The clumping transition in niche competition: a robust critical phenomenon

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Abstract. We show analytically and numerically that the appearance of lumps and gaps in the distribution of $n$ competing species along a niche axis is a robust phenomenon whenever the finiteness of the niche space is taken into account. In this case, depending on whether the niche width of the species $\sigma$ is above or below a threshold $\sigma_c$, which for large $n$ coincides with $2/n$, there are two different regimes. For $\sigma > \sigma_c$ the lumpy pattern emerges directly from the dominant eigenvector of the competition matrix because its corresponding eigenvalue becomes negative. For $\sigma \leq \sigma_c$ the lumpy pattern disappears. Furthermore, this clumping transition exhibits critical slowing down as $\sigma$ is approached from above. We also find that the number of lumps of the species distribution versus $\sigma$ displays a stair-step structure. The positions of these steps are distributed according to a power law. It is thus straightforward to predict the number of groups that can be packed along a niche axis and this value is consistent with field measurements for a wide range of the model parameters.

Keywords: pattern formation (theory), pattern formation (experiment), population dynamics (theory), population dynamics (experiment)
## 1. Introduction

An important problem in ecology is that of how closely species can be packed in a natural environment [1]. A usual way to approach this issue is by considering the species distributed along a hypothetical one-dimensional niche axis [1]. To fix ideas one may consider the niche axis as a gradient that is related to the size of organisms. Each species $i$ is represented by a normal distribution $P_i(\xi) = \exp[-(\xi - \mu_i)^2/2\sigma^2]$ centered at $\mu_i$, corresponding to its average position $\xi$ on this niche axis, and with a standard deviation $\sigma$, which measures the width of its niche. The competition for finite resources among the $n$ species can be described by a Lotka–Volterra competition model (LVCM):

$$\frac{dN_i}{dt} = r_i \frac{N_i}{K_i} \left( K_i - \sum_{j=1}^{n} a_{ij} N_j \right),$$

(1)

where $N_i$ is the density of species $i$, $r_i$ is its maximum per capita growth rate, $K_i$ is the carrying capacity of species $i$ and the coefficient $a_{ij}$ is the coefficient of competition of species $j$ with species $i$. It seems natural to assume that the intensity of the interaction between two species $i$ and $j$ depends on how close they are along the niche axis. A measure of this is provided by the niche overlap, i.e. the overlapping between $P_i(\xi)$ and $P_j(\xi)$. The competition coefficients $a_{ij}$ can be computed by using the MacArthur and Levins overlap (MLO) formula [2]:

$$a_{ij} = \frac{\int_{-\infty}^{\infty} P_i(\xi)P_j(\xi) d\xi}{\int_{-\infty}^{\infty} P_i^2(\xi) d\xi} = e^{-(\mu_i-\mu_j)/2\sigma^2}.$$

(2)

Recently Scheffer and van Nes [3] found by simulations that the combination of LVCM (1) with MLO (2) yields long transients of lumpy distributions of species along the niche axis.
the niche axis. (For asymptotic times, the lumps are thinned out to single species unless a stabilizing mechanism/term is included, as was shown in [3].)

This phenomenon of spontaneous emergence of self-organized clusters of look-alikes separated by gaps with no survivors was dubbed by the authors self-organized similarity (SOS). It was recognized as an important new finding in an established model in ecology [4, 5]. In addition, there is empirical evidence for self-organized coexistence of similar species in communities ranging from mammal [6] and bird communities [7] to lake plankton [8].

However, there has been some controversy as regards whether this lumpy distribution of species is indeed a robust result or rather depends strongly on details of the model, like the competition kernel [9, 10].

Here we show that the lumpy pattern is a robust phenomenon provided one takes into account the finiteness of the niche axis. Thus, truncation, besides being a crucial assumption which guarantees clustering, allows the analytical computation of the eigenvalues and eigenvectors of the competition matrix $A$ with elements $a_{ij}$ given by (2). Furthermore, we show that ultimately solving the linear problem is enough to get both the transient pattern—lumps and gaps between them—and the asymptotic equilibrium. The plan of this work is as follows.

