

Notes and Comments

The Moran Effect and Phase Synchronization in Complex Spatial Community Dynamics

Bernard Cazelles^{1,2,*} and Gérard Boudjema³

1. Laboratoire d'Écologie, Centre National de la Recherche Scientifique Unité Mixte de Recherche 7625, Université Pierre et Marie Curie, 7 quai St. Bernard, Batiment A, case 237, 75252 Paris Cedex 05, France;

2. Département de Biologie, Université Paris 7, 2 place Jussieu, 75251 Paris Cedex 05, France;

3. Laboratoire de Physique Statistique, École Normale Supérieure, 24 rue Lhomond, 75230 Paris Cedex 05, France

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Population biologists have long been interested in the possible causes of population cycles and synchronized population fluctuations. Many studies published within the past few years have shown that spatial population synchrony is a general phenomenon (Ranta et al. 1997*b*; Bjørnstad et al. 1999; Hudson and Cattadori 1999; Koenig 1999). However, full synchronization, considered as the complete coincidence in population abundance between two populations, appears unrealistic in ecological systems where demographic and environmental stochasticity is ubiquitous. Blasius et al. (1999) recently employed the concept of phase synchronization (Winfree 1980; Rosenblum et al. 1996) to explain the observed synchronization of complex oscillations in theoretical and observed ecological communities. Phase synchronization of two interacting nonidentical chaotic oscillators is the perfect locking of their phase while their amplitudes remain chaotic and uncorrelated (Rosenblum et al. 1996). The results of Blasius et al. (1999) suggest that the concept of phase synchronization may be of considerable relevance to ecology (Lloyd and May 1999) as in other biological fields (Schäfer

et al. 1998; Tass et al. 1998; Neiman et al. 1999*b*; Mormann et al. 2000; Pavlov et al. 2000).

Blasius and coworkers (Blasius et al. 1999; Blasius and Stone 2000) employed a spatial tritrophic food web model in which patches of herbivores and predators interacted through a process of dispersal. They showed that all populations of the patch lattice, while oscillating chaotically, were phase locked to the same collective rhythm although their abundances remained uncorrelated. Local interpatch dispersal is the critical synchronizing process here. Nonetheless, in this system, as the distance between populations increases, the degree of synchrony between them remains identical only the lag between the phases of the populations increases.

Dispersal between populations is not, however, the only explanation for spatial synchrony in population fluctuations. Indeed, observations reviewed recently (Bjørnstad et al. 1999; Hudson and Cattadori 1999; Koenig 1999) have shown the existence of population synchrony over large geographical regions. A mechanism typically used to explain this phenomenon, known as the Moran effect (Moran 1953; Royama 1992), suggests that two populations, regulated by the same density-dependent factors, may become spatially synchronized when exposed to similar environmental fluctuations. If these environmental fluctuations are temporally correlated, the fluctuations in population size will also be correlated.

This Moran effect (Moran 1953; Royama 1992) is typically associated with linear systems. Theoretical works have shown that the Moran effect alone is capable of synchronizing population dynamics, but these results were only verified with linear or simple models. In contrast, and for a more complex system, Jansen (1999) demonstrated that the Moran effect alone is unable to synchronize identical dynamics of two periodic predator-prey models. Bjørnstad et al. (1999) pointed out that regionally correlated noise can fail to synchronize populations with chaotic dynamics (see their figs. 1*c* and 1*f*). These results confirm those of Ranta et al. (1995, 1997*a*), who also found that for highly nonlinear (chaotic) models the Moran effect

* E-mail: bcazelle@snv.jussieu.fr.

alone cannot easily synchronize populations. All of these results lead to the conclusion that the nonlinearity of the density dependence undermines the synchronization of oscillating systems.

Here we extend the generality of the idea of phase synchronization in population dynamics (Blasius et al. 1999; Blasius and Stone 2000) by showing that the Moran effect can induce phase synchronization in two nonlinked tri-trophic communities even when their dynamics are non-identical chaotic. Hence, we demonstrate evidence that a noisy forcing can induce phase synchronization of non-linked chaotic populations, generalizing the Moran effect to nonlinear complex dynamics.

Model and Method

We used the two-patch model proposed by Blasius and coworkers (Blasius et al. 1999; Blasius and Stone 2000), with parameters selected to induce chaotic behavior. We added a noisy periodic forcing on the right-hand side of the model equations to mimic environmental stochasticity. The model reads

$$\begin{aligned}\frac{du_i}{dt} &= au_i - \alpha_1 f_1(u_i, v_i) + \xi_{ui}, \\ \frac{dv_i}{dt} &= -b_i v_i + \alpha_1 f_1(u_i, v_i) - \alpha_2 f_2(v_i, w_i) + \xi_{vi}, \\ \frac{dw_i}{dt} &= -c(w_i - w^*) + \alpha_2 f_2(v_i, w_i) + \xi_{wi},\end{aligned}\quad (1)$$

where $i = 1, 2$ is the patch index, u is the primary producers, v is the herbivores, w is the predators, a is the primary producer growth rate, b_i is the natural mortality of the herbivores, c is the mortality rate of the predators, and α_1 and α_2 are the strength of the interactions between primary producers and herbivores and between herbivores and predators, respectively. The interactions are modeled by a Holling Type II function, $f_i(x, y) = (xy)/(1 + k_i x)$, where k_i is the carrying capacities. As in Blasius et al. (1999), we employed parameter values that induce chaotic behavior, but with two different herbivore mortality rates for each patch, b_1 and b_2 .

