

# Noise can prevent onset of chaos in spatiotemporal population dynamics

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**Abstract.** Many theoretical approaches predict the dynamics of interacting populations to be chaotic but that has very rarely been observed in ecological data. It has therefore risen a question about factors that can prevent the onset of chaos by, for instance, making the population fluctuations synchronized over the whole habitat. One such factor is stochasticity. The so-called Moran effect predicts that a spatially correlated noise can synchronize the local population dynamics in a spatially discrete system, thus preventing the onset of spatiotemporal chaos. On the whole, however, the issue of noise has remained controversial and insufficiently understood. In particular, a well-built nonspatial theory infers that noise enhances chaos by making the system more sensitive to the initial conditions. In this paper, we address the problem of the interplay between deterministic dynamics and noise by considering a spatially explicit predator-prey system where some parameters are affected by noise. Our findings are rather counter-intuitive. We show that a small noise (i.e. preserving the deterministic skeleton) can indeed synchronize the population oscillations throughout space and hence keep the dynamics regular, but the dependence of the chaos prevention probability on the noise intensity is of resonance type. Once chaos has developed, it appears to be stable with respect to a small noise but it can be suppressed by a large noise. Finally, we show that our results are in a good qualitative agreement with some available field data.

## 1 Introduction

Irregular fluctuations of population densities typically observed in field observations is a signature of ecosystem dynamics [1]. However, their origin and implications often remain obscure and have been a long-standing challenge in theoretical ecology. In particular, since early works of May [2,3] where he showed that even seemingly very simple models of population dynamics can exhibit an extremely complex behaviour called chaos, it has been linked to the predictability of ecosystem dynamics. An essential feature of chaos is the system's high sensitivity to small variation of the initial conditions [4] which, since the actual initial conditions are never known precisely, makes a mid-term prediction of the ecosystem state impossible [5]. Identification of factors that can affect the irregularity of population fluctuations making them either chaotic or regular (e.g. periodic) is therefore a problem of significant importance.

Theoretical findings of May [2,3] triggered a vigorous quest for chaos in ecological data [6–9]. The results turned to be somewhat discouraging, though. Although chaos in population dynamics was finally discovered in a laboratory

population of flour beetle [10] and in some microbial populations [11], there has been a growing opinion that chaos in ecosystem dynamics is more likely to be an exotic rather than common phenomenon. One reason why chaos is not commonly seen is thought to be an insufficient length of ecological time series. To make it worse, the time series are usually smeared by the impact of transient environmental conditions. However, these arguments yet leave open the principal question whether the inherent ecosystem dynamics can or cannot be chaotic and under what conditions.

Moreover, there seems to be a discrepancy between the lack of evidence from ecological data and a broad variety of theoretical/mathematical approaches predicting chaos in models of population dynamics [12–19]. In particular, it was shown that spatially explicit models are, in general, much more likely to exhibit chaos than the non-spatial ones [20–24]. It was also shown that chaos, especially a spatiotemporal one when population densities' irregular oscillations in time are combined with their irregular fluctuations in space, may be beneficial for community functioning and persistence [25,26].

In order to close the gap between theory and reality, a question was brought forward about a possibility of ecosystems regulation, through the impact of either exogenous or endogenous factors, that helps keeping their

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dynamics regular. One factor that is thought to affect the type of ecosystem dynamics is the impact of stochastic factors [27–31], which is often referred to as noise. Indeed, a general theory predicts that inclusion of stochastic forces can change the properties of a dynamical systems essentially [32–34]. In particular, it was proved in [35] that noise increases system’s sensitivity to the initial conditions and hence can make it chaotic even when the corresponding deterministic system is not (but see [31] for a different point of view). However, on the whole the interplay between the deterministic and stochastic factors is a non-trivial one and, in spite of many recent insightful studies [36–39], the question about its outcome yet remains largely open. One reason for that is that the dynamics of a mixed deterministic/stochastic system is usually much richer than the dynamics of its deterministic and stochastic parts considered separately [39,40]. Correspondingly, theoretical/modelling results are often case-specific and hence it becomes difficult to identify general properties of such systems, at least, until a considerable amount of empiric information is accumulated.

While a certain degree in understanding has been reached for nonspatial systems, the situation is worse for spatially explicit systems. The spatial aspect makes the dynamics of a population system much more complex, e.g. allowing for the onset of chaos when it would be impossible in the corresponding nonspatial case [24,41].

The higher complexity of the system’s “deterministic skeleton” (i.e. the dynamics of the corresponding deterministic system) obviously opens a much wider variety of possible effects of noise. The goal of this paper is, along the lines of the earlier debate with regards to nonspatial systems [31,40], to consider what can be an outcome of the interaction between the deterministic chaos and noise. We are particularly interested in the question whether noise can be a factor regularizing the ecosystem’s dynamics. Since predator-prey interaction is a constituting block in the dynamics of any ecosystem, we focus on the predator-prey system.

There have been a large number of studies of spatiotemporal stochastic processes in the last quarter of 20’s century, e.g. see [42–46]. However, we want to emphasize that the problem of the interplay between noise and the deterministic skeleton of a spatially explicit system in the case of oscillatory predator-prey dynamics has, to the best of our knowledge, never been studied. Moreover, most of the earlier studies have been done using generic models such as the Ginzburg-Landau equation or lambda-omega systems (the latter being a real-valued version of the GL equation). However, as we have showed in our recent paper [47] the predictions made for lambda-omega systems under the impact of noise may not always be true for a more specific predator-prey system. The reason is that the lambda-omega system appears to be too symmetric to grasp the dynamical features of the less symmetric predator-prey system; see [47] for details.

The paper is organized as follows. In Section 2, we briefly recall the main features of a deterministic predator-prey system continuous in space and time. We then argue

that the standard approach to include stochasticity, originally developed for physical applications, might be not immediately relevant to population dynamics and consider its modification in order to build a mixed deterministic/stochastic model. In Section 3, we present the results of numerical simulations that appear to be rather counter-intuitive. In Section 4, we show that our theoretical results are in a good qualitative agreement with some available ecological data. Section 5 provides discussion and conclusions.

