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 the 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 dynamics 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; Molinan 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; Mugglestone and Renshaw, 1998; Keitt, 2000; Lunnquist 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 16th neighbourhood was a $(2i+1) \times (2i+1)$ square ($i = 1, \ldots, 5$), which held 81 cells. Colonizers from a given cell were then expected on average to reach $C$ cells with $C = \sum_{i=1}^{5} 8i \times c(i)$. 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 $c(i) = (m/r)\exp(−i)/\sum_{k=1}^{5}8k\exp(−k)$. 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
sets of simulations (522 simulations in each set), accounting for different random initial population distributions. It allowed us controlling the generality of patterns found across replicates.

2.3. Characterizing the steady occupancy state

To investigate spatial properties of metapopulations at their steady occupancy state, we averaged the cell binary occupancies over \( N \) time steps. Since the estimates may depend on \( N \), we computed such occupancy probabilities for a wide range of \( N \) values (from 1 to 300). We will call hereafter \( \bar{X} = \{ \bar{X}_i \} \) this estimated spatial variable (\( i \) is the spatial index of cells \((x_i, y_i)\) over the lattice). Each simulated map is characterized by a \((p, q, r)\) triplet, so that we may write \( \bar{X}(N, p, q, r) \). The variation of the three parameters \((p, q, r)\) allows generating a wide diversity of spatial occupancy patterns (Fig. 1a). For instance, the spatial extent of the occupied area over \( N \) population generations can be very small compared to the extent of suitable habitat, even for \( N = 300 \) (Fig. 1b). For all our simulations and analyses on occupancy maps, we used the Mathematica 5.0 software (Wolfram Research, 2003).

2.4. Spectral analysis

Analysing a spatial pattern using the position information in space or time is known to imply statistical caveats, especially because of statistical dependencies according to distance (auto-correlation problems). Instead, spectral analysis allows transforming such information into statistically independent frequency classes. Intrinsically, spectral analysis would be particularly suited to analyse the spatial aggregation of populations, under a localized extinction–colonisation process (Mugglestone and Renshaw, 1996; Couteron, 2001). However, the often non-intuitive nature of the results has largely hampered its use in ecology. Here, we will try to reap the advantages of spectral analysis while still producing intuitively straightforward results.

The spatially structured variable \( \bar{X} \) can be fully described either by its values at sampling points \((x, y)\) or by a series of periodic spatial functions of frequencies \( f_x \) and \( f_y \), and of amplitude \( A \). Hence the \((x, y, \bar{X})\) formulation and the \((f_x, f_y, A)\) spectral formulation are equivalent (space-frequency duality). The power spectrum decomposition relies on this formulation and allows partitioning the variance of \( \bar{X} \) in the spectral domain. It emphasizes spatial scales at which the properties of population dynamics may express themselves.

We hence conducted a 2D spatial Fourier analysis on the 100 \times 100 discrete occupancy maps at the steady occupancy state (time-averaged occupancy maps \( \bar{X}(N, p, q, r) \)), and computed the power spectra. In order to focus on the spatial structure, we did not consider the constant component of spectra, which features the mean population occupancy (see Appendix A). The power spectrum \( PS(\bar{X})((k – 1)/n, (l – 1)/n) \) provided the fraction of the variance in \( \bar{X} \) that relates to the spatial frequency \((f_x = (k – 1)/n, f_y = (l – 1)/n) \) (see Platt and Denman, 1975).

![Fig. 1 – Examples of spatial patterns of metapopulations. (a) Averaged cell occupancies \( \bar{X}(N, p, q, r) \). Three types of spatial structures are exemplified. Unoccupied habitat cells are in black. In occupied cells, time averaged occupancy probabilities (300 generations) are shown in grey levels from 0 (black) to 1 (white): lighter cells have higher mean occupancy. (1) Diffuse metapopulation \((p = 0.8, q = 0.8, r = 0.7)\): overall low local occupancy probability in an extended habitat. (2) Archipelago metapopulation \((p = 0.3, q = 0.7, r = 0.2)\): contrast between high and low occupancy areas in a fragmented habitat. (3) Uniform metapopulation \((p = 0.9, q = 0.9, r = 0.1)\): overall high local occupancy probability in an extended habitat. (b) Occupied habitat at the steady occupancy state. Black cells are unsuitable, grey cells represent potentially suitable sites that were never colonised during the sampling period. White cells indicate sites that were colonised at least once.](image)
An important and well-documented issue in spectral analysis is the necessity for spectral smoothing (e.g. Platt and Denman, 1975). Indeed the power spectrum decomposition provides as many spectral estimates as observations (here 100 × 100 = 10,000 estimates). Smoothing reduces the number of spectral components by pooling them into classes (Appendix A.2), so that more than one degree of freedom is available to estimate the smoothed spectral components. Fixing an upper limit on frequencies, according to the Nyquist criterion, allows avoiding the well-documented aliasing artefact (see Platt and Denman, 1975 and Appendix A). All spectral calculations were performed using Mathematica 5.0 (Wolfram Research, 2003), and statistical analyses using S+Plus 6.2 (Venables and Ripley, 2002).

