QUASI-DETERMINISTIC POPULATION DYNAMICS IN STOCHASTIC COUPLED MAPS

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We studied the stochastic dynamics of coupled map lattices for small local populations. Quasi-deterministic dynamics is lost when considering one isolated population or two populations linked by dispersal. In a one-dimensional ring linked by closest neighbors some intermittent synchronization is observed. Finally we show that in two-dimensional lattices long-term synchronization take place above a critical value of the dispersal probability and the system displays a quasi-deterministic dynamics.

1. Introduction

Discrete time population models are used to describe populations with discrete (non-continuous) generations. The simplest and most studied model is the classical logistic map in which the population in generation $t+1$ is obtained from the population in generation t by

$$x(t+1) = rx(t)\left[1 - \frac{x(t)}{K}\right] = x(t)F[x(t)] \equiv g(x(t)) \tag{1.1}$$

where r is the replacement rate at low densities and the carrying capacity K fix the maximum population allowed. The per-capita replacement rate F captures, in a fenomenological way, the density dependent intra-specific competition which is the mechanism of population regulation.

This model became popular after the 1977's paper by May[17] and was vastly used and studied since then. Simple models like the logistic map or many others with a somewhat similar density dependence form for the per-capita replacement rate are attractive because its solutions display a rich dynamics controlled by only one parameter (r for the logistic map). For $1 < r < 3$ there is a single stable point, while for $r > 3$ exists a 2^k period-doubling route to chaos.

Since the seminal works by Kaneko (see for example[14,15]) coupled map lattices has been extensively studied (see for example[3,13,22,23]) and used to study theoretical problems in spatial ecology,[4,6,11,16,18–20] statistical physics[7] among other fields.

Most work were done in the deterministic limit $K \mapsto \infty$, and in few cases a small additive noise were considered.[9,10] However density-dependent competition takes place at some spatial scale, where individuals share the resources. Therefore, if we ignore spatiality, local populations (subject to 1.1) cannot be arbitrarily large. Surprisingly the realistic case of small populations were not considered[a].

For small populations demographic stochasticity plays a significant role with stochastic fluctuations of the order of the square root of the population.[2] Larger populations are then considered as spatial distributed collection of local populations linked by dispersal.

In this work we explore the consequences of stochastic demography and dispersal in the emergence of quasi-deterministic dynamics at different spatial scales using coupled map lattices.

2. Modelling Demographic Stochasticity and Dispersal

2.1. *Deterministic Models*

2.1.1. *Local dynamics*

In this work we will consider a theoretical population with non overlapping generations. For an insolated population we assume that the dynamics is governed by the logistic map 1.1.

For $x > K$, $g(x) < 0$ and therefore the constraint $x \geq 0$ must be enforced separately. The carrying capacity K provides a ceiling for the population. When x is allowed to take continuous values in $(0,K)$ the solutions of the equation 1.1 include (depending on the value of the reproduction rate r) fixed points, cycles of period 2^k and chaos.

In this work we considered only discrete, integer, values for the populations, This is achieved by considering a new map f which is the integer part of g, and therefore

$$x(t+1) = f(x(t)). \tag{2.1}$$

The fact that only integer values of the population are allowed imposes new constrains and chaos is no longer possible. For $K \mapsto \infty$ solutions of (2.1) converge to the solutions of (1.1).

2.1.2. *Dispersal*

Spatiality is modelled using a metapopulation approach. We assume that new recruited individuals (R) from the previous generation t in population $x_i(t)$ is given by the integer logistic map f, that is

$$R_i(t+1) = f(x_i(t))$$

[a]At our best knowledge.

after recruitment individuals may disperse. We assume a constant probability of dispersion per individual D and therefore we expect $DR_i(t+1)$ individuals leaving population i to other populations. After dispersal, the population i is obtained as the balance equation

$$x_i(t+1) = (1-D)R_i(t+1) + \sum_j Df_{ij}R_j(t+1)$$

where f_{ij} is the fraction of the dispersers from population j who moved to population i. We may write the evolution equation in terms of x alone as

$$x_i(t+1) = (1-D)f(x_i(t)) + \sum_j Df_{ij}f(x_j(t)). \tag{2.2}$$

Two Patch Model. The most simple setting with some spatiality is two connected populations. In this case model (2.2) reads:

$$x_1(t+1) = (1-D)f(x_1(t)) + Df(x_2(t)), \tag{2.3}$$

$$x_2(t+1) = (1-D)f(x_2(t)) + Df(x_1(t)). \tag{2.4}$$

One dimensional ring. A more realistic case is a linear arrangement of patches connected by first neighbors. We considered periodic boundary conditions, or in other words, a ring. If the total number of patches is N and dispersal is symmetric ($f_{i,i-1} = f_{i,i+1} = 1/2$), model (2.2) becomes

$$x_i(t+1) = (1-D)f(x_i(t)) + \frac{D}{2}\left[f(x_{i-1}(t)) + f(x_{i+1}(t))\right] \tag{2.5}$$