## 2 Model

### 2.1 Deterministic model

We begin with a brief overview of some typical properties of a spatially explicit predator-prey system in a deterministic environment, i.e. without noise. Its dynamics can be described by the following equations [22,48–51]:

$$\frac{\partial U(X, T)}{\partial T} = D \frac{\partial^2 U}{\partial X^2} + F(U) - G(U)V, \quad (1)$$

$$\frac{\partial V(X, T)}{\partial T} = D \frac{\partial^2 V}{\partial X^2} + \kappa G(U)V - M(V), \quad (2)$$

where  $U$ ,  $V$  are the densities of prey and predator, respectively, at time  $T$  and position  $X$ ,  $F(U)$  is the prey growth rate,  $G(U)V$  describes predation,  $M(U)$  is the predator mortality, and coefficient  $\kappa$  describes the efficiency of food utilization. Coefficient  $D$  describes the intensity of spatial mixing or dispersal due to individual mobility [48]; for simplicity we consider it to be the same for both species. Environmental properties are considered to be homogeneous, so that none of the coefficients in equations (1, 2) depends on space.

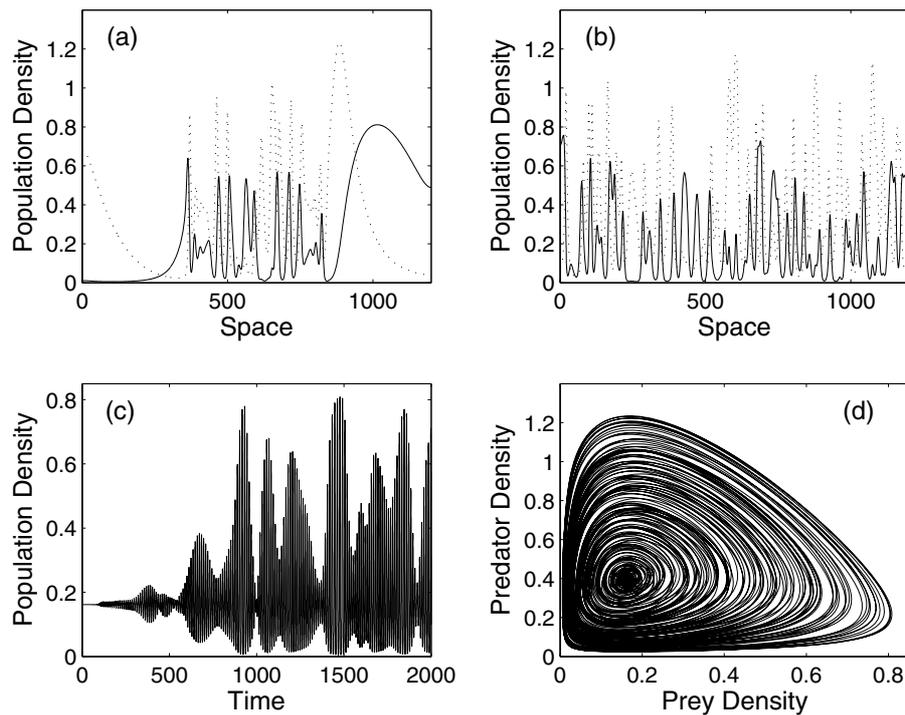
Since our study is essentially based on numerical simulations, we need to specify a parametrization for the functions  $F$ ,  $G$  and  $M$ . Here we assume that the prey growth is logistic (hence neglecting the Allee effects), predator response is of Holling type II and the predator mortality is density independent. Then, by rescaling the variables in a standard way [49,51], we arrive at the following dimensionless Rosenzweig-MacArthur system:

$$\frac{\partial u(x, t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \alpha u(1 - u) - \frac{uv}{u + h}, \quad (3)$$

$$\frac{\partial v(x, t)}{\partial t} = \frac{\partial^2 v}{\partial x^2} + k \frac{uv}{u + h} - mv, \quad (4)$$

where  $\alpha$ ,  $k$ ,  $h$  and  $m$  are dimensionless parameters. We consider the domain of finite length  $L$ , so that  $0 < x < L$ .

The corresponding nonspatial system, i.e. equations (3, 4) without diffusion terms, is known to possess a few steady states. There are always (i.e. for any parameter values) the extinction state  $(0, 0)$  and the prey-only state  $(1, 0)$ . Under some restrictions on parameter values, there is also a coexistence state  $(\bar{u}, \bar{v})$ , which can be either stable or unstable. In the latter case, the system’s dynamics becomes periodical due to a limit cycle that is born through the Hopf bifurcation [51], Section 10.1.



**Fig. 1.** Dynamics of the system (3–4) without noise, (a, b): population distribution over space (solid curves for prey, dashed curves for predator) at (a)  $t = 500$  and (b)  $t = 2000$  obtained for parameters  $\alpha = 1$ ,  $k = 2$ ,  $h = 0.3$ ,  $m = 0.7$  and the initial conditions (5) with  $x_* = 600$ ,  $\epsilon = 10^{-4}$ ; (c) prey distribution vs. time at fixed position in space at  $x = 600$ ; (d) the phase plane of the local population densities at  $x = 600$ .

Note that, although some properties of the system (1, 2) may depend on the particular choice of the functional responses  $F$ ,  $G$  and  $M$ , the existence of a (unique) coexistence steady state which is stable inside a certain parameter range has been observed for many different parameterizations [52] and therefore seems to be a generic property for a class of predator-prey systems.

Dynamics of the spatial system (3, 4) depends, to a large extent, on the properties of the coexistence steady state. It is well known that, when  $(\bar{u}, \bar{v})$  is unstable, the system may evolve to spatiotemporal chaos [22–24, 41, 51]. The specific routes to chaos depend on the initial conditions. In particular, in the case of the following constant-gradient type conditions, that is,

$$u(x, 0) = \bar{u}, \quad v(x, 0) = \bar{v} + \epsilon(x - x_*), \quad (5)$$

where  $x_*$  and  $\epsilon$  are auxiliary parameters, for  $0 < x_* < L$  chaos first emerges in a vicinity of the critical point  $x = x_*$  and then gradually spreads over the domain through the propagation of the “wave of chaos” – a travelling front separating the spatial domains with different type of dynamics [24]; see Figure 1a.

Chaos in the system (3, 4) is persistent and self-sustained. Once chaotic oscillations have invaded over the entire domain (see Figs. 1b, 1c and 1d), the dynamics of the system will not undergo any further changes. The properties of the system’s chaotic dynamics were considered in detail in [53]. In particular, the dominant

Lyapunov exponent  $\lambda_D$  was proved to be positive, its value being estimated to lie between 0.003 and 0.01.

## 2.2 Model with environmental stochasticity

The goal of this paper is to consider how the generic properties of the predator-prey spatiotemporal dynamics outlined above can be affected by environmental stochasticity. A particular focus is on a possibility of routes to chaos to be averted by the impact of noise so that, instead of developing spatiotemporal chaos, the system would stay in a regular dynamical regime.