2.5. Principal component analysis on spectra

In order to describe the variation of the smoothed power spectra, we performed a principal components analysis (PCA), using spatial frequencies as variables and simulations as observations (Couteron et al., 2006). Importantly, in accordance with the general practice, the average over the spectra was set to 0 for each frequency component (centring). Hence, extinct metapopulations had no impact and the analysis focused on persisting metapopulations. We computed correlation values between resulting PCA components and simulation parameters at the steady occupancy state. For a given set of (p, q, r) values, the five replicated patterns obtained with different random initial conditions yielded very similar spectral results (not shown). Hence, we focus the following analysis on one arbitrary reference replicate, for which 227 simulations out of 522 did not go extinct at equilibrium.

3. Results

As expected, the model produced highly diversified spatial occupancy patterns (Fig. 1). We performed spectral analysis on simulated metapopulations over a wide range of (p, q, r) parameters at the steady occupancy state. For a given set of (p, q, r) values, the five replicated patterns obtained with different random initial conditions yielded very similar spectral results (not shown). Hence, we focus the following analysis on one arbitrary reference replicate, for which 227 simulations out of 522 did not go extinct at equilibrium.

3.1. Population turnover versus habitat structure

We consider the Fourier power spectra of time-averaged metapopulation maps \(X(N, p, q, r)\), with \(N = 300\) time steps. There are 25 frequency components, with five classes over the abscissa \(i\), and five classes over the ordinates \(j\) (e.g., Fig. 2). The PCA was performed over all 227 simulations spectra using these 25 components as variables. The first Fourier principal component (FPC1) explained 49.7% and the two first ones (FPC1 + FPC2) 90.8% of total spectra variance. Hence most of the spatial variance at the steady occupancy state can be summarized by two independent gradients in the spectral domain.

The spectral signatures of principal components were characteristic (Fig. 2). FPC1 had positive, slightly decreasing loadings with respect to spatial frequencies \(I_{ij}\) (Appendix A.2). This was a scale-free component, with a power law shape. In contrast, FPC2 revealed opposite contributions of high and low spatial frequencies, with negative and positive loadings, respectively. Hence, FCP2 evidences long distance spatial structuring.

Importantly, FCP1 and FCP2 were correlated with the variables of interest. FPC1 was highly and significantly correlated with the metapopulation parameter \(r\), but not with the aggregation parameter \(q\), while it was weakly though significantly linked to \(p\) (Pearson correlation coefficients; Table 1, above the diagonal). Fig. 3 illustrates the relationship between \(r\) and FPC1 and FCP2. FCP2 was correlated to habitat structure through a high and significant correlation with \(q\), whereas it was not correlated to \(r\). Again there was a lower correlation with \(p\). Finally, there was a high correlation between \(q\) and \(r\).

We conclude that FPC1 and FPC2 captured the uncorrelated part of the variation of \(q\) and \(r\) and that spectral analysis of cell occupancy at the steady occupancy state separated a first scale-free component associated with metapopulation dynamics (FPC1), and a second one associated with habitat
Table 1 – Correlation analysis on metapopulation parameters and principal components for two time ranges of occupancy statistics: over 300 generations (above the diagonal) and over 2 generations (below the diagonal)