Two dimensional lattice. Finally we considered two dimensional arrays of populations connected by the four closest neighbors in a torus (periodic boundary conditions). Thus, if the population in the patch (i,j) is x_{ij} the dynamics of the system is governed by the difference equation:

$$\begin{aligned} x_{ij}(t+1) &= (1-D)f(x_{ij}(t)) \\ &+\frac{D}{4}\left[f(x_{i-1,j}(t)) + f(x_{i+1,j}(t)) + f(x_{i,j-1}(t)) + f(x_{i,j+i}(t))\right] \end{aligned} \tag{2.6}$$

2.2. *Stochastic demography and dispersal*

Density dependent processes take place during finite periods of time and involve many events like birth and death at different stages. Here we simplified the situation by considering only one event, recruitment of new individuals from those in the patch in the previous generation. Therefore if the expected number of new recruits in generation $t+1$ is $f(x(t))$ the actual number is a random variable with (approximate) Poisson distribution with parameter $f(x(t))$. Realizations of this process are obtained then as

$$x(t+1) = Poisson(f(x(t))) \tag{2.7}$$

where $Poisson(\lambda)$ is a (positive integer) number drawn from a Poisson distribution of parameter λ. For $\lambda > 5$ Poisson distribution is approximately normal with mean and variance equal to λ. In such a case (2.7) becomes approximately

$$x(t+1) = f(x(t)) + \eta\sqrt{f(x(t))}$$

where η is a random variable normally distributed with zero mean and unitary variance.[2] As K increases the additive noise term becomes less significant and the dynamics becomes quasi-deterministic.

On the other hand, we considered a per-individual probability of dispersal D independent of the density. Therefore the number of individuals dispersing from a population of size x is a random variable with binomial distribution with probability of success D and x trials. This number is further divided among the j recipient populations according to a multinomial distribution with probabilities Df_{ij} (where f_{ij} are the fractions of the dispersers from population i what move to populations j).

3. Results

Period two cycle is the more robust non-trivial dynamics and therefore in this work we considered $r = 3.2$ for all the populations. We also considered a small value for the carrying capacity ($K = 250$) as we are interested in cases where stochasticity has a significant effect on the dynamics.

In this case realizations of model (2.7) do not show a clear two period behavior with the population taking almost all allowed values (see Fig.1).

The two-patch model 2.3 is the most simple setting with some spatiality. The deterministic case was extensively studied by Hasting[10] who found a complex dynamics including fractal basin boundaries. In our case ($r = 3.2$) the dynamics is very simple. For low values of the dispersal both patches are almost uncoupled and the solutions for each patch are in phase or out of phase depending on initial conditions. Eventually, as we increase the value of the dispersal parameter D, the patches synchronize for any initial condition. However the stochastic counterpart does not show any clear period two solution at any spatial scale: one single patch behaves in the same way as the total population. The deterministic dynamics is completely blurred by the intrinsic stochasticity of the demography and dispersal processes.

Can we recover the period two cycle for larger populations? When considering $N = 100$ patches in a linear arrangement like in model 2.5 stochasticity still prevents long term synchronization. This results are markedly different to the obtained in the deterministic case[7]

In the figure 2 we show the dynamics observed in one patch together with the evolution of the total population for two values of the dispersal D. For low dispersion, each patch follows its own dynamics which is determined by the (randomly chosen) initial conditions. Total population averages to the (unstable) equilibrium of the logistic map $x^* = NK(1 - 1/r)$. For large values of the dispersal ($D = 0.5$)

there some intermittent and weak synchronization. For some periods of time the total population oscillates in a somewhat clear way, but far from the values expected for a full synchronized population (see Fig. 2). To understand the dynamics better we consider the state of the system mod 2 (i.e. only for even values of t). In a typical realization the total population stay above the equilibrium value x^* for some period of time, then approaches to the equilibrium value to stabilize for some other period of time below the equilibrium value.