Note that emergence or prevention of chaos can be linked to the issue of synchronization. Indeed, chaos in a two-species spatially explicit space- and time-continuous predator-prey model becomes possible due to dynamical splitting of the whole space to a number of sub-domains with mutually uncorrelated dynamics [41]; chaos in the corresponding spatially homogeneous predator-prey system is impossible. Therefore, in the case that the population oscillations become, for any reason, synchronized over the whole domain, chaos cannot appear.

Mechanisms of oscillations synchronization has long been a topic of interest in ecology [28, 54] as well as in complex systems in general [55, 56]. In particular, a process that leads to coupling of different parts of a fragmented habitat and can result in synchronization of their

population dynamics (provided the coupling is sufficiently strong) is dispersal [57,58].

While the impact of dispersal on synchronization is intuitively clear, a similar effect can be achieved through a completely different mechanism, i.e. noise. A phenomenon that we recall here is known as the Moran effect or Moran theorem [29,59]: a spatially correlated noise applied to a discrete system of oscillators may result in oscillations synchronization.

Surprisingly, the whole body of published literature concerned with synchronization focuses either on spatially discrete systems or on spatially continuous systems with a special “excitable” type of local kinetics [56,60]. To the best of our knowledge, the baseline case that seems to be the most ecologically relevant – i.e. limit cycle-induced oscillations in a spatially continuous population system (1, 2) – has never been addressed.

Reformulating the available results on the synchronization conditions in terms of different dynamical regimes of the predator-prey system (3, 4), a prediction that we seemingly can make is that, under the impact of a sufficiently strong spatially-correlated noise, spatiotemporal chaos is unlikely to be observed.

A comprehensive approach should take into account the fact that noise can be only partially correlated over the space. However, development of a complete theory lies beyond the scope of this paper. Instead, our aim is to make an insight into the issue of what can possibly be the effects of the interplay between stochastic and deterministic factors in a spatially continuous population system on the type of the system’s dynamics and spatiotemporal pattern formation. Therefore, we consider a particular but important case of purely temporal noise which is homogeneous in space. In ecological terms, it corresponds to a situation when noise is primarily associated with processes acting on a spatial scale much larger than the habitat size, e.g. fluctuations in the solar activity [61] or dynamics of large-scale atmospheric systems [28,62] such as North Atlantic Oscillation, El Niño, etc.

In order to investigate this issue, we consider system (3, 4) with some stochasticity added by assuming that some coefficients in (3, 4) are not constant but depend on time in a random manner. Specifically, we consider that the prey growth rate  $\alpha$  and the predator mortality  $m$  depend on time in the following way:

$$\begin{aligned}\alpha(t) &= \langle \alpha \rangle [1 + \sigma_1 \xi(t)], \\ m(t) &= \langle m \rangle [1 + \sigma_2 \xi(t)],\end{aligned}\quad (6)$$

where  $\xi(t)$  is a random noise with zero mean,  $\sigma_1$  and  $\sigma_2$  are the noise intensities, and the brackets stand for the mean value.

Note that predator and its prey usually belong to different taxonomic groups (e.g. birds and insects) with their biological trait differing considerably. Therefore, their response to the same environmental change, as well as their sensitivity to environmental noise, can be very different. For instance, a 50% drop in the autumn rainfall would unlikely change birds mortality in any significant way but it may have crucial consequences for soil insects [63,64].

Correspondingly, in order to distinguish between the impact of noise on prey (through its growth rate  $\alpha$ ) and on predator (through its mortality  $m$ ), in this paper we focus on a special case when only one of the species is affected by noise, i.e. either prey or predator but not both of them, so that either  $\sigma_1$  or  $\sigma_2$  is set to zero.

As a next step, we need to make assumptions about the noise properties taking into account ecological reasons. Multiplication rates of terrestrial species are known to depend on environmental factors such as air temperature, amount of sunshine, humidity and/or rainfall etc. The values of these factors are linked to ‘weather systems’, i.e. large-scale atmospheric structures with low or high pressure (often referred to as cyclones and anticyclones). Parameters of any two weather systems are usually not correlated or only weakly correlated (recall that the atmospheric dynamics is chaotic). Taking into account a typical size of such structures, which is on the order of  $10^3$  km [65], once a weather system arrives at a given region, it determines its weather conditions for a period of up to several weeks. However, a change between different weather systems usually occurs on a much shorter time scale.

Taking the above observations into account, the corresponding environmental noise is best described by a kangaroo-type process [45]. Correspondingly, we assume that the stochastic variable  $\xi$  takes a new value, randomly chosen with a certain probability, after each fixed interval  $T_0$ :

$$\xi(t) = g_n \quad \text{for } t_n < t < t_{n+1}, \quad (7)$$

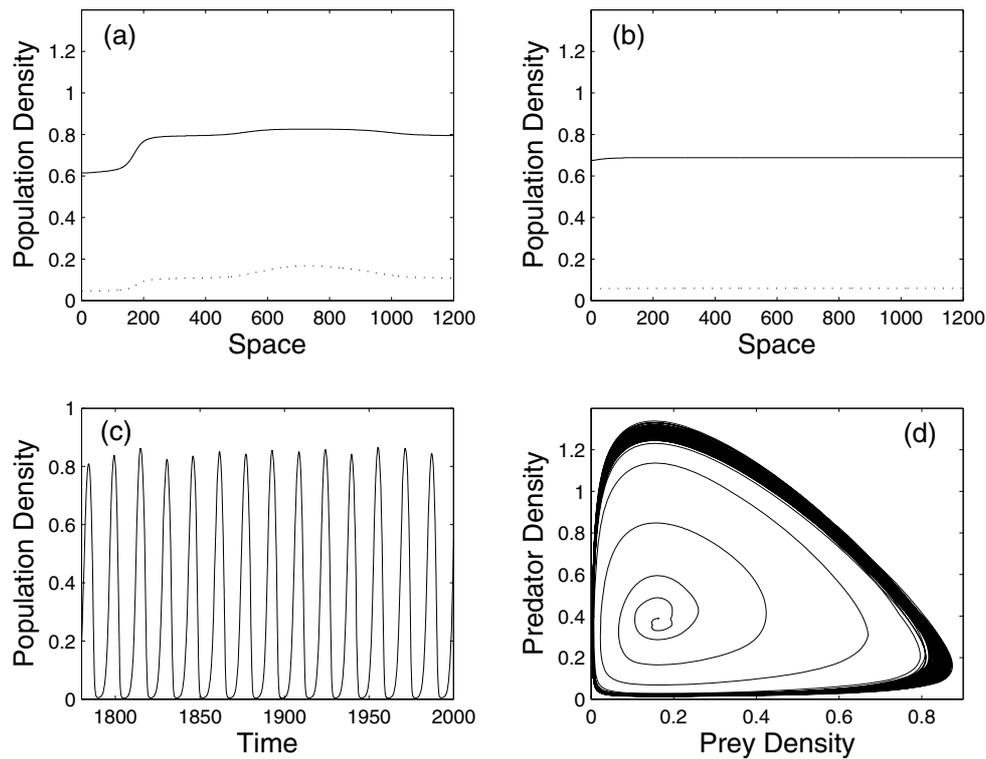
where  $t_{n+1} = t_n + T_0$ ,  $n = 0, 1, 2, \dots$ , where  $T_0$  is a positive parameter and  $\{g_n\}$  is a sequence of random numbers.

