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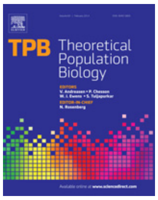

The demography of a metapopulation in an environment changing in time and space

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ABSTRACT

The persistence of populations living in heterogeneous environments crucially depends on the interaction between changes of the environment in space and time, and the way individuals move between locations. Here an approximation for the multiplicative growth rate of a metapopulation is derived, as a function of the properties of the spatial heterogeneity and temporal change in local habitat quality, and the dispersal pattern. This analysis reveals that the growth rate depends on (i) the geometric mean of the average growth rate in the metapopulation, (ii) whether individuals tend to be more numerous in high quality demes and (iii) temporal fluctuations in the spatial distribution of individuals. The two latter effects had been previously identified but mostly in simulation studies. Here I identify them in a unified analytical framework which helps clarifying previous studies. This analysis reveals that the shape of temporal variability interacts with the dispersal rate to determine the growth of the metapopulation, and in particular that the effects of dispersal depend on the level of temporal correlation of the environment.

0. Introduction

Natural populations often experience heterogeneity in environmental conditions, for example in temperature, chemical composition, moisture, or the biotic environment. Heterogeneity in the environment causes the vital rates of populations to change both in space and in time. Such variations have profound consequences on the demography and evolution of populations. Understanding what these consequences are is important in many contexts, for example, pest control in crop management (Levins, 1969), management of antibiotic resistance in bacteria (Bourguet et al., 2013) or conservation of endangered species. The probability of persistence of a population depends on the interaction between the properties of environmental variability (spatial and temporal correlations), and the pattern of dispersal. These phenomena have been extensively studied in empirical and theoretical studies.

One classical study showed that lynx population abundance in Canada exhibits spatially correlated cyclic dynamics, which may be driven by spatially correlated changes in resources (Moran, 1953) or by dispersal (Lande et al., 1999). Spatial correlations in abundance increase the probability of extinction (Heino et al., 1997). This result has prompted many measures of the spatial scale of correlation in population abundance in the field (Koenig, 1998, 2001). Another major concept is that of "source–sink" dynamics (Pulliam, 1988), whereby spatial variability in environmental conditions creates an asymmetry between "source" populations, which enjoy favorable conditions and have positive growth rates, and "sink" populations, which experience bad conditions, have negative growth rates, and can only be sustained by the influx of migrant coming from source populations. Many studies have sought to detect "source–sink" dynamics in wild populations (Johnson, 2004; Ringsby et al., 2002; Runge et al., 2006; Sæther et al., 1999; Schaub et al., 2006; Smith et al., 1996; Stacey and Taper, 1992). Recently, a particular attention has been paid to source–sink systems where the status of source or sink changes through time for each deme (Gonzalez and Holt, 2002; Holt et al., 2003; Jansen and Yoshimura, 1998; Roy et al., 2005; Schreiber, 2010). A striking result is that a metapopulation may persist in a changing and heterogeneous environment thanks to dispersal between patches, even if each patch individually is on average a sink habitat. Last, much work has taken the shortcut of describing patches of suitable habitat as either "empty" or "occupied", and followed the dynamic of extinction and colonization of these patches ("metapopulation dynamics"; Hanski, 1998; Levins, 1969). This work has led to important insights into the demography of populations in variable environments (e.g., Saccheri et al., 1998)

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or the evolution of dispersal (Hanski and Mononen, 2011), but conceptual links with models with explicit demography are not easy to draw (but see Engen and Sæther, 1998; Hanski and Mononen, 2011; Sæther et al., 1999).

The focused research effort reviewed above has brought key insights into the dynamics of populations in variable environments, but also raised several questions. The very abundant literature can be split into studies considering density independent growth on one hand, and those considering density dependent growth and/or multispecies models (e.g., predator–prey or host–parasite models) on the other hand. For simplicity, the following review is focused on density-independent populations—as we will see, even in this simple scenario, many different concepts have been introduced to understand population growth. First, although it seems well established that spatial correlation in the environment impedes persistence of the metapopulation, the impact of the properties of *temporal* change has been less studied. Simulations suggest that positive temporal correlation in the growth rates tends to enhance persistence (called the "inflationary effect" or "growth–density covariance"; Jansen and Yoshimura, 1998; Chesson, 2000; Schiegg, 2003; Roy et al., 2005). In these studies, the fluctuations in the environment are random, autocorrelated, and it is not known whether the "inflationary effect" holds for other shapes of environment fluctuations (e.g., periodical fluctuations). More generally, explicit analytical results characterizing how this effect depends on environmental variability and dispersal are lacking. Second, the effects of dispersal are many and seem to depend on the shape of temporal variability. Indeed, studies which consider uncorrelated random fluctuations in habitat quality (white noise) find that full dispersal enhances persistence relative to no dispersal (Kuno, 1981; Metz et al., 1983; Venable and Brown, 1988, 1993). Other studies with some level of temporal correlation in the environment find, on the contrary, that growth is maximal for an intermediate rate of dispersal (Jansen and Yoshimura, 1998; Roy et al., 2005; Schreiber, 2010). The diversity of assumptions of these studies and the lack of analytical results make it unclear what are the phenomena behind these effects of dispersal. Dispersal has complex effects, as it stabilizes local fluctuations in population abundance ("dispersal-induced stability"), but at the same time tends to synchronize population dynamics in space which would on the contrary impair persistence (Abbott, 2011). In sum, the study of demography in variable environments has generated a great profusion of concepts and identified many interesting phenomena. Yet few analytical results exist encompassing all these phenomena within a set of general principles governing the fate of a population in a variable environment.

