Species Clustering in Competitive Lotka-Volterra Models

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We study the properties of general Lotka-Volterra models with competitive interactions. The intensity of the competition depends on the position of species in an abstract niche space through an interaction kernel. We show analytically and numerically that the properties of these models change dramatically when the Fourier transform of this kernel is not positive definite, due to a pattern-forming instability. We estimate properties of the species distributions, such as the steady number of species and their spacings, for different types of interactions, including stretched exponential and constant kernels.

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It is widely believed that competition among species greatly influences global features of ecosystems. One of the most relevant is the fact that ecosystems can host a limited number of species. The common explanation is the so-called limiting similarity [1] and involves representing species as points in an abstract *niche space*, whose coordinates quantify the phenotypic traits of a species which are relevant for the consumption of resources, such as the typical size of individuals, but also preferred prey, optimal temperature, and so on. One expects that a species experiences a stronger competition with the closer species in this space. As a consequence, a species can survive if it is able to maintain its distance with the others above a minimum value which depends on the competition strength. On the contrary, a species will outcompete another when the distance between them becomes too small, due to the unavoidable difference in how efficiently they feed on the resources. This is the phenomenon of competitive exclusion [2], which is a basis of the concept of the ecological niche. Thus, a stable ecosystem should be made up of a finite number of species, approximately equidistant in a niche space. The finiteness of the number of species has been observed in several competition models [3] and rigorously demonstrated for a general class of them [4].

Deviations from the above scenario have aroused renewed interest when it was observed numerically [5] that the equilibrium state of such models is not always characterized by a homogeneous distribution of species in a niche space. Instead, clumpy distributions, with clusters of many species separated by unoccupied regions, have been observed. Evidences of a similar phenomenon have been observed also in evolutionary models [6], suggesting that a theoretical explanation of these patterns could bring new insights in the study of speciation mechanisms [7].

In this Letter, we study the Lotka-Volterra (LV) competitive model as the prototype of competitive systems (i.e., population models in which the growth of a species negatively affects the growth rate of others). The statistical properties of many-species LV models have been studied using particular symmetries of the interaction matrix [8], but not much is known on the statistics of a competitive case. In this Letter, we use the language of ecological species competition, but the competitive LV system appears also in contexts as multimode dynamics in optical systems [9], technology substitution [10], mode interaction in crystallization fronts [11], or spin-wave patterns [12]. Our main result is that the macroscopic clustering of species is related to a pattern-forming transition that separates two different regimes. The feature which is relevant for this transition is the functional form of the competition kernel: Patterns occur when its Fourier transform takes negative values. A similar phenomenon is found in birth-death particle systems with interaction at a distance, in which individuals aggregate, forming clusters arranged in an ordered pattern [13], with the physical space playing the role of the niche space. We will exemplify our results with a family of stretched exponential kernels and a long-range, constant one.

We consider here the LV competitive model:

$$\dot{n}_i = n_i\left(r - a_i \sum_{j=1}^{N} g(|x_i - x_j|)n_j\right), \qquad i = 1, \ldots, N. \tag{1}$$

N is the number of species, and n_i denotes the population of species i. Each species is characterized by a growth rate r and a competition parameter $a_i > 0$ (we take into account differences among species only in the latter parameter). A species is also characterized by a position x_i in a niche space that we assume, for simplicity, to be the segment $[0, L]$ with periodic boundary conditions. Generalization to a multidimensional niche space is straightforward, and we expect the unrealistic boundary conditions to be irrelevant except close to the interval end points. The competition kernel $g(x)$ is a non-negative and nonincreasing function. Note that the sum in Eq. (1) contains the self-interaction term $g(0)n_i$.