Since an analytic solution for realistic conditions—species randomly distributed along a finite and non-periodic niche axis, each with a different per capita growth rate $r_i$ and carrying capacity $K_i$—is not possible, we will consider in section 2 a series of simplifications. We get an analytic expression for the state of this simpler system, in terms of the dominant eigenvector of $A$. It provides a qualitatively good description of the system for not too short times and becomes very good for asymptotic times. Part of the material of this section was presented in a previous short paper [11], but there are some important differences like considering a less rough approximation together with some steps being better explained.

In section 3 we show, using simulations, that all these simplifications do not destroy SOS: lumps and gaps remain in the case of a finite linear niche axis no matter whether the niche is non-periodic (i.e. it has borders), or the species are randomly distributed, or $r$ and $K$ change from species to species. Indeed we go further and show that SOS occurs in niches of more than one dimension or when interaction kernels different from the Gaussian kernel are considered.

In section 4 we show that the prediction of the number of lumps as a function of $\sigma$ is in good agreement with measures in several ecosystems [1], provided $\sigma$ is greater than a threshold value $\sigma_c$. For this critical value there occurs a bifurcation which is responsible for the clumping transition.

Section 5 is devoted to conclusions and to putting our results in a proper perspective, addressing some general concerns about SOS and comparing with other different approaches.

2. An analytical proof of self-organized similarity in a simplified case

We start by considering the following simplifications:

$S1$—The $n$ species are evenly distributed along a finite niche axis of length $L = 1$, i.e. $\mu_i = (i - 1)/n (i = 1, \ldots, n)$.

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To avoid border effects, the niche is defined as circular, i.e. periodic boundary conditions (PBC) are imposed. This is done by just taking the smallest of $|\mu_i - \mu_j|$ and $1 - |\mu_i - \mu_j|$ as the distance between the niche centers.

All species have the same per capita growth rate which we take equal to 1: $r_i = 1$ for all $i$.

The carrying capacity $K$ is also homogeneous: $K_i = K$ for all $i$.

Under the simplifying conditions $S3$ and $S4$ the system of equations (1) reduces to

$$\frac{dx_i}{dt} = x_i \left( 1 - \sum_{j=1}^{n} a_{ij} x_j \right),$$

where $x_i$ is the density of species $i$, normalized by its carrying capacity $K_i (x_i = N_i/K_i)$.

An equilibrium of the system (3) is specified by a set of densities $x_i^*$, one for each species $i$, verifying

$$x_i^* \left( 1 - \sum_{j=1}^{n} a_{ij} x_j^* \right) = 0.$$ (4)

A standard procedure for checking the stability of this equilibrium is linear stability analysis—that is, considering initially small, disturbances $y_i(0)$ from the equilibrium values $x_i^*$ and studying their fate $y_i(t)$ as the time grows. Let us take $x_i^* = x^* \forall i$ which, by virtue of conditions $S1$ and $S2$, is an exact equilibrium. The evolution equation for $y_i(t)$ can be written as

$$\frac{dy_i}{dt} = -(x^* + y_i(t)) \sum_{j=1}^{n} a_{ij} y_j(t).$$ (5)

Since the coefficients of the matrix $A$ given by (2) are symmetric, in the eigenvector basis $\{v_i\}$ it becomes diagonal with all its eigenvalues $\lambda_i$ real. Hence integrating equation (5), and using that $y_i(0)$ is small, $y_i(t)$ can be approximated by

$$y_i(t) \simeq y_i(0) e^{-x^* \lambda_i t}.$$ (6)

Thus, for asymptotic times, $y$ becomes proportional to the dominant eigenvector $v_m$, the one associated with the minimum eigenvalue of $A$, $\lambda_m$, i.e.

$$y(t) \propto e^{-x^* \lambda_m t} v_m \quad \text{for large times.}$$ (7)

We will show that, for a wide range of the parameters $n$ and $\sigma$, $\lambda_m(n, \sigma)$ is in general negative (see below). Hence, from (7), $y$ is amplified over time instead of decaying to zero (as would happen in the case of a positive $\lambda_m$). Therefore, for large times, from (5) we can express the time derivative of $x$ as

$$\frac{dx}{dt} = -x(t) \lambda_m v_m,$$ (8)

and by integration we get the approximated solution given by

$$x(t) \approx e^{-\lambda_m v_m t} \quad \text{for large times.}$$ (9)