The small number of analytical studies combining spatial and temporal heterogeneity is somewhat surprising as general principles have been captured long ago for the case of a population growing in a temporally changing but spatially homogeneous environment (Lewontin and Cohen, 1969, who introduced the idea that population persistence depends on the *geometric* mean fitness). Schreiber (2010) derived expressions for the growth rate of a metapopulation when the population is almost "fully mixed" (full mixing occurs when all individuals of the metapopulation are gathered in a common pool of migrants before being re-distributed among all demes regardless of their origin). He found a general expression for the growth rate, which revealed in particular that temporal correlations increase the growth rate, while spatial correlations decrease it. Here I set up a similar model to derive the growth rate of a density-independent metapopulation in an environment variable in time and space. The present study extends previous work in two ways: first, a general approximation for the growth rate in any scenario of environmental variability and any dispersal pattern is derived. This expression unifies a disparate body of theoretical work by encapsulating all the above-mentioned phenomena in a single analytical expression. Second, this new approximation allows accurate prediction of the growth rate when the dispersal pattern is not necessarily close to a "fully mixed" model, and in particular allows examining how the properties of environmental variability (shape of the temporal change, temporal correlation, spatial variability, etc.) and the rate of dispersal influence growth in these conditions.

1. The model

We describe a metapopulation where individuals are distributed across K demes. At each time step, the outcome of the events of reproduction and survival is described by the local growth rate $r_{i,t}$ and the rate of dispersal from population j to i is represented by $d_{j\to i}$. From one time step to the next, thus, local population size in deme i changes as:

$$N_{i,t+1} = d_{i\to i} N_{i,t} r_{i,t} + \sum_{\substack{j=1\\ j\neq i}}^{K} d_{j\to i} r_{j,t} N_{j,t} \qquad (1)$$

with $d_{i\to i} + \sum_{\substack{j=1\\ j\neq i}}^{K} d_{i\to j} = e$. e is the probability of successful establishment and lies in the $[0, 1]$ interval. If $e = 1$, dispersal is not costly and the metapopulation size is not affected by dispersal.

Eq. (1) is a system of K linear equations with fluctuating coefficients $r_{i,t}$ describing the spatial heterogeneity and the change of the environment. In the following these coefficients $r_{i,t}$ will be called the *local* growth rates, and they must not be confused with the "growth rate", which refers to the growth rate of the entire metapopulation. The total population size at time t as $N_t = \sum_{j=1}^{K} N_{j,t}$. In such model, the metapopulation grows exponentially, and the aim of the following sections is to derive expressions for its growth rate. To this end I define the fractional size of deme i as $w_{i,t} = \frac{N_{i,t}}{N_t}$ and the spatial average of the local growth rates weighted by local population sizes as $\bar{r}_t = \sum_{j=1}^{K} w_{j,t} r_{j,t}$. The expected growth rate of the metapopulation from time 0 to t is given by (Appendix A):

$$\lambda_t = \mathrm{E}\left[\frac{1}{t}\log\left[\frac{N_t}{N_0}\right]\right] = \log[e] + \mathrm{E}\left[\frac{1}{t}\sum_{\tau=0}^{t-1}\log[\bar{r}_\tau]\right]. \qquad (2)$$

In the scenarios of environmental variability that we will examine, for large t, λ_t converges to a limit λ which is independent of time. This is not always necessarily the case: for example, if the environment changed in a directional fashion, the growth rate would always depend on t. The limit λ is the Lyapunov exponent of the process defined in Eq. (1) (Metz et al., 1983, 1992). λ depends on the average of the local growth rates (i) over all demes weighted by their local population size (the bar of $\bar{r}_\tau$), (ii) over time ($\frac{1}{t}\sum_{\tau=0}^{t-1}$) and (iii) over the realizations of the random process determining the $r_{i,t}$ (E[ ]). In this model, λ determines population persistence: if $\lambda < 0$, the population goes extinct; if $\lambda > 0$, the population grows exponentially with rate λ. Population growth is density-independent, but the model is also a good approximation of density-dependent population growth when populations are small. In the case of negative density dependence, positive growth rate at the limit of small population ensures the population will converge to a positive solution (Benaïm and Schreiber, 2009). In the presence of demographic stochasticity (which we do not model here), $\lambda > 0$ is a necessary condition for the population to persist, but not a sufficient one, because demographic stochasticity may cause small populations to get extinct by chance even if $\lambda > 0$.

2. General expression for the growth rate of a metapopulation in a variable environment

Finding general expressions for the growth rate λ_t is not possible in the general case. To go further, following Metz et al. (1983), I apply the change of variables $r_{j,t} = R(1 + \rho_{j,t})$, and $w_{j,t} = \frac{1}{K}\left(1 + \epsilon_{j,t}\right)$, where R is the expected value of the time average of the spatial average of $r_{j,t}$ (i.e. $R = \mathrm{E}\left[\frac{1}{t}\sum_{\tau=0}^{t-1}\mathrm{E}^S\left[r_{j,\tau}\right]\right]$), $\rho_{j,t}$ is the excess growth rate in deme j at time t relative to the average growth rate, and $\epsilon_{j,t}$ is the excess fraction of individuals in deme j at time t. I assume both $\rho_{i,t}$ and $\epsilon_{i,t}$ are of the order of a small dummy variable δ. In practice, this assumption allows good prediction of the growth rate when the local growth rates do not fluctuate more than four-fold (i.e., $r_{j,t}$ range from 0.5 to 2), when the dispersal rates are greater than 0.01, and when the environment fluctuates in time (if the environment is constant, most of the individuals will reside in the highest quality deme and $\epsilon_{j,t}$ will not be small). The quantity $\bar{r}_\tau$ in Eq. (2) is approximated as a second order Taylor series in δ, yielding the following approximation for λ:

$$\lambda = \underbrace{\log[e]}_{\text{cost of dispersal}} + \underbrace{\mathrm{E}[\log[R]] - \frac{1}{2}\mathrm{V}[\mathrm{E}^S[\rho]]}_{\text{geometric mean}} + \underbrace{\mathrm{E}[\mathrm{C}^S[\epsilon,\rho]]}_{\text{inflationary effect}} + o\left(\delta^2\right). \tag{3a}$$

