When Two and Two Make Four: A Structured Population Without Chaos

ISTVÁN SCHEURING† AND IMRE M. JÁNOSI‡

Institute for Advanced Study, Collegium Budapest, Szentháromság utca 2, H-1014 Budapest, Hungary and Höchstleistungsrechenzentrum, KFA-Jülich, D-52425 Jülich, Germany

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Because a large number of theoretical models suggest chaos in populations, field biologists have been trying for decades to confirm the existence of chaos in nature. In spite of their efforts, chaotically evolving populations have been found in extremely low numbers. In this article we consider a metapopulation model which was built up by the interaction of local populations. Local populations interact with their nearest neighbours via migrations, but migration occurs only if the local population density exceeds a threshold level (overcrowding). Depending on the strength of the interaction, the metapopulation density shows noiselike dynamics of many degrees of freedom, periodical evolution, or tends to a fixed point. Low dimensional collective chaos has not been detected. Moreover, the migration size distribution indicates the emergence of self-organized criticality, if the interaction is strong enough.

1. Introduction

It has been known for more than 20 years (May 1974, 1976, 1986) that populations may exhibit complex dynamics, including chaos, but the evidence for chaotic behaviour in natural populations is scarce (Berrymann & Millstein, 1989; Turchin, 1990; Turchin & Taylor, 1992; Witteman et al., 1990; Godfray & Grenfell, 1993). There may be (at least) three reasons for this discrepancy. First, it is difficult to distinguish low dimensional deterministic chaos from coloured noise originated from stochastic environmental effects (Stone, 1992), especially in short-time series. Second, it is possible that natural selection keeps populations away from chaos (Berrymann & Millstein, 1989). Recent theoretical investigations suggest, however, that natural selection could not destroy chaos efficiently, on the contrary, it often promotes the emergence of chaos (Altenberg, 1991; Ferrière & Gatto, 1992; Doebeli, 1994). The third possible hypothesis states that the spatial and dynamical complexity of natural habitats and populations prevents the emergence of chaos (Stone, 1993). Diffusion-like processes, for example, generally decrease the chaotic domain of population dynamical models (Gonzales-Andujar & Perry, 1993; Hastings, 1993). There are model systems, however, where diffusion leads to the emergence of chaos (Pascual, 1993), or increases the chaotic region (Solé & Valls, 1992; Bascomte & Solé, 1994). If dynamical and diffusional processes are modelled by individually based cellular automata, the emergence of spatio-temporal chaos is quite common (Wolfram, 1983, 1984, 1986; Pacala & Silander, 1985; Molofsky, 1994).

Our aim is to study the dynamical behaviour of a spatially structured single species population model, which tries to take account of a self-regulation mechanism in a more adequate manner than reaction-diffusion equations or cellular automata do. The spatial scale in this study is different from the scale of individual based models. A metapopulation is considered, which is built up by local sub-populations. Nearest neighbouring local populations interact via migrations. The local populations, in agreement with individual-based simulations and the
differential or difference equation descriptions, are allowed to evolve in a chaotic way.

One important question is how to implement the mechanism of migration. The simplest idealisation assumes that there is no distance and density dependence in migration (Levins, 1970). More sophisticated models introduce either density (Gadgil, 1971; Hanski & Gilpin, 1991; Hastings, 1993) or distance dependence (MacArthur & Wilson, 1967).

To describe the distance dependence of migrations in our model, we use the so called “stepping stone” picture, i.e. population fragments can disperse farther away by a series of elementary migrational steps to the nearest neighbouring habitats. These elementary migrations are supposed to be much faster than the reproduction rate, thus a timescale separation is also introduced. Another basic ingredient of our dispersal rule is a threshold condition. Migration begins from a habitat only if the local population is overcrowded, i.e. the population density exceeds a critical level. We would like to emphasize that these assumptions are motivated by field observations, flying insects of long migrational rules are as follows: migration is subcritical (migration phase). Note that this rule introduces the timescale separation: migration is much faster than reproduction. (As an illustrative example think of the cockchafer, Polyphylla fullo: It has a synchronized reproduction cycle of 4–5 years, but is able to migrate several kilometers in a few days.) The updating occurs simultaneously during the migration phase. This means that several avalanches of different origins can run parallel in a large system. The migrational avalanches are “transparent” to each other, avalanche collision does not stop migrations in opposite directions. The neglection of avalanche interaction is necessary to mimic the natural situation, where opposite migrations occur at the same time with low probability, but opposite migrations at different times do not interact. As the time interval of the migrational phase in our model is considered as an instant on the reproduction timescale, there is no way to resolve avalanches shifted in time to each other but in the same migrational phase.