The environmental stochasticity is modeled, for each trophic level j , as a noisy periodic forcing:

$$\xi_{ji} = A_j \cos(\omega t) + \zeta_{ji}, \quad (2)$$

where A_j and ω are the amplitude and the frequency of the forcing signal, respectively, and ζ_{ji} an additive noise component for the trophic level j and the patch i . The noise effect is restricted so that at any time step each

population abundance remains positive. Different types of additive noise are used: global periodic forcing contaminated by Gaussian noise, in which each trophic level is influenced by the same environmental fluctuation, $\zeta_{j1} = \zeta_{j2} = \epsilon_j$; each trophic level influenced by the same global periodic forcing contaminated by colored (red) noise, $\zeta_{j1} = \zeta_{j2} = \zeta(t) = \rho \zeta(t-1) + \gamma \epsilon_j$; and global forcing plus local, but correlated, noise. In this last case, the noise component experienced by each trophic level in the first patch is correlated with the noise experienced in the second patch, $\zeta_{j1} = \epsilon_{j1}$ and $\zeta_{j2} = \rho \zeta_{j1} + \gamma \epsilon_{j2}$. In each case, ϵ_j and ϵ_{ji} are Gaussian-distributed independent random variables with standard deviation σ and $\gamma = (1 - \rho^2)^{1/2}$; hence, the process ζ_{ji} will always have the same variance.

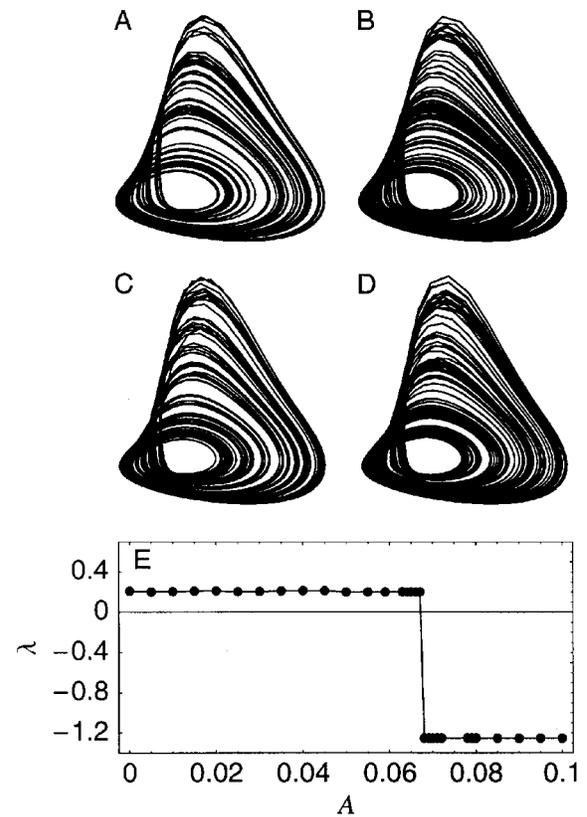


Figure 1: Dynamics of the tritrophic food web model proposed by Blasius et al. (1999), with parameters selected to induce chaotic behavior. The parameter values are $a = 1$, $c = 10$, $\alpha_1 = 0.2$, $\alpha_2 = 1$, $k_1 = 0.05$, $k_2 = 0$, $w^* = 0.006$, and $b_1 = 1.1$. A–D, Model’s attractor obtained by plotting u versus v versus $10w$: A, without forcing, $A_j = 0$, $\sigma = 0$; B, with noisy Gaussian disturbances, $A_j = 0$, $\sigma = 0.001$; C, with periodic forcing, $\omega = 1$, $A_j = 0.025$, $\sigma = 0$; and D, with noisy periodic forcing, $\omega = 1$, $A_j = 0.025$, $\sigma = 0.001$. E, Dependence between the estimated first Lyapunov exponent on the amplitude of the periodic forcing. The Lyapunov spectrum has been computed for noisy free equations with the classical Eckmann-Ruelle method (Eckmann and Ruelle 1980; Parker and Chua 1989).

