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New approaches to source–sink metapopulations decoupling demography and dispersal

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ABSTRACT

Source–sink systems are metapopulations of patches with different, and possibly temporally varying, habitat qualities, which are commonly used in ecology to study the fate of spatially extended populations.

We propose new techniques that disentangle the respective contributions of demography and dispersal to the dynamics and fate of a single species in a source–sink system. Our approach is valid for a general class of stochastic, individual-based, stepping-stone models, with density-independent demography and dispersal, provided that the metapopulation is finite or else enjoys some transitivity property.

We provide (1) a simple criterion of persistence, by studying the motion of a single random disperser until it returns to its initial position; (2) a joint characterization of the long-term growth rate and of the asymptotic occupancy frequencies of the ancestral lineage of a random survivor, by using large deviations theory. Both techniques yield formulas decoupling demography and dispersal, and can be adapted to the case of periodic or random environments, where habitat qualities are autocorrelated in space and possibly in time.

In this last case, we display examples of coupled time-averaged sinks allowing survival, as was previously known in the absence of demographic stochasticity for fully mixing (Jansen and Yoshimura, 1998) or partially mixing (Evans et al., 2012; Schreiber, 2010) metapopulations.

1. Introduction

1.1. Ecological background

Metapopulation models (Hanski and Gilpin, 1997) are models of population dynamics where the spatial structure is explicit. They are used to infer the processes which have shaped contemporary range distributions, to predict migration trends or invasion fronts in response to biotic or abiotic changes, to understand the evolution of dispersal, to design protected areas and natural reserves, etc. When the landscape is heterogeneous in terms of habitat suitability, even the mere question of predicting persistence can be a complicated task, since persistence is the result of the intricate interplay between population growth in suitable habitats, population depletion in unsuitable habitats and of how dispersal connects different habitat patches.

In ecology, metapopulation models where habitat suitability is spatially heterogeneous are commonly referred to as *source–sink systems* (Dias, 1996; Holt, 1985; Pulliam, 1988). Roughly speaking, even if the definition of sources and sinks have been subject to debate (Pulliam, 1988; Runge et al., 2006), sources designate habitat patches where the habitat is suitable enough for the population to persist in the absence of dispersal (fundamental niche), and sinks are habitat patches where the population would become extinct in the absence of dispersal, or from which mortality during dispersal is too high to compensate growth. Spatial heterogeneity can be due to biotic environmental variables (predation risk, resource availability) or to abiotic environmental variables, which can either be constant through time (altitude or depth, latitude) or variable through time (precipitation, moisture, irradiance, pH, salinity).

To study the persistence of a single species in a metapopulation, it is common to further assume that population dynamics are *density-independent*. This assumption does certainly not hold for all natural populations, but can at least be used for populations whose persistence is guaranteed whenever their abundance is

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large enough to make this approximation unrealistic. It is also particularly relevant when asking about the establishment success of a new variant arising in few copies (immigrants, genetic mutants, infectives).

The assumption of density-independence allows theoretical ecologists to make use of linear models: *matrix population models* (Caswell, 2001) for deterministic dynamics and *multitype branching processes* (Asmussen and Hering, 1983; Athreya and Ney, 2004; Haccou et al., 2007; Jagers, 1975) for stochastic dynamics. These models are parsimonious in the number of parameters, and the associated mathematical theory is extremely well developed. The extinction probability has a very simple power dependence upon initial population size and composition, and under suitable assumptions, conditional on long-term survival, the geographic distribution of the population stabilizes over time, whereas its overall abundance grows exponentially with an exponent called the *Malthusian growth rate*, or *long-term growth rate*, or simply *growth rate*. In addition, the stable geographic distribution and the long-term growth rate are solutions to a well-known spectral problem. Namely, the growth rate is the maximal eigenvalue of the mean offspring matrix (encompassing both demography and dispersal), and the stable distribution is an associated eigenvector (Li and Schneider, 2002; Seneta, 2006).

A lot of work has been dedicated to extend these results to more complicated situations, like infinite metapopulations (Metz and Gyllenberg, 2001), or, as earlier stressed, because spatial heterogeneity can itself be time-variable, to multitype branching processes in random environment (Athreya and Karlin, 1971b,a; Benaïm and Schreiber, 2009; Haccou and Iwasa, 1996; Haccou and Vatutin, 2003; Kaplan, 1974; Tanny, 1977). More ecologically-related work has investigated in which dispersal strategies are more likely to persist in metapopulations with random environment (Gonzalez and Holt, 2002; Schreiber, 2010; Schreiber and Lloyd-Smith, 2009), which such metapopulations are more prone to persistence (Bascompte et al., 2002), and which introduction strategies are more successful (single large vs. several small) (Haccou and Vatutin, 2003; Wilcox and Murphy, 1985). Specific attention has been given to coupled sinks, that is, metapopulations where each habitat patch is a (time-averaged) sink, but where populations might still persist thanks to dispersal in sparse favorable periods (Evans et al., 2012; Jansen and Yoshimura, 1998; Roy et al., 2005; Schreiber, 2010).