The dynamics are then as follows. Each site evolves simultaneously according to eqn (1) from a random initial density value (reproduction phase). When one (or more) local population densities exceeds the threshold value \( N_{c,i} \), the time evolution stops on the whole lattice, and migrations run until every site becomes subcritical (migration phase). Note that this rule introduces the timescale separation: migration is much faster than reproduction. (As an illustrative example think of the cockchafer, Polyphylla fullo: It has a synchronized reproduction cycle of 4–5 years, but is able to migrate several kilometers in a few days.) The updating occurs simultaneously during the migration phase. This means that several avalanches of different origins can run parallel in a large system. The migrational avalanches are “transparent” to each other, avalanche collision does not stop migrations in opposite directions. The neglection of avalanche interaction is necessary to mimic the natural situation, where opposite migrations occur at the same time with low probability, but opposite migrations at different times do not interact. As the time interval of the migrational phase in our model is considered as an instant on the reproduction timescale, there is no way to resolve avalanches shifted in time to each other but in the same migrational phase.

The model defined above is very close to the so-called self-organized critical (SOC) model family. A typical SOC system consists of many locally interacting degrees of freedom, and reaches a dynamic critical state without adjusting any external parameter (Bak et al., 1987, 1988). Important ingredients are external driving, some dissipation mechanism ensuring a steady state, the presence of a threshold condition, and timescale separation. To illustrate the general idea, let us briefly describe the sandpile model of self-organized criticality (Bak et al., 1987). Take a horizontal plane, and drop sand randomly onto it.
grain by grain. A pile grows and its slope slowly increases. If the pile becomes too steep locally, some grains move downhill, occasionally creating large sand avalanches. After a while, the average slope of the pile attains a critical value, which does not increase further. This is a dynamical critical state: a new single grain may trigger off an avalanche of any size (limited by the system size only). The distributions of avalanche sizes and durations show characteristic power-law shapes defining dynamical critical exponents.

On the other hand, our model is also closely related to the coupled map lattice (CML) models (Kaneko, 1992). Perhaps the most widely investigated CMLs consist of diffusive nearest neighbour coupling, which has the following form in two dimensions:

$$x'_{i,j} = (1 - \epsilon) f(x_{i,j}) + \frac{\epsilon}{4} \sum_{k,l \in \text{nn}} f(x_{k,l}),$$

(4)

where \(x_{i,j}\) and \(x'_{i,j}\) are the state variables at time \(t\) and \(t+1\), respectively, \(f(x_{i,j})\) is an appropriate function governing the local dynamics, \(\epsilon\) denotes the coupling parameter (or diffusional constant), and the summation runs over the nearest neighbours \((nn)\) in a square lattice. It is easy to recognize that our migrational rule eqn (3) involves the same form of discretized Laplacian as eqn (4). The local dynamical function in eqn (4) can be, for example, the logistic map \(f(x_{i,j}) = rx_{i,j}(1 - x_{i,j})\) with the control parameter \(r\) (Kaneko, 1992; Solé & Valls, 1992), or eqn (1) (Bascompte & Solé, 1994). The main difference between our system and the diffusively coupled CMLs is that in our model diffusion occurs only occasionally, above the threshold level, and it is an instantaneous process as a consequence of the timescale separation.

3. Characteristics of the System

In the following we focus attention on the global behaviour of the lattice. As the overwhelming part of the field data involves population census over a given area, its behaviour should be closer to global dynamics than local ones. We think that the local dynamics, i.e., the behaviour of a single site in the interacting lattice, is hardly comparable to the dynamics of a natural subpopulation. One reason is that a local habitat in nature is not as well defined as a unit as a site in a lattice model is: the area, location, borders etc. are changing dynamically in time, it is difficult to define them at all.

The question is now the following: what is the characteristical global behaviour of a metapopulation built up by chaotically evolving, interacting local subpopulations? To answer it, we have performed extended numerical experiments in the model defined above. The parameters of eqn (1) were chosen to drive subpopulations chaotically: \(\lambda = 100.0, a = 1.0,\) and \(\beta = 8.8\) (Hassel et al., 1976). The key parameters of our studies were the threshold level, \(k\), triggering migrations and the system size, \(L\). We found that the subcritical level \(N_{sc}\) in eqn (2) did not play an important role in the dynamics, thus in most cases it was fixed to the threshold level as \(N_{sc} = 0.7k\).