The extra connections provided by the two-dimensional lattice where each patch interacts with its closest four neighbors is enough to produce long term synchronization (see Fig. 3). For low values of the dispersal dynamics of each patch is independent of the dynamics of its neighbors and the total population fluctuates around the equilibrium value $x^* = NK(1 - 1/r)$. As the value of D increases we observed a sharp transition to a state where most of the patches are synchronized. In Fig. 3 we show a typical realization for a high value of the dispersal $D = 0.5$. Total population values are close to the deterministic solution corresponding to full synchronization (solid lines in Fig. 3). However, even in this case we may observe a destabilization of the system with a (relatively abrupt) transition to the other state (for example from above $x*$ to below it, as displayed in fig 4).

For high values of dispersal ($D = 0.5$ for example) total population displays a quasi-deterministic dynamics with a well defined two-period cycle and small fluctuations. However local dynamics observed at a single patch is still greatly dominated by stochasticity (see Fig. 3). Distribution of population values, however, show a bimodal distribution as opposed to the case of low diffusion (see Fig. 1 top panel).

In order to characterize the transition to (long-term) synchronization as we increase the dispersal probability D we proceeded as follow. For low values of D the total population fluctuates around the equilibrium value $x^* = NK(1 - 1/r)$. We defined a diffusion region as the interval $(x^* - \sqrt{x^*}, x^* + \sqrt{x^*})$. For a given realization we computed each pair of consecutive values of the total population and checked if the difference of them was greater than $2\sqrt{x^*}$. We then computed the proportion of those pairs to the total number of pairs in the simulation. For each value of D we repeated this numerical experiment 10 times and computed the average proportion P. The results displayed in Fig. 5 show that the transition to high synchronization takes place about the critical value $D_c \sim 0.35$.

4. Discussion and Conclusions

Models for spatially extended populations play a key role in the development of ecological theory. Levins[21] metatapopulation theory provided a simple explanation for population persistence and species coexistence. While small and isolated populations are prone to extinction a collection of such population may persist by a process of local extinction and recolonization from other patches. Low levels of dispersal contributes to stability while higher dispersal promotes synchronization, and therefore may increase the probability of global extinction (see[1,24] for a review, but

see also[20]).

Coupled map lattices has been studied for many decades but the great majority of the works considered the deterministic case. Among the few works in which stochasticity was included we can mention the paper by Hastings.[10] If well most of the results were obtained for the deterministic case, Hastings included an additive white noise of variance 10^{-3} (he considered the normalized logistic map $x_{t+1} = rx_t[1-x_t]$). Stochastic demography produce fluctuations with Poisson distribution, and therefore variance is of the same order of the mean. Hastings choice imply that the population is of the order of 10^6. However competition is a local process and therefore we should not to expect such large populations in local competition. In this work we focused in the more realistic, but surprisingly almost not studied, case of small local populations where stochasticity almost dominates the dynamics.

When considering an isolated local population, and for the population sizes considered in this work, stochasticity blurred the deterministic dynamics. The same is observed in a two-patch model. All the complexity described in the work of Hastings is lost. Quasi-deterministic dynamics is recovered only for larger population but the connectivity of the metapopulation plays a fundamental role. For 100 patches arranged in a ring and linked by the two closest neighbors there is no an appreciable synchronization and quasi-deterministic dynamics appear in an intermittent, not well defined, way. Periods of partial synchronization may be followed for long periods of lack of synchronization what may last hundreds of generations (see Fig. 2, see also[5,11,18,19] for a discussion of long transients in spatially extended populations).

In a two dimensional lattice where each patch is in contact with its four closest neighbors a sharp transition to synchronization is observed for dispersal D above the critical value $D_c \sim 0.35$. In this case a clear period-two cycle is observed with relatively small fluctuations. The values of the total population oscillates close to the values expected for a fully synchronized deterministic coupled map lattice, an indication of the high level of synchronization. However, even in this case deterministic dynamics is not apparent at local level. In Fig. 3 (bottom panel) we show the dynamics for the total population together with the dynamics observed in one random chose patch. While the total population oscillates between two quite well defined values, local population wander over a wide range in phase space. However the dynamics is qualitatively different from the observed in an isolated population. In this last case the distribution of the frequency of population values presents only one peak close to the upper deterministic value of the period two cycle (see Fig. 1, top panel). On the other hand, the distribution observed in a local population of a two-dimensional synchronized lattice is (slightly) bi-modal. Although period two cycle is not clearly apparent at local level, the synchronization among populations produce a well defined bimodal distribution for the total population.

