}_\eta \\ \gamma^1_\eta \sum_{\alpha=1}^r m^\alpha_\eta v^{1,\alpha}_\eta & \gamma^2_\eta \end{pmatrix} \in \mathbb{R}^{2 \times 2} \,, \, \eta \in \mathcal{I}. \tag{17}$$

The reduced systems (13) and (16) are not scalar and so in general they are not analytically tractable. There are, however, several particular cases in which analytical calculations are possible. Here we focus on one of such cases.

Let us suppose that the parameters that govern demography are independent of the environment (and therefore in the notation we drop subindex η) and that migration rates depend on the environment through a common multiplicative random variable, i.e., different environments increase or decrease all migration rates by the same factor. Specifically, for each $i = 1, 2$ and $\alpha \neq \beta$ we have $p^{i,\alpha\beta}_\eta = \xi^i_\eta t^{i,\alpha\beta}$ where $\xi^i_\eta \in (0, 1]$ and the $t^{i,\alpha\beta} \geq 0$ verify that $\Sigma_{\beta \neq \alpha} t^{i,\alpha\beta} \leq 1$. For $\beta = \alpha$ we have $p^{i,\alpha\alpha}_\eta = 1 - \xi^i_\eta \sum_{\beta \neq \alpha} t^{i,\alpha\beta}$. Then it is easy to check that the eigenvector v^i_η of $\mathbf{P}^i_\eta$ associated to 1 is independent of η, i.e., $v^i_\eta = v^i = (v^{i,1}, ..., v^{i,r})^\top$ for all $\eta \in \mathcal{I}$. So, we have that, although systems (12) and (15) are stochastic, the reduced systems (13) and (16) are deterministic. More specifically we have $\hat{\mathbf{H}}_\eta = \hat{\mathbf{H}}$, $\tilde{\mathbf{H}}_\eta = \tilde{\mathbf{H}}$ where $\hat{\mathbf{H}}$ and $\tilde{\mathbf{H}}$ are given by (14) and (17) by dropping subindex η. Therefore, $\hat{\lambda}_S$ and $\tilde{\lambda}_S$ are, respectively, the dominant eigenvalues of matrices $\hat{\mathbf{H}}$ and $\tilde{\mathbf{H}}$ whereas $\hat{\sigma}^2 = \tilde{\sigma}^2 = 0$.

3.3. Comparison of the two modelling approaches

In this section we use a very simple setting to illustrate the differences between models (1) and (2). Due to the large number of parameters involved in the general case, we restrict our attention to the case of Section 3.1 of a population without structure and, further, we assume a deterministic setting and that the environment is constituted by two patches. We present a first particular case that yields the same growth rates for both systems. Then, a second situation in which the re-scaled system always possesses a smaller growth rate. And, finally, a third case where, depending on parameter values, the growth rate of any of the two systems can be larger than the other. In the latter, we show in particular that using one of the models can predict exponential growth whereas, for the same parameter values, the use of the other predicts extinction.

Following the notation in Section 3.1, let the demographic parameters of the model be $d^1 = \tilde{d}^1 s^1$ and $d^2 = \tilde{d}^2 s^2$ where $\tilde{d}^1$ and $\tilde{d}^2$ denote the fertility coefficients in each patch. The fast process is then represented by matrix

$$\mathbf{P} = \begin{pmatrix} 1 - m_2 & m_1 \\ m_2 & 1 - m_1 \end{pmatrix},$$

where $m_1 \in (0, 1)$ represents the migration rate from patch 2 to patch 1 and $m_2 \in (0, 1)$ the one from patch 1 to patch 2. $\mathbf{P}$ is a primitive stochastic matrix with associated stable probability distribution vector $v = (v^1, v^2) = (m_1/(m_1 + m_2), m_2/(m_1 + m_2))$. In this case model (1)

reads:

$$x_k(t+1) = \begin{pmatrix} \tilde{d}^1 s^1 & 0 \\ 0 & \tilde{d}^2 s^2 \end{pmatrix} \begin{pmatrix} 1 - m_2 & m_1 \\ m_2 & 1 - m_1 \end{pmatrix}^k x_k(t), \tag{18}$$

and model (2)

$$\tilde{x}_k(t+1) = \begin{pmatrix} \tilde{d}^1 & 0 \\ 0 & \tilde{d}^2 \end{pmatrix} \begin{pmatrix} (s^1)^{\frac{1}{k}}(1 - m_2) & (s^1)^{\frac{1}{k}} m_1 \\ (s^2)^{\frac{1}{k}} m_2 & (s^2)^{\frac{1}{k}}(1 - m_1) \end{pmatrix}^k \tilde{x}_k(t). \tag{19}$$