For simplicity, E[] and V[] now denote the expectation/variance over the realization of the random variables at each time point *and* the average/variance over time (e.g., from now on, $\mathrm{E}[X]$ stands for $\mathrm{E}\left[\frac{1}{t}\sum_{\tau=0}^{t-1}X_\tau\right]$). $\mathrm{E}^S[]$ and $\mathrm{C}^S[]$ denote the *spatial* average and covariance. Leaving aside the effect of the cost of dispersal (first term), two very different effects impact the growth rate of the metapopulation. The first only depends on the parameters ρ defining the properties of the environment. It is an approximation of the geometric mean of the average local growth rates (variance-discounted arithmetic mean), and constitutes a direct application of the "geometric mean principle" at the level of the metapopulation (Lewontin and Cohen, 1969). The variance term "$\mathrm{V}\left[\mathrm{E}^S[\rho]\right]$" means that fluctuations of the environments at the level of the metapopulation tend to reduce growth (this can be the case, for example, if fluctuations in the environment are very correlated across demes). The second effect depends not only on the parameters ρ, but also on the variables ϵ. Indeed, in a spatially structured population, the growth rate is also impacted by how individuals are distributed in the demes. It is quantified by the covariance in space between the excess growth rates and the excess fractional sizes of demes, the last term "$\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]$" in Eq. (3). The growth rate of the metapopulation is increased when there are more individuals in high-quality demes such that the covariance is positive. Such phenomenon has been called "growth–density covariance" (Chesson, 2000; Snyder and Chesson, 2004) and the "inflationary effect" (Roy et al., 2005). It may allow a metapopulation to persist even when each single population would not have persisted alone (Jansen and Yoshimura, 1998).

In cases where the environment is weakly temporally autocorrelated, the inflationary effect may be much reduced and other properties of the spatial distribution of individuals are important. The predictions of Eq. (3a) may be refined to account for such situations by approximating $\bar{r}_\tau$ with a Taylor series in δ up to the 4th order (details in Appendix A):

$$\lambda = \log[e] + \underbrace{\mathrm{E}[\log[\mathrm{R}]] - \frac{1}{2}\mathrm{V}[\mathrm{E}^S[\rho]] + \frac{1}{3}\mathrm{E}[\mathrm{E}^S[\rho]^3] - \frac{1}{4}\mathrm{E}[\mathrm{E}^S[\rho]^4]}_{\text{geometric mean}} + \underbrace{\mathrm{E}[\mathrm{C}^S[\epsilon,\rho]]}_{\text{inflationary effect}} - \frac{1}{2}\mathrm{V}\left[\mathrm{C}^S[\epsilon,\rho]\right] + \mathrm{o}\left(\delta^4\right). \tag{3b}$$

As in Eq. (3a), the growth rate of the metapopulation first depends on the geometric mean fitness at the scale of the metapopulation. The more precise approximation of the geometric mean reveals that an asymmetry in the distribution of average growth rates is beneficial to growth (term depending on the skew: $\frac{1}{3}\mathrm{E}\left[\mathrm{E}^S[\rho]^3\right]$), while extreme events are detrimental (term depending on the kurtosis: $-\frac{1}{4}\mathrm{E}\left[\mathrm{E}^S[\rho]^4\right]$). In addition, Eq. (3b) reveals that the growth rate is not only affected by the expected value of the covariance $\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]$ already interpreted above, but also by the temporal variance of this covariance $\mathrm{V}\left[\mathrm{C}^S[\epsilon,\rho]\right]$. The latter term tends to decrease the growth rate of the metapopulation. In other words, a population whose "inflationary effect" $\mathrm{C}^S[\epsilon,\rho]$ fluctuates little in time enjoys a higher growth rate. Such phenomenon has been identified before in the specific scenario of white noise fluctuations in the local growth rates (Metz et al., 1983; Venable and Brown, 1993). Eqs. (3a) and (3b) predict the growth rate of a metapopulation for any scenario of environmental variability in time and space and for any dispersal pattern. The conceptual distinction between the "inflationary effect", and the temporal fluctuations in this effect, is important. Both terms have been identified separately in previous studies before, but have never been identified together in a general scenario of environmental variability and dispersal.

Although Eq. (3) gives interesting insights into the multiple effects contributing to the growth rate of a metapopulation, it is not a closed equation because it does not inform on how individuals are arranged in the demes. To have a full understanding on how the properties of the environmental variability, the number of demes in the metapopulation, and the dispersal pattern determine the growth rate of a metapopulation, the next step is to find how the expected value $\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]$ and variance $\mathrm{V}\left[\mathrm{C}^S[\epsilon,\rho]\right]$ change and equilibrate. We find that the vector of local population sizes at time t $\boldsymbol{E}_t$ is approximately (Appendix A2):

$$\boldsymbol{E}_t \approx \frac{1}{e^t}\boldsymbol{E}_0\boldsymbol{D}^t + \sum_{\tau=1}^{t}\frac{1}{e^\tau}\left(1 + \boldsymbol{R}_{t-\tau}\right).\left(\boldsymbol{D} - \frac{e}{K}\right).\boldsymbol{D}^{\tau-1} \tag{4a}$$

where $\boldsymbol{D}$ is the matrix of dispersal rates (the element of the ith row and jth column is $d_{i\to j}$) and $\boldsymbol{R}_t$ is the vector of local growth rates. The first term will vanish for large t ($\boldsymbol{D}^t$ tends to $\mathbf{0}$ as all elements of the matrix $\boldsymbol{D}$ are smaller than 1). Plugging Eq. (4a) in Eqs. (3a) and (3b) results in an explicit expression for the growth rate. Thus, the approximation of weak heterogeneity in the environment and high migration allows finding a general approximation for the growth rate of a metapopulation for any dispersal pattern and any spatio-temporal variability in the environment. Moreover, we will see later on that the approximation is not very restrictive and allows predicting the growth rate with a good accuracy over a wide range of parameters (migration rate $\geqslant 0.01$ and variation in local growth rates smaller than four fold between bad environments and good environments).