We later checked by means of simulations that all the derivations below are independent from the initial condition: the same results are obtained when starting from a completely random assigning of densities.
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Analytic expressions for the eigenvalues and eigenvectors of \( A \) are not known for the general case of random distributions of species on a niche axis with arbitrary boundary conditions. However, for the simpler case when the \( n \) species are evenly spaced along the niche axis, \( \mu_j = (j - 1)/n \) (with the index \( j = 1, \ldots, n \)), and PBC (the simplifying conditions S1 and S2), \( A \) becomes a matrix whose rows are cyclic permutations of the first one:

\[
\begin{bmatrix}
c_1 & c_2 & \cdots & c_{n-1} & c_n \\
c_n & c_1 & \cdots & c_{n-2} & c_{n-1} \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
c_2 & c_3 & \cdots & c_n & c_1 \\
\end{bmatrix}
\]

with \( c_j(n, \sigma) = e^{-(\tilde{j} - 1)/2n} \), where the tilde stands for \((\text{mod } (n + 2)/2)\), implementing the PBC. For this case, the eigenvalues \( \lambda_k \) and the components of the eigenvectors \( v^k \) \((k = 1, \ldots, n)\) are given by [12]

\[
\lambda_k = \sum_{j=1}^{n} c_j(n, \sigma)e^{2\pi (k-1)\mu_j} = \sum_{j=1}^{n} c_j(n, \sigma)e^{2\pi (k-1)(j-1)/n},
\]

(10)

and

\[
v^k_j = n^{-(1/2)}\left[\cos(2\pi(k-1)\mu_j) + \sin(2\pi(k-1)\mu_j)\right] = n^{-(1/2)} \left[\cos \left( \frac{2\pi (k-1)(j-1)}{n} \right) + \sin \left( \frac{2\pi (k-1)(j-1)}{n} \right) \right].
\]

(11)

Since the matrix \( A \) is symmetric, \( c_j = c_{n+2-j} \). Therefore, from (10) one can see that the eigenvalues occur in pairs: \( \lambda_k = \lambda_{n-k} \), with the exception of \( \lambda_1 \) (and of \( \lambda_{n/2+1} \) if \( n \) is even). Furthermore, these paired eigenvalues can be expressed as

\[
\lambda_k = 2 \sum_{j=2}^{n/2} c_j(n, \sigma) \cos[2\pi (k-1)(j-1)/n].
\]

(12)

Equation (10) can be used to determine the index \( k = m \) that gives the minimal eigenvalue, for \( n \) and \( \sigma \) given, \( \lambda_m(n, \sigma) \) (as we have just seen, the index \( k = n - m + 2 \) produces the same value). The surface depicted in figure 1 corresponds to \( \lambda_m(n, \sigma) \) computed for a grid \( 2 \leq n \leq 200, \) and \( 0.05 \leq \sigma \leq 0.5 \). Notice that \( \lambda_m \) is negative except for small values of \( \sigma \) and becomes positive when \( n < 8 \). The substitution of the dominant eigenvector \( v^m \), which from (11) has \( m - 1 \) peaks and \( m - 1 \) valleys, into (9) allows us to predict the distribution of species for long enough times.

The results that we got were checked by numerical simulations. In these simulations the initial values for the \( x_i \) are random numbers between 0 and 1. Then the system of differential equations (ODE) is integrated for a given final time. In figure 2 we compare this analytical approximation with simulations. For instance, if \( n = 200 \) and \( \sigma = 0.15 \) we get \( m = 5 \) (and \( m = 200 - 5 + 2 = 197 \)), \( \lambda_m = 0.3938 \) and the components of \( v^m \) are given

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Figure 1. The minimal eigenvalue of $A$, $\lambda_m$, determined from equation (10), as a function of $n$ and $\sigma$. The black spot denotes the point $n = 200$ and $\sigma = 0.15$. Inset: a zoom of $\lambda_m$ versus $\sigma$ for $n = 200$ in the interval $0.05 \leq \sigma \leq 0.1$.