The noise introduced in this way is therefore red on a short time-scale  $t < T_0$  but it is white on the time-scale greater than  $T_0$ . Here we want to mention that the question as to what are the actual properties of environmental noise remains a controversial issue. Along with an increasing number of papers considering models with a colored noise, there is also a strong opinion that white noise can be a suitable approximation [66,67].

### 3 Simulations

System (3, 4) with (5), (6) and (7) was solved numerically by finite differences in the domain  $0 < x < 1200$ . At the boundaries of the domain, the zero-flux boundary conditions were used. Throughout our simulations we assume  $T_0 = 1$ . The numerical mesh step  $\Delta t$  was chosen accordingly so that  $\Delta t/T_0 \ll 1$ . Note that, having defined the noise properties as given by (7),  $\alpha(t)$  and  $m(t)$  become piecewise constant function, and hence numerical integration of equations (3, 4) does not bring any difficulty and can be done using standard numerical schemes for PDEs.

For a given value of  $T_0$ , different properties of the noise are quantified by the distribution function of the random sequence  $\{g_n\}$ . Following [29], we use  $\{g_n\}$  uniformly distributed over the interval  $(-1, 1)$ , giving rise to a bounded kangaroo-type stochastic process. In order to



**Fig. 2.** Dynamics of the system (3, 4) with noise intensity  $\sigma = 10\%$ , (a, b): population distribution over space at (a)  $t = 500$  and (b)  $t = 2000$ ; (c) prey distribution vs. time at fixed position in space at  $x = 600$ ; (d) the phase plane of the local population densities at  $x = 600$ . Here and below  $\langle\alpha\rangle = 1$ , other parameters and the initial conditions are the same as in Figure 1.

generate  $\{g_n\}$ , we used the linear congruential generator  $X_{n+1} = (aX_n + b) \bmod(j)$  which is known to provide a sufficiently long sequence of numbers with good randomness properties for appropriately chosen parameters  $a$ ,  $b$  and  $j$  [68]. The sequence  $\{X_n\}$  was then scaled to obtain the uniformly distributed numbers  $\{g_n\}$ .

With regard to noise intensity, according to the argument made above (see the paragraph below Eqs. (6)) we have considered two different cases and run two series of numerical experiments accordingly. In Case 1,  $m$  is considered to be constant and  $\alpha$  a random function of time (as given by (6, 7)) so that  $(\sigma_1, \sigma_2) = (\sigma, 0)$ . In Case 2,  $\alpha$  is constant and  $m$  is a random function so that  $(\sigma_1, \sigma_2) = (0, \sigma)$ . The impact of noise is therefore quantified by a single parameter  $\sigma$ . Simulations were made for different values of  $\sigma$ , having other parameters fixed at some hypothetical values.

### 3.1 Case 1: $m = \text{const}$ , $\alpha$ is noisy

We have found that, in the case that the noise intensity is very small (less than 1%), i.e.  $\sigma \leq 0.01$ , the system dynamics does not differ from the one observed for a deterministic system, cf. Figure 1. However, when a noise of a higher intensity is applied, the system dynamics can become qualitatively different; see Figure 2. Now the phase singularity in the initial conditions at  $x = x_*$  does not

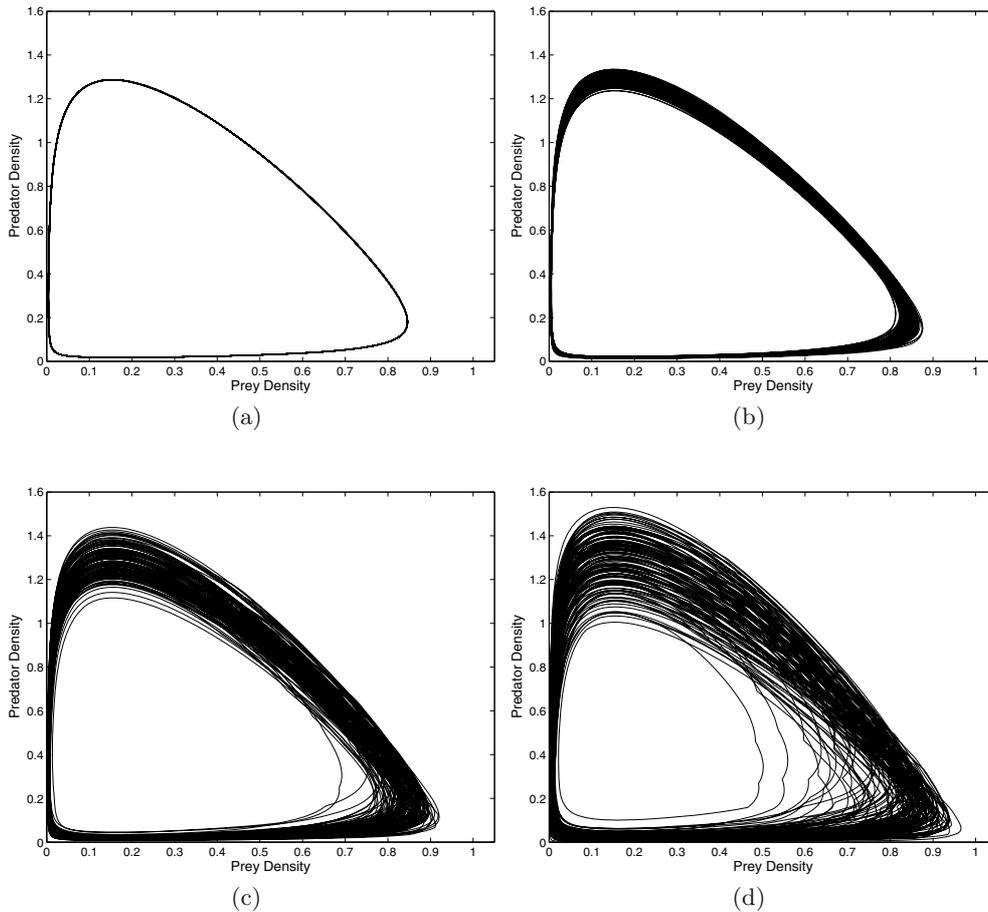
necessarily lead to formation of a chaotic domain. Local population oscillations (i.e. at a fixed position in space) are almost perfectly periodical (Fig. 2c). Irregular spatial fluctuations do not appear either and, at any time, the spatial distribution remains smooth (cf. Figs. 2a and 2b) and highly correlated throughout the domain.

