



# 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.

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## 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  $d_{j \rightarrow i}$ . From one time step to the next, thus, local population size in deme  $i$  changes as:

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

with  $d_{i \rightarrow i} + \sum_{\substack{j=1 \\ j \neq i}}^K d_{i \rightarrow j} = e$ .  $e$  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):

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

In the scenarios of environmental variability that we will examine, for large  $t$ ,  $\lambda_t$  converges to a limit  $\lambda$  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  $\lambda$  is the Lyapunov exponent of the process defined in Eq. (1) (Metz et al., 1983, 1992).  $\lambda$  depends on the average of the local growth rates (i) over all demes weighted by their local population size (the bar of  $\bar{r}_t$ ), (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,  $\lambda$  determines population persistence: if  $\lambda < 0$ , the population goes extinct; if  $\lambda > 0$ , the population grows exponentially with rate  $\lambda$ . 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  $\lambda_t$  is not possible in the general case. To go further, following Metz et al. (1983),

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