by $\sqrt{1/n} \sin[8\pi\mu_j] + \sqrt{1/n} \cos[8\pi\mu_j]$. Panel (A) of figure 2 is for $t = 1000$ generations. The agreement is quite good and the quality of the agreement improves with time, until it becomes very good when the lumps are thinned to single lines as is shown in panel (B). This happens because we are not considering any lump stabilizing term like the one considered in [3]. Notice that ultimately the lumps and gaps coincide, respectively, with the $m - 1$ maxima and minima of $v^m$. The integer $m$, which gives the minimal eigenvalue, is a function of the width $\sigma$ of the niche, $m = m(\sigma)$. It does not depend on $n$ provided $n$ is large enough. Nevertheless, as we will show in section 4, $m$ becomes a function of $n$ and $\sigma$ for small values of both these parameters. For example, for $\sigma = 0.15$, $m - 1 = 4$ for all even $n$ greater than or equal to 8. This lower $n$ limit arises because the maximum possible number of peaks that can be accommodated with $n$ vector components is $n/2$ (half of the components of $v^m$ pointing up and the other half down). So in this particular case $n/2$ must be greater than or equal to 4, and, in general, $n/2$ must be greater than or equal to $m - 1$.

Another remarkable result as regards $m$ is that it is always an odd number (and then the number of clumps is even). The reason for this can be traced to the cosines appearing in (12) making contributions to the eigenvalues of opposite signs: positive for odd $k$ and negative for even $k$. As a consequence, the number of peaks, equal to $m - 1$, is always even.

4 The gray lines, generated from $v^m$, are actually lines. They were drawn thick just to show their coincidence with the black thin lines produced by simulations.

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3. Self-organized similarity persists under more realistic assumptions

In order to consider more realistic assumptions, abandoning the simplifying conditions S1–S4, we rely in the following exclusively on simulations. Since the emphasis in SOS is on transient maintenance of clumps of similar species, one might wonder about how initial conditions determine the results, and how species that are being driven extinct ever managed to get up to high density in the first place. So, as before, the ODE system is integrated starting from initial $x_i$ which are random numbers between 0 and 1. We checked in all the cases that changes in the initial populations do not introduce qualitative changes.

3.1. From evenly to randomly distributed species

What happens in the general case of species randomly distributed over the niche axis? In this case the spectrum and $\mathbf{v}_m$ are obtained numerically from $\mathbf{A}$. It turns out that simulations produce quite similar results. We illustrate this in figure 2 where we plot the population fractions normalized to 1, $\hat{x}_i = x_i / \sum_{i=1}^{n} x_i$, for the particular parameter values $n = 200$ and $\sigma = 0.15$. The resemblance is clear when comparing panels (C) and (D) with, respectively, (A) and (B). In fact, the spectra of eigenvalues in the two cases are

Figure 2. Population fractions $\hat{x}_i$ for $n = 200$ and $\sigma = 0.15$. In black results from a simulation after $t$ generations and in gray $\exp[-\lambda_m \mathbf{v}_m^m t]$. (A) and (B): species evenly spaced along the niche axis for $t = 1000$ and $t = 10000$ generations, respectively. (C) and (D): species randomly distributed along the niche axis for $t = 1000$ and $t = 10000$. 

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Table 1. Eigenvalues of $A$ for $n = 200$ and $\sigma = 0.15$, ordered from small to large, i.e. $\lambda_m = \lambda_1 = \lambda_2$.

|                | Evenly spaced | Randomly distributed |
|----------------|---------------|----------------------|
| $\lambda_1$   | $-0.3938$     | $-0.4 \pm 0.01$     |
| $\lambda_2$   | $-0.3938$     | $-0.4 \pm 0.01$     |
| ...            |               | ...                  |
| $\lambda_{198th}$ | $45.391$     | $46 \pm 0.96$       |
| $\lambda_{199th}$ | $45.391$     | $46 \pm 0.96$       |
| $\lambda_{200th}$ | $104.387$    | $105 \pm 1.93$      |

very similar as is shown in table 1 (the values on the right correspond to averages among simulations).

