Comments

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Comment on "Absence of chaos in a self-organized critical coupled map lattice"

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Csilling and collaborators [Phys. Rev. E **50**, 1083 (1994)] present a coupled map lattice representing a collection of linked populations with nonoverlapping generations. They report that their model fails to predict both chaos and spatial organization. In this comment, I highlight a number of published studies using similar models which (by contrast) commonly report both chaos and spatial organization. After careful comparison of two of these models, I suggest that the root of the highly unusual results of Csilling *et al.* may lie in their separation of the time scales on which dispersal and reproduction occur. Further, I suggest how this theory could be tested.

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The recent article by Csilling *et al.* [1] presents a coupled map lattice (CML) that is used to investigate the likelihood of chaos being observed in natural populations. They conclude that chaos is unlikely to be observed in spatially distributed populations. In fact, there has been a flourishing literature in ecological journals, unmentioned by Csilling *et al.*, which addresses essentially the same question using CML's and other models of coupled populations. The general consensus of these publications takes the completely opposite viewpoint: that chaos is more likely in models of spatially distributed populations than in the equivalent nonspatial models.

It is particularly interesting to compare the results of Csilling *et al.* (hereafter CJPS) with that of Bascompte and Solé (hereafter BS) [2]. Both papers use CML's with the same function describing the intrinsic growth rate of the population on each site. Both assume movement by diffusion only to nearest-neighbor sites. However, there are two important differences. CJPS assume that diffusion of individuals from a population only occurs if that population has a size greater than a fixed threshold value; BS do not have such a condition. Second, CJPS consider dispersal and reproduction to occur on separate time scales, whereas BS assume that they occur together. Specifically, CJPS assume that all sites undergo reproduction, and then dispersal to nearest neighbors is allowed. This dispersal phase continues until all population values are below threshold. Hence, several rounds of dispersal may occur before the next round of reproduction. In the BS model, each site undergoes both reproduction and dispersal at the same time, hence each site experiences equal numbers of reproductive and dispersal phases.

The two models behave very differently. CJPS report that "when the threshold is small enough, the time evolution (of the collective system) is strictly periodic or shows a stable fixed point equilibrium. We have not been able to find any threshold value at which the collective dynamics show low dimensional chaos." In contrast, BS found that space acts as a bifurcation parameter. Even for parameter values where the steady state of an isolated population would be stable, enlarging the lattice leads to a series of bifurcations leading eventually to chaos. They conclude that "chaos appears for a wide range of parameter values and hence it is structurally stable."

In large lattices, BS do suggest that the ensemble dynamics of their model can resemble a steady state with added noise. However, they never observe the "strictly oscillatory or stable" behavior of CJPS. The amplitude of the "noise" shown in Fig. 7 of BS is sufficiently high that it would be surprising if anyone were to describe the signal as "strictly stable."

Why do these similar models produce such different behavior? CJPS begin their discussion section with the sentence: "We have demonstrated that the global metapopulation does not show collective chaotic behavior if local habitats interact via a threshold rule." However, even at very low threshold values, the behavior of their model is completely different from that of BS. Hence, it may be that the key feature leading to the difference in behavior may be the other major difference between the models: the separation of time scales. Future investiga-

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tion of a hybrid model that could be forced, under limiting conditions, to mimic either of the two current models would allow this point to be investigated further.

There has been a considerable number of other publications in the ecological literature that present CML models of one or two species [3–8]. All these models commonly predict chaotic dynamics. In further contrast to CJPS, these models commonly report strong spatial self organization within the ensemble. CJPS report that for their model, "there is no sign of spatial organization, even when the system settled down to a strictly periodic oscillatory state." There has also been investigation of the dynamics of spatially extended populations where space is treated as a continuous variable [9,10]. Again, these papers commonly report both chaos and spatial organization.

CJPS conclude their paper as follows. "The simulation results agree well with the overwhelming part of field observations, where only in some exceptional cases a partially chaotic time evolution was found." True, there is, as yet, no unequivocal evidence for the widespread existence of chaos in a time series obtained from field observation. However, this may be because the identification of chaos is very difficult in a biological time series, which are typically both short and noisy [11,12]. The dynamics of childhood diseases, such as measles and chicken pox, in humans have been subjected to particularly intense study because of the relatively long time series available. Analysis of these data provides considerable evidence that chaos is present in at least some of the time series [13]. Moreover, recent modeling work suggests that movement of people between subgroups in a population must be represented in order to reproduce the observed field time series effectively [14].

It is somewhat surprising that CJPS do not make a comparison with the existing literature on models similar to theirs. Such a comparison would highlight how interesting and iconoclastic the results of CJPS really are. This can easily be seen by comparing the conclusion of CJPS with the view taken by Pascual [10] in interpreting the predictions of his model: "These results suggest that complex temporal dynamics in natural populations may arise through the spatial dimension. Spatially induced chaos may have an important role in spatial pattern generation." However, by very good fortune, the models of BS and CJPS share so many similarities that, hopefully, further experiment with modified versions of these models should yield an understanding of those properties of the CJPS model that make it behave so differently from all the other models discussed here. My personal belief is that the difference will lie in CJPS's unusual (at least in the ecological literature) treatment of time scales. If this proves to be correct, our next question will be to examine how well the treatment of time scales matches the behavior of real populations. No matter what, I believe that the results presented by CJPS will form the cornerstone of a useful collaboration between the physical and ecological sciences.

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