Their corresponding reduced systems are, respectively,

$$y(t+1) = \hat{h} \, y(t) = (v^1 \tilde{d}^1 s^1 + v^2 \tilde{d}^2 s^2) y(t),$$

and

$$\tilde{y}(t+1) = \tilde{h} \, \tilde{y}(t) = (s^1)^{v^1}(s^2)^{v^2}(v^1 \tilde{d}^1 + v^2 \tilde{d}^2) \tilde{y}(t).$$

Thus, we have to compare $\hat{h} = v^1 \tilde{d}^1 s^1 + v^2 \tilde{d}^2 s^2$ and $\tilde{h} = (s^1)^{v^1}(s^2)^{v^2}(v^1 \tilde{d}^1 + v^2 \tilde{d}^2)$.

Case 1: Assuming equal survival rates, $s^1 = s^2$, we have

$$\tilde{h} = s^{v^1} s^{v^2}(v^1 \tilde{d}^1 + v^2 \tilde{d}^2) = s(v^1 \tilde{d}^1 + v^2 \tilde{d}^2) = \hat{h}.$$

There is no difference between the asymptotic growth rates of systems (18) and (19).

Case 2: Assuming equal fertility rates, $\tilde{d}^1 = \tilde{d}^2 = \tilde{d}$ and using the inequality relating the (weighted) arithmetic mean and the (weighted) geometric mean, we obtain

$$\tilde{h} = s^{v^1} s^{v^2}(v^1 \tilde{d} + v^2 \tilde{d}) = s^{v^1} s^{v^2} \tilde{d} \leq (v^1 s^1 + v^2 s^2) \tilde{d} = \hat{h},$$

i.e., the asymptotic growth rate of the re-scaled model (19) is always smaller than the one of system (18).

We would like to stress that the first two cases can be straightforwardly extended to an environment with an arbitrary number of patches.

Case 3: Assuming a uniform distribution of individuals between patches, $v^1 = v^2 = 1/2$, we can find, depending on parameters values, the same results as in cases 1 and 2 and, in addition, the reverse inequality $\hat{h} < \tilde{h}$. The expressions for $\hat{h}$ and $\tilde{h}$ in this particular case are

$$\hat{h} = \frac{1}{2}(\tilde{d}^1 s^1 + \tilde{d}^2 s^2) \quad \text{and} \quad \tilde{h} = \frac{1}{2}\sqrt{s^1 s^2}(\tilde{d}^1 + \tilde{d}^2).$$

Considering $\tilde{d}^1$ and $\tilde{d}^2$ constant, we can write the fraction of the survival rates in both patches, $C := \hat{h}/\tilde{h}$, as a function of variable $\alpha := s^2/s^1 \in (0, \infty)$ in the following way:

$$C(\alpha) = \frac{1}{\sqrt{\alpha}} \frac{\tilde{d}^1}{\tilde{d}^1 + \tilde{d}^2} + \sqrt{\alpha} \frac{\tilde{d}^2}{\tilde{d}^1 + \tilde{d}^2}.$$

An elementary analysis yields that C is decreasing in $(0, \alpha_{min})$ and increasing in (α_{min}, ∞), with $\alpha_{min} = \tilde{d}^1/\tilde{d}^2$ and

$$C(\alpha_{min}) = \frac{\sqrt{\tilde{d}^1 \tilde{d}^2}}{(\tilde{d}^1 + \tilde{d}^2)/2} \leq 1.$$

On the other hand, for $\tilde{d}^1 \neq \tilde{d}^2$, equation $C(\alpha) = 1$ has two roots, $\alpha_1 = 1$ and $\alpha_2 = (\tilde{d}^1/\tilde{d}^2)^2$, one in $(0, \alpha_{min})$ and the other in (α_{min}, ∞).

