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# Spectral analysis of simulated species distribution maps provides insights into metapopulation dynamics

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## ABSTRACT

Modelling the spatial dynamics of populations is a basic approach in ecology, in order to understand their observed spatial and temporal patterns, which can be diverse and complex. From the metapopulation perspective, the spatial distribution of populations results from colonization–extinction random process over a network of suitable habitat cells. Hence, evaluating such dynamic is an important issue for the follow-up of populations. Our aim here is to demonstrate that Fourier spectral analysis of population distribution maps can provide insights into metapopulation dynamics in a heterogeneous habitat. We simulated metapopulation dynamics in spatially structured habitat maps and investigated the steady spatial occupancy patterns using Fourier analysis. We showed that there were separable spectral signatures of habitat structure and of population dynamics. Fourier spectral analysis thus provides a promising tool for inferring independent characteristics of metapopulation dynamics and habitat structure from species occurrence data.

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## 1. Introduction

Much literature in ecology is devoted to the study of spatial population dynamics, e.g., for conservation purpose. In this respect, the metapopulation formalism has provided an important contribution. A metapopulation is defined as a set of populations perpetuating itself through a random succession of colonization and extinction events, which is assumed as widely independent from the demography inside populations (Levins, 1969) (for a debate on the assumptions, see Freckleton and Watkinson, 2002). Basically, the metapopulation model with localized colonization events is a contact process (Weitz, 1997; Franc, 2004), which depicts, in physics, binary switching states on a lattice, with a constant death

rate (or inhibition), and a birth rate depending on the state of neighbours (activation) (Harris, 1974; Liggett, 1999). Such processes may result in particular patterns in space and time (Snyder and Nisbet, 2000; Szabó et al., 2002). Diverse models of metapopulations have been investigated, ranging from spatially fully implicit mean field models, where only mean occupancy statistics are considered (e.g., Levins, 1969; Lande, 1987), to fully spatially explicit models, where the binary states are fully modelled in space and time, using for instance cellular automata (e.g., Bascompte and Sole, 1996; Hanski and Gilpin, 1997; Keymer et al., 2000). Our purpose, here, is to provide a new and simple way to characterize the spatial structure of a metapopulation in a spatially structured environment.

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Recent and popular “spatially realistic models” of metapopulations provide analytically tractable solutions to predict the future of a metapopulation in a complex, spatially structured habitat (Hanski, 1997; Moilanen and Hanski, 1998; Hanski and Ovaskainen, 2000). We investigate further the idea that some synthetic spatial statistics can provide relevant and robust insights on the spatial structure of metapopulations. To some extent, the field of landscape ecology has significantly contributed to study the properties of diverse spatial statistics. The purpose was to characterize the structure of complex spatial patterns (O’Neill et al., 1988, 1989; Cain et al., 1997; Li, 2000), and to generate “neutral” models of landscape patterns as null hypotheses (Gardner et al., 1987; Gardner and O’Neill, 1991; O’Neill et al., 1992). Among investigated approaches, spectral analysis has been used to feature, in space and/or time, the frequencies instead of the positions of objects disseminated on a lattice. It indeed allows separating small and large-scale variations, and hence proved to be efficient to analyze patterns induced by multi-scale processes (Platt and Denman, 1975; Muggleston and Renshaw, 1998; Keitt, 2000; Lundquist and Sommerfeld, 2002). Nevertheless, it has never been used for analyzing the complex spatio-temporal patterns produced by metapopulation models in structured habitats.

In this paper, we show that spectral analysis is a valuable tool, which allows interpreting spatial patterns of metapopulations in heterogeneous habitats in terms of simple, ecologically meaningful, components. Specifically, our purpose is to evaluate the capacity of spectral analysis to retrieve in spatial patterns the imprint of key ecological parameters of a metapopulation model. We therefore refer to a metapopulation model using three input parameters: (1) one defining the population turnover (colonization versus extinction), (2) one defining the density of suitable habitat patches, and (3) one defining the aggregation of suitable habitat patches. We then demonstrate the relevance of the Fourier spectral decomposition according to two criteria: (1) its capacity to reflect the variations of the input parameters of the metapopulation model and (2) its capacity to separate the effects of the different input parameters introduced into the model.