<table>
<thead>
<tr>
<th></th>
<th>FPC1</th>
<th>FPC2</th>
<th>( p )</th>
<th>( q )</th>
<th>( r )</th>
</tr>
</thead>
<tbody>
<tr>
<td>FPC1</td>
<td>1</td>
<td>0</td>
<td>0.2914***</td>
<td>-0.0202</td>
<td>-0.6985***</td>
</tr>
<tr>
<td>FPC2</td>
<td>0</td>
<td>1</td>
<td>0.2727***</td>
<td>-0.667***</td>
<td>-0.069</td>
</tr>
<tr>
<td>( p )</td>
<td>0.6220***</td>
<td>0.2513***</td>
<td>1</td>
<td>0.197**</td>
<td>0.2553***</td>
</tr>
<tr>
<td>( q )</td>
<td>-0.0037</td>
<td>-0.6180***</td>
<td>0.197**</td>
<td>1</td>
<td>0.4320***</td>
</tr>
<tr>
<td>( r )</td>
<td>-0.3914***</td>
<td>-0.11</td>
<td>0.2553***</td>
<td>0.4320***</td>
<td>1</td>
</tr>
</tbody>
</table>

The occupancy probabilities are estimated over 300 generations and 2 generations. The Pearson’s correlation coefficients are tested against the null hypothesis with no correlation, using a \( t \)-test (computed with SPlus). Rejecting this hypothesis with a type I error of *5%, **1% and ***0.1%.

aggregation (FPC2). Habitat density \( p \) appeared to be correlated to both principal components, hence our analysis allowed separating out independent effects of \( r \) and \( q \), but not of \( p \).

### 3.2. Temporal sampling effects

The results presented up to now were obtained for time-averaged metapopulation occupancy maps with \( N = 300 \). We also computed several maps with time-averaging over \( N = 1 \) (binary presence–absence from a single observation), 2, 5, 10, 20, 50, 100, 150, 200 and 300 consecutive generations, in order to control for the effect of the number of sampled generations on spatial statistics and spectral patterns. The proportion of variance explained by PCA axes 1 and 2 stabilized when the number of sampled generations, \( N \), was greater than 20 (Fig. 4), a value above which spatial features were broadly unchanged. For lower values of \( N \), more variance was explained by FPC1, and less by FPC2. The sum of both remains fairly constant.

The analysis of correlations between \( p \), \( q \), \( r \), FPC1 and FPC2 showed that the decoupling property on the effects of parameters \( q \) and \( r \) was significant as soon as \( N = 2 \) (Table 1, below the diagonal). Noticeably, the correlation of \( p \) with FPC1 increased as \( N \) decreased, so that its confounding effect was reinforced. It is important to note that spectral decoupling no longer worked for \( N = 1 \); and that at least two successive generations were needed to decouple features of population turnover from those of habitat spatial structure. This implied that we could not capture independent insights for both habitat structure and population dynamics with presence–absence data.

### 4. Discussion

We aimed at identifying through Fourier analysis the spatial features of cell occupancy that are driven by the structure of suitable habitat (binary representation) and those driven by metapopulation dynamics. We demonstrated that the Fourier power spectrum analysis of population occupancy patterns at
equilibrium effectively distinguished one structural feature of habitat \( q \) and a parameter of population turnover \( r \). Below we discuss the potential applications and limitations of the approach.

### 4.1 Insights from spectral analysis

Most of the variance among simulations spectra could be expressed on only two independent PCA axes, one representing populations dynamics (parameter \( r \)), and the other representing habitat structure (parameter \( q \)). The decoupling between dynamics and structure is a new and significant result in the field of metapopulation modelling. By pooling spectral components into classes of frequency, spectral smoothing remove most of the spatial noise introduced by the stochastic nature of simulated maps (Platt and Denman, 1975; see Appendix A.3 for an illustration), and also by the stochastic variation in metapopulation dynamics. Hence, smoothing Fourier spectra allowed us to only retain general features on habitat structure and population dynamics. Moreover, the method may have considerably limited the incidence of the suitable habitat density, \( p \), by removing from spectra the constant component, which features the mean population occupancy.

Interestingly, although the colonization process was very local in our modelling, namely a decreasing function over the neighbours within a path of five cells, we observed that its spatial imprint could be perceptible not only locally but also at large spatial scales. Such emergence is a signature of larger-scale dynamical features, which are known in the more general field of contact processes (Weitz, 1997; Oborný et al., 2005), and result from self-organization. For low habitat occupancy rates (large \( r \) values), large parts of the suitable habitat remained unoccupied over \( N = 300 \) generations, whereas the occupied part was very aggregated (see Fig. 1b left). The spatial structures of metapopulations are largely independent from habitat spatial structure.