We can conclude from the above that, if $\tilde{d}^1 < \tilde{d}^2$, then $\hat{h} < \tilde{h}$ for $s^2/s^1 \in ((\tilde{d}^1/\tilde{d}^2)^2, 1)$ and $\hat{h} > \tilde{h}$ for $s^2/s^1 \in (0, (\tilde{d}^1/\tilde{d}^2)^2) \cup (1, \infty)$. An analogous reverse result is obtained in the case $\tilde{d}^1 > \tilde{d}^2$.

An important additional question is whether $\hat{h}$ and $\tilde{h}$ can be one larger than 1 and the other less than 1, since this would mean that one of the models predicts extinction whereas the other predicts exponential growth. The answer is positive. Let us fabricate an example to illustrate this fact. Take, for instance, the previous case with $\tilde{d}^1 < \tilde{d}^2$ and $s^2/s^1 \in ((\tilde{d}^1/\tilde{d}^2)^2, 1)$, what implies $\hat{h} < \tilde{h}$. Now just change parameters $\tilde{d}^1$ and $\tilde{d}^2$ into $2\tilde{d}^1/(\hat{h} + \tilde{h})$ and $2\tilde{d}^2/(\hat{h} + \tilde{h})$. It is immediate to see that the corresponding growth rates, that we call $\hat{h}'$ and $\tilde{h}'$, verify the required condition:

$$\hat{h}' = \frac{2}{\hat{h} + \tilde{h}}\hat{h} < 1 < \frac{2}{\hat{h} + \tilde{h}}\tilde{h} = \tilde{h}'.$$

The previous discussion corresponds to a deterministic setting. If we introduce stochasticity, the number of parameters is highly increased, what renders the model difficult to analyze. However, one can check that the three aforementioned cases still hold.

4. Discussion

We have dealt with the issue of distinguishing time scales in discrete systems to help in their analysis. The setting is, on the one hand, simple because we deal with a linear structured metapopulation model and, on the other hand, complex due to the fact that the model considers environmental stochasticity and admits an arbitrary numbers of individual classes and spatial patches.

When there are two processes acting at different time scales that must be gathered in a single discrete model, it is reasonable to choose the slow time unit to express it. In this way, the action of the fast process can be represented by letting it act a number of times approximately equal to the ratio between the two time scales. It is not easy to establish a criterion to classify processes between those that occur at the slow time scale and those happening at the fast time scale. Indeed, let us consider processes, such as mortality, predation and others, which are often measured at the slow time scale. If they act almost continuously, then it can be argued that they should be better considered as occurring at the fast time scale.

We have analysed the particular case of survival in a linear stochastic structured metapopulation model. First, we have proposed a model in which survival is included in the slow process. In a second step, we have shown how to express its action on a much shorter interval of time by performing a sort of k-th root of their action in a slow time unit. Using this we have proposed a second model, to be compared with the first one, in which survival has been re-scaled to the fast time scale.

The comparison of the two models is done through their SGRs and SLVs, as they are the main parameters describing their asymptotic behaviour. In general, it is not possible to calculate them exactly, and so the available course of action is to estimate them by means of computer simulations or other approximations. The obtained reduction results simplify this task by performing it for the associated reduced models, what is much less costly.

Considering the particular case of unstructured populations, their reduced models are scalar, what allows one to obtain closed expressions for their SGRs and SLVs, that approximate the SGRs and the SLVs of the original models.

In this setting of unstructured populations, we carry out a comparison of the two models and we present cases where the re-scaling of survival makes no difference in the dynamics, other cases where considering survival at the fast scale reduces population growth rate and, finally, some cases where the population growth can be larger in any of the two models depending on parameters values.

5. Conclusion

We have shown the relevance of using time scales when modelling through dynamical systems. This is done in the framework of linear matrix models with environmental stochasticity.

A key point to build an accurate two time scale model is the choice of the time scale that it is associated to each of the processes involved. For a given process, data can be obtained on a certain time scale and, at the same time, they are better included in the model on a different time scale. To deal with this issue, we have considered the procedure of re-scaling applied to the survival process. Survival data are translated from the slow to the fast time scale. We have proposed some cases where including survival at either the slow or the fast time scale can mean the difference between exponential growth or extinction of the population. This illustrates how important the appropriate choice of time scale can be.