3.2. Taking into account border effects in a linear niche axis

We also analyzed what happens when a linear, instead of a circular, niche axis (PBC) of length $L$ is considered. The competition coefficients for these open boundary conditions (OBC) are now given by

$$a_{ij} = e^{-(\mu_i - \mu_j)^2/2\sigma^2} \frac{\text{erf}((2L - \mu_i - \mu_j)/2\sigma) + \text{erf}((\mu_i + \mu_j)/2\sigma)}{\text{erf}((L - \mu_i)/\sigma) + \text{erf}(\mu_i/\sigma)}. \quad (13)$$

When using competition coefficients given by (13) with $L = 1$, again, a lumpy pattern emerges although it shows some quantitative differences. For example, a four-lump pattern occurs for smaller values of $\sigma$, e.g. $\sigma = 0.12$ instead of $\sigma = 0.15$ (panel (A) in figure 3). Additionally, although $\lambda_m$ is still negative, due to the factor multiplying the Gaussian in (13), the matrix $A$ is no longer symmetric and so there appear complex eigenvalues.

3.3. The effect of a non-uniform growth rate

Simplification $S3$ was to consider a uniform $r$. Indeed it is simple to realize that an $r$ varying from species to species does not introduce major changes. This is because what are relevant for the equilibrium values $x_i^*$ are the terms between brackets in the LVCM equations (see panel (B) in figure 3).

3.4. The effect of the heterogeneity in the carrying capacity

We find that when variations $\pm \delta K_i$ of the carrying capacity around an average value $\bar{K}$ occur in such a way that the amplitude of these fluctuations, $\delta K_{\text{max}}$, is no greater than 10% of $\bar{K}$, the lumpy pattern changes but is similar to the one corresponding to the homogeneous case. If, in addition, one assumes that neighbor species along the niche axis have similar carrying capacities, and larger variations are only possible for species which are far away on the niche axis, then larger values of $\delta K_{\text{max}}/\bar{K}$ still preserve SOS (panel (C) in figure 3). On the other hand, strong random variations of the carrying capacity along the niche axis in general destroy the SOS pattern.

In figure 3 we show the population fractions obtained when the more realistic conditions 2–4 are gradually taken into account. In the three panels we plot the results

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Figure 3. Fraction of species $\hat{x}_i$ (black bars, left vertical axis) for $n = 200$, $\sigma = 0.1$ and open boundary conditions (coefficients given by (13) with $L = 1$) after 500 generations and the corresponding entropy for each lump and gap region $S_r$ (gray dashed lines, right vertical axis). (A) Uniform maximum growth rate $r$ and carrying capacity $K$. (B) Varying $r$ (the $r_i$ are random numbers with average value equal to 1) and uniform $K$. (C) Varying $r$ (the $r_i$ are random numbers with average value equal to 1) and $K$ ($\delta K_{\text{max}}/\bar{K} = 0.2$; see the text) from species to species.

produced by simulations starting from the same initial distribution of populations. Panel (A) corresponds to OBC and homogeneous $r$ and $K$, panel (B) to OBC, heterogeneous $r$ and homogeneous $K$ and panel (C) to OBC and heterogeneous $r$ as well as $K$. Notice that although the lumpy structure becomes less clear as the original restrictions are lifted, it is still recognizable in panel (C). In order to provide a more quantitative test for the clumping to the favorable niches, it is necessary to introduce an observable which measures species coexistence or diversity. Among the different indices proposed to measure species diversity perhaps the most common is the Shannon–Wiener index [13], [14], or in physics language the well known entropy $S$, defined by

$$S = -\sum_{i=1}^{n} \hat{x}_i \ln \hat{x}_i.$$  

Moreover, entropy analysis has been used to quantify species diversity and niche breadth [15] and to recognize ecological structures (see [16] and references therein). Therefore we proceed as follows. From the homogeneous $r$ and $K$ situation we obtain the modulation along the niche axis determining the number and positions of lumps and

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gaps. In this specific case there are four lumps separated by gaps all of the same length. Thus we divide the niche axis into nine regions: four lumps and three gaps between them, all seven of length 0.125, plus two smaller gaps at the niche borders completing the remaining length of 0.125. The amount of entropy \( S_r \) calculated for each region \((r = 1, 2, \ldots)\), measures the species diversity (represented by gray dashed lines in panels (A)–(C)). Notice that the profiles of \( S_r \) for the three situations are similar although, as expected, they offer more clear cut evidence of lumps and gaps for the homogeneous situation of panel (A): the entropy is in general lower (higher) at the gaps (lumps of coexistence) than in panels (B) or (C). Therefore, we conclude that the simplifications considered do not introduce substantial changes and that SOS survives in more realistic conditions.