Expectedly, since the system (3, 4) has now acquired probabilistic properties, the actual dynamics of the system can be different between different simulation runs<sup>1</sup>, even if all the parameters are the same. Indeed, we have found that, for a not very small value of the noise intensity  $\sigma$ , different noise realizations can result in either spatiotemporal chaos (similar to that observed for the deterministic system, cf. Fig. 1) or in chaos prevention and regular dynamics, see Figure 2. That makes it possible to quantify the system properties with respect to noise in terms of probability of these two different types of dynamics. Specifically, we define the ‘experimental probability’ of the event that the system is driven to chaos ( $P_{cha}$ ) and of the event that it remains in a regular regime ( $P_{reg}$ ) as

$$P_{cha} = \frac{N_{cha}}{N} \quad \text{and} \quad P_{reg} = \frac{N_{reg}}{N}, \quad (8)$$

where  $N_{cha}$  and  $N_{reg}$  are the number of numerical experiments where the system dynamics is observed to be

<sup>1</sup> where different simulation runs correspond to different noise realizations.



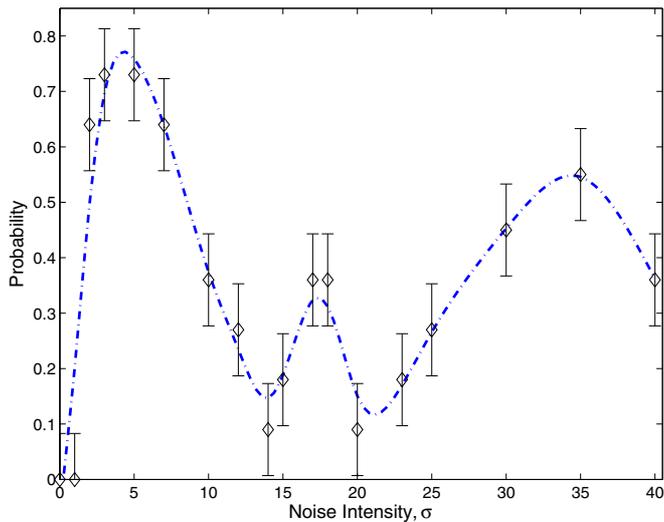
**Fig. 3.** Phase plane of the spatially homogeneous system when noise is applied to the growth rate, (a) for  $\sigma = 0$ , (b) for  $\sigma = 10\%$ , (c) for  $\sigma = 30\%$ , (d) for  $\sigma = 50\%$ . Here  $\langle \alpha \rangle = 1$ , other parameters are the same as in Figure 2.

chaotic and regular, respectively, and  $N = N_{cha} + N_{reg}$  is the total number of experiments; obviously,  $P_{cha} + P_{reg} = 1$ . Note that experimental probabilities (8) become real probabilities only in the large- $N$  limit; for any finite value of  $N$ , they are calculated up to a certain statistical error.

We then considered system's properties for different values of the noise intensity. A subtle issue is what should be a meaningful range of  $\sigma$ . The point is that, while for small and intermediate values of noise the system dynamics appears as an interplay between the deterministic factors and stochastic factors, for a large noise intensity (e.g.  $\sigma \approx 1$ ), the system dynamics becomes largely stochastic. The properties of stochastic system are likely to be considerably different, and hence a comparison between an 'almost deterministic' and 'almost stochastic' dynamics may be not instructive. (Indeed, below we will show that, for large values of the noise intensity, the system acquires qualitatively new features). Therefore, it seems reasonable to restrict our study to the range of  $\sigma$  where the system (3, 4) still retains essential features of its deterministic structure, such as the oscillations along the limit cycle. For convenience, we will call this range a "small noise."

In order to reveal what is the upper bound of this range, we ran simulations in the non-spatial counterpart of (3, 4) for increasing values of  $\sigma$ , and check how the dynamics changes. The simulation results are shown in Figure 3. It is readily seen that, while for  $\sigma = 10\%$  (Fig. 3b) the dynamics is almost the same as in the system without noise (Fig. 3a), for  $\sigma = 50\%$  (Fig. 3d) the system's trajectory in the phase plane hardly resembles the limit cycle. Therefore, we restrict our simulations to the interval  $0 \leq \sigma \leq 40\%$ .

Having thus decided about a plausible upper bound for the noise intensity, we then accomplished simulations for different values of  $\sigma$  in the spatial system (3, 4). We have obtained that the probability of chaos suppression  $P_{reg}$  is different for different  $\sigma$ ; see Figure 4. Since calculation of  $P_{reg}$  for any given value of  $\sigma$  requires a lot of computational resources, in order to reveal the structure of the dependence of  $P_{reg}$  on  $\sigma$  and yet to minimize the amount of simulations, we used an 'adaptive grid strategy'. Simulation were first made for a few equidistant values of the noise intensity, e.g.  $\sigma = 5\%, 10\%, \dots, 30\%$ . Once the general structure of the function  $P_{reg}(\sigma)$  becomes clear, we then make simulations for additional values of



**Fig. 4.** (Color online) Probability  $P_{reg}$  of chaos suppression vs. noise intensity when noise is applied to the prey growth rate. Other parameters are the same as in Figure 2. The blue dashed-and-dotted curve is drawn using cubic spline approximation with the purpose to provide an easier visual perception of the results.

$\sigma$  which were chosen, in order to provide a better resolution, around the positions of the humps and hollows.