Directly linked to the time scales models are the methods to reduce them. They are the tools to simplify their analysis. In Appendix B we have presented an extension of an already existing reduction technique for linear matrix models with environmental stochasticity. This new result has lead to reducing the model with re-scaled survival, but it can be apply in more general situations.

The re-scaling in the case proposed in this work is rather straightforward, but this is not always the case and it would be very interesting to study the influence of time scale choice on other demographic processes. Nguyen-Huu et al. (2011) proposed a more general approach to re-scaling in a deterministic setting that can be extended to the stochastic case along the guidelines and the reduction results presented here.

Appendix A. Matrix models with environmental stochasticity

This section presents the basic form of the matrix models that consider environmental stochasticity when the environmental process is a Markov chain. We assume that the population lives in an ambient in which there are different environmental states that, for simplicity, we suppose finite and label with $\eta \in \mathcal{I} := \{1, ..., n\}$; a nonnegative matrix $\boldsymbol{A}_\eta \in \mathbb{R}^{N \times N}$ represents the vital rates of the population in environment η. The environmental variation is characterized by a Markov chain τ_t, $t = 0, 1, 2, ..$ defined on a certain probability space $(\Omega, \mathcal{F}, p)$ over the state space $\mathcal{I}$. For each realization $\omega \in \Omega$ of the process, the population is subject to environmental conditions $\tau_{t+1}(\omega)$ between times t and $t + 1$. Thus, the model reads

$$\boldsymbol{z}(t + 1) = A_{\tau_{t+1}}\boldsymbol{z}(t), \tag{20}$$

where $\boldsymbol{z}(t) = (z^1(t), ..., z^N(t))^{\mathsf{T}}$ represents the population vector at time t for each $t = 0, 1, ...$. We assume that $\boldsymbol{z}_0$ is a fixed nonzero nonnegative vector.

The following theorem gives important information on the distribution of the total population size $||\boldsymbol{z}(t)||_1 = |z^1(t)| + \cdots + |z^N(t)|$ (in the sequel the subscript in the norm will be omitted):

Theorem 1. *Let us assume that Markov chain τ_t is homogeneous, irreducible and aperiodic and, further, that the set $\mathcal{A} = \{\boldsymbol{A}_\eta, \ \eta = 1, ..., n\}$ of vital rate matrices is ergodic, i.e., there exists a positive integer g such that any product of g matrices (with repetitions allowed) drawn from $\mathcal{A}$ is a positive matrix (i.e., its components are all positive). Then we have:*

1. We can define the stochastic growth rate (SGR) λ_S for system (20) through $\log \lambda_S := \lim_{t \to \infty} \log||\boldsymbol{z}(t)||/t$ with probability one. Moreover, λ_S is finite, and is independent of the initial probabilities of the chain states and of the initial (nonzero) population vector $\boldsymbol{z}_0 \geq \boldsymbol{0}$ and can be calculated through

$$\log \lambda_{\mathrm{S}} = \mathbb{E}_F \log \| \boldsymbol{A}_{\tau_{t+1}} \frac{\boldsymbol{z}(t)}{\|\boldsymbol{z}(t)\|} \|, \tag{21}$$

where F denotes the stationary distribution for $(\tau_t, \boldsymbol{z}(t)/\|\boldsymbol{z}(t)\|)$ (whose existence is guaranteed (Cohen, 1977)).

2. We can also define the "scaled logarithmic variance" (SLV) as $\sigma^2 := \lim_{t \to \infty} \mathbb{V} [\log\|\boldsymbol{z}(t)\|]/t$ where $\mathbb{V}$ denotes variance and where σ^2, which is finite, is independent of the initial probabilities of the chain and of the initial (nonzero) population vector $\boldsymbol{z}_0 \geq \boldsymbol{0}$.

