



Spatial synchrony and harvesting in fluctuating populations: Relaxing the small noise assumption



Steinar Engen

Department of Mathematical Sciences, Centre for Biodiversity dynamics, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

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ABSTRACT

In spatio-temporal population dynamic models, the most important concept, in addition to mean and variance of local density fluctuations, is the spatial scale of fluctuations in density expressed by studying the spatial autocovariance function. Analytical formulas for this scale in models with local density regulation, dispersal and spatially autocorrelated noise, are rather simple when based on asymptotic theory giving linear models in the limit as the environmental variance approaches zero. The accuracy of these analytical small noise approximations has, however, not been investigated theoretically. Here, we work out improved approximations for the scale as well the spatial autocorrelation function using non-linear logistic local dynamics and going to the next order of approximation with respect to the environmental variance. Generally, it turns out that the asymptotic results are remarkably accurate under moderate fluctuations in density but may be inaccurate for very large fluctuations. For populations with small dispersal capacity, the main error comes from the fact that the logistic dynamics is non-linear, and this error is partly wiped out as dispersal increases. Proportional harvesting has a large effect on the dynamics in spatial as well as non-spatial models, increasing population fluctuations and their spatial scale. The optimal harvesting rate with respect to expected yield per time unit, however, is only to a small extent affected by the magnitude of population fluctuations unless these are very large, so that asymptotic results are applicable over a large range of population fluctuations.

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1. Introduction

In populations located in small areas, individuals may all have the same chance of interacting with each other in reproduction as well as competition for resources. The dynamics may then be described realistically by simply studying temporal variation in number or density of individuals. However, most populations are spread out in space so that vital rates are generated locally through interaction between individuals located close to each other. Then, the dynamic properties can only be understood by studying spatial aspects of population dynamics, which is an area of increasing interest for single species (Shigesada and Kawasaki, 1997; Tilman and Kareiva, 1997; Bascompte and Solé, 1998; Turchin, 1998; Ovaskainen and Cornell, 2006; Cantrell et al., 2009; Rai, 2013) as well as communities (Lande et al., 2003; Ovaskainen and Soininen, 2011). Spatial modeling in ecology was first approached through meta-population dynamics by Levins (1969, 1970), modeling dynamics on islands connected by migration, and taken further with more ecological realism by Lande et al. (1998) and Hanski (1999). General analytical results have also been reached by considering the density as a smooth stochastic field with temporal changes

(Morozov and Poggiale, 2012) although most studies are based on simulations using islands governed by local density regulation, dispersal of individuals (Kendall et al., 2000; Girard et al., 2002; Ranta et al., 2006) as well as stochastic environmental noise affecting vital rates locally (Ranta et al., 1997; Grenfell et al., 1998; Koenig, 1999; Lande et al., 2003; Liebhold et al., 2004; Bjørnstad et al., 2008). Observations have confirmed that synchrony in population fluctuations decreases with spatial distance between populations and are affected by individual migration rates as well as spatial correlations of temporal fluctuations in environmental variables affecting vital rates (Hanski and Woiwood, 1993; Sutcliffe et al., 1996; Koenig, 1998). Moran (1953) showed that in linear models for fluctuations in populations with no migration between them, the synchrony in population fluctuations will be the same as that in the stochastic environments driving the fluctuations, the so-called Moran effect. This was confirmed empirically for isolated populations by Grenfell et al. (1998) and populations spread out over large areas by Lindström et al. (1996).

The basic properties of spatio-temporal fluctuations can often be expressed by three parameters, the mean and variance of local density as well as some measurement of spatial scale of fluctuations in density. In general, the spatial scale is some maximum distance at which two densities are expected to have similar values, often expressed by their correlation (Bjørnstad et al., 2008).

E-mail address: steinaen@math.ntnu.no.

The spatial scale is the single most important parameter in spatial models as compared to simple models with no spatial structure. It is related to many different properties of the dynamics such as local density regulation, dispersal rate and distance, as well as the permanent or temporally variable spatial distribution of the habitat expressed through climate variables as well as amount of resources or predation risk. Models explaining spatial scales therefore have a number of important ecological implications. Understanding the mechanisms generating the scale is crucial for understanding the effects of different kinds of human activities implying physical forcing of environmental variables. Landscape fragmentation and other changes in the spatial pattern of the environments of a species has a direct effect on the spatial dynamics by its effect on dispersal and migration of the focal species as well as competitors or predators. Another example is harvesting, usually performed at different rates in areas with different densities, which therefore has large impact on the spatial dynamics (Hsieh et al., 2006; Fryxell et al., 2010). Even spatially uniform harvesting will reduce realized growth rate and strength of local density dependence and thereby affect the spatial scaling (Lande et al., 1999).