1.2. Goals and outline of the paper

In the present paper, we develop new methods in order to disentangle the contributions of demography and dispersal to the dynamics and outcome of source–sink systems with possibly varying environment. We are interested in criteria for global persistence and in the computation of the long-term growth rate, and of the occupation frequencies of long-lived lineages.

One of the main problems of the spectral approach to the study of metapopulations is that the computation of eigenvalues and eigenvectors is totally opaque to biological interpretation. In particular, the respective contributions of dispersal and demography to the value of the long-term growth rate are very hard, if not impossible in general, to disentangle. As regards the question of persistence, we could ask for an alternative criterion, equivalent to, but simpler than, the positivity of this growth rate, which would avoid computing directly this eigenvalue. Similarly as in Evans et al. (2012), Hastings and Botsford (2006), Krkošek and Lewis (2010), Runge et al. (2006) and Schreiber and Lloyd-Smith (2009), we seek initially to provide such an alternative criterion.

For example, in (st)age-structured models, it is easy to compute the net reproductive number R_0, which is the expected total progeny produced in the lifetime of a single individual. Then thanks to a simple renewal argument, the condition $R_0 > 1$ is seen to be equivalent to possible survival. More rigorously, the set of juvenile offspring of a focal juvenile ancestor forms what is called a *stopping line*, for which it is known that an extended branching property holds (Chauvin, 1986). This idea of the next generation-stopping line has been adapted to the spatial context in Krkošek and Lewis (2010) and Runge et al. (2006), but remains of limited applicability. In the first part of this work, the key idea is to use as an alternative stopping line the set of descendants of a focal ancestor who are the first to return to the ancestor patch. Then by the extended branching property, the population persists with positive probability if and only if the expected number, say G, of individuals on the stopping line is larger than one.

If, as we first assume, the dispersal scheme does not depend on the state of the environment, then G can be expressed separately in terms of the mean offspring numbers in each patch (and in each environmental state) and of the motion of a single random disperser. More specifically, a random disperser is an individual on the metapopulation which follows the dispersal stochastic scheme. We denote by X_n its position at time n so that (X_n) is a Markov chain with transitions given by the dispersal matrix which is denoted by D. In the case when the environment is constant, we let m_i denote the mean number of offspring begot per individual dwelling in patch i, which includes survival during one time-step, regardless of migration. We prove that

$$G = m_1 \mathbb{E}\left(\prod_{n=1}^{T-1} m_{X_n}\right),$$

where T is the first time the random disperser returns to patch 1 (assumed to be the initial patch), which is well defined under some irreducibility assumption. The population persists with positive probability if and only if $G > 1$. It is worth noting that under the irreducibility assumption, the criterion $G_i > 1$ does not depend on the initial patch i. Thus, $G_i > 1$ if there exists some supercritical dynamics somewhere in the graph of the metapopulation, which ensures persistence with positive probability. This way, our formulas are seen to disentangle the effects of demography and dispersal. If all other habitat patches than patch 1 have the same mean offspring m, then the last equality specializes into

$$G = m_1 \mathbb{E}\left(m^{T-1}\right),$$

where the expectation in the last display can now be seen as the probability generating function of the random variable $T - 1$ evaluated at m. We also compute this expectation in some special cases of interest.

In a second part, we use large deviations techniques to prove that the logarithm of the long-term growth rate ρ and the asymptotic fraction (φ_i) of time spent in each patch of the ancestral lineage of a random survivor are given respectively by the maximum and the unique argmax of a functional $R - I$ defined on the set

$$\mathcal{F} = \{(f_i : 1 \le i \le K) : f_i \ge 0,\ f_1 + \cdots + f_K = 1\}$$

of frequencies indexed by the metapopulation, where K is the number of patches, R only depends on the reproduction/survival scheme and I only depends on the dispersal scheme. Our second formula also decouples the demography and dispersal. Namely, denoting $f = (f_i : 1 \le i \le K)$,

$$\log(\rho) = \sup\{R(f) - I(f) : f \in \mathcal{F}\} = R(\varphi) - I(\varphi),$$

where R is a linear functional of frequencies only depending on the mean offspring numbers in each patch

$$R(f) := \sum_i f_i \log(m_i),$$