Hence, we highlight that local metapopulation processes can produce patterns at large scales, so that cross-scale spatial information might be important and informative. Spectral analysis, though little used in ecology, may provide a most interesting tool to capture such ecological determinants of metapopulation spatial structure. Alternative methods currently focusing on potential habitat modeling, and invoking ad hoc spatial structures (Lichstein et al., 2002), may not be able to clearly distinguish the real determinants.

### 4.2 Applications and limitations

We showed that sampling effects became strong for a very low number of sampled generations, i.e., for low \( N \) values. In particular, when \( N = 1 \) (presence–absence binary data), that is, with a single temporal observation, spectral decoupling was no longer present. The Fourier decomposition technique is indeed a useful and powerful tool for analyzing continuous signals, but, in a finite space, it becomes less efficient for discrete signals. Therefore, the Fourier power spectrum analysis is not suited to binary presence–absence maps, and this may explain why we failed to detect spectral decoupling in binary maps. It is an open question whether the use of more suited methods, such as the Haar wavelet decomposition (Chui, 1992), would reveal the patterns we obtained with time averaged data.

We used Fourier spectral analysis because it relies on a rather simple numerical transformation, with well-documented properties, and because very powerful algorithms are available (such as fast Fourier transform, FFT). Hence, it is very powerful for treating large data sets on regular grids and this allowed us to draw strong conclusions. However, this method is not suited for the more frequently used irregular sampling designs, and that may be an important limitation when studying real datasets. It remains to be determined whether the use of other spectral methods, such as the Principal Coordinates of Neighbor Matrices (Borcard and Legendre, 2002), may detect similar patterns in situations involving irregular spatial sampling.

We noticed that a local colonization/extinction process could induce on FPC1 a characteristic scale-free pattern, probably self-organized and self-similar in space and time (see also Weitz, 1997), whereas the large-scale structure of the habitat was highlighted on FPC2. The method highlights the difference between a scale free pattern due to contact processes and a scaled habitat pattern. It is an open question whether the decoupling is conserved if the habitat structure is itself scale free. Another limitation is the use of a local binary habitat, which depicts the realm of many experimental metapopulation systems, yet with very specific requirements (e.g., cliff dwelling Centaurea corymbosa, Colas et al., 1997). Alternatively, we should further generalise the habitat model to account for continuous gradients, especially to deal with ecologically important bioclimatic gradients.

Inference will obviously be the ultimate goal. The decoupling property suggests that we can extract from species distribution spectra some unambiguous information on metapopulation dynamics. We assumed that the metapopulation parameter, \( r \), did not vary across space or time, within the limits of ecological time and space scales, thus being consistent with the framework in conservation biology (Hanski, 1998). Although Fourier analysis might fail with binary presence–absence data, we showed that only two time steps were required to get some characteristic spectral decoupling properties. However, in order to get a clearer pattern, it may be more reasonable to use at least five generations for capturing the spectral decoupling. Moreover, it is an important topic to deal with a true metapopulation system, and to accordingly work on an appropriate spatial and temporal scale (Ehrén and Eriksson, 2003; Freckleton and Watkinson, 2003; Baguette, 2004). Specifically, to account for the basic assumptions, the time step must be clearly longer that the required time to reach demographic equilibrium within populations, and the spatial extent of local lattice cells must be large enough to feature entire populations. Noticeably, for instance, the time step would be shorter when considering any metapopulation of ruderal, annual plant, which may reach the demographic equilibrium very fast, than any metapopulation of long-lived plants. This is a matter of species biological strategies. This implies that our technique could be applied directly to study highly dynamic species, for which data over only several years are available. Metapopulation data concerning butterflies (e.g., Melitaea cinxia, Hanski et al., 1994;
Proclossiana eunomia, Schtickzelle et al., 2002) appear to meet such requirements.

In summary, our metapopulation model relied on only three ecological variables: population turnover $r$, binary habitat density $p$ and habitat aggregation $q$. Although these variables were somewhat correlated because of constraints on the metapopulation persistence and on the habitat spatial structure, the Fourier analysis retained two characteristic structures that are independently related to parameters $r$ and $q$, that is, to population turnover and habitat aggregation, respectively. Hence, this study offers a new ecological application of spectral analysis that can provide independent insights on species habitat spatial structure and population dynamics from field occurrence data.