To fully specify the dynamics, we should state how the x_i are assigned to species and eventually changed. We consider an immigration mechanism by which new species, characterized by a random phenotype $x \in [0, L]$, are introduced in the system with a rate I. This choice is appropriate to model a situation such as an ecological community on an island [14]. We consider extinct, and remove from the system, species whose population goes below a threshold n_T. When I^{-1} is very large compared to the time scales of population dynamics, the system has time to relax to a quasisteady state after each immigration event. Our interest here is in the features of these states, in which immigration plays almost no role. An efficient way to obtain them is by integrating (by a second-order Runge-Kutta method) Eq. (1) while introducing a new species with population δn with the proper rate. To ensure that the reached states are stable, we "switch off" the immigration mechanism after some time. By a choice of the time and the population units, we can set $r = 1$ and $n_T = 1$ (thus, the parameters a_i are really $a_i n_T / r$). We take units in the niche space so that $L = 1$.

In Fig. 1, we show numerical simulations of our model. In the top row, we compare the distribution of species with kernels $g_1(x) = \exp(-x/R)$ and $g_4(x) = \exp[-(x/R)^4]$, R being the typical competition range. In the exponential case (left), species occupy the whole niche space. Although they are not perfectly equispaced and there are differences in the population sizes, there is a clear average interspecies distance, which corresponds to $1/N$. In the quartic-exponential case (right), a much more regular pattern emerges, with different species perfectly equidistant (and all with the same population). Since growth limitation is known to affect species distribution [5], we plot in the bottom row results for kernels $g_1(x) + \delta_{x0}$ and $g_4(x) + \delta_{x0}$, i.e., the same kernels but with an enhanced value of the self-competition coefficient $g(0)$. Here the difference is even more striking: The exponential case is similar to the previous one, but the quartic case shows clear clusters of species separated by empty regions. Since our model does not include mating, the sharp distinction between self- and interspecific competition introduced by the delta function could be questionable. We have checked, however, that the same clusters of species appear when the singular delta function is replaced by continuous kernels sufficiently peaked at the origin.

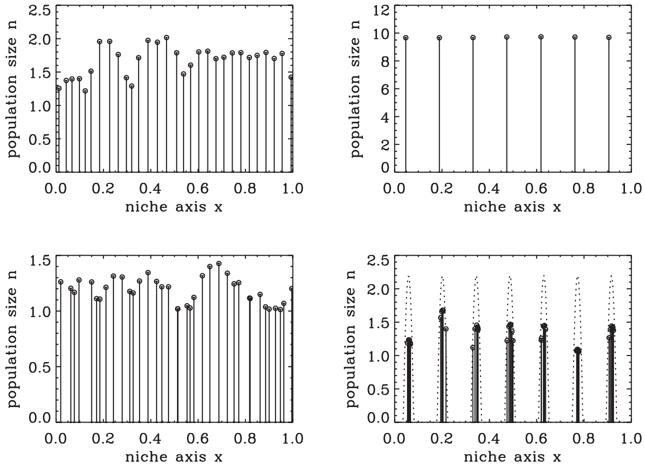

FIG. 1. Steady states of system (1), with $a_i = a = 0.1$, obtained by evolving a random configuration, initially of 200 species, for a time $t = 5 \times 10^5$. The immigration rate was initially $I = 0.004$ and was switched off after half of the simulation. Top panels: Competition kernel $g_1(x) = \exp(-x/R)$ (left) and $g_4(x) = \exp[-(x/R)^4]$ (right), with $R = 0.1$. In the bottom panels, we added a Kronecker delta δ_{x0} to the kernels above. In the last panel, the dotted line is a steady solution of (2), arbitrarily scaled in the vertical to fit in the same plot.

To understand the origin of the periodic patterns, we write a continuum evolution equation for the field $\phi(x, t)$, the expected density of individuals in a given point x of the niche space as a function of time:

$$\partial_t \phi(x, t) = \phi(x, t)\left(1 - a \int g(|x - y|)\phi(y, t) dy\right) + s, \tag{2}$$