In the following, we go further in the interpretation of Eqs. (3) and (4) by examining the island model of dispersal. In this model, at each time step a fraction m of each deme goes in a pool of migrants and is re-distributed in all demes at random. Assuming only a fraction c of the migrants successfully establish after dispersal, the dispersal coefficients in the island model are $d_{i\to i} = 1 - m + \frac{m(1-c)}{K}$, and $d_{j\to i} = \frac{m(1-c)}{K}$ for all $j \neq i$. Replacing in (4a) yields, when t is large:

$$\epsilon_{i,t} \approx \sum_{\tau=1}^{t}\left(\frac{1-m}{1-c\,m}\right)^\tau\left(\rho_{i,t-\tau} - \mathrm{E}^S[\rho]\right). \tag{4b}$$

Eq. (4b) can be used to show that the covariance quantifying the inflationary effect stabilizes, in the island model, to (Appendix B):

$$\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]^* \approx \sum_{\tau=1}^{t}\left(\frac{1-m}{1-c\,m}\right)^\tau\mathrm{E}\left[\mathrm{C}^S[\rho_{t-\tau},\rho_t]\right]. \tag{5a}$$

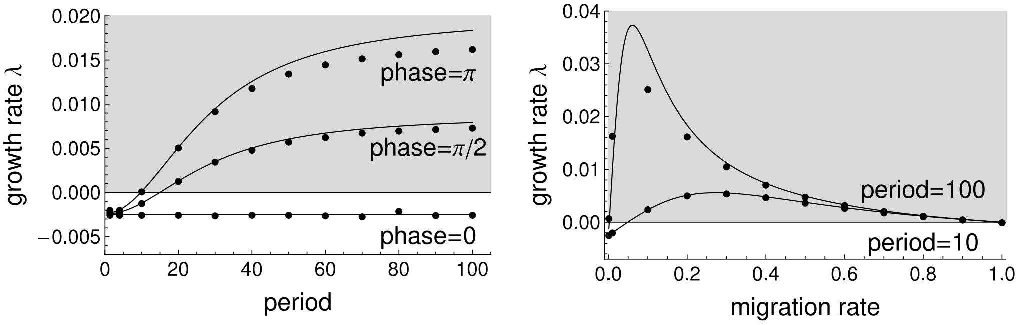

Fig. 1. Growth rate of the metapopulation in a sinusoidally changing environment. On the left, the growth rate is shown as a function of the period for three values of the phase between sine waves ψ, when the dispersal rate is $m = 0.2$. On the right, the growth rate is shown as a function of dispersal for two values of the period $T = 10$ and $T = 100$ when the sine waves are out of phase ($\psi = \pi$). Lines are analytical predictions, and points are the result of simulations. The zone where the population persists ($\lambda > 0$) is highlighted in gray. The fluctuations in habitat quality are sine waves with mean 1 and amplitude 0.1, and the number of demes is $K = 2$.

The inflationary effect depends on the covariances, taken over the metapopulation, between the current local growth rates and the local growth rates of the past $\mathrm{E}\left[\mathrm{C}^{\mathrm{S}}\left[\rho_{t-\tau}, \rho_t\right]\right]$. Furthermore, the sum integrates all past environments, but more recent environments have more impact on the covariance. This is because dispersal progressively erases the footprint of past environments on the spatial distribution of individuals. If the covariances between the environments at successive time intervals are positive (positive temporal autocorrelations), individuals will manage to accumulate in good demes and the metapopulation may persist even if each deme, individually, would not have allowed population persistence. Moreover, spatial correlations in the local growth rate tend to decrease the covariance in (5a), which decreases the inflationary effect and is detrimental to growth. Note that the right hand side of Eq. (5a) may in principle depend on time. However, in the scenarios of environmental variability considered here, it converges to a time-independent limit for large t.

An explicit equilibrium expression for the variance of temporal fluctuations in inflation can similarly be found under low autocorrelation (Appendix A):

$$\mathrm{V}\left[\mathrm{C}^{\mathrm{S}}\left[\epsilon_t, \rho_t\right]\right]^* \approx \sum_{\tau=1}^{t}\left(\frac{1-m}{1-c\,m}\right)^{2\tau}\mathrm{V}\left[\mathrm{C}^{\mathrm{S}}\left[\rho_{t-\tau}, \rho_t\right]\right]. \qquad (5b)$$

The variance in inflationary effect depends in turn on the variance of the temporal fluctuations in the covariance over space of the local growth rates of several time points ($\mathrm{C}^{\mathrm{S}}\left[\rho_{t-\tau}, \rho_t\right]$).

In summary, in many situations the growth rate of a metapopulation is predicted by Eq. (3a) together with Eq. (5a). In the special case of weak temporal autocorrelation in the growth rates, the effect of fluctuating covariance is also important, and Eq. (3b) with (5a) and (5b) may be used. These equations allow predicting the growth rate of the population for any scenario of spatial and temporal heterogeneity of the growth rate. In the following we apply these equations to several scenarios of environmental change.

3. Examples

Here Eqs. (3)–(5) are illustrated in two scenarios of environmental variability. These examples allow to make precise in which circumstances the various components of the growth rate are important and to show how the shape of the temporal variability, the spatial variability, the speed of environmental change, and the dispersal rate impact the growth rate of the metapopulation.

3.1. Deterministic periodical environments

In the first example, I assume there are two demes in which the environment fluctuates sinusoidally, $r_{1,t} = R\left(1 + \sin\left[\frac{2\pi}{\beta}\,t\right]\right)$ and $r_{2,t} = R\left(1 + \sin\left[\frac{2\pi}{\beta}t + \psi\right]\right)$, where $2\pi/\beta$ is the period and ψ is the phase difference in the cycles of the two demes. These periodical fluctuations may represent seasonal fluctuations in habitat quality, or the effect of periodical fluctuations in prey abundance for a predator. An analytical expression for the growth rate was derived using Eq. (3a) (Eq. (B5), Appendix B).