3. If $\sigma^2 > 0$ the population size is asymptotically lognormal in the sense that

$$\frac{\log\|\boldsymbol{z}(t)\| - t \log \lambda_{\mathrm{S}}}{t^{1/2}\sigma} \xrightarrow{\mathcal{L}} \mathcal{N}(0, 1)$$

where $\mathcal{N}(0, 1)$ denotes a normal distribution of zero mean and unit variance and $\mathcal{L}$ denotes convergence in distribution.

Proof. The result is essentially Lemma 4 in Tuljapurkar and Orzack (1980) except for a technical detail. See Theorem 2.3. in Alonso and Sanz (2009) for the proof. $\square$

Appendix B. Reduction of matrix models with environmental stochasticity

We present here a general class of matrix models with environmental stochasticity which can be reduced, as well as the reduction technique. We also include a result that relates the behavior of the original and the reduced model. These models and results generalize those of Alonso and Sanz (2009), which are only valid for models of the kind (1), to more general models like (2). For the sake of simplicity, in this work we deal with a finite number of environments, but the general technique is valid even when there is an infinite (denumerable or not) number of environments.

Let N, $n \in \mathbb{N}$ and $\mathcal{I} = \{1, ..., n\}$. For each k large enough, we consider a set of nonnegative matrices $\mathcal{A}_k = \{\boldsymbol{H}_{k,\eta}, \ \eta \in \mathcal{I}\}$ with $\boldsymbol{H}_{k,\eta} \in \mathbb{R}_+^{N \times N}$ and denote the population vector $\boldsymbol{x}_k(t) = (x_k^1(t), ..., x_k^N(t)) \in \mathbb{R}^N$. Let τ_t be the Markov chain defined in Appendix A that selects the environment in each time step. Then we define the so called *complete model*

$$\boldsymbol{x}_k(t + 1) = \boldsymbol{H}_{k,\tau_{t+1}} \boldsymbol{x}_k(t), \tag{22}$$

where we assume that $\boldsymbol{x}_k(0)$ is a fixed nonzero vector $\boldsymbol{x}_0 \geq \boldsymbol{0}$.

In order to reduce system (22), we suppose that k is large enough and we impose some conditions which are specified in the following two hypotheses:

Hypothesis 1. For all $\eta \in \mathcal{I}$ there exists a matrix $\bar{\boldsymbol{H}}_\eta$ such that
$$\lim_{k \longrightarrow \infty} \boldsymbol{H}_{k,\eta} = \bar{\boldsymbol{H}}_\eta.$$

Hypothesis 2. There exist $q \in \mathbb{N}$, $q < N$, such that for all $\eta \in \mathcal{I}$ we can decompose $\bar{\boldsymbol{H}}_\eta$ in the form
$$\bar{\boldsymbol{H}}_\eta = \boldsymbol{D}_\eta \boldsymbol{G}, \tag{23}$$

where $\boldsymbol{G} \in \mathbb{R}_+^{q \times N}$, independent of environment η, and $\boldsymbol{D}_\eta \in \mathbb{R}_+^{N \times q}$ are nonnegative matrices.

In what follows we accept Hypotheses 1 and 2. Then, we proceed to reduce system (22) in two steps.

First, we define the so-called *auxiliary system* which approximates (22) when $k \to \infty$. Denoting its vector of variables at time t by $\boldsymbol{x}(t)$, this auxiliary system reads

$$\boldsymbol{x}(t + 1) = \bar{\boldsymbol{H}}_{\tau_{t+1}} \boldsymbol{x}(t) = \boldsymbol{D}_{\tau_{t+1}} \boldsymbol{G} \boldsymbol{x}(t). \tag{24}$$

The set of environmental matrices for the auxiliary system is $\mathcal{A}_{\mathrm{aux}} = \{\bar{\boldsymbol{H}}_\eta, \ \eta \in \mathcal{I}\}$.

Now we define *global variables*, which will play the role of state variables of the reduced, or *aggregated*, system

$$\boldsymbol{y}(t) := \boldsymbol{G}\boldsymbol{x}(t) \in \mathbb{R}_+^q. \tag{25}$$

Multiplying both sides of (24) with $\boldsymbol{G}$, we obtain the aggregated system

$$\boldsymbol{y}(t + 1) = \boldsymbol{G}\boldsymbol{x}(t + 1) = \boldsymbol{G}\boldsymbol{D}_{\tau_{t+1}}\boldsymbol{G}\boldsymbol{x}(t) = \boldsymbol{G}\boldsymbol{D}_{\tau_{t+1}}\boldsymbol{y}(t),$$

which is a stochastic system for the global variables $\boldsymbol{y}(t)$ that we use as an approximation of system (22).