which is a mean field version of Eq. (1) for $a_i = a$. In this *macroscopic* description, we neglect fluctuations in the immigration process by using a constant rate $s = I\delta n$. The stationary homogeneous solutions of Eq. (2) are $\phi_0 = (1 \pm \sqrt{1 + 4s\hat{a}})/(2\hat{a})$, where $\hat{a} = a\mathcal{N}$, with $\mathcal{N} = \int g(x) dx$. Of the two solutions, only the one with the plus sign is acceptable, since the other leads to a negative density (this second solution corresponds to the extinct absorbing state when $s = 0$). We analyze the stability of the positive solution by considering a small harmonic perturbation $\phi = \phi_0 + \epsilon \exp(\lambda t + ikx)$. Substituting into (2), the first order in ϵ gives the following dispersion relation:

$$\lambda(k) = 1 - \phi_0 \hat{a}\left(1 + \frac{\tilde{g}(k)}{\mathcal{N}}\right), \tag{3}$$

where $\tilde{g}(k) = \int g(x) \exp(-ikx) dx$ is the Fourier transform of $g(x)$. When λ becomes positive for some values of k, the constant solution of (2) is unstable, signaling a pattern-forming transition [15] with the characteristic length scale of the pattern determined by the value of k at which $\lambda(k)$ is maximum. In the limit $s \rightarrow 0$, one has $\phi_0 \hat{a} \rightarrow 1^+$, and it is a sufficient and necessary condition for instability that the Fourier transform of the kernel $\tilde{g}$ takes negative values.

To exemplify this mechanism, we consider the family of kernels $g_\sigma(x) = \exp[-(x/R)^\sigma]$, $\sigma \geq 0$ and R being the typical competition range. For $0 \leq \sigma \leq 2$, this family of functions has non-negative Fourier transform [16]. Interestingly, the commonly adopted Gaussian kernel [1,5] corresponds to the marginal case. This may imply that some results previously obtained for this case could be nonrobust and largely affected by the way immigration is introduced, the presence or absence of diffusion processes in the niche space, etc.

We quantify the pattern-forming transition in terms of the structure function $S(k) = |\sum_j n_j \exp(ikx_j)|^2$ of the stationary distribution of species obtained from the simulations. The position and height of its maximum identify periodic structures. In Fig. 2, we plot (left panel) the maximum height of S as a function of the exponent σ of the kernel. The sharp increase of max$S$ for $\sigma > 2$ indicates the formation of periodic structures. This is confirmed by the right panel plot, where we show the position k_m of the peak of S, together with the value k_L at which the linear growth [expression (3)] has a maximum. Note that the location of this maximum is independent of the parameters a and s, being dependent only on the parameters in $g_\sigma(x)$ (R and σ; the dependence on R disappears when considering $k_L R$). The striking agreement between k_m and k_L for $\sigma > 2$ confirms that the linear pattern-forming instability of the homogeneous distribution is the mechanism responsible for the periodic species arrangement observed in that range. Except when $\sigma \approx 2$, the value of $k_L R$ is in the range 4.0–5.0, so that the pattern periodicity would be $d \approx 2\pi/k_L \approx \alpha R$, with $\alpha \approx 1.3$–1.6, as observed in Fig. 1 (right panels).

Another difference between $\sigma \leq 2$ and $\sigma > 2$, visible in Fig. 1, is the existence in the latter case of *exclusion zones* around established species, in which immigrants have not been able to settle. We can understand the presence of these regions also from the density equation (2), for $s = 0$, by noticing that its steady stable solutions $\phi_{\rm st}(x)$ necessarily have regions with $\phi_{\rm st}(x) = 0$ in the pattern-forming case. This can be seen from the steady state condition $\int dy g(|x - y|)\phi_{\rm st}(y) = 1/a$, which is valid for all x in which $\phi_{\rm st}(x) \neq 0$. If, in fact, these locations cover the full niche space $[0, 1]$, we can solve the steady state condition by Fourier transform and find that the only solution [for nonconstant $g(x)$] is the homogeneous one $\phi_{\rm st}(x) = (a\mathcal{N})^{-1}$. Since this is linearly unstable when the Fourier transform of $g(x)$ is not positive definite, we conclude that steady stable solutions of (2) in the pattern-forming case must have exclusion zones, i.e., regions of zero density. Given the absorbing character of the $\phi = 0$ state, many steady solutions exist, differing in the amount and location of the $\phi_{\rm st} = 0$ segments, but the most relevant are the ones attained when $s \to 0^+$. Figure 1 (bottom right) shows one of these solutions, numerically obtained [for a kernel $g_4(x) + \delta(x)$]. The steady solution corresponding to the $g_4(x)$ kernel of the top right panel is zero everywhere except at a set of periodically spaced delta functions. In both cases, the discrete species distribution is well represented by the solutions of (2).