In general, the analytical approximation based on Eq. (3a) very accurately predicts the true growth rate, even for small dispersal rates ($m = 0.01$) (the true growth rate was found by simulating the exact system defined in Eq. (1)). Temporal fluctuations in the inflationary effect (extra term in Eq. (3b)) do not have an important impact on the growth rate. This analysis yields several insights. First, the growth rate always increases as the local growth rates are less synchronized across demes (Fig. 1). Thus spatial variability in the local growth rates always enhances growth. Indeed less synchronized environmental fluctuations result in a higher geometric mean and also a higher inflationary effect (see Eq. (3a)). Second, the inflationary effect may spectacularly improve the growth rate as compared to isolated populations. This effect is maximal when the fluctuations are slow and, interestingly, for an intermediate rate of dispersal (Fig. 1, right panel). Dispersal helps the population keep track of the changing environmental quality, even though there is no habitat choice or habitat-dependent dispersal. Mathematically, this relates to the presence of negative autocovariance functions in Eq. (5a) in a periodically changing environment. The rate of dispersal that maximizes the growth is given by (Eq. (B5)):

$$m^* = \left(\sin[\beta] + \cos[\beta] - 1\right)\sec[\beta] \quad \text{if } \beta \leqslant \pi/2 \text{ (period} \geqslant 4) \qquad (6)$$
$$m^* = 1 \quad \text{if } \beta > \pi/2 \text{ (period} < 4).$$

This optimal dispersal rate depends only on the period of fluctuations (Fig. 3). It is 1 when fluctuations are rapid, then decreases and eventually falls down to 0 in the limit of very slow cycles. Interestingly, it does not depend on the amplitude of fluctuation, nor on the phase difference ψ.

3.2. Stochastic autocorrelated environment

The second scenario is one where there are K demes in which the local growth rates follow a normal autocorrelated random process with mean μ, variance σ^2 and autocorrelation parameter ϕ. That is, the temporal sequence of local growth rates in a deme is obtained recursively using the relationship $r_{i,t+1} = \phi r_{i,t} + (1-\phi)\,a_{i,t}$ where $a_{i,t}$ is drawn in a normal distribution with mean μ and standard deviation σ. The standard deviation σ is assumed to be small so that the local growth rates do not vary a lot through time and space. ϕ is the autocorrelation parameter and lies between 0 (white noise) and 1 (constant environment). This process has

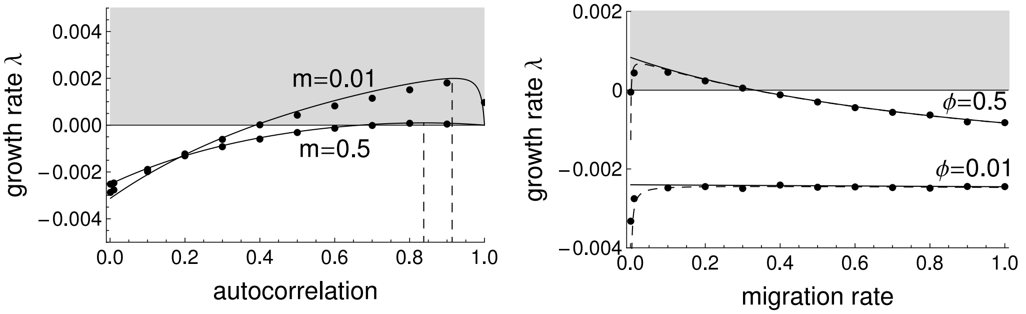

Fig. 2. Growth rate of the metapopulation in a random autocorrelated environment. On the left, the growth rate is shown as a function of the autocorrelation parameter with dispersal rates $m = 0.01$ and $m = 0.5$. An intermediate value of the autocorrelation parameter maximizes the growth rate. On the right, the growth rate is shown as a function of dispersal for two values of the autocorrelation parameter $\phi = 0.01$ and $\phi = 0.5$. Lines are analytical predictions, and points are the result of simulations. On the right panel, the plain line is the analytical prediction given by Eq. (3a), and the dashed line is that given by Eq. (3b) (with the effect of temporal fluctuations in inflationary effect). The autocorrelated random fluctuations are based on a normal distribution with mean 1 and standard deviation 0.1, and the number of demes is $K = 2$.

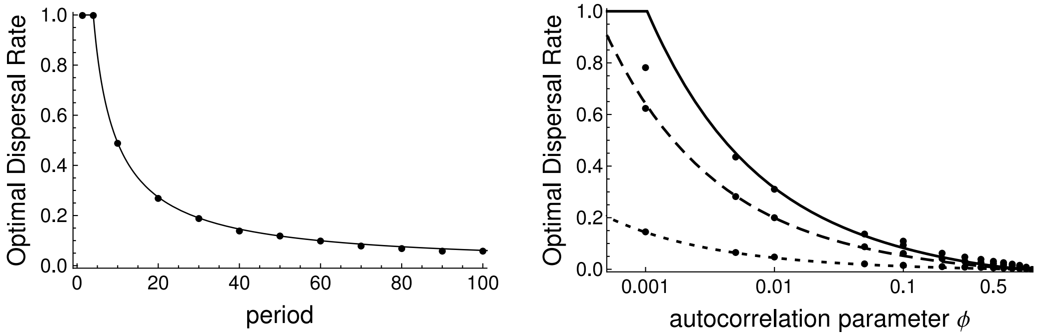

Fig. 3. Optimal dispersal rate for sinusoidally fluctuating local growth rates (left), and for autocorrelated random change in local growth rates (right). For the autocorrelated random change, the optimal dispersal rate is shown for $K = 2$, 5 and 100 demes in plain, dashed and dotted lines respectively. Lines are analytical predictions, and points are the result of simulations. Other parameters are the same as in Figs. 2 and 3.

average μ and temporal variance $\mathrm{V}[r] = \frac{1-\phi}{1+\phi}\sigma^2$. Such a shape of environmental change may represent, for example, changes in temperature or changes in soil composition. The processes are not correlated across demes, but we explore later on the consequences of relaxing this assumption (see Section 4). For this scenario of environmental variability, the temporal autocorrelation decays exponentially with time.

Analytical expressions for the growth rate were found using Eq. (3b) (Appendix B, Eq. (B17)). Accuracy of the approximations was verified with simulations of the exact dynamic of the metapopulation as specified by Eq. (1). The analytical result is accurate when dispersal is not too low ($m \geqslant 0.01$). At very low dispersal ($m = 0.001$), differences in local population size across demes are so important that the recursion equation for ϵ (Eq. (A14)) may be inaccurate, but the qualitative pattern is nevertheless well predicted (Fig. 3). The analysis yields the following insights.