3.5. Other competition kernels and multi-dimensional niches

It was argued that the formula (2) is a special case and that competition coefficients are typically non-Gaussian \([9, 17]\). Some recent analyses explore more general non-Gaussian competition kernels of the form \([18]\)

\[
a_{ij} = e^{-\frac{(\mu_i - \mu_j)^2}{2\sigma^2}},
\]

which reduces to the Gaussian one for \(p = 2\). Moreover, it was claimed that Gaussian competition does not lead to patterns but is a borderline case between pattern and non-pattern regimes \([10]\). However, this depends on whether or not one takes into account the finiteness of the niche axis. When it is taken into account, as we do by using a truncated kernel, \(p = 2\) is no longer a border case. Rather, the lumpy pattern occurs for any real kernel exponent \(p\) above 1, for example, \(p = 1.5\), as is shown in panel (A) of figure 4 for \(\sigma = 0.19\). This is because the only change in the formula for the eigenvalues (10) is in the coefficients \(c_j(n, \sigma)\) which, for a general value of the exponent \(p\), are given by \(c_j(n, \sigma) = e^{-\frac{(j-1)^2}{2\sigma^2}}\), while the expression (11) for the eigenvectors remains unchanged.

Panel (B) of this figure is a plot of the components of the \(v^m\) showing that its peaks (valleys) coincide with the lumps (gaps). Another common criticism is that it is not very realistic to consider a one-dimensional niche; rather, niches (utilizations) in general are multi-dimensional \([19, 20]\). It turns out that a multi-dimensional niche only makes the mathematics a little bit less straightforward. Suppose that the \(n\) species are distributed at random in a two-dimensional niche with axes \(\mu_1\) and \(\mu_2\). Then one can assign an index \(i\) to each population, located at the point in the niche space given by a couple \((\mu_1, \mu_2)\), and group them into a vector of \(n\) components. Therefore, the expression for the competition coefficient between species \(i\), located in this niche space at a point of coordinates \((\mu_{1i}, \mu_{2i})\), and species \(j\), at \((\mu_{1j}, \mu_{2j})\), can be written as

\[
a_{ij} = e^{-\frac{(\mu_{1i} - \mu_{1j})^2 + (\mu_{2i} - \mu_{2j})^2}{2\sigma^2}}.
\]

It turns out that this preserves the cyclic property of the \(A\) matrix—its rows are cyclic permutations of the first one—a property required to get the expressions for the eigenvalues (10) and the eigenvectors (11) \([12]\). Figure 5 shows the results for \(\sigma = 0.2\). It shows a general result that we found: if in the case of a one-dimensional niche \((d = 1)\), for a given value of \(\sigma\), there are \(m - 1\) lumps, for a two-dimensional niche \((d = 2)\) there occur \((m - 1) \times (m - 1)\) lumps (for \(\sigma = 0.2\) there are two lumps for \(d = 1\) while for \(d = 2\) there are four lumps).
4. The dependence of clumping on the niche width and the clumping transition

How close species can be packed along the niche axis is commonly measured by the parameter $d/\sigma$, where $d$ is the separation between species [1]. In the case of the model under consideration, $d$ can either measure the separation between (a) lumped groups of species, persisting during long transients, or (b) surviving species (one per lump), for asymptotic times. So we get either an estimate for the species packing or one for the group packing. In any event, this distance coincides with the inverse of the number of peaks of $v^m$, which depends on $\sigma$, and is given by $n_\infty(\sigma) = m(\sigma) - 1$. Figure 6 shows $n_\infty$ for $\sigma$ ranging from 0.05 to 0.5 and the number of species fixed to $n = 200$. There are a series of steps, located at values $\sigma_s$, that become wider as $\sigma_s$ increases. The height of these steps is always 2. This is because, as we have seen in section 2, the number of peaks of $v^m$ is always an even number. That is, if $\sigma^-_s$ ($\sigma^+_s$) corresponds to $\sigma$ tending to $\sigma_s$ on the left (right), then $n_\infty(\sigma^-_s) = n_\infty(\sigma^+_s) + 2$. For example, if $\sigma > \sigma_s \simeq 0.169$ then $v^m$ always has two peaks, below this value the number of peaks jumps to 4, and so on. We find that when $\sigma$ tends to $\sigma^+_s$, $n_\infty$ can be fitted with the power law $0.099\sigma_s^{-1.73}$ (the dashed line in figure 6). The packing parameter in the different step regions can be approximated, by taking the number of peaks at each $\sigma_s$ as the semi-sum of the numbers of peaks on each
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Figure 5. Distribution of species in a two-dimensional niche of coordinate axis $\mu_1$ and $\mu_2$ for $n = 15 \times 15 = 225$ species, and $\sigma = 0.2$, PBC after 100 generations. $2 \times 2 = 4$ clumps are observable.