Here we want to remark that in all cases presented in this work detection of density dependent regulation is out of question. However the details vary from case to case. For low dispersal, the oscillatory deterministic skeleton may be detected at

local level but not a global level (see Fig. fig-lattice, top panel) where the system behaves as having a growth rate at low densities $r < 3$.

For dispersal above the critical value, synchronization of populations, changes the picture. Local populations oscillate in an irregular way while populations at larger scales display a clear quasi-deterministic two-period cycle (see Fig. 3, bottom panel). In this case our results are in the opposite direction of the Hastings:[10] Density dependence is more detectable at larger spatial scales.

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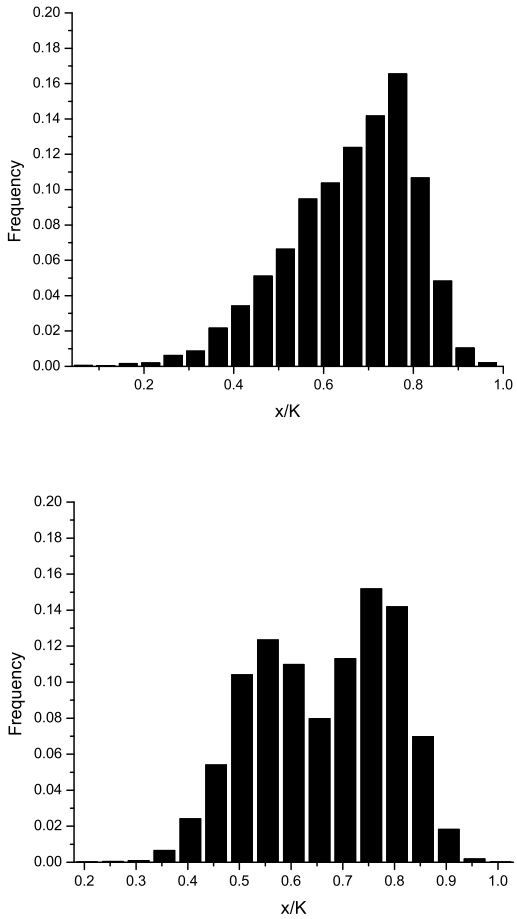

Fig. 1. Distribution in the phase space obtained with model 2.7 (top panel) and with the two-dimensional coupled map lattice (bottom panel, $D = 0.5$) for one randomly chose patch. After transients we run the model for 10^4 time steps and computed the frequency of occurrence of different population values (expressed as proportions x/K). Normalized deterministic solutions of model 2.1 (x/K) oscillates between 0.516 and 0.796. For the one patch model distribution does not show any sign of the two period cycle. Dynamics in a typical patch in the 2D lattice shows a bi-modal distribution with peaks around the deterministic values . In all cases $r = 3.2$ and K=250.

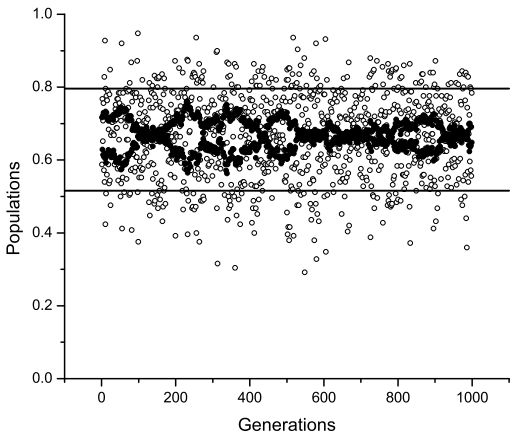

Fig. 2. Local and global dynamics in a ring of 100 patches for high dispersal. Total population (solid dots) presents some intermittent oscillations. Local populations (open circles) show large fluctuations in the available range $(0, K)$. Continuous lines are the deterministic values between the fully synchronized metapopulation oscillates. ($D = 0.5$, $r = 3.2$, K=250, $D = 0.5$.)