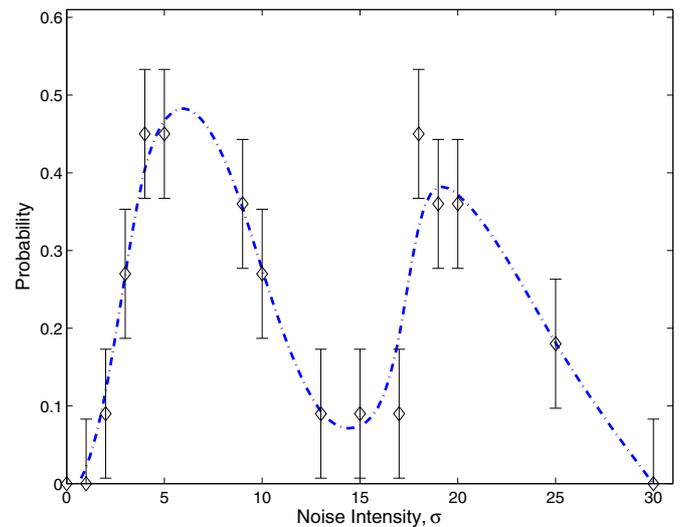
It is readily seen that, when the noise intensity is small,  $\sigma \ll 1$ , an increase in  $\sigma$  leads to an increase in  $P_{reg}$ . However, in a broader interval of  $\sigma$ , the dependence  $P_{reg}(\sigma)$  appears to be more complicated. We have obtained that, rather counter-intuitively, the probability dependence on  $\sigma$  appears to be nonmonotone, showing three maxima of different height.

We want to mention that, although we have thus demonstrated that noise can prevent the onset of chaos, small noise cannot suppress chaos if/after it has developed. In our simulations with small noise, we did not observe a single case when chaos would give way to regular dynamics.

### 3.2 Case 2: $\alpha = \text{const}$ , $m$ is noisy

Now noise is applied to the predator mortality. As above, we first investigate what is the reasonable range of  $\sigma$  where the system retain its deterministic skeleton. We do it by applying noise to the corresponding non-spatial system, i.e. Equations (3, 4) without diffusion terms. We have found that the system is slightly more sensitive to noise than it was previously, so that it becomes largely stochastic already for  $\sigma = 40\%$ . Correspondingly, we restricted our simulations to  $0 \leq \sigma \leq 30\%$ .

We obtained that the system properties are similar to those observed in the previous case. The system exhibits a similar response to noise when  $\sigma \ll 1$ , i.e. the probability  $P_{reg}$  of chaos suppression grows with  $\sigma$ . However, the dependence  $P_{reg}(\sigma)$  appears to be essentially nonmonotone when considered in a broader range of the noise intensity



**Fig. 5.** (Color online) Probability  $P_{reg}$  of chaos suppression vs. noise intensity when noise is applied to the predator mortality. Other parameters are the same as in Figure 2. The blue dashed-and-dotted curve is drawn using cubic spline approximation with the purpose to provide an easier visual perception of the results.

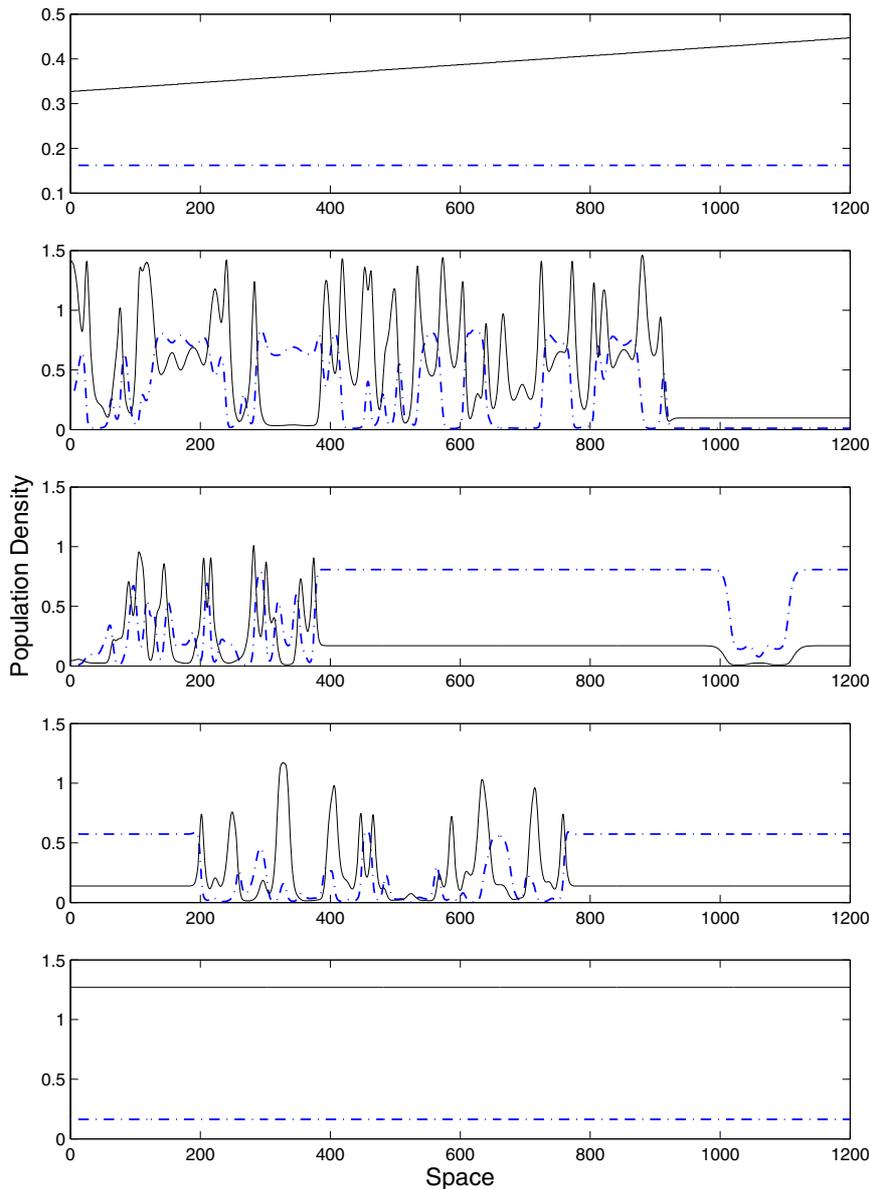
showing two maxima of different height; see Figure 5. As well as in the previous case, a small noise can prevent the onset of chaos (with the probability  $\approx P_{reg}$ ) but it cannot suppress it once chaos has developed.

### 3.3 The effects of large noise

In the above, we have shown that onset of spatiotemporal chaos in a predator-prey system can be prevented if noise is applied to either the prey growth rate or to the predator mortality. We also obtained that chaos, once it appears, is very stable to the impact of noise.

