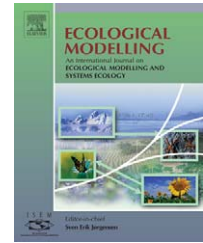


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The estimation of dispersal rates using the covariance of local populations

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ARTICLE INFO

Article history:

Received 7 June 2005

Received in revised form 17 January 2006

Accepted 9 February 2006

Published on line 17 April 2006

Keywords:

Time series analysis

Autoregressive process

Migration

Dispersal rate

Metapopulation

ABSTRACT

Dispersal has important implications on an individual, population and metapopulation level. Dispersal rates, however, are difficult to measure. In this paper we introduce a method that uses census data, i.e. repeated counts of number of individuals per location and point in time, to estimate dispersal rates. The rationale underlying this method is that local stochastic disturbances which dissipate in subdivided populations create a covariance structure, the details of which depend on how strongly the local populations are coupled. This covariance structure can be used to estimate dispersal rates. We describe this process using a stochastic model for growth and dispersal which explicitly accounts for the geometry of the patchy population. A regression of the covariance structure of this model is then used to infer the growth rate near equilibrium and the dispersal rate. We study the distribution of the estimated parameters and obtain confidence intervals using a bootstrap analysis and a Monte Carlo technique. We study how the confidence intervals depend on the model's parameters, the robustness of the estimating scheme, and discuss the applicability of our method.

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1. Introduction

Many natural populations are subdivided and occur in habitat patches (Husband and Barrett, 1996; Hanski, 1999; Thrall et al., 2000; Barton, 2001; Chesson, 2001). Ecologists and geneticists have formulated models describing metapopulations, i.e. populations consisting of "local populations", each of which have a substantial probability of extinction, but which can persist at a regional level (Wright, 1940; Levins, 1970; Hanski, 1999, 2001). Dispersal between these local populations is an essential feature of a spatially structured population.

The importance of dispersal has been recognised in empirical and theoretical studies. However, quantification of dispersal is difficult as measuring dispersal rates in natural populations is a time and labour consuming enterprise. (For re-

cent reviews on this issue see Clobert et al., 2001; Nathan et al., 2003; Cain et al., 2003 and other papers in same issue of *Ecology*.) So far two different methodologies have been used to measure dispersal: (1) one can observe marked individuals and track movement and redistribution (Stensteth and Lidicker, 1992; Kaiser, 1995), (2) one can infer dispersal by the redistribution of a population of markers (Slatkin, 1985; Barton, 2001).

Individual movement-redistribution methods use data on observations of individuals. In most cases, animals will be captured, a mark applied, and the animal released. Subsequent reobservation generates (a) recovery data, in which animals are recovered dead, (b) recapture/resighting data, or (c) known-status data, in which marked animals are re-observed alive or dead at specified times. Evaluation of the data using an appropriate model yields dispersal-related parameters (Bennets et al., 2001). Direct tracking of individuals involves the use of

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doi:10.1016/j.ecolmodel.2006.02.031

radio tags, satellite tags or electronic data storage tags (see references in Nathan (2001)). Although this approach potentially gives good results, its main disadvantages are associated technical difficulties, the labour-intensive way of collecting the data, and above all the high costs of the tags. Moreover, the data gathered using these direct methods might not represent the full distribution of individual movements and are temporarily and spatially restricted (Koenig et al., 1996).

In case of the redistribution of a population of markers, the markers used are mostly genetic e.g. microsatellite loci, mitochondrial DNA, ribosomal DNA or allozymes. The distribution of neutral genetic markers can be predicted from a model and the observed distribution can be compared to the distribution predicted by the model. The data necessary for these indirect techniques are easy to gather: a single sampling event in time generates a snapshot of the current state of genetic variation which is used to calculate the number of migrants under a certain model. Coalescence methods and F -statistics are mostly based on the island model (Wright, 1940) and are widely used to measure gene flow within and among populations and infer dispersal rates. This model is the most widely used, and is based on a large number of assumptions, which are all too often violated in real populations. This is the main reason why studies using F -statistics to infer dispersal patterns have been widely criticized (Whitlock and McCauley, 1999; Cain et al., 2000; Barton, 2001; Rousset, 2001 and references therein). While a stepping stone model is often more realistic, and is also used as a basis to calculate statistics of interest in theoretical papers (Slatkin and Barton, 1989; Rousset, 1996), it is rarely applied to determine dispersal rates in studies of natural populations.

