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Spatially Synchronous Extinction of Species under External Forcing

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More than 99% of the species that ever existed on the surface of the Earth are now extinct and their extinction on a global scale has been a puzzle. One may think that a species under an external threat may survive in some isolated locations leading to the revival of the species. Using a general model we show that, under a common external forcing, the species with a quadratic saturation term first undergoes spatial synchronization and then extinction. The effect can be observed even when the external forcing acts only on some locations provided the dynamics contains a synchronizing term. Absence of the quadratic saturation term can help the species to avoid extinction.

Consider two important phenomena concerning populations of different species. First is the spatial synchronization of populations of a species. Many examples of spatially synchronized populations have been observed in nature [1–12]. These include synchronization of vole populations by predatory birds [1], synchronization of caribou and musk oxen by climate [4,12], and synchronization of lynx populations probably by climate [8] and/or dispersal [9]. Several other examples are documented in Ref. [10]. The second important phenomenon is the extinction of species. More than 99% of the species that ever existed on the surface of the earth are now extinct. One example of such extinctions is the statistically homogeneous $K - T$ (Cretaceous-Tertiary) extinction intensities observed for marine molluscs on a global scale [13]. (In this Letter, extinction will mean extinction on the global scale.) Such global extinctions are still a puzzle. It is possible that when a species is under threat it may survive in some isolated locations and afterwards lead to the revival of the species. This is the ''rescue effect'' [14]. Various factors affecting extinction such as migration, chaos, noise, etc., have been discussed in the literature [15,16]. It is believed that spatial synchronization can promote global population extinctions [15,16]. However, there is no clear understanding of the relation between spatial synchronization and extinction and whether they will always coexist. This underscores the need for a general theory of spatial synchronization and extinction of populations under external forcing which will clarify this relation.

In this Letter we investigate the time scales of spatial synchronization and extinction. Using a general model of population dynamics under a common external forcing we show that the saturation term (decay term) decides these time scales. If the dynamics has a quadratic saturation term, the species first undergoes spatial synchronization and then extinction. The populations will remain synchronized as they are driven towards extinction. Thus, the

rescue effect [14] can be avoided. On the other hand, the species which do not possess the specific saturation term in the dynamics, will show a natural resistance towards extinction through the rescue effect.

We present the details of our argument by considering a general model of population dynamics. We follow the experimental set up of Ref. [1] that considered 28 enclosed vole populations that were fenced to prevent predatory mammals and vole dispersal. It was found that the vole populations synchronized due to predatory birds. Following this experimental set up, let $P_i(t)$ denote the population of a species at ith patch, $i = 1, \ldots, N$, at time t and let $Q(t)$ denote an external variable (e.g., meteorite impacts, volcanic eruptions, predator population, climate, etc.) which interacts with the population of the species at different patches. The coupled dynamics can be written as

$$\frac{dP_i}{dt} = f_1(P_i(t)) + \epsilon_1 g_1(P_i(t), Q(t)) + I, \quad (1a)$$

$$\frac{dQ}{dt} = f_2(Q(t)) + \frac{\epsilon_2}{N} \sum_i g_2(P_i(t), Q(t)), \quad (1b)$$

where f_1 and f_2 represent the uncoupled dynamics, g_1 and g_2 represent the interactions, and ϵ_1 and ϵ_2 are interaction constants. The term I represents the interaction terms between populations of species in different patches and is not important for our basic argument. We will consider its effect later.

We are interested in the spatially synchronized state, $P_1(t) = \ldots = P_N(t) = P(t)$. Linear stability of this state can be analyzed using the Jacobian J of the vector field defined by P_i's and Q. The eigenvectors of J split into two orthogonal subspaces A and B [17]. The subspace A has dimension two and it defines the synchronization manifold. The subspace B has dimension $N - 1$ and it defines the transverse manifold. The eigenvectors of B are of the type $\hat{\alpha}_t = (\alpha_1, \ldots, \alpha_N, 0)^T$, $\Sigma_{i=1}^N \alpha_i = 0$ and the eigenvalues

are $N - 1$ fold degenerate and are given by $\frac{\partial}{\partial P}(f_1 + \epsilon_1 g_1)$. We note that under time evolution the two subspaces A and B do not mix with each other and the subspace B has the same eigenvectors for all the time. Thus, it is possible to take the time average of the degenerate eigenvalue of B to obtain the transverse Lyapunov exponent. For the stability of the spatially synchronized state we require the transverse Lyapunov exponent to be negative. Imposing this, we obtain the condition for the stability of the synchronized state as

$$\left\langle \frac{\partial}{\partial P}(f_1(P) + \epsilon_1 g_1(P, Q)) \right\rangle < 0, \qquad (2)$$

where $\langle \rangle$ represents the time average.