side of the step, as

$$
\frac{d}{\sigma_s} \approx \frac{1}{\sigma_s \frac{1}{2}(n_\infty(\sigma_s^+)) + n_\infty(\sigma_s^-))} = \frac{1}{\sigma_s + 0.09\sigma_s^{-0.75}}.
$$

(16)

This quotient varies from approximately 1.96 for the first step, at $\sigma_s \simeq 0.169$, to 1.1 for the last step, at $\sigma_s \simeq 0.05$. This is in good agreement with many field measurements that found a species packing ratio always lying between 1 and 2 [1]. It is worth remarking that when $\sigma$ decreases, $\lambda_m$—which is in general negative—increases, until at some critical value, $\sigma_c$, it becomes 0—that is, in Thom’s catastrophe theory language [21], a degenerate critical point or a non-Morse critical point. This $\sigma_c$ depends on the number of species: it decreases with $n$. We computed $\sigma_c(n)$ as the values such that $\lambda_m(n, \sigma_c)$ becomes 0. In figure 7 we show this. Notice that for $n \geq 40$, $\sigma_c$ scales as $2n^{-1}$, i.e. double the initial average separation between species. As $\sigma$ is decreased in simulations—for a fixed value of $n$—so that it becomes closer and closer to $\sigma_c$ and $\lambda_m$ moves towards 0, we observe that the time for reaching the lumpy pattern grows unboundedly. This is the well known phenomenon of critical slowing down [22]: the characteristic relaxation time of the dominant eigenmode is proportional to $1/\lambda_m$. In fact, taking $n = 200$, for $\sigma = 0.15$ the

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four lumps are noticeable after typically 500 generations while the six lumps for $\sigma = 0.1$ require around 20,000 generations, and for $\sigma = 0.075$ it takes a huge number of generations (more than 500,000) to produce the ten-lump pattern. The inset of figure 1 is a zoom of $\lambda_m$ versus $\sigma$. It shows that, at least for all practical purposes, the clumping becomes noticeable at $\sigma \simeq 0.075$.

5. Conclusions and final comments

A realistic mathematical description of the dynamics of a large number of species placed along a resource spectrum is a complicated issue for which an exact solution is not available. In fact, analytical work looks at the long-term equilibria of models. The alternative for dealing with the transients is to use simulations.

However a simulation approach, like the one used by Scheffer and van Nes [3], may leave room for doubt as regards whether things might be artifacts. We made a series of simplifications which allow an analytic proof, by working directly with the community matrix $A$, of the emergence of SOS. Roughly, the lumpy pattern that one is seeing is the exponential of the dominant eigenvector $v^m$ of $A$ (multiplied by the time).

We later showed that this is indeed a robust result. The clumping phenomenon does not depend on the boundary conditions or on the kernel exponent $p$ (provided it is greater than 1); it is quite independent on the heterogeneity of species parameters $r$ and $K$, and it occurs for a wide range of $\sigma$, and in more than one niche dimension. In addition, Roelke and Eldridge [23] found similar patterns in a different resource competition model. They
also suggest that this mechanism is not very fragile. Additional supporting evidence can be found in [24].