The above results were obtained for the noise intensity sufficiently small, so that the system was supposed to retain its deterministic structure. A question still remains, however, whether a noise of larger intensity can bring any new features. Although a detailed insight into this issue lies beyond the scope of this paper, a general tendency that we observed in our simulations is that the probability of regular dynamics increases considerably for a large  $\sigma$  ( $\sigma \geq 50\%$ ). Moreover, for a large  $\sigma$ , chaos does not appear to be stable with respect to the impact of noise and can be suppressed even after its onset. An example is shown in Figure 6 obtained for  $\sigma = 50\%$ . In this case, noise does not prevent onset of chaos from the initial conditions (5), so by  $t = 500$  it has already invaded over most of the spatial domain. However, the spread of chaos does not appear to be irreversible, and the chaotic domain shrinks by  $t = 1000$ , although it may then grow again as was observed at  $t = 1500$ . Finally, however, the spatially homogeneous distribution wins, so that chaos disappears completely.

Our simulations with large noise show that suppression of chaos in the manner described above, cf. Figure 6, is a



**Fig. 6.** (Color online) Example of spatiotemporal chaos suppression observed for  $\sigma = 50\%$ , noise is applied to the prey growth rate. Population densities vs. space are shown at  $t = 0$ ,  $t = 500$ ,  $t = 1000$ ,  $t = 1500$  and  $t = 2000$  (top to bottom, respectively). Dashed-and-dotted curves for prey, solid curves for predator. Parameters are the same as in Figure 2.

typical rather than exotic phenomenon. In particular, for  $\sigma = 50\%$ , the probability of chaos suppression is estimated to be about 0.4.

#### 4 Comparison with field observations

An important question is to what extent the above results are in agreement with ecological observations. It evokes a question of relevant data that the simulation results can be confronted with. A possibility of a straightforward comparison looks rather unlikely. Indeed, it would imply a series of field experiments with manipulated level of environmental noise; however, in a typical ecological situation, there are numerous factors contributing to noise and many

of them are poorly understood and/or hardly possible to control.

Instead, we use another approach. We analyze available data on spatiotemporal population dynamics on several species of the same taxa. A species is described by its biological traits such as average body mass, offspring number, survival rate, etc. The corresponding parameter values are different for different species. We then assume that different value of the parameters correspond to different sensitivity to the environmental noise.

As a sample case, we use the data on birds in the UK. Population dynamics of British birds have been under intensive study for a few decades and vast amount of data has been collected. These data have been recently recovered, processed and analyzed in [69] and almost

**Table 1.** Distribution of the global spatial correlation coefficient (GSC). Parameter values with 95% confidence intervals, proportion of variance explained  $R^2$ , difference in AIC  $\Delta$  and Akaike weight  $w$  for five statistical models fitted to the GSC.

Model	Parameters	$R^2$	$\Delta$	$w$
$a + bX$	$a = 0.27 \pm 0.14$ $b = -0.39 \pm 0.24$	0.20	6.7	0.028
$aX^{-b}$	$a = 0.04 \pm 0.02$ $b = -1.028 \pm 0.52$	0.22	5.29	0.057
$aX \exp(-bX)$	$a = 4.40 \pm 3.14$ $b = -6.93 \pm 2.01$	0.21	6.01	0.040
$a_1 \exp \left[ - \left( \frac{X-m_1}{\sigma_1} \right)^2 \right] + a_2 \exp \left[ - \left( \frac{X-m_2}{\sigma_2} \right)^2 \right]$	$a = 0.26 \pm 0.08$ $m_1 = 0.22 \pm 0.05$ $\sigma_1 = 0.09 \pm 0.05$ $a_2 = 0.15 \pm 0.06$ $m_2 = 0.47 \pm 0.02$ $\sigma_2 = 0.04 \pm 0.002$	0.40	4.96	0.068
$a_1 \left[ 1 + \left( \frac{X-m_1}{\sigma_1} \right)^2 \right]^{-1} + a_2 \left[ 1 + \left( \frac{X-m_2}{\sigma_2} \right)^2 \right]^{-1}$	$a = 0.26 \pm 0.08$ $m_1 = 0.19 \pm 0.07$ $\sigma_1 = 0.13 \pm 0.07$ $a_2 = 0.3 \pm 0.2$ $m_2 = 0.44 \pm 0.01$ $\sigma_2 = 0.011 \pm 0.008$	0.47	0	0.807

comprehensive information about essential features of the population dynamics of 60 avian species has been obtained. A focus of the study was on the spatial dynamics. For each species under study, the analysis of spatial cross-correlations between local population abundances at approximately 1000 locations was made and described by the cross correlation functions (CCF). In particular, for each pair of sites the correlation of oscillations of birds' population sizes has been computed. The obtained CCFs were then averaged over the pairs in order to produce a single index, i.e. global spatial correlation coefficient or the mean CCF, which thus quantifies the synchrony in population dynamics of a given species on a large (countrywide) spatial scale. All details about estimating the variance of the mean CCF can be found in the cited paper.

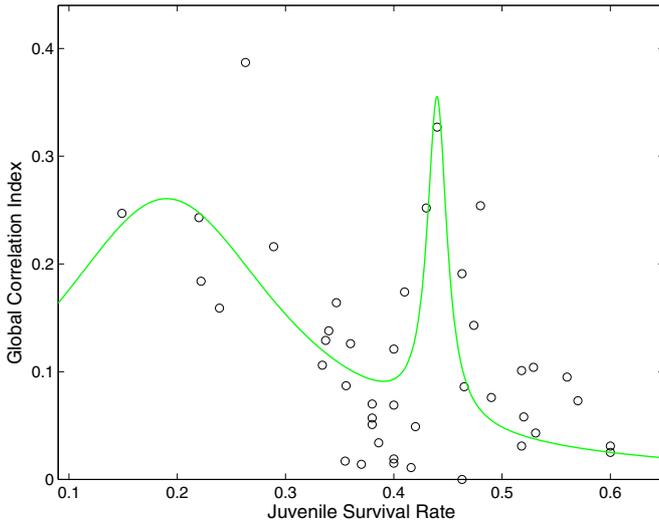
Now we want to link these field data on birds to our theoretical results. For any given bird species, its abundance fluctuate in time (although the amplitude of the fluctuations can be considerably different) and here we hypothesize that, in agreement with the conceptual model (3, 4), this is a cycle generated by predator-prey interspecific interaction between the birds and their food, e.g. insects. We therefore neglect other factors such as the effect of top predators, diseases and/or parasites, details of the demographic mechanisms, anthropogenic impact etc. We want to mention here that, although we are not aware of an ecological study proving that fluctuations in birds numbers are directly caused by predator-prey type interactions, predator-prey induced cycles in other species is a well established phenomenon [9,70,71]. In terms of the spatially explicit predator-prey model, a high degree of spatial correlation can be regarded as synchronization in population fluctuations and hence the absence of the spatiotemporal chaos, and a low degree of correlation may be

taken as an indication of desynchronization and a possibility of chaos.

