Spatial synchrony in population dynamics: The effects of demographic stochasticity and density regulation with a spatial scale

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ABSTRACT

We generalize a previous simple result by Lande et al. (1999) on how spatial autocorrelated noise, dispersal rate and distance as well as strength of density regulation determine the spatial scale of synchrony in population density. It is shown how demographic noise can be incorporated, what effect it has on variance and spatial scale of synchrony, and how it interacts with the point process for locations of individuals under random sampling. Although the effect of demographic noise is a rather complex interaction with environmental noise, migration and density regulation, its effect on population fluctuations and scale of synchrony can be presented in a transparent way. This is achieved by defining a characteristic area dependent on demographic and environmental variances as well as population density, and subsequently using this area to define a spatial demographic coefficient. The demographic noise acts through this coefficient on the spatial synchrony, which may increase or decrease with increasing demographic noise depending on other parameters. A second generalization yields the modeling of density regulation taking into account that regulation at a given location does not only depend on the density at that site but also on densities in the whole territory or home range of individuals. It is shown that such density regulation with a spatial scale reduces the scale of synchrony in population fluctuations relative to the simpler model with density regulation at each location determined only by the local point density, and may even generate negative spatial autocorrelations.

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1. Introduction

In population dynamics spatial synchrony is measured by parameters expressing how correlations in population size or their temporal fluctuations changes with distance between sites. Such correlations are of great interest because they in general affect the dynamics and in particular extinction risks [2,6,11,23,30,42]. Populations can be synchronized by the effects of spatially correlated environmental variables [5,28,33,42] such as weather [18], by biological interactions like predation [24,47] as well as dispersal rates and distances [16,43]. These effects may differ considerably among species [30,39], leading to large interspecific differences in the spatial scale of population synchrony [43].

Spatial population dynamics was first studied by metapopulation models introduced by Levins [31,32], and then extended especially by Hanski and collaborators [21,22]. Later models in continuous time and space have proved useful in analyzing how environmental noise, density regulation and dispersal rates in general influence population synchrony [10,12,27,29,30] that in turn may have considerable effects on extinction processes [11].

In the absence of migration, linear spatial population models (or log population size models) in discrete or continuous time have the simple property, known as the Moran effect [36], that the spatial autocorrelation of population size (or log population size) equals the spatial autocorrelation in the noise, provided that the strength of density regulation is constant in space [12]. However, spatial dynamic models with migration has shown that dispersal may have a substantial additional effect on the scale [10,29]. In particular, under weak local density regulation even small migration over short distances may lead to a spatial scale of population synchrony that is much larger than the scale of the environmental noise. Lande et al. [29] expressed this by a simple result, using a linearized model. Defining the spatial scale of a function of spatial distance as the standard deviation of the distribution obtained by scaling the function, they showed that the squared spatial scale of population density was $l_0^2 + m l_g^2/\gamma$, where l_0 and l_g are the scales of environmental noise and dispersal distance, respectively, m is

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the dispersal rate, and γ the strength of local density regulation. A similar formula was given by Engen [10] for log density with larger population fluctuations but smooth migration modeled as spatial diffusion.

In addition to using linear models as approximation to more complex dynamics, the result of Lande et al. [29] is based on two other simplifying assumptions. First, there is no demographic stochasticity acting independently on the survival and reproduction of each individual, only spatially correlated environmental stochastisity affecting all individuals sufficiently close to one another in the same way. This is realistic only for large densities, or very large spatial scale of environmental effects. Second, the models are based on the assumption of strictly local density regulation, that is, the temporal changes in density at a given location is only affected by the density at that particular point, with no direct effect from the density at nearby locations.

Here, we consider the linear model of Lande et al. [29], generalized to include demographic stochasticity acting locally. Furthermore, the density regulation at a given point in space is assumed to act through a given weighted average of densities in the neighborhood of the point, defining a more realistic competition for resources in space. These two additional components still lead to rather transparent analytical results and are shown to create substantial effects on the spatial autocorrelation of population density.