First, in contrast to the periodical scenario above, it is often necessary to take into account the impact of temporal fluctuations in the inflationary effect on the growth rate (that is, the more precise Eq. (3b)). In particular, these temporal fluctuations are relevant to the growth of the population when the environment is weakly autocorrelated ($\phi < 0.1$), when the number of demes is small, and also when dispersal is reduced ($m = 0.01$) (Figs. 2 and 4). Such cases may be common in natural populations (Lande et al., 2003). Second, growth is enhanced as there are more demes in the metapopulation. More demes means fewer fluctuations at the scale of the metapopulation, and also a higher inflationary effect. Third, the growth rate is maximized for an intermediate value of the autocorrelation parameter (Fig. 2). This relationship follows from the two opposite effects of temporal autocorrelation on growth. At higher autocorrelation, the environment changes more slowly (which increases the inflationary effect, thus favoring growth), but is also less spatially variable (which impedes growth), because spatial variation is proportional to temporal variation when fluctuations are independent across demes. These two opposite effects result in the growth rate being maximal for an intermediate value of autocorrelation. Last, as in a periodically changing environment, growth is maximized for an intermediate rate of dispersal (Fig. 2). However, here this pattern is driven by quite different effects: in such an environment dispersal always reduces the inflationary effect, but it stabilizes fluctuations at the scale of the metapopulation. As a result, a little dispersal dramatically increases the growth rate and may allow persistence of the population (Fig. 2). More specifically, the dispersal rate that maximizes the growth rate is given by:

$$m^* = \min\left(\frac{\sigma}{2\mu}(1-\phi)\sqrt{\frac{1-\phi}{K\phi(1+\phi)}}, 1\right) \tag{7}$$

which is an increasing function of the standard deviation of fluctuations σ, and a decreasing function of the number of populations K, and the autocorrelation ϕ. Thus, the optimal dispersal rate would be largest in an environment with high variability, no temporal correlation and very few demes (Fig. 4).

To conclude, the ability of dispersal to distribute individuals in high quality habitats (inflationary effect) depends on the presence of negative temporal autocovariances (Eq. (5a)). This happens in a periodical environment where, for example, the environment half a period after a low quality environment is necessarily a high quality environment. In contrast, random environments with positive autocorrelation do not exhibit this kind of predictability, such that the inflationary effect is maximal when the dispersal rate is zero. Dispersal also influences the growth of metapopulation through its impact on the temporal variance in the inflationary effect (Eq. (5b)). Specifically, dispersal reduces the temporal variance in the inflationary effect, which tends to enhance growth

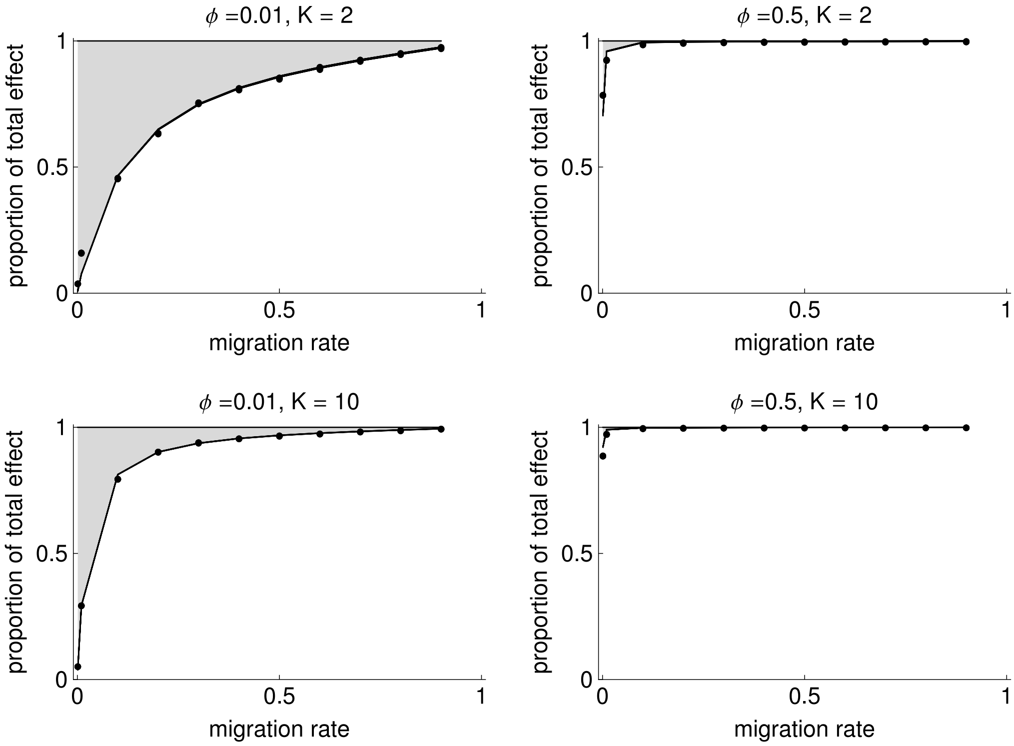

Fig. 4. Relative contributions of inflationary effect, fluctuations in inflationary effect and other effects on the growth rate, for two values of the autocorrelation parameter $\phi = 0.01$ and $\phi = 0.5$ and two metapopulation sizes $K = 2$ and $K = 10$. To calculate these contributions; we focused on the five terms $\mathrm{E}\left[\mathrm{C}^S\left[\epsilon, \rho\right]\right]$ (inflationary effect), $-\frac{1}{2}\mathrm{V}\left[\mathrm{C}^S\left[\epsilon, \rho\right]\right]$ (fluctuations in inflationary effect), and $-\mathrm{E}\left[\mathrm{E}^S\left[\rho\right]\mathrm{C}^S\left[\epsilon, \rho\right]\right]$, $\mathrm{E}\left[\mathrm{E}^S\left[\rho\right]^2\mathrm{C}^S\left[\epsilon, \rho\right]\right]$, $-\frac{1}{2}\mathrm{E}\left[\mathrm{C}^S\left[\epsilon, \rho\right]\right]^2$ (other effects), in Eq. (A8), that describe the impact of the distribution of individuals across demes on the growth rate. The contribution of inflationary effect $\mathrm{E}\left[\mathrm{C}^S\left[\epsilon, \rho\right]\right]$ is shown in white and the contribution of fluctuations in inflationary effect $-\frac{1}{2}\mathrm{V}\left[\mathrm{C}^S\left[\epsilon, \rho\right]\right]$ in gray. All other effects are shown in between these two effects, but they are not distinguishable because they contribute very little to the growth rate. Relative contribution of each of these five effects was calculated as $\frac{|\mathit{focal\ effect}|}{\left|\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]\right|+\left|\mathrm{E}\left[\mathrm{E}^S[\rho]\mathrm{C}^S[\epsilon,\rho]\right]\right|+\left|\mathrm{E}\left[\mathrm{E}^S[\rho]^2\mathrm{C}^S[\epsilon,\rho]\right]\right|+\left|\frac{1}{2}\mathrm{E}\left[\mathrm{C}^S[\epsilon,\rho]\right]^2\right|+\left|\frac{1}{2}\mathrm{V}\left[\mathrm{C}^S[\epsilon,\rho]\right]\right|}$. These contributions are between 0 and 1, and they sum to 1. The points are the results of simulations, and lines the analytical results. The autocorrelated random fluctuations are based on a normal distribution with mean 1 and standard deviation 0.1.