A population with spatial autocorrelation close to one for any pair of locations within its habitat behaves very differently from a population where fluctuations are approximately uncorrelated even at rather small distances. In the first case, even a very large population will have dynamics similar to much smaller subpopulations. Studying the dynamics at a single location is then sufficient for exploring the total population by multiplication of the local population size with an approximately constant factor. As a consequence, large spatial scale indicates that the number of individuals in large areas may show considerable fluctuations relative to its mean, which may result in quasi extinctions of the whole population (Bolker and Grenfell, 1996; Heino et al., 1997; Ranta et al., 1997; Engen, 2007). If, on the other hand, the spatial scale is small, fluctuations in large areas will be small due to practically independent fluctuations in density between most locations, giving smaller fluctuations in total population size and more sustainable population fluctuations by the law of large numbers.

Theoretical studies of spatial dynamics are most commonly done by subdividing the population into discrete subpopulations or islands (Levins, 1969, 1970; Lande et al., 1998; Hanski, 1999), using specific assumptions of local dynamics as well as dispersal between islands. Analyses of such systems can be performed by simulating temporal changes in local densities or by individual based models defined by rules describing vital rates and movements of each individual. Such variation in environmental variables affecting vital rates can be explored by methods in spatial statistics and linked statistically to measurements of scales of population synchrony. An advantage of simulation studies is the possibility of including permanent spatial heterogeneity in the habitat expressing variation in local climate, physical conditions or densities of interacting species, which may be a major component of temporal variance as well as spatial scale of population densities. Some analytical results on permanent heterogeneity are also available (Engen et al., 2002).

Here, we use a model describing continuous variation in population density over a large (infinite) area, and in order not to make the model too complicated we assume no permanent spatial variation in the habitat. However, the environment varies in space with a given spatial scale. Lande et al. (1999) generalized Moran's result (Moran, 1953) by added migration and local density regulation to the model and showing, assuming small environmental noise giving approximately a linear dynamics, that this increased the spatial scale through a term proportional to the dispersal rate and inversely proportional to the local strength of density regulation. Non-linearities (Greenman and Benton, 2001; Cazelles and Boudjema, 2001; Engen and Sæther, 2005; Sæther et

al., 2007) in combination with dispersal complicate these relations considerably.

The spatial scale of population fluctuations is known to vary considerably among species. For small individuals where environmental effects may show local variation over small distances and dispersal distances are small, such as for example butterflies, the scale may be only one or a few kilometers varying with dispersal capacity (Sutcliffe et al., 1996; Lande et al., 2003). Birds and mammals often fluctuate at an intermediate scale at the order of 10 kilometers (Ims and Andreassen, 2000; Grøtan et al., 2005, 2008), while oceanic fish species with large migration capacity living in water with large scale of temperature fluctuations may have spatial scale as large as several hundred kilometers (Myers et al., 1997; Anderson et al., 2008; Frank et al., 2016).

Many populations show rather large temporal fluctuations in density, with a coefficient of variation even bigger than 0.5 (Lande et al., 2003). This poses the important question of how robust the asymptotic scaling result of Lande et al. (1999) is against the magnitude of environmental fluctuations. Here, we address this problem using local logistic dynamics, which is often realistic even for large fluctuations, and assuming that the spatial autocorrelation of the environmental noise has a Gaussian form. In the limit as the environmental variance σ_e^2 (defined as the temporal variance in local logarithmic growth rate) approaches zero, the spatial autocovariance function is proportional to σ_e^2 and hence vanishes completely in the limit. In order to investigate larger and more realistic environmental fluctuations in density we therefore derive an accurate approximation for the autocovariance function under logistic local dynamics and use that to find the first order approximation in σ_e^2 to the spatial scale of density fluctuations, generalizing the result of Lande et al. (1999). These results are finally also used to study the effects of proportional harvesting in space, which preserves the logistic type of model but modifies parameter values.

We shall in general assume that densities are large enough to neglect the influence of demographic noise generated by local between individuals differences in vital rates (see Engen and Sæther, 2016 for details), so that the noise is determined only by a fluctuating environment affecting equally individuals located close to one another. Furthermore, to avoid complex descriptions near the border of some closed area it is convenient to model the dynamics over the entire two-dimensional space and assuming that there are no permanent spatial heterogeneity affecting dispersal or vital rates, giving models that are invariant with respect to transitions in space.

After starting by showing some basic required results for proportional harvesting in a logistic non-spatial model and presenting shortly the linearized model of Lande et al. (1999), the derivation of the results for the spatial logistic model are based on the following steps: First, the spatio-dynamic equations with local logistic density regulation, dispersal and spatially structured environmental noise are presented. The model parameters are chosen so that the total population can neither go extinct nor grow towards infinity. Then, the dynamics is stationary in space and time so that the spatial autocorrelation between the densities at two locations only depends on the distance between them, not on the actual positions or the time. Using this fact, it is possible to write up balance equations for the spatial autocorrelation function. These equations are most easily solved using the Fourier transform of the unknown autocovariance function and the other known functions of distances in the model and derive the corresponding simplified balance equation including all these Fourier transforms. This equation can be solve for the unknown Fourier transform of the autocovariance function. From this function, it is possible to derive the spatial scale of the autocovariance defined as the standard deviation of the autocovariance function after it has been

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