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Appendix A

A.1. Fourier spectral analysis

The mean occupancy map, $\bar{X}$, features, at coordinates $(x, y)$ throughout the lattice, the time average occupancy probabilities, with float values. The two-dimensional discrete Fourier transform for $\bar{X}$ is a function depending on the two dimensions of geographical frequencies, hereafter indexed $f_x = (k - 1)/n$ and $f_y = (l - 1)/n$:

$$\gamma(\bar{X})\left(\frac{k-1}{n}, \frac{l-1}{n}\right) = \frac{1}{n^2} \sum_{j=1}^{n^2} \bar{X}_j e^{2\pi i [(x_j - 1)(k - 1) + (y_j - 1)(l - 1)]/n}$$

It is a complex number, with $k = \{1, \ldots, n\}$ and $l = \{1, \ldots, n\}$. $(k - 1)/n$ and $(l - 1)/n$ are spatial frequencies according to abscissa and ordinates, respectively. When these frequencies are both set at 0, we have $\gamma(\bar{X})(0, 0) = 1/n^2 \sum_{j=1}^{n^2} \bar{X}_j = \bar{X}$, which is the general mean over space and time. As we wished to focus on the spatial structure of populations, we

Fig. A1 – Fourier power spectrum of the noisy, regular point pattern (a), before smoothing (b), and after smoothing (c). The lattice (a) features cells of value 1, among which are spread regularly spaced cells, with an average value of 0. These cells actually feature values between $-0.2$ and $0.2$, drawn in a uniform random distribution. Their regular spacing is 10 in both horizontal and vertical directions.
chose to subtract this constant component when investigating spectra.

For a discrete map, the Nyquist sampling theorem states that high spatial frequency Fourier components are biased and must be set to 0. It leads to only retain the frequencies for \( k = \{1, \ldots, n/2\} \) and \( l = \{1, \ldots, n/2\} \) (see Platt and Denman, 1975), with \( n/2 = 50 \) for the lattice we used.

The power spectrum is derived from the expression of the basic Fourier spectrum through its modulus: \( PS(\bar{X})(f_x, f_y) = \frac{1}{2} \bar{X}(f_x, f_y) \bar{X}(f_x, f_y) \).

### A.2. Smoothing formula

Given an integer \( s \) divisor of \( n \), we partitioned the initial spatial frequencies \((f_x, f_y)\) into intervals \( I_{i,j} \): \[
I_{i,j} = \left( \frac{s(i-1)}{n}, \frac{s(i-1)}{n} \right), \quad \text{for} \quad i, j = 1, \ldots, \text{Int}\left(\frac{n}{s}\right)
\]

Int is the integer part function (rounded to the lower integer in absolute value). The smoothed power spectrum is then:

\[
\text{smooth } PS(\bar{X})(l_{i,j}) = \sum_{(f_x, f_y) \in I_{i,j}} PS(\bar{X})(f_x, f_y) / k. \quad \text{We took } s = 10.
\]

### A.3. Illustration

We provide in Fig. A1 an example of Fourier analysis, using a simple, regular point pattern over a square lattice, with \( n = 100 \). Cells are of value 1, except in regularly spaced cells of average value 0, but which actually range between 0.2 and 0.2 according to a random uniform variation (Fig. A1a). The raw Fourier spectrum (Fig. A1b) features, on a lattice, the components \( \Im(\bar{X})(k-1)/n, (l-1)/n \) with \( k \) as abscissa and \( l \) as ordinates, their upper limit being \( n/2 = 50 \), according to the Nyquist’s rule. After removing the constant component \( (k=1, l=1) \), one can detect prominent, regular spatial frequencies (white cells), yet being blurred by a large noise on all the components (grey levels). When smoothing the spectrum, we provide smooth component \( PS(\bar{X})(l_{i,j}) \) on intervals \( I_{i,j} = [s(i-1)/n, (s(i-1)-1)/n] \times [s(j-1)/n, (s(j-1)-1)/n] \), with width \( s \) being set to 5 (Fig. A1c). The regular frequency components become obvious, with no noise left. This illustrates the importance of smoothing, in order to remove noise in spectra.

**References**