We now return to the problem of synchronization and extinction. Near extinction, We analyze the problem by retaining the lowest order terms in the Taylor series expansion of various functions in Eq. (1a) in terms of the population $P_i(t)$.

$$f_1(P_i) = aP_i - bP_i^2 + \mathcal{O}(P_i^3). \qquad (3)$$

The first term in the expansion is a growth term and $a > 0$. The second term is a saturation term if $b > 0$. Neglecting the higher order terms, we get the stable solution $P_i = b/a$. If $b < 0$, then we must include higher order terms in Eq. (3) to get a stable solution. The interaction function g_1 to lowest order in P_i can be written as $-P_i h(Q)$ where $h(Q)$ is some function of Q.

Let us first consider the case $b > 0$. The condition (2) for the stability of synchronized state now becomes

$$\lambda_s = \langle a - 2bP - \epsilon_1 h(Q) \rangle < 0. \qquad (4)$$

For extinction the forcing must be able to compensate the growth and the condition for extinction is

$$\lambda_e = \langle a - \epsilon_1 h(Q) \rangle < 0. \qquad (5)$$

This condition can also be obtained by considering the stability of $P = 0$ state. Comparing the conditions (4) and (5), we find that as $\langle a - \epsilon_1 h(Q) \rangle$ starts decreasing, the condition (4) will be satisfied before the extinction condition (5) is satisfied. If both the synchronization and extinction conditions are satisfied then the time scale associated with synchronization ($\tau_s = 1/|\lambda_s|$) will be less than the time scale associated with extinction ($\tau_e = 1/|\lambda_e|$). Thus, we conclude that the populations in different locations will synchronize before the extinction of the species. They will remain synchronized as the populations at different patches start decreasing. Hence we expect the extinction of populations in different patches to take place almost simultaneously.

We demonstrate that spatial synchronization precedes extinction using a simple prey-predator model [18]. For this model, the different functions in Eq. (1) are given by $f_1(P) = aP - bP^2$, $g_1(P, Q) = -g_2(P, Q) = -PQ$, $f_2(Q) = -u(Q - Q^*)$. We allow the predator to maintain

a low equilibrium level $Q = Q^*$ even when its usual prey, P, is rare [11]. For the above model, the synchronization condition becomes $\langle a - 2bP - \epsilon_1 Q \rangle < 0$ and the extinction condition is given by $\langle a - \epsilon_1 Q \rangle < 0$. In Fig. 1(a), we plot populations of different patches as a function of time starting from random initial populations. The parameters used are: $a = 0.5$, $b = 50.0$, $u = 0.1$, $\epsilon_1 = 4.8$, $\epsilon_2 = 1.0$, $N = 100$, $Q^* = 0.5$. We see that the populations of different patches synchronize and then are driven to extinction. To better understand the time scales involved, we plot the following two parameters as a function of time in Fig. 1(b): Synchronization parameter $S = [2/N(N-1)]\sum_{i=1}^{N}\sum_{j=1}^{i-1}(P_i - P_j)^2$, which measures the mean square deviation between pairs of populations and extinction parameter $E = (1/N)\sum_{i=1}^{N} P_i^2$, which measures the mean square populations. We observe that initially the synchronization parameter S (solid line) goes to zero with a rate greater than that of the extinction parameter E (dotted line). As the populations become very small, λ_s and λ_e [Eqs. (4) and (5)] become nearly identical and the rates of decrease of S and E become nearly equal as can be seen from Fig. 1(b).

In the dynamics of the populations we have neglected the effect of intraspecies interactions or diffusion within the populations in different patches [I in Eq. (1a)]. It is easy to see that these effects do not affect the conclusion of
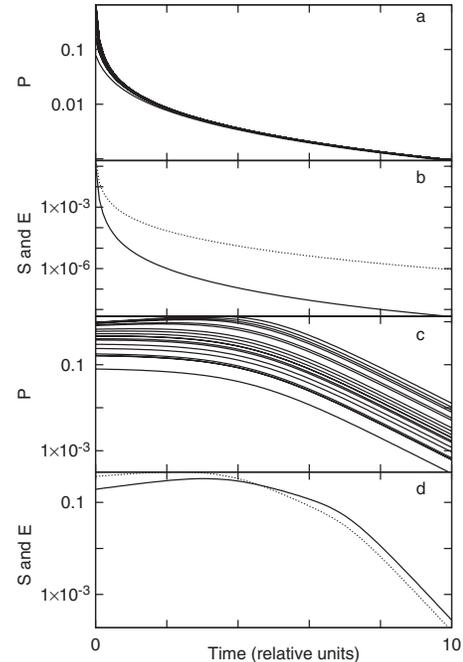