When $\tilde{g}(k)$ remains positive, as for $g_\sigma(x)$ with $\sigma \leq 2$, $\lambda(k)$ remains negative, and there are no patterns nor exclusion zones surviving in steady solutions of the density equation for $s \to 0^+$. Thus, the characteristic distance between species observed in Figs. 1 and 2 should be determined by a qualitatively different mechanism from the case $\sigma > 2$. We explore it for the exponential kernel $g_1(x) = \exp(-x/R)$, because it allows an analytical estimate. Figure 3 shows the number of species at equilibrium for $a_i = a$ and also in the heterogeneous situation in which the a_i's are independent random variables uniformly distributed between $0.95\bar{a}$ and $1.05\bar{a}$, $\bar{a}$ being an average value.

In the nonheterogeneous case, we observe that, when the species evolve far from the extinction threshold, a new species can always settle between two existing ones, thus reducing their populations. This brings the n_i's closer to n_T as the number of species increases, and eventually no new species will be admitted. Thus, for $\sigma < 2$, the mechanism fixing a maximum number of species and the characteristic

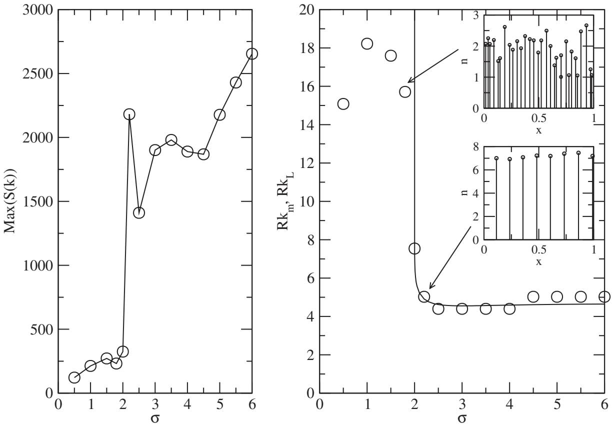

FIG. 2. Left panel: Maximum of $\langle S(k)\rangle$, the structure function averaged over 1000 realizations of stationary distributions of species (obtained after a time $t = 10^5$, without immigration during the last half of it) as a function of σ, for $R = 0.1$, $a_i = a = 0.1$. Right panel: Position of the peak k_m vs σ (circles), together with the linearly fastest growing mode k_L (line), from (3). For $\sigma > 2$, the difference between k_m and k_L is always smaller than the finite-size discretization of the values of k_m. We show configurations for $\sigma = 1.8$ and $\sigma = 2.2$, close to the critical value $\sigma = 2$.

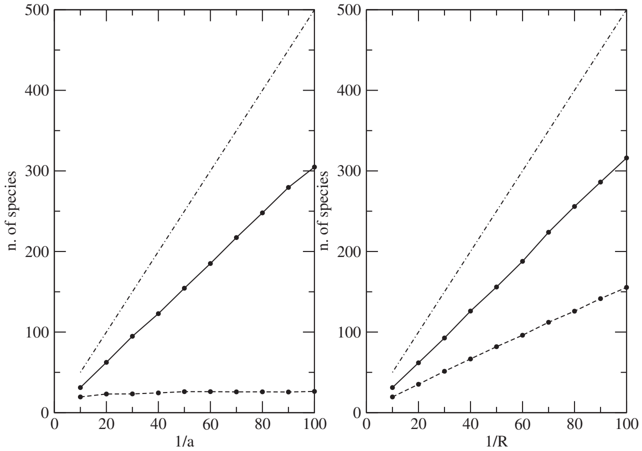

FIG. 3. Number of species as a function of competition coefficient a (left panel, $R = 0.1$) and the interaction distance R (right panel, $a = 0.1$). Symbols joined by dashed and solid lines are for the cases of $a_i's$ heterogeneity (for which $\bar{a}$ is plotted instead of a) and nonheterogeneity, respectively. The upper dotted-dashed lines are from the approximation (4).

mean distance d among them is the presence of an extinction threshold n_T.