The most common approach to studying population dynamics in space is to use so-called individual based models, simulating the dynamics based on the performance of each individual in relation to reproduction, survival and dispersal [46]. Such an approach has the advantage that one can study very complex forms of spatial structure and non-linear dynamics. The drawback, on the other hand, is that one cannot obtain general analytical results but only investigate the performance of the system for a limited choice of parameter values compared to all realistic combinations. Another approach is to start with small cells in space and define birth and death processes with possible increase or decrease of a single individual at each cell during an infinitesimal time step, and allow for smooth dispersal of individuals by spatial diffusion [7,35,38]. Historically, this was also the approach first used to describe stochastic dynamics of populations with no spatial structure [3], but during the 1970s one became aware of the practical limitations of these models due to large environmental effects affecting all individuals in the same or similar way [17,25,26,34,45,54]. For large populations demographic noise, which by definition is independent among individuals, has practically no effect compared to environmental noise [30]. Starting with pure demographic noise and generalizing by including temporal environmental variation in parameters has so far not given any transparent analytical results. At the other extreme, the vast literature on time series analysis on log population sizes using constant variance in the noise [53] only includes the environmental component with no demographic noise and may therefore be inadequate for small population sizes.

Here we follow the approach of Lande et al. [29] using the concept of population density with no reference to positioning of each individual in the population. The underlying basic idea is that individuals move around in their habitat and thereby contribute to a continuous spatial density function expressing the mean number of individuals in areas relative to these stochastic movements [13]. Demographic stochasticity is generated by within year variation among individuals in survival and reproduction [30] and thereby operates directly on the point process but indirectly also on the density function. Each death or reproduction, however, only affects the density function over a very small area where the individuals are most likely to stay. Density regulation, on the other hand, reflects the competition between individuals for resources spread out over larger areas where individuals search for and collect their food items. Hence, individuals with substantial difference

in mean positions may still compete with one another during foraging due to overlapping search areas. This may in particular be the case in a seasonal environment, where individuals from large areas may compete intensively during periods with limited food supplies [15,41]. Accordingly, competition for food creates a density regulation in such a way that the density at a given point is affected not only by the local density at that point, but also by the densities in a surrounding area where foraging is likely to occur. Here we do not model the spatial position of each individual but still take the independent contributions from individuals into account by adding a demographic noise component to the density, which is actually a spatial white noise component. This is defined in such a way that it leads to the correct magnitude of fluctuations in small areas in agreement with models without spatial structure [30].

Let z denote points in the two-dimensional space and write $\mu(z, t)$ for the population density at z at time t meaning that the mean number of individuals in a small (infinitesimal) area dz at position z at a given time t is $\mu(z, t)dz$. We consider each individual to contribute to the density according to its movements in its home range so that the integral over the entire space of the density contribution from a single individual is one. The density $\mu(z, t)$ therefore is a mean value in the sense that the expected number of individuals in an area A during a discrete time step with given density field $\mu(z, t)$ is $\int_A \mu(z, t)dz$. Our aim is to analyze how the field $\mu(z, t)$ changes through time by births and deaths of individuals affected by density, as well as migration. Stochastic contributions to the next generation will typically have demographic components generated by independent stochastic variation in vital rates among individuals a given year, as well as environmental components generated by a stochastic environment affecting all individuals at nearby locations in the same or a similar way. In simple models with no spatial components, the relative effect of demographic and environmental variance is determined by the population size, the demographic and environmental variance components of the temporal increment in a population of size N being proportional to N and N^2, respectively. This variance is written as $\sigma_d^2 N + \sigma_e^2 N^2$ where σ_d^2 and σ_e^2 are the demographic and environmental variances [9]. We shall see that a similar result holds for spatial models in which the relative effects of these components in an area depend on the number of individuals expected to be in that area. One interesting question is how these variance components act together in generating the spatial autocorrelation function, in particular what their role is in determining the spatial scale of synchrony. Here we show that the demographic variance in relation to environmental variance acts in space through a *spatial demographic coefficient* $s = \sigma_d^2/(\sigma_e^2 N_0)$, where N_0 is a *characteristic population size* defined by the mean density and the autocovariance function for environmental noise.

2. Deterministic model

In the absence of migration and stochastic noise we assume that the density regulation at z acts through the weighted mean $\int \mu(z - u, t)f(u)du$, where $f(u)$ is a two-dimensional distribution obeying $\int f(u)du = 1$. The continuous model for temporal change in density then takes the form

$$\frac{d\mu(z, t)}{dt} = r\mu(z, t)\left\{1 - D\left[\int \mu(z - u, t)f(u)du\right]\right\},$$

where D is an increasing function describing how the densities in the neighborhood of z affects the expected growth in density and r is the growth rate in the absence of density regulation. This formulation defines an overall carrying capacity K for population density defined by $D(K) = 1$. For a spatially constant population density $\mu(z, t) = K$ the growth at any point in space is accordingly zero.