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Population distribution and synchronized dynamics in a metapopulation model in two geographic scales



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ABSTRACT

In this paper, a metapopulation model composed of patches distributed in two spatial scales is proposed in order to study the stability of synchronous dynamics. Clusters of patches connected by short-range dispersal are assumed to be formed. Long distance dispersal is responsible to link patches that are in different clusters. During each time step, we assume that there are three processes involved in the population dynamics: (a) the local dynamics, which consists of reproduction and survival; (b) short-range dispersal of individuals between the patches of each cluster; and (c) the movement between the clusters. First we present an analytic criterion for regional synchronization, where the clusters evolve with the same dynamics. We then discuss the possibility of a full synchronism, where all patches in the network follow the same time evolution. The existence of such a state is not always ensured, even considering that all patches have the same local dynamics. It depends on how the individuals are distributed among the local patches that compose a cluster after long-range dispersal takes place in the regional scale. An analytic criterion for the stability of synchronized trajectories in this case is obtained.

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1. Introduction

A metapopulation is composed of populations that live in fragments called patches and are often connected via dispersal processes [20]. An interesting phenomenon related to the dispersal process is the synchronized dynamics where the population densities in all patches evolve with the same amplitude and phase [24]. Its importance lies in the fact that synchronized dynamics can make the whole metapopulation vulnerable to extinction. On the other hand, if the metapopulation is not synchronized and a local population is extinct, it can be recolonized by individuals that migrate from neighboring patches ("rescue effect"), favoring the population persistence [2,3]. The synchronization phenomenon is important from the ecological and epidemiological point of view [8]. In ecology, synchronization may have a deleterious effect on population persistence, because it may lead to the impossibility of a recolonization, and can be dangerous for species that need to be preserved. In epidemiology, synchronization can be beneficial in order to control and improve efforts against a disease. In Thailand [5], time series analyzes of dengue cases between 1984 and 1996 showed a spatial synchrony in the number of dengue cases between the cities indicating that the increase in number of cases in a city may be reflected over the entire country. Another example is the seasonal dynamics of the influenza virus which epidemics occur annually with the highest activity occurring during winter months [38].

Systems of discrete equations are often used to model metapopulations [1,7,13,32,34]. A metapopulation model with patches linked by migration and subjected to external perturbations was considered in [1]. Through numerical simulations, it was shown that chaos can prevent global extinctions when coupling is weak. In [13] the patches were linked by considering dispersal process and distance and it was concluded that this asynchrony reduces the synchronization likelihood. In [7] was established a positive correlation between the degree of coherence of the oscillations in each patch and the risk of extinction of the metapopulation. They also obtained an analytical result for the stability of synchronized trajectories by considering a model with an arbitrary number of patches linked by dispersal. An analytical result examining a special case of density-dependent dispersal was obtained in [34], concluding that this mechanism reduces the stability of the synchronous dynamics. These results are based on the calculation of the transversal Lyapunov number that depends on the local dynamics of each patch, and a parameter that depends on the whole migration process. Symmetric and asymmetric dispersion [6,12,16,18,21], density-dependent dispersion [29,33,34,37] studies were done in order to show the different trends of





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metapopulation dynamics and its implications on the persistence and conservation of species.

The dispersal process often involves two modes, short-distance and long-distance dispersal [30]. Short-distance dispersal refers to movement to other sites on a local scale usually by the individual's own way of transport such as flying or swimming. The long-distance dispersal occurs in a regional scale and it takes place usually through passive transport on wind, water flow, birds or artificial transportation. Examples of long-range dispersal have been reported on insects [22,26,27], and in aquatic invertebrates [11,17]. Long-range dispersal events may be rare but they are crucial to population spread since it allows recolonization and counteracts genetic drift and inbreeding in fragmented environments [36]. In [14] the genetic structure of the medfly *Ceratitis capitata* in South Africa was analyzed and molecular approaches were employed to obtain estimates of the dispersal ability of the Mediterranean fruit fly at three spatial scales. The results in [14] suggested that the structure observed in South African medflies maybe the result of complex interactions at local scales (limited dispersal ability) and at broad scales (human-mediated and other forms of long-range dispersal).

In this paper we propose a model of a network of local populations linked by a dispersal process that takes into account shortand long-distance movements. The environment is assumed to be fragmented in such way that clusters of patches connected by short-range dispersal are formed. We assume that these clusters are too far away to admit connection by short-range dispersal and thus, long-range dispersal is responsible for establishing connections between some patches that are distant apart. We then describe the synchronization phenomenon. The analysis is done by linearizing the equations of the model around the synchronized trajectories and further decomposition of perturbation vectors into components in the synchronized manifold and other components that are transversal to it, obtaining conditions to its local asymptotic stability. These conditions are obtained from the block decomposition of the Jacobian Matrix that presents a fundamental role in the stability analysis of the synchronous manifold [4.28].

In Section 2 we introduce the metapopulation model with patches distributed in two geographic scales. In Section 3 we analyze the asymptotic local stability of synchronized trajectories and obtain a criterion to its stability based on the calculation of the transversal Lyapunov numbers. In Section 4 we present numerical simulations considering different distributions of individuals in the patches that compose a cluster. Final comments and discussion are done in Section 5.