Figure 1 shows the typical results of bifurcation tests, where the values of 1000 iterations (after discarding 1000 initial points) were plotted for different thresholds. Figure 1(a) refers to a single map with open boundaries: When the populational density...
exceeds the threshold \( k \), at the next step the value will be \( N_c = 0.7k \) as a consequence of outward migrations. The threshold rule destroys chaos immediately after becoming effective (\( k < 4.4304 \)). Compare it with Fig. 1(b), where the appropriate values for a single site in a lattice of \( L = 8 \times 8 \) are plotted. In this spatially extended system, the local evolution remains chaotic (or at least complex) in a wide threshold range (\( 2.35 < k < 4.43 \)), where an isolated map shows strict periodicity. This result is reminiscent of earlier observations (Pascual, 1993; Solé & Valls, 1992; Bascompte & Solé, 1994), where local chaos was found in a wider parameter range if spatial dispersion was switched on.

Figure 1(c) shows the asymptotic values for the whole lattice. The global dynamics are represented by the time evolution of the lattice average:

\[
\langle N \rangle \text{ or } \bar{N}(t) = \frac{1}{L^2} \sum_{i,j} N_{i,j}(t).
\]

Average values were measured after finishing all migrations. At larger threshold values (\( k > 2.65 \)), the behaviour is noiselike in the sense that the lattice average fluctuates around a (temporal) average with a Gaussian amplitude distribution. At smaller threshold values, period four, period two, and fixpoint behaviour settle down, but low dimensional collective chaos has not been found at any parameters.

Obviously, the noiselike behaviour of the lattice average at the range \( k > 2.65 \) is not “real noise”, because the fluctuations in the average are the consequences of deterministic rules there is no external source of perturbations. This also means that the global dynamics may obey “high dimensional chaos”, from the point of view of practical evaluation of field observations, however, this makes no significant difference when compared with real noise.

To establish the last statement in a more convincing way, we measured the standard deviation of the fluctuations as a function of system size. The standard deviation \( \sigma \) is defined as usual:

\[
\sigma = \sqrt{\langle (N) \rangle^2 - \langle N \rangle^2},
\]

where the inner/outer brackets denote spatial/temporal averaging. In the case of stochastic noise, \( \sigma \) decreases with the square-root of the number of independent degrees of freedom contributing to the signal. In Fig. 2 we plotted \( \sigma(L^2) \) at two different thresholds: \( k = 5.0 \) refers to a non-interacting case (totally independent degrees of freedom), while at \( k = 3.2 \) extended migrations are present (cf. Fig. 1). The solid line shows the theoretical scaling for the non-interacting situation, i.e. a power-law with an exponent \(-1/2\). The difference between the interacting and non-interacting cases is very moderate, apart from the fact that the amplitude of fluctuations is slightly higher if the interaction is switched on. Of course, there are advanced methods to distinguish pure noise from high dimensional chaos (e.g. Bauer et al., 1993 and references therein), the length of time series necessary for the unambiguous decision, however, (\( \sim 10^5-10^6 \) data for noiseless cases) makes these methods almost unusable for practical purposes.

Low dimensional collective chaos would mean that there exist one or a few at most “master” degrees of freedom governing the time evolution of the otherwise complex system—in this case the search for the equation(s) of motion would be more promising.

We have also checked the behaviour of our model by plotting the first return maps and calculating the power spectra of time sequences (Csilling et al., 1994) at several parameter sets, no deviation from the above mentioned characteristics were observed.

The lack of collective chaos is a more or less well-established fact in noiseless coupled map lattice models with nearest neighbour diffusive coupling (Kaneko, 1992; Solé & Valls, 1992; Bascompte & Solé, 1994). In our model, however, the situation is not so clear. We have pointed out by analysing the migrational avalanches (Csilling et al., 1994), that below a critical threshold, \( k, \approx 2.35 \), self-organized criticality emerge with long-range correlations. To illustrate the birth of SOC, we plotted in Fig. 3 the distribution \( P(s) \) of the migrational avalanche sizes \( s \) at different thresholds. The size \( s \) of an avalanche is defined as the total number of elementary migration steps starting from a single overcrowded site. To avoid difficulties in accounting migrations at avalanche collisions, we implemented the so-called local-perturbation method, for details see Csilling et al. (1994). When the interaction is weak.
At $k \approx 4.0$, the distribution function can be fitted by an exponential function:

$$P(s) \sim \exp\left(-\frac{s}{s_*}\right),$$  \hspace{1cm} (7)

where the characteristic length $s_* \approx 1$ indicating local and uncorrelated migrations. In an intermediate range $2.35 < k < 2.8$, $P(s)$ has an exponentially damped power law shape:

$$P(s) \sim s^{-\tau} \exp\left(-\frac{s}{s'}\right),$$  \hspace{1cm} (8)

where the exponent is in the range $1.0 < \tau < 1.3$, and the characteristic length $s' > 3.0$ quickly diverges to the infinity as the threshold decreases to a critical level $k_c \approx 2.35$. Below this critical value, power-law behavior arises:

$$P(s) \sim s^{-\tau},$$  \hspace{1cm} (9)

where $\tau = 1.2 \pm 0.08$ slightly depends on $k$. Obviously, in a finite system scaling breaks down exponentially at sizes comparable to the system size. We tested the presence of power law behaviour by finite-size scaling analysis as well (Csilling et al., 1994). The emergence of power law distributions indicates the build-up of long range correlations in the lattice, and characterizes self-organized criticality.

The appearance of long range correlations extends the range of the effective interaction beyond nearest neighbours. In the SOC state migrational avalanches of system size occur, however, according to the power law distribution, not very often. Thus synchronized collective chaos is not probable in large systems, but it might be present at small sizes. Another way to promote synchronization is to decrease the divergence rate of neighbouring trajectories, i.e. to decrease the Lyapunov exponent. We tested both possibilities to find collective chaos.

First, let us consider a metapopulation of size $L = 3$, without changing the dynamical parameters. (This is the smallest system containing not only boundary sites.) In Fig. 4 the first return maps for the central site and for the lattice average are plotted at different thresholds. Not surprisingly, without interaction each site evolves chaotically [Fig. 4(a)], and the lattice average shows the noiselike behaviour [Fig. 4(b)]. As the threshold decreases (i.e. the interaction increases), new arms appear in the first return map of the central site [Fig. 4(c)] indicating the coupling to the neighbours, while the evolution of the metapopulation remains almost the same as in the

![Fig. 3. Distributions of migrational avalanche sizes in a system $L=16$, $\lambda=100.0$, $a=1.0$, $\beta=8.8$, $\Delta=1.0$, and $N_{sc}=0.7k$. For the sake of clearness, the curves are shifted. The solid lines are fitted functions, see text.](image1)

![Fig. 4. First return maps for the central site (left column) and for the lattice average (right column) in a system of $L=3$, $\lambda=100.0$, $a=1.0$, $\beta=8.8$, $\Delta=1.0$, and $N_{sc}=0.7k$. (a) $k=3.20$, (b) $k=3.0466955$, and (c) $k=3.0466960$.](image2)
non-interacting case [Fig. 4(d)]. A further very small decrease of the threshold level ($\Delta k = 5 \times 10^{-7}$) causes the emergence of perfect periodicity [Fig. 4(e) and (f)]. The transition in this small system is extremely sharp. Based on simulations at different system sizes, we concluded that the larger the metapopulation, the wider the transition range. The size dependence of different properties is generally known, though not well understood from similar CML models (Kaneko, 1992). In models like ours, the vanishing effect of the open boundaries at growing systems may certainly contribute significantly to behavioural changes.

Next, we investigated the behaviour of small systems with “weak” chaotic driving (Fig. 5). We selected the dynamical parameters $\lambda = 100.0$, $a = 1.0$, and $\beta = 7.275$, where the isolated map eqn (1) has a positive Lyapunov exponent $\gamma = 0.0230 \pm 0.0005$ (Csilling et al., 1994). The transition from complex to strictly periodic evolution is smeared out, compared with the cases shown in Fig. 4. In a narrow threshold range, even some low dimensional structure appears in the first return map of the lattice average [Fig. 5(b)]. Further analysis, however, gave the result that this is not low dimensional chaos. We implemented a simple but robust method to calculate the largest Lyapunov exponent (Kantz, 1994), but a positive value has not been obtained. The power spectra [Fig. 5(c) and (f)] of the time series suggest period two motion with a smeared, uncorrelated background, which originates probably from the intermittent bursts of the otherwise almost perfectly oscillating local populations [Fig. 5(d)].

In natural metapopulations the dissipation parameter $\Delta$ of eqn (3) should usually be less than one. We made some simulations with $\Delta$ smaller than one, but the only remarkable observations were the further widening of the transition range from the complex to the periodic state, and the decrease of migrational avalanche sizes. Extremely strong dissipation obviously leads to the decoupling of local populations and the ceasing of SOC behaviour.