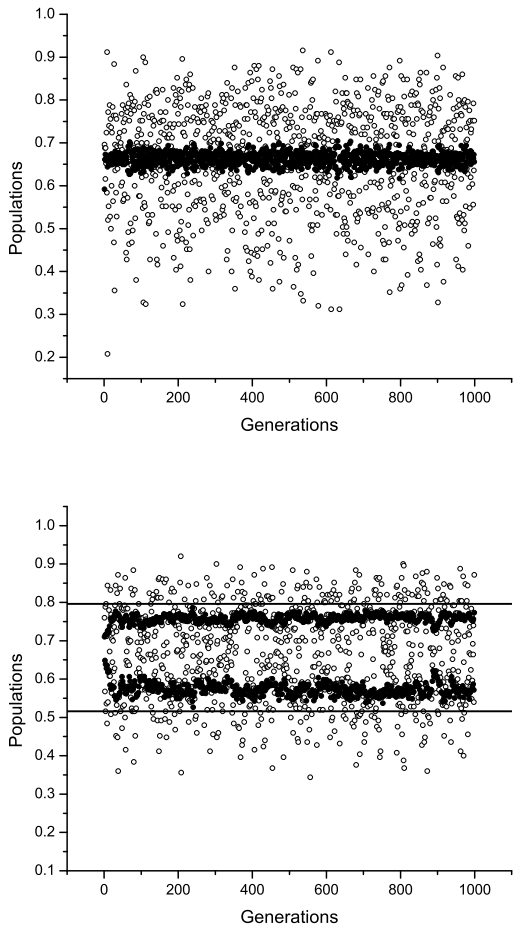

Fig. 3. Local and global dynamics in a lattice of 10×10 patches for low ($D = 0.05$, top panel) and high dispersal ($D = 0.5$, bottom panel). For high dispersal the total population (black dots) oscillates close to the deterministic values for a fully synchronized lattice. $r = 3.2$, K=250, $D = 0.5$.

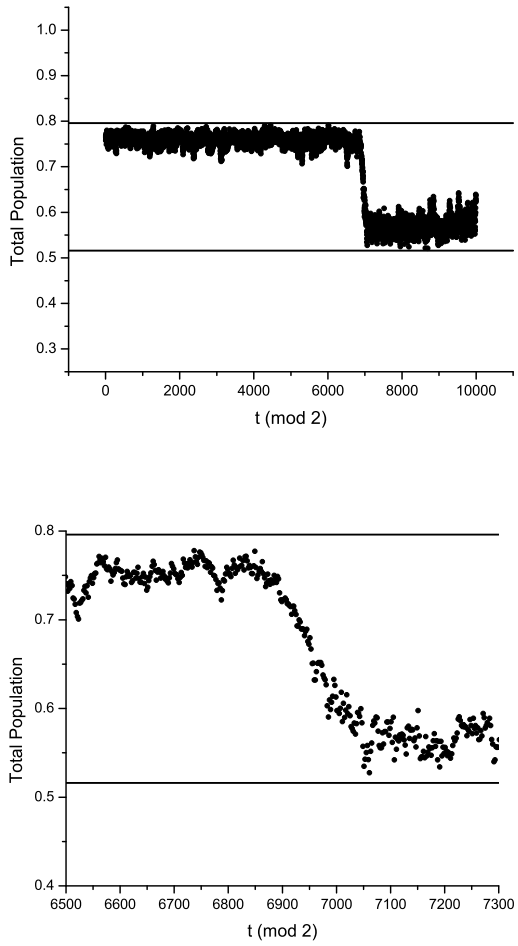

Fig. 4. Total population (mod 2) in a lattice of 10 × 10 patches. Around $t \sim 6900$ the system change its state in a relatively short window of time of approximately 150 time steps (see bottom panel). $r = 3.2$, K=250, $D = 0.4$

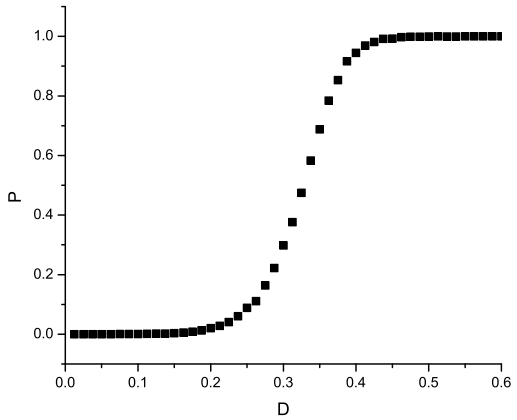

Fig. 5. Transition to synchronization in a lattice of 10 × 10 patches. For each value of D we computed the average proportion of consecutive pairs (P) above and below the diffusion region using ten replicas.