2. The mathematical model

We consider a network of patches distributed in two spatial scales. In a local scale, nearby patches are connected by short-range dispersal forming clusters or conglomerates. We assume that these clusters are too far away from each other to be linked by short-range dispersal. Thus, in a regional scale, patches of different clusters are allowed to be connected by long-range dispersal (see Fig. 1). Fig. 1 is just a schematic representation but it resembles real networks topologies [15]. In [15] the network topology showing patch conglomerates was obtained with data on the grasshopper *Stethophyma grossum* distributed in a fragmented agricultural landscape.

2.1. The isolated cluster

We start describing the basic habit unit of our network viewed in a broad scale, a cluster of patches linked by short-range dispersal. If there is no long range dispersal, the clusters are isolated. This will be a metapopulation in a more classical sense, a collection of patches linked by short-range dispersal as in [1,7,13]. Assume that the processes of survival and reproduction which compose the local dynamics is described by a map f on $[0,\infty)$ of class C^1 . In the absence of dispersal between patches, the time evolution of the population is given by

$$x_{t+1} = f(x_t), \quad t = 0, 1, 2, \dots,$$
 (1)

where x_t represents the number of individuals at time t. Important examples of f used in ecology are given in [25,35], and the single patch model (1) can display rich dynamical behavior including stable cycles, periodic-doubling cascades and chaos.

We assume that a fraction *m* leave patch *i* and disperse to the neighboring patches. Thus, the density of individuals that leave patch *i* is given by $mf(x_t^i)$, where x_t^i denote the population density in patch *i* at time *t*, for all i = 1, ..., d, t = 0, 1, ... Moreover, from the individuals that disperse from the neighboring patches *k*, a fraction γ_{ik} reach patch *i*. Clearly $\gamma_{kk} = 0$, and $\sum_{k=1}^{d} \gamma_{ki} = 1$, for all i = 1, ..., d. We now can write the equations describing the dynamics of the isolated cluster as

$$\mathbf{x}_{t+1}^{i} = (1-m)f(\mathbf{x}_{t}^{i}) + \sum_{k=1}^{d} \gamma_{ik} m f(\mathbf{x}_{t}^{k}).$$
⁽²⁾

The first term in Eq. (2) represents the individuals that did not leave patch *i* at time *t*, while the second term is the sum of all contributions of individuals of the neighboring patches.

2.2. A system of linked clusters

The metapopulation model in two spatial scales consist of *n* equal clusters, as described in the previous subsection, labelled as 1, 2, ..., n, each one containing *d* equal patches. The total number of patches in the whole network is *nd*. Let \mathbf{x}_t^l the number of individuals in patch *i* of cluster *l* at time *t*. Let $\mathbf{x}_t^l = (x_t^{l1}, x_t^{l2}, ..., x_t^{ld})$ the *d*-dimensional vector representing the distribution of individuals among the patches of cluster *l*. In the absence of long-range dispersal the dynamics of cluster *l* is given by $\mathbf{x}_{t+1}^l = \mathbf{f}(\mathbf{x}_t^l)$, where $\mathbf{f} : R^d \to R^d$ is given by

$$\mathbf{f}(\mathbf{x}_{t}^{l}) = \begin{pmatrix} (1-m)f(\mathbf{x}_{t}^{l1}) + \sum_{k=1}^{d} \gamma_{1k}mf(\mathbf{x}_{t}^{lk}) \\ (1-m)f(\mathbf{x}_{t}^{l2}) + \sum_{k=1}^{d} \gamma_{2k}mf(\mathbf{x}_{t}^{lk}) \\ \vdots \\ (1-m)f(\mathbf{x}_{t}^{ld}) + \sum_{k=1}^{d} \gamma_{dk}mf(\mathbf{x}_{t}^{lk}) \end{pmatrix}.$$
(3)

Let $\mathbf{f}(\mathbf{x}_t^l) = (y_t^{l_1}, y_t^{l_2}, \dots, y_t^{l_d})$. Thus after the local dynamics (within patch dynamics) and short-range dispersal the number of individuals of patch *i* of cluster *l* is $y_t^{l_i}$.

We now describe the long distance movement between patches in different clusters. Let μ_i be the fraction of individuals that leave patch *i* in any cluster in a long-range movement to establish in another cluster. Of course $0 \le \mu_i \le 1$, i = 1, ..., d. Thus, the number of individuals that leave patch *i* of cluster *l* at time *t* is $\mu_i y_t^{li}$. From these individuals only a fraction will move to cluster *j*. This process is governed by a nonnegative $n \times n$ matrix *C*, satisfying $\sum_{j=1}^{n} c_{jl} = 1$ and $c_{ll} = 0$ for all l = 1, ..., n. Thus, the number of organisms that leave patch *i* of cluster *l* and reach cluster *j* at time *t* is $c_{jl}\mu_i y_t^{li}$. Let patch *k* of cluster *l* be the final destination of these migrants. Only part of them will settle in patch *k* with proportion w_{ki} . This process of distribution of migrants among the patches of the new cluster is governed by the $d \times d$ matrix *W*, with entries w_{ki} , with $0 \le w_{ki} \le 1$ for all *i*, k = 1, ..., d. Adding the contribution of all patches in clusDownload English Version:

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