## 2. Methods

### 2.1. Simulating habitat maps

We built a  $100 \times 100$  discrete landscape lattice, in which each cell was either suitable or unsuitable for a given species. Different kinds of “neutral”, yet spatially structured landscapes, have been proposed, some of them emphasizing self-similar structures (O’Neill et al., 1992; Keitt, 2000). We considered a simple representation characterized by the density  $p$  of favourable sites along with an aggregation parameter  $q$ , which is the conditional probability for a cell to be suitable if a neighbouring cell is (see Hiebeler, 2000). One thus estimates  $q$  by counting horizontal and vertical pairs of suitable cells over the lattice. Noting 1 and 0 the suitable and unsuitable cells, respectively, and  $P(00)$  the probability of an adjacent vertical or horizontal pair of cells to be 0–0,  $P(11) = pq$  to be 1–1, and  $P(01) = p(1 - q)$  to be 0–1, maps exist if and only if  $P(00) = 1 - p(11) - 2P(01) = 1 - pq - 2p(1 - q) \geq 0$  (Hiebeler, 2000).

Hence a necessary and sufficient constraint on  $p$  and  $q$  is  $q \geq 2 - (1/p)$ . Maps were generated using the C program of Hiebeler (2000), which starts from a random distribution of suitable cells, with density  $p$ , then iteratively moves suitable cells so that to increase  $q$  to the desirable value. Parameters  $p$  and  $q$  were made to vary from 0.1 to 0.9, with 0.1 increments, to build the experimental set of 58 binary habitat maps.

### 2.2. Simulating metapopulation dynamics

For each habitat map, we simulated the dynamics of a metapopulation, under the constraint that populations could not persist in an unsuitable cell, whereas it could be either present or absent in a suitable cell. At each time step, extinction and colonization events occurred. For a given cell at a given time, extinction events followed a binomial distribution with fixed probability  $m$ , which meant that extinction events were independent between neighbouring cells. An occupied cell provided colonizers to neighbouring cells following an exponentially decreasing probability  $c(i) = A \times \exp[-i]$ , where  $i$  was the rank of the neighbourhood ( $i \leq 5$ ). The factor  $A$  controlled the global rain of colonizers. The first neighbourhood contained all cells in the  $3 \times 3$  square around the focal cell, and hence the  $i$ th neighbourhood was a  $(2i + 1) \times (2i + 1)$  square ( $i = 1, \dots, 5$ ), which held  $8i$  cells. Colonizers from a given cell were then expected on average to reach  $C$  cells with  $C = \sum_{i=1, \dots, 5} 8i \times c(i)$ . Interestingly, results obtained in this paper were found to be robust to the choice of the colonisation function, that is, were unchanged when a function decreasing with Euclidean distance was used instead, so we chose to use the simplest representation.

The ratio  $r = m/C$  is the turnover parameter (see Levins, 1969), and has been shown to be a good descriptor of metapopulation properties in spatially realistic models (Hanski and Gyllenberg, 1997). In the basic mean field formulation of metapopulation dynamics (Levins, 1969), the equilibrium density in a uniform habitat directly depends on the turnover  $m/C$  (cf. Hanski and Gilpin, 1997). This ratio also determines the stationary density in a spatially realistic formulation with dispersal limitation (Ovaskainen and Hanski, 2001), as we assumed in our simulations. Moreover, a simple but important necessary condition for local population persistence in uniform habitat is  $C > m$ . We used a set of  $r$ -values ranging from 0.1 to 0.9, with 0.1 increments. The extinction rate  $m$  was set to 0.09 so that setting the  $r$ -value directly gives the colonization function  $c(i) = (m/r)(\exp(-i)/\sum_{k=1, \dots, 5} 8k \exp(-k))$ . Setting  $m$  to a different value would mainly change the time needed to reach equilibrium, yet without effect on the investigated occupancy statistics (see Etienne and Nagelkerke, 2002). Finally, we initiated all metapopulations with a 10% random occupancy of the habitat.

Metapopulation dynamics were then simulated over 8000 generations, in order to reach the equilibrium density of populations (Hanski and Gilpin, 1997). We checked for temporal steadiness of density values over the last 300 generations, and referred to such equilibrium as the steady occupancy state. The model yielded a null equilibrium density of populations when the metapopulation went deterministically extinct. A set of 522 simulations was required to cover the desired variations of parameters  $p$ ,  $q$  and  $r$ . We further made five replicate

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