Denoting

$$\hat{\boldsymbol{H}}_\eta := \boldsymbol{G}\boldsymbol{D}_\eta \quad \eta \in \mathcal{I}, \tag{26}$$

we can write the aggregated system as

$$\boldsymbol{y}(t + 1) = \hat{\boldsymbol{H}}_{\tau_{t+1}}\boldsymbol{y}(t), \tag{27}$$

for which the set of environmental matrices is $\mathcal{A}_{\mathrm{ag}} = \{\hat{\boldsymbol{H}}_\eta, \ \eta \in \mathcal{I}\}$.

Note that through the previous procedure we have constructed an approximation of (22) for k large enough that allows us to reduce a system with N variables to a new system with q variables. In most practical applications (Caswell, 2001; Rogers, 2015), q will be much smaller than N.

In order to obtain asymptotic results of the original system (22) from the aggregated system (27) we proceed to relate the distribution of the total population size for both systems. For the results to hold we need to impose the following hypothesis:

Hypothesis 3. For all $\eta \in \mathcal{I}$, matrices $\boldsymbol{D}_\eta$ are row-allowable (i.e., each row has at least a nonzero component) and matrix $\boldsymbol{G}$ is column-allowable (i.e., each column has at least a nonzero component).

Proposition 2. *Assume that the environmental process τ_t is an irreducible and aperiodic homogeneous Markov chain and that Hypotheses 1, 2 and 3 hold. Then, if $\mathcal{A}_{\mathrm{ag}}$ is ergodic, the set $\mathcal{A}_{\mathrm{aux}}$ is also ergodic and there exists $k_0 \in \mathbb{N}$ such that $\mathcal{A}_k$ is ergodic for all $k \geq k_0$. Therefore, if $\mathcal{A}_{\mathrm{ag}}$ is ergodic, the aggregated system meets the sufficient conditions of Theorem 1 for the SGR and SLV to exist, and those sufficient conditions are also met by the auxiliary system and by the*

original system for $k \geq k_0$.

Proof. A straightforward generalization of the proofs of Proposition 4.1. and Corollary 4.2. in Alonso and Sanz (2009). □

Therefore, if $\mathcal{A}_{ag}$ is an ergodic set, we have, under the hypotheses of Proposition 2, that we can define the following characteristics for the Aggregated system: $\log \hat{\lambda}_S := \lim_{t \to \infty} \frac{\mathbb{E} \log \| \boldsymbol{y}(t) \|}{t}$; $\hat{\sigma}^2 := \lim_{t \to \infty} \frac{1}{t} \mathbb{V} [\log \| \boldsymbol{y}(t) \|]$;

Original system: $\log \lambda_{S,k} := \lim_{t \to \infty} \frac{\mathbb{E} \log \| \boldsymbol{x}_k(t) \|}{t}$; $\sigma_k^2 := \lim_{t \to \infty} \frac{1}{t} \mathbb{V} [\log \| \boldsymbol{x}_k(t) \|]$.

Next theorem shows that, when k is large, we can approximate $\lambda_{S,k}$ and σ_k through $\hat{\lambda}_S$ and $\hat{\sigma}$, respectively, which are easier to compute.

Theorem 3. *Let us assume the same Hypotheses of Proposition 2 and, in addition, that $\mathcal{A}_{ag}$ is an ergodic set. Then we have*

$$\lim_{k \to \infty} \lambda_{S,k} = \hat{\lambda}_S, \quad \lim_{k \to \infty} \sigma_k = \hat{\sigma},$$

and so the lognormal asymptotic distribution for the original system can be approximated through the parameters $\hat{\lambda}_S$ and $\hat{\sigma}$ that correspond to the reduced system.

Proof. A quite technical generalization of the proof of Theorem 4.3. in Alonso and Sanz (2009) that will appear published elsewhere. □

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