![Fig. 5. Time series, first return map, and power spectrum of the time series for the lattice average (upper row) and for the central site (lower row) in a system of $L = 3$, $\lambda = 100.0$, $a = 1.0$, $\beta = 7.275$, $\Delta = 1.0$, $N_0 = 0.7k$, and $k = 3.150$.](image-url)
4. Possible Tests of the Model

A possible direct check of the biological relevance of our model would be a statistical analysis of natural migrational avalanches. As this is hardly applicable in practice, we turn our attention to other, more promising methods, which are based on data analysis in local habitats.

The migration activity depends primarily on the coupling strength, i.e. on the threshold level $k$. The larger the value of $k$, the smaller the frequency of dispersal events; this can be observed following the time evolution of a local subpopulation. A possible characteristic is then, for example, the distribution $D(T)$ of “silent” periods $T$, i.e. the number of reproduction cycles during which no population fragments arrive in a given habitat. We measured $D(T)$ in the site $(i=8,j=7)$ of a lattice $L=16$ at parameter values $\lambda=100.0$, $a=1.0$, and $\beta=8.8$, and at several threshold $k$. The results are plotted in Fig. 6. The distribution density functions decay exponentially (see inset):

$$D(T) \sim \exp\left(-\frac{T}{T^*(k)}\right),$$

if $k>k_c$. Here $T^*(k)$ is a threshold dependent characteristic time. This behaviour changes abruptly at the critical threshold $k_c$, where also the power law scaling in avalanche sizes appears. Instead of a broad distribution of $T$, only a narrow peak remains near the origin, indicating inward migrations in almost every cycle. In fact, the observed longest silent interval in this system was $T=3$ at $k<k_c$. In the $k>k_c$

regime, the following assumption gives a good fit for the characteristic times:

$$T^*(k) = \frac{1}{c_0 - c_1 k},$$

where $c_0=1.7 \pm 0.05$ and $c_1=0.37 \pm 0.04$ are empirical parameters. This fit also gives a satisfactory estimation of the divergence limit $k_c = 4.60 \pm 0.35$, where the coupling disappears (the exact value is close to 4.5).

Another useful test may be based on the analysis of the size distribution of incoming population fragments to a local habitat. We measured two related quantities in our model: first, the distribution $D(n)$ of the arriving population $n$ during an elementary migrational step; second, the distribution $D(m)$ of the total immigrated population $m$ until subcriticality is reached in the whole system. The latter quantity, $m$, accounts for only the arriving population fragments, it is not corrected by the possible outward migrations. The results are plotted in Figs (7 and 8) for the same system as before. At the critical connection strength,
5. Summary and Discussion

We have suggested a possible mechanism that defends natural populations against low-dimensional chaos. We have introduced a metapopulation model, a population which is a spatially dispersed system of local subpopulations interacting with each other via migrations. Migration obeys a threshold condition and timescale separation, i.e. reproduction is supposed to be much slower than diffusive dispersal.

In spite of the fact that local populations may evolve chaotically, the metapopulation shows either noise-like behaviour of many degrees of freedom, or periodic evolution without the presence of collective, low-dimensional chaos. The lack of collective chaos is not trivial in our model, because we observed long range correlations below a critical coupling strength. The main characteristics are in close analogy with thorough analysis of field observations of insects and vertebrates (Turchin et al., 1990; Turchin & Taylor, 1992; Witteman et al., 1990), and the behaviour of simple one-dimensional coupled “single-humped” maps with constant immigration (Stone, 1993).

Unexpectedly, the lack of collective chaos also characterizes extremely small metapopulations. Thus, it is possible that dispersal events triggered off by overcrowding inhibit the emergence of collective chaos very efficiently. Moreover, we found that the smaller the metapopulation, the sharper the transition from complex evolution to perfect oscillatory state. This implies practical conclusions: very strict periodicity in natural populations may reflect a small metapopulation containing only a few local subpopulations, and even a very small decrease in local connection (increasing of $k$) may change the behaviour of these metapopulations dramatically.

Periodicity in the local reproductional laws is not necessary to achieve periodic collective state. The marked differences between the collective and the local behaviour show that selection of the sampling scale in field observations is a crucial step. As every field measurement was intended to use the best available statistics, probably most of them refer to metapopulations instead of isolated subpopulations. Thus, to find adequate models for the interpretation, the consideration of interactions between local subpopulations is inevitable.

We pointed out that, besides the time series analytical methods, migrational avalanche statistics may help in understanding the properties of interacting subpopulations. We proposed to measure migrational data locally, i.e. on local habitats. We hope that similar “unconventional” analysis may contribute to the understanding of why low-dimensional chaos is not widely present in nature.

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