FIG. 1. The interplay between synchronization and extinction in a simple prey-predator model [18]. (a) and (c) show the populations of different patches as a function of time for b positive and negative, respectively. (b) and (d) show the synchronization and extinction parameters S and E (solid and dotted lines, respectively) as a function of time.

spatial synchronization before extinction. For example, consider Eq. (1a) with

$$I = \frac{1}{N}\sum_{j=1}^{N} h_1(P_j) + \frac{1}{N}\sum_{j=1}^{N} h_2(P_j - P_i), \qquad (6)$$

where the first term gives a mean field type interaction while the second term represents a diffusive type interaction. The conditions for the stability of the synchronized state and the condition for extinction now become, respectively,

$$\langle [F(P,Q)] + H \rangle < 0, \qquad (7a)$$

$$\langle [F(P,Q)]_{P=0} + H \rangle < 0, \qquad (7b)$$

where $F(P,Q) \equiv \frac{\partial}{\partial P}[f_1(P) + \epsilon_1 g_1(P,Q)]$ and $H = -[\frac{\partial h_2(Y)}{\partial Y}]_{Y=0}$. Note that h_1 does not contribute to the above conditions and h_2 in general helps synchronization. We see that our conclusion about spatial synchronization before extinction is still valid. Higher order interaction terms of the type $h_3(P_i, P_j) = P_i^\mu P_j^\nu$ have to be treated more carefully. In general, there will be both productive and competitive terms [19]. If they balance out or if the competitive term dominates, our conclusions remain valid. But, if the productive terms dominate, then survival in isolated locations may be possible and the rescue effect can take place.

Our basic finding of synchronization before extinction can be tested in an ecological experiment similar to those described in Ref. [1]. The food source of the vole population can be decreased progressively to see whether the synchronization persists and whether the extinction is almost simultaneous. Similar experiments could be carried out with other populations such as insects, etc.

In the above argument we have neglected the effect of higher order terms in the Taylor series expansion of various functions appearing in Eqs. (1a). When higher order terms are retained two possibilities arise. First chaotic attractors can occur and second there can be multiple stable solutions [20]. It is believed that when the isolated patches are individually chaotic with a weak coupling then it can lead to asynchrony between different patches thus preventing global extinction [14]. However, we find that such chaotic solutions do not prevent spatial synchronization when the effect of common external forcing is included. It is well known in the nonlinear dynamics literature and also as shown above, that a common forcing, including common external noise, can synchronize chaotic systems [21,22].

When there are multiple stable solutions, it is possible that depending on the initial conditions populations in different patches may converge to different stable solutions. In this case extinction is difficult due to the rescue effect and neither is there a spatial synchronization.

So far we have neglected the effect of variation in parameters from patch to patch and also the effect of local noise. Both these factors, if they are large, can lead to spatial asynchrony. However, we have verified that small

parameter variations and noise do not affect our conclusions. The effect of small parameter variations is demonstrated afterwards in Fig. 2.

We now discuss the case $b < 0$ in Eq. (3). It is easy to see that in this case the time scale for extinction will be less than that for synchronization. Clearly, spatial synchronization cannot take place before extinction. Thus, it is possible that the rescue effect can prevent extinction. In Fig. 1(c), we show the populations of different patches as a function of time for $b = -4.0$ We see that the patches do not show any spatial synchronization and the species may survive due to the rescue effect if the external forcing is switched off after some time. Figure 1(d) shows the synchronization and extinction parameters, S and E, as a function of time for $b = -4.0$. We see that initially the rate of decrease of E is greater than that of S and afterwards the two rates become almost equal.

Thus, we see that the parameter b can be treated as a measure of the resistance of a species towards extinction. Smaller the value of b, more is the resistance. The second term in Eq. (3) corresponding to parameter b represents interaction between two members of a species. The parameter b is in general positive due to competition between members. This is also reflected in various population models used in the literature which are known to give good fit for experimental observations [18,23,24]. However, a high degree of cooperation between the members may be able to make b negative and the species more resistant to extinction.