A crucial element for getting clumping is taking into account the finiteness of the niche axis. This, besides being realistic, leads to a $\lambda_m$ with a negative real part (and then to lumps and gaps). We want to remark that OBC or the standard implementation of PBC implies a niche which is finite. This explains the remarkable differences from the outcomes reported in [10]. The procedure that they use to implement PBC consists in taking a periodic array of copies of the same system. These ‘perfectly periodic’ boundary conditions mimic an infinite niche axis. The first such difference is that, in our case, the SOS is robust against variations in the kernel: a negative $\lambda_m$ is obtained whenever the exponent $p$ of the kernel interaction is a real number greater than 1. The second difference is that the parameter $\sigma$, controlling the width of each species distribution, plays a fundamental role. There is a critical value, $\sigma_c$, below which there is no clustering. On the other hand, in a virtually infinite niche axis, since it is always possible to set $\sigma = 1$ by rescaling $\mu$, the clustering should not depend on $\sigma$. However it seems natural that things in ecosystems depend on $\sigma$, and usually the interest is precisely in measuring this effect. This is another powerful reason for choosing an implementation of boundary conditions like the one that we are using.

Figure 7. Log-log plot of $\sigma_c$ versus $n$ for $n$ between 20 and 200. The dashed line corresponds to $2/n$. 

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Similar approaches for determining pattern formation in phenotype space have also been used by Levin and Segel [25], Sasaki [26] and more recently Meszéna and co-workers [27,28]. The main difference of our approach is that a discrete set of phenotypes is considered, instead of a continuum. This is an important feature, since firstly it can affect the assessment concerning how robust SOS is. That is, in the case of a continuous set of phenotypes, it was shown that an arbitrarily small perturbation can destroy the continuous coexistence, making the species distribution discrete [27,28]. And this could be taken as an evidence of the breaking of SOS. On the other hand, in our model, from the very beginning, the distribution of species is discrete and SOS is rather understood as a strong overlap of the species distributions. Secondly, it allows us to go beyond the large \( n \) limit and carry out applications to real communities, involving a number of species \( n \) of intermediate size. For example, this was tested for the case of phytoplankton communities in a lake ecosystem involving between 50 and 100 species and the agreement between theory and empirical data is quite good [29]. Moreover, in this real ecosystem the fact that \( \sigma \) is not the same for all species, but rather varies from species to species, does not spoil the lumpy pattern.

There are interesting parallels with similar phenomena in physical systems, including:

- The fact that the emergence of the lumpy pattern is related to the eigenvector with the minimum eigenvalue and the number of lumps is determined mostly by the model parameter \( \sigma \) resembles the spinodal decomposition\(^5\). That is, under the spinodal decomposition the system develops a spatially modulated order parameter whose amplitude grows continuously from zero and extends throughout the entire system. This results in domains of a characteristic length scale called the spinodal length \( \lambda_{sp} \) which usually depends strongly on temperature (because the second derivative of the free energy becomes increasingly negative deep inside the region delimited by the spinodal) [30].

- The emergence of power laws and critical slowing down are attractive ingredients for physicists since they are signatures of self-organized criticality (SOC) [31]. This tendency to spontaneously self-organize into a critical state, without any significant ‘tuning’ of some control parameter, usually reflects a share of the same fundamental dynamics for many different systems referred to as universality. While the origin of critical slowing down is clearly explained by the existence of a degenerate critical point, the power law distribution for the plateaus of the number of lumps versus \( \sigma \) is not completely understood and deserves further analysis.

- The application of techniques and concepts of statistical mechanics to very different realms like ecosystems might be of interest to ecologists, statistical physicists and the growing community at the intersection of the two fields. In that sense, the analytical proof of clumping is based on statistical mechanics results from Berlin and Kac [12] obtained when they were analyzing the spherical model of a ferromagnet.

- The calculation of the entropy for different regions of a system, to get an overview of the level of correlation between elements in each of the regions, has been used in several contexts closer to physics—for example: cellular automata [32], deterministic models of nonlinear dynamics [33], glass-forming materials [34], astrophysics of galaxies and

\(^5\) In fact we are grateful to one of the anonymous referees who pointed this out.
clusters [35], image processing [36], to mention but a few. In our case it has proved to be useful for identifying the lumpy structure.

To conclude, it is remarkable that the predictions for the number of groups of species that can be packed along the niche axis are quantitatively consistent with field data for a wide range of values of both the width of the niche and the number of species.

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