The next step is to chose a controlling parameter, i.e. which of the bird's biological traits quantifies best their sensitivity to environmental noise. We hypothesize that it is the survival rate of the offspring during the first year of their life. Obviously, birds of this age (as indeed juveniles of any species) are more susceptible to adverse environmental conditions than adult individuals and hence can be regarded as a 'bottleneck' in the population functioning; the larger is the survival rate, the less sensitive is the population to the noise.

The field data<sup>2</sup> on the mean CCF vs. the juvenile survival rate are shown in Figure 7. In order to reveal the tendency in the data, we checked several standard statistical models, see Table 1. The statistical measures such as the proportion of the variance explained  $R^2$  and the Akaike weight  $w$  immediately rule out simple monotone distributions like a straight line or a power law (see the first and second rows of Tab. 1). A single humped linear/exponential distribution is not supported either due to unacceptably low values of  $R^2$  and  $w$  (the third row of Tab. 1). The fitting becomes better for the two-hump shaped sum of two Gaussian distributions (see the fourth row of Tab. 1), even in spite of the fact that it has much more parameters. The best fitting is found to be given by a sum of two Lorentzian distributions which not only provides the highest value of  $R^2$  but is also overwhelmingly supported by the Akaike weight; see the bottom row of Table 1.

<sup>2</sup> In order to make the species more homogeneous taxonomically, we did not include data on migrating birds and on predatory birds.



**Fig. 7.** (Color online) Index of the global spatial cross-correlation (mean CCF) of population abundance vs. juvenile survival for birds in the UK, circles show the field data from [69], the curve shows the best-fitting of the data by the sum of two Lorentzians. The choice of this statistical model is clearly supported by Akaike weights, see Table 1.

Therefore, statistical analysis of the data unambiguously shows that the value of the mean CCF (which we denote as  $\langle CCF \rangle$ ) vs. the juvenile survival rate is a two humped distribution. The best fitting function (a sum of two Lorentzians) is shown in Figure 7 by the solid curve. Recalling that the mean CCF quantifies the degree of the spatial synchrony in the population dynamics, we can make one step further and interpret  $\langle CCF \rangle$  as a probability of a regular dynamics, so that the probability of spatiotemporal ‘chaos’ is  $1 - \langle CCF \rangle$ . Now, if we take into account that, according to our argument above, juvenile survival can be linked to the noise intensity, a good qualitative agreement between Figures 7 and 5 becomes obvious.

We want to emphasize it here that we do not claim quantitative agreement (such as position, height and width of the peaks) between the data and our theoretical predictions. Indeed, it would hardly be possible in terms of the very schematic predator-prey model. However, the bimodal structure of the mean CCF shown in Figure 7 is a statistically confident result, and its agreement with our conceptual modelling approach (see (3, 4) with (6, 7)) seems to be encouraging.

## 5 Concluding remarks

Mechanisms of ecosystems regulation and self-regulation that potentially affect their dynamics by enhancing or hampering development of chaos have long been attracting considerable attention [10,15-20,28]. In this paper, we have shown that a nonspatial stochastic forcing (“noise”) applied to a space-explicit predator-prey system can prevent system’s transition to spatiotemporal chaos. We have

considered two cases, i.e. (i) noise applied to the prey growth rate and (ii) noise applied to the predator mortality rate. Having performed extensive numerical simulations, we obtained that noise can increase the probability of regular dynamics  $P_{reg}$  (which is exactly 0 in the corresponding deterministic system) to as much as 0.5 or even higher. We have found that the dependence of  $P_{reg}$  on the noise intensity is a nontrivial one showing a few maxima of different height, which may be interpreted as a stochastic resonance [4,34]. Remarkably, our findings seems to be in a good agreement with available field data.

Prevention of the onset of chaos due to the impact of small noise can be explained heuristically if we recall that the corresponding deterministic skeleton exhibits bistability [24]: depending on the initial conditions the system (3, 4) may either evolve to a fully synchronized spatially homogeneous population distribution or it may evolve to spatiotemporal chaos. For the parameter range where the initial condition is within the basin of the chaotic attractor but not far away from the basin’s boundary, a small noise can then push the solution to the other basin, i.e. to the non-chaotic attractor. The mechanism is therefore different from the standard mechanisms of synchronization by entrainment of the characteristic frequencies and by phase locking [4]. This heuristic interpretation also helps to understand why synchronization/chaos suppression has not been observed after the onset of chaos: a ‘fully developed’ chaotic solution is far away from the basin’s boundary and the probability that small noise pushes it out of the basin should be negligibly small.

Note that the system (3), (4), (6) does not exhibit intermittent behaviour. The reason is that the spatially homogeneous, temporarily periodic solution of the system is linearly stable and hence possesses a non-empty basin of attraction. Therefore, a small heterogeneous perturbation to this solution tends to zero in the large-time limit. Therefore, once a heterogeneous solution of the system (3), (4), (6) becomes sufficiently flat (cf. Fig. 2b) to get into the basin, it will remain there indefinitely.

A comment should be made about generality of our findings. The results shown in Figures 4 and 5 are obtained for a given set of parameter values. However, we want to emphasize that, as we checked it in our simulations, the observed effect of noise on the system’s spatiotemporal dynamics remains qualitatively the same for any parameter values when the local kinetics is oscillatory (which is a necessary condition of chaos in the system (3, 4)), although the strength of the effect (i.e. the height of the peaks in Figs. 4 and 5) and the shape of the curves can be somewhat different.

Our attention was mostly focused on the case of a small noise when the stochastically perturbed system still retains its deterministic skeleton such as periodicity induced by a stable limit cycle. Small noise decreases the probability of chaos onset; however, if/when chaos has developed, it appears to be self-sustained and persistent. The situation changes in the case of a large noise when the system’s dynamics is driven away from

the skeleton; e.g. see Figure 3d. Large noise can suppress chaos even after its onset, cf. Figure 6. Therefore, large noise also acts as a regularizing factor, although the scenario is different.

Summarizing, our main finding is that the outcome of the interplay between the noise and the deterministic skeleton appears to be essentially different in spatial and nonspatial cases. In the nonspatial systems, a general result seems to be that noise makes the system dynamics “more chaotic” by amplifying the system’s sensitivity to the initial conditions [35,40]. Although this inference is well built theoretically, it is at odds with observations because noise is indeed a very common factor but chaos has been rarely detected in population dynamics. Our results provide a possible solution to this apparent paradox by showing that the impact of noise in a spatially explicit system makes the onset of chaos less likely to occur.

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