A more fundamental shortcoming of such methods is that for population ecological purposes one usually needs estimates of dispersal rates at the timescale of generations, such as the “instantaneous” dispersal rates determined by direct measurements. The rates obtained by genetic approaches reflect an average over a period of time whose length depends on mutation rates and genetic drift. This means that these indirect (genetic) methods of estimating dispersal rates are of limited use for population ecologists (Hanski, 2001).

Here, we will illustrate how spatial census data, i.e. repeated counts of number of individuals per location and point in time, can be used to estimate dispersal rates. The rationale underlying this method is that natural populations are subject to local stochastic disturbance due to, for instance, demographic stochasticity or the effect of local weather. The creation and dissipation of such perturbations will create a typical covariance structure. These perturbations will dissipate quickly through the population if the population is highly connected and there is much dispersal, if there is limited dispersal the dissipation will be slow.

Various formalisms to describe dispersal have been used in the formulation of ecological models (see Czaran, 1998 for a comprehensive review). Among the different approaches are models that describe a continuum of space in the form of partial differential equations, individuals based models, and multi-patch or metapopulation models. The last category forms a convenient middle ground between realism and tractability and this explains the popularity of this approach (for recent examples in the ecological modelling literature see

Etienne (2004), Hein et al. (2004), Hovestadt and Poethke (2006), Matter (2001), Metzger (2005), Reed and Levine (2005), Pfenning et al. (2004) and Singh et al. (2004).) Here, we describe a generic model for dispersal in coupled populations using a model for population growth and dispersal and from this description derive a method to infer dispersal rates from census data. The model describes an ecological system of coupled local populations which are reasonably close to their equilibrium. As the equilibrium value, its stability properties and the topology of the spatial system can be chosen freely, this approach provides a generic description of diffusive systems. The model thus generalises the description of dispersal used previously (see e.g. Hassell et al., 1991; Rohani et al., 1996; Czaran, 1998; Bascompte and Sole, 1998). Our model extends earlier work in that it explicitly accounts for a large class of topologies and thus avoids simplifying assumptions on the geometry of the habitat. We develop a statistical method to analyze these data and estimate parameters from the covariance structure, this provides a novel and generic way to estimate dispersal rates and is an advance compared to other methods, in particular those based on genetics, in that this provides an estimate at an ecological relevant timescale. We study the distribution of the estimator, and we obtain confidence intervals of the dispersal rate. Finally, we discuss the robustness of this estimation scheme.

2. A generic model for dispersal

We will start this section with a brief explanation of the model structure. For ease of explanation we will start with a strictly deterministic model. We will next use this model as a basis for a stochastic model. For clarity we have formulated the model as a non-structured, single species model without density-dependent dispersal. These model can be easily generalised, in Appendix A we outline how this can be done.

2.1. The deterministic model

The model we will use is a simple linear model describing the changes in population size. The model describes the population dynamics of a local population in the vicinity of its equilibrium.

Let us assume that the population consists of n sub-populations. In the absence of dispersal the linearised dynamics take the form

$$x_{j,t+1} = ax_{j,t}, \quad j = 1, \dots, n \quad (1)$$

where $x_{j,t}$ is the deviation of the density of population j from its equilibrium density at time t . Note that the first index refers to location, and the second to time. The parameter a can be interpreted as the *per capita* growth rate of the population near equilibrium. This is a generic description that can cover a large class of growth models. To see this, suppose that the local population grows according to some growth function F : so that $N_{j,t+1} = F(N_{j,t})$. Suppose there exists an equilibrium population size \bar{N} defined as $F(\bar{N}) = \bar{N}$. The constant a is the derivative of F evaluated at the equilibrium point: $a = (dF/dN)|_{N=\bar{N}}$. If $x_{j,t} = N_{j,t} - \bar{N}$ is the deviation from the equilibrium density \bar{N} ,

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