Figure 3 shows that the number of species N (in the steady state obtained after switching off immigration) grows linearly with $1/R$ and with $1/a$ in the case of equal species, while heterogeneity slows down the increase with $1/R$ and almost stops it with $1/\bar{a}$. Notice that decreasing a is the same as decreasing the threshold value n_T due to our rescaling of the equations. We can explain these dependences by considering an ideal steady state made of equidistant species, at distance d, and having the same population n^*. The equilibrium condition for the system of equations (1) in the exponential kernel case becomes $\tanh(d/2R) = an^*$, which gives $d \approx 2aRn^*$ in the limit $(d/2R) \ll 1$. Recalling that $N = 1/d$, each population n^* decreases as the number of species increases during immigration. The limit, setting the steady state, will be the situation in which $n^* = n_T = 1$, for which no new immigrant can be accepted. Thus, we estimate the equilibrium number of species in this case as

$$N \approx (2aR)^{-1}. \tag{4}$$

This is only a rough approximation, since species are not equidistant nor equipopulated in the true equilibrium, but it provides an explanation for the observed linear scaling of N with $1/a$ and $1/R$. Figure 3 shows that it gives an upper estimation for the number of species in the less ordered distributions actually found.

The case with heterogeneity of Fig. 3 shows a clearly different mechanism: The number of species does not change with $\bar{a}$ and, consequently, with n_T. This scenario is qualitatively similar to the pattern-forming case: There is a distance in the niche space, not related to the threshold value, of the order of the interaction range. Two species cannot survive due to heterogeneity if they are closer than this distance, independently on the mean competition strength.

To clarify this third mechanism, we consider the role of heterogeneity in the long-range case of a constant kernel $g(x) = 1$ for all x. This may be interpreted as a case in which the kernel-decaying distance goes to infinity. Summing all of the equations in (1), we obtain an equation for the total population $N_{\text{tot}} = \sum_j n_j$:

$$\dot{N}_{\text{tot}} = N_{\text{tot}}(1 - \langle a \rangle N_{\text{tot}}), \tag{5}$$

where $\langle a \rangle = (\sum_j a_j n_j)/N_{\text{tot}}$. After a short time, the equilibrium value $N_{\text{tot}} = \langle a \rangle^{-1}$ would be attained, and we can plug this value back into Eq. (1) to obtain $\dot{n}_i = n_i(1 - a_i/\langle a \rangle)$, valid at longer times. In the case of equal species, one has $a_i = \bar{a} = \langle a \rangle$, and all possible states with $a\sum_j n_j = 1$ are allowed. In the heterogeneous case, species having $a_i < \langle a \rangle$ will grow, while the others will decrease their population and finally go extinct. Meanwhile, it is easy to realize that $\langle a \rangle$ will increase, sending more and more species below the extinction threshold. The final result, valid for any initial distribution of the a_i's if $g(x) = 1$, is that just one species will survive, as confirmed by simulations (not shown).

To conclude, we studied analytically and numerically the collective behavior of competitive Lotka-Volterra systems. Our main message is that the form of the competition kernel changes drastically the equilibrium distribution of species. Species clustering with periodic spacings of the order of the interaction range can occur at one side of a pattern-forming transition, whereas smaller spacings, depending on the interaction strength a, occur at the other. Surprisingly, the Gaussian kernel, the one usually considered in the literature, corresponds to a frontier case. Diversity has been shown to alter qualitatively the competition outcome. Diffusion in a niche space, modeling mutations [5], can be introduced and has a stabilizing effect similar to that of the immigration rate.

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