of the metapopulation. Overall, for any scenario of environmental variability, it is necessary to integrate the multiple forces that affect the growth rate of the metapopulation to understand how the properties of environmental variability and dispersal influence growth.

4. Discussion

This work extends the geometric mean principle to a metapopulation. The growth rate of a metapopulation in an environment changing in time and space depends not only on the geometric mean of the average local growth rates, but also on the way individuals are distributed in demes. The impact of the distribution of individuals on the growth rate can be decomposed into two effects: the growth rate is increased when individuals preferentially reside in high quality demes (“inflationary effect”), but is decreased when the covariance characterizing this distribution fluctuates a lot through time. These two effects have been described in previous studies but they have never been identified together in a single study and they have not been captured by an explicit analytical expression. The analysis reveals that these two effects are affected in different ways by the shape of environmental change, the number of demes, and dispersal.

Specifically, the analysis brings several clarifications regarding previous work. First, the inflationary effect is also present in a periodically fluctuating environment. Second, temporal fluctuations in the inflationary effect are most important to determine the growth rate when there are very few demes, the environment is weakly autocorrelated and migration is not too strong (Fig. 4). Specifically, the effects of temporal fluctuations are more important than the inflationary effect when the temporal autocorrelation fulfills the condition $0 < \phi < \frac{(1-m)\sigma^2}{2K(2-m)m\mu^2}$ (Appendix B, after Eq. (B17)). Third, dispersal has a different impact on the inflationary effect depending on the shape of temporal fluctuations. Dispersal may increase the inflationary effect when the environment is changing periodically, but always decreases it when the environment changes in a random, positively autocorrelated fashion. This implies that it is crucial to characterize the pattern of temporal variability to assess the impact of dispersal on persistence. In the context of a single population, the risk of population extinction is often projected using white noise temporal variations in the environment (Lande et al., 2003). When considering a metapopulation, such a simplification may lead to erroneous conclusions regarding the role of dispersal. Fourth, the optimal dispersal rate is often intermediate, as shown in previous studies, but the underlying reasons for this pattern are various. In a random environment dispersal stabilizes fluctuations at the scale of the metapopulation, but this effect becomes less important when the number of demes in the population is larger or the environmental fluctuations get more correlated in time. In a periodically fluctuating environment, dispersal boosts the inflationary effect by helping individuals keep track of environmental change and distributing them in higher quality demes.

These results clarify and extend previous studies. A previous analytical study has found an expression for the growth rate of a metapopulation in a high dispersal limit (Schreiber, 2010). The approximation proposed here allows accurate prediction of the growth rate even when the dispersal rate is small ($m = 0.01$).

These results confirm that in general, temporal correlations in the local growth rate are beneficial to growth through their positive effect on the inflationary effect, while spatial correlations are detrimental because they increase metapopulation-level temporal fluctuations and reduce the inflationary effect. However, one result not anticipated by Schreiber's study is that at low dispersal rates, fluctuations of the inflationary effect at the scale of the metapopulation are important to determine the growth rate. This phenomenon was evidenced before in several studies (Metz et al., 1983; Venable and Brown, 1993), but never identified jointly with the inflationary effect in a unifying framework. It explains, in particular, the positive effect of dispersal on growth at low dispersal rates (Fig. 2), a fact not captured by Schreiber's approximation. In another theoretical study, Evans et al. (2013) examine the problem in the case of white noise fluctuations in the environment. They find an equation for the growth rate (analogous to Eqs. (3) in this study) but do not solve explicitly the expression, except in the case of two demes. Consistent with previous studies, I find that full dispersal maximizes the growth rate when fluctuations in habitat quality are uncorrelated in time (Kuno, 1981; Metz et al., 1983; Venable and Brown, 1988, 1993). This effect of temporal fluctuations must not be confused with the inflationary effect, because it has the very different properties of disappearing as the number of demes gets large and temporal correlation gets higher. For example, Jansen and Yoshimura (1998) find an optimal intermediate dispersal rate in positively correlated, random environment. Results of the present study suggest that this pattern is due to temporal fluctuations at the scale of the metapopulation, and should therefore disappear when considering a large number of independent demes.

4.1. *Evolution of life-history strategies*

Which strategy should populations adopt to face an uncertain world? Migration helps population keep track of the changing habitat quality in a periodically changing environment, and helps stabilize fluctuations at the scale of the metapopulation. Note that some authors (Venable and Brown, 1988, 1993) have interpreted the role of migration in the latter case as a "bet-hedging" strategy, which helps stabilizing temporal fluctuations in growth. If the ability to disperse is genetically variable, the dispersal rate that maximizes the growth rate will evolve (Appendix C; Metz et al., 1983). Thus, in an environment where habitat quality fluctuates in time, an intermediate rate of dispersal often evolves (Cohen and Levin, 1991; Comins et al., 1980). Strikingly, the dispersal rate that evolves in a periodically changing habitat (Eq. (6)) is exactly identical to the one that would evolve if *selection* changed periodically in time (Eq. (12) in Blanquart and Gandon, 2011, with no recombination between the locus under selection and the locus modifier of migration). Thus a strong conceptual link exists between the role of dispersal in helping populations keep track of changing habitat quality and changing selection.