We now consider a situation of great practical importance. It is easy to establish that if the coupling parameter ϵ_1 has a small variation, it does not alter the above conclusions. However, it may happen that some patches escape the effect of the external forcing, i.e., $\epsilon_1 = 0$ for these
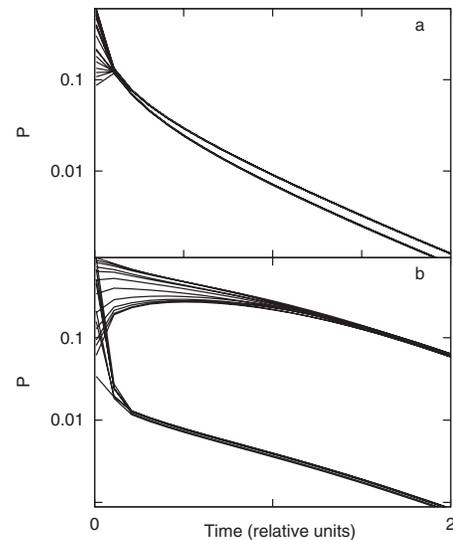

FIG. 2. The time evolution of populations in different patches is shown when only 50% of the patches interact with the external forcing. (a) $b = 50.0$, (b) $b = -4.0$.

patches. We now show that our conclusions based on the parameter b are still valid provided there is some synchronizing interaction among the patches. Let N_2 patches escape the effect of external forcing and the remaining $N_1 = N - N_2$ patches be affected by the forcing. We choose the interaction term $I = \frac{d}{N}\sum_j(P_j - P_i)$. In this case, by using an argument similar to the one used to show the stability of the synchronized state for Eq. (1a), it is possible to show that we get a two-cluster synchronized state. The N_1 patches synchronize to one value of the population say $\bar{P}_1$ and the remaining to another value say $\bar{P}_2$. The conditions for the two-cluster synchronized state are $\langle a - b\bar{P}_1 - d - \epsilon_1 h(Q)\rangle < 0$ and $\langle a - b\bar{P}_2 - d\rangle < 0$ for the two clusters, respectively. The difference $\Delta\bar{P} = \bar{P}_2 - \bar{P}_1$ evolves as

$$\frac{d\Delta\bar{P}}{dt} = [a - b(\bar{P}_1 + \bar{P}_2) - d]\Delta\bar{P} - \epsilon_1 h(Q)\bar{P}_1. \quad (8)$$

When the extinction condition for N_1 cluster is satisfied, i.e., $\langle a - \epsilon_1 h(Q) - d\rangle < 0$ and $b > 0$, the synchronization of $\bar{P}_1$ will precede that of extinction due to the b term. The N_2 cluster will also synchronize due to b term if $\bar{P}_2$ is large. Further, this cluster will decay according to Eq. (8). Now as $\bar{P}_1$ becomes smaller the second term on the right-hand side of Eq. (8) becomes small and if $[a - b(\bar{P}_1 + \bar{P}_2) - d] < 0$ then $\bar{P}_2$ will start decreasing in some sort of generalized synchrony with $\bar{P}_1$.

In Fig. 2 the time evolution of populations in different patches is shown when only 50% of the patches interact with the external forcing. We also introduce a 5% patch to patch variation in all the parameters about their respective mean values. For b positive [Fig. 2(a)] we initially see the formation of the two-cluster synchronized state. Following this, the N_1 cluster rapidly decays and is closely followed by the N_2 cluster. For b negative [Fig. 2(b)] the populations again separate into two distinct groups. The N_1 cluster shows a rapid decay but the N_2 cluster shows a very small decay. This small decay comes from the pulling down effect of Eq. (8). We note that as the N_1 cluster becomes extinct the effect of Eq. (8) will also vanish and the N_2 group will start its independent evolution thus escaping extinction.

In this Letter, we have established a clear connection between extinction and spatial synchronization of populations. Under reasonably general conditions with external forcing we showed that spatial synchronization precedes extinction when the parameter $b > 0$, thus avoiding the rescue effect. On the other hand, for $b < 0$, the species can show a natural resistance to extinction. These conclusions are valid even if the external forcing acts only at some locations provided there is some synchronizing interaction between the populations. Clearly, in mass extinction events where there is a strong common external shock, the above conclusions should be valid. Even in other situations, we expect our general conclusions to hold since they are based only on the parameter b of the local dynamics.

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