The system of equations we analyzed may describe populations structured not by space, but by genotype. In this interpretation, Eq. (1) would be akin to equations classically set up in studies interested in the evolution of mutation or stochastic switching and the $d_{i\to j}$ would be interpreted as switching rates. Such studies have mostly focused on special shapes of environmental change, e.g. white noise (Gillespie, 1981) or periodically fluctuating environments (Gaál et al., 2010; Ishii et al., 1989; Kussell et al., 2005; Kussell and Leibler, 2005; M'Gonigle et al., 2009). The present study finds more general expressions for the growth rate of a genotypically or phenotypically diverse population for arbitrary fluctuations in the environment, when the rates of switching are sufficiently high.

4.2. *Theoretical perspectives*

Eqs. (3) and (4a) are general with respect to the pattern of dispersal, but only the island model where there is no isolation by distance was investigated in details. To investigate the impact of isolation by distance on growth, I calculated the growth rate of the metapopulation in the case of a stepping stone model of dispersal with $K = 5$ demes arranged on a circle. This dispersal pattern results in growth rates very similar to those obtained under the island model of dispersal (Fig. 5). When the environment is strongly spatially autocorrelated, one would expect that "stepping stone" migration has less impact on the growth rate than "island" migration because individuals move to nearby patches which are very similar—however, again I find growth under the stepping stone model is very similar to what it is under the island model (Fig. 5).

Another critical assumption is that of density-independent population growth. This assumption is suitable to study small populations or populations that are not limited by resources. The demography of a density-dependent population in a heterogeneous and changing environment may certainly be very different. It would be an interesting challenge, in particular, to try to define an "evolutionarily maximum principle" (similar to the growth rate λ of our study) in such a population. Finding such a principle when the environment changes is challenging even in a single population because of the alternating regimes of "r" and "K" selection (Lande et al., 2009). In the presence of density dependence, dispersal would be more advantageous on average, because it would allow to recolonize empty or near-empty patches in which individuals enjoy a growth advantage.

Last, persistence of populations also depends on their genetic composition (Ezard et al., 2009). It would be interesting to investigate the consequences of dispersal for persistence of small populations when its impact on the genetic composition of populations is also considered.

4.3. *Experimental perspectives*

The theoretical clarification of the various forces that impact the growth rate of a metapopulation in a variable environment may have implications for empirical work. Demographic studies of wild populations have mainly focused on the spatial scale of synchrony in population fluctuations, and the detection of source and sink populations. Eq. (3) suggests that population persistence is mainly driven by (i) the geometric mean growth rates at the scale of the metapopulation; (ii) whether there are more individuals in good habitats; and (iii) the temporal fluctuations in the covariance quantifying the spatial distribution. Estimating these quantities in wild populations may enhance our understanding of their demography. Besides, experimental systems which allow precise control on the environmental variability and direct measurements of population sizes offer exciting perspectives to test the predictions of this study (Matthews and Gonzalez, 2007).

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.tpb.2014.03.001.

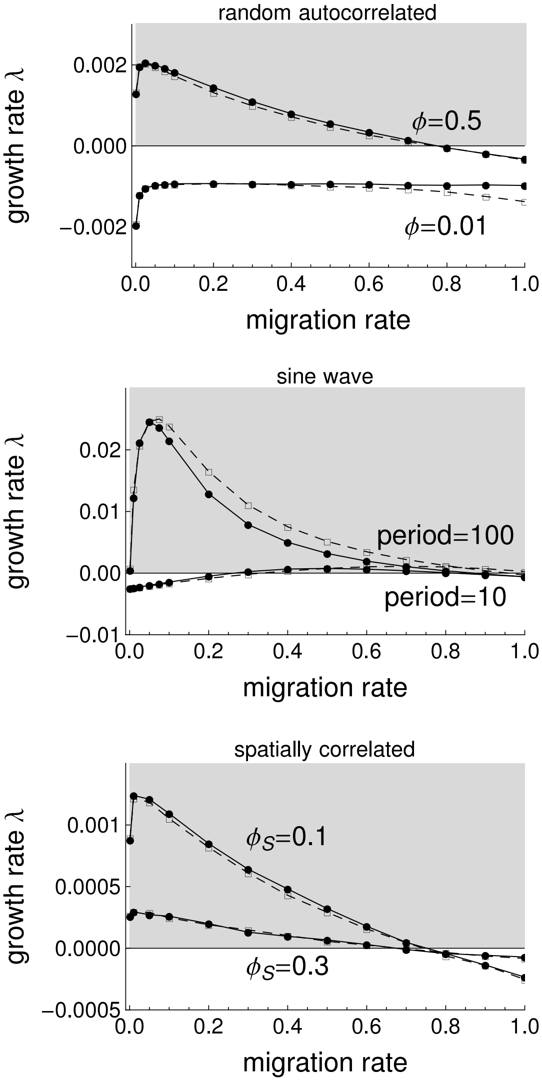

Fig. 5. Growth rate of the metapopulation with the stepping stone dispersal rate versus the island model of dispersal, in a random autocorrelated environment (top), a periodical environment (middle) and a random autocorrelated environment with some level of spatial correlation (bottom). In the three panels there are $K = 5$ demes in the metapopulation. Growth rate for the island model of dispersal is shown in filled circle and plain line, and the growth rate for the stepping stone model is shown in empty squares and dashed line. The demes are arranged circularly for the stepping stone model of dispersal (e.g., migrants from population #1 end up to populations #2 or #5). Top panel: growth rate in a random environment with autocorrelations $\phi = 0.5$ and $\phi = 0.01$. Middle panel: growth rate in a sinusoidally changing environment with periods $T = 10$ and $T = 100$. The phases of the sine waves are $\left\{0, \frac{\pi}{4}, \frac{\pi}{2}, \frac{3\pi}{4}, \pi\right\}$ respectively in the five demes. Bottom panel: growth rate in a random environment with temporal autocorrelations $\phi = 0.5$ and spatial autocorrelation $\phi_S = 0.1$ (top curve) and $\phi_S = 0.3$ (bottom curve).

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