Following the lead of Blasius and coworkers (Blasius et al. 1999; Blasius and Stone 2000) in studying the relationship between populations and the potential effect of environmental forcing, we employed the concept of phase synchronization. Any time series can be decomposed into phase and amplitude. The first step in applying phase analysis is to estimate the phase of the observed time series. One general approach has been based on the analytic signal concept in which the phase of the signal is obtained by the Hilbert transform (Pikovsky et al. 1997). But in many cases the time series considered can be reduced to quasi-cycles with maxima and minima. In this case, a simple way to define the phase is to use the maxima. The interval between two maxima corresponds to one complete quasi-cycle; therefore, the phase increases during this time period by exactly 2π . Hence, one can assign to the times t_n the values of the phase $\phi(t_n) = 2\pi n$ and take it linearly growing for the interval $[t_n, t_{n+1}]$. Thus, in a more mathematical form, one has

$$\phi(t) = 2\pi \left[\frac{t - t_n}{t_{n+1} - t_n} + (n - 1) \right], \quad t_n \leq t < t_{n+1}, \quad (3)$$

with t_n being the time of the n th maxima. The period lengths between successive maxima are then given by $T_n = t_{n+1} - t_n$ and instantaneous (angular) frequencies can be defined as $\Omega(t_n) = 2\pi/T_n$. Then, for two time series, the next step will be to define the phase difference as $\Delta\phi(t) = \phi_1(t) - \phi_2(t)$ and the cyclic phase difference as $\psi(t) = \Delta\phi(t) \bmod 2\pi$, with $\phi_1(t)$ and $\phi_2(t)$ the phases of the first and second populations considered.

The influence of noise on phase synchronization of linear oscillators has been studied (e.g., Stratonovich 1963). In these noisy systems, phase synchronization must be

understood only in a statistical sense, and the distribution of $\Delta\phi(t)$ or $\psi(t)$ must be taken into account.

Results

We know of no other study that examines the effects of noise-contaminated periodic forcing on the behavior of an ecological tritrophic such as model equation (2). Then we inspected the influence of the forcing used (eq. [2]) on the behavior of the tritrophic model. Figure 1A–1D displays the attractor of the model without forcing (the nominal attractor), with additive noise, with periodic forcing, and with noisy periodic forcing, respectively. This figure reveals that with “weak” forcing, the phase space is explored slightly more than the nominal attractor, but for all practical purposes the envelope of the attractor remains hardly changed. Moreover, the dynamics without and with “weak” periodic forcing are identical—similar peaks in the power spectrum (not shown) and almost identical first Lyapunov exponent (fig. 1E). Note that when the amplitude of the periodic forcing is above a threshold, the chaotic dynamics are destroyed and a periodic regime appears (fig. 1E); simulations show that the negative Lyapunov exponent indicates limit cycles rather than fixed equilibrium dynamics.

We explored the dynamics of the predators of two nonlinked tritrophic food web models to different types of forcing and disturbance. First, as expected, pure periodic forcing can induce phase synchronization of these chaotic nonidentical dynamics (fig. 2A), but pure common random disturbances cannot induce phase synchronization (fig. 2B). From an ecological point of view, noisy periodic forcings appear more realistic. We then focused on these cases. We examined the trajectories of the model and the

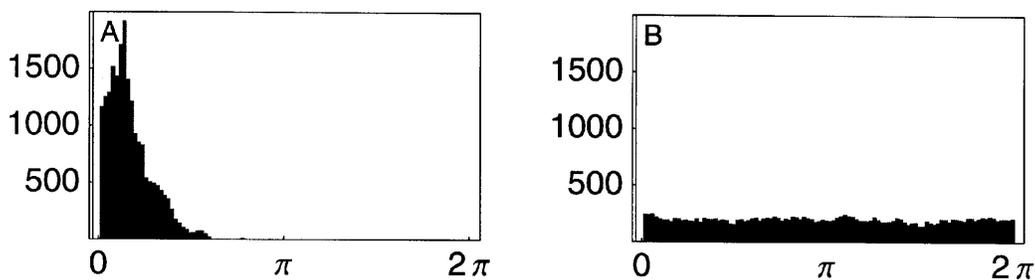


Figure 2: Distribution of the cyclic phase difference ($\psi = \Delta\phi \bmod 2\pi$) in nonlinked nonidentical chaotic populations. A, Distribution of the cyclic phase difference with pure global periodic forcing ($\omega = 1$, $A_j = 0.05$, $\sigma = 0$); B, with common Gaussian noise ($\omega = 0$, $A_j = 0$, $\sigma = 10^{-2}$). The other parameter values are $a = 1$, $c = 10$, $\alpha_1 = 0.2$, $\alpha_2 = 1$, $k_1 = 0.05$, $k_2 = 0$, $w^* = 0.006$, $b_1 = 1.1$, $b_2 = 1.055$. For each distribution, 10 runs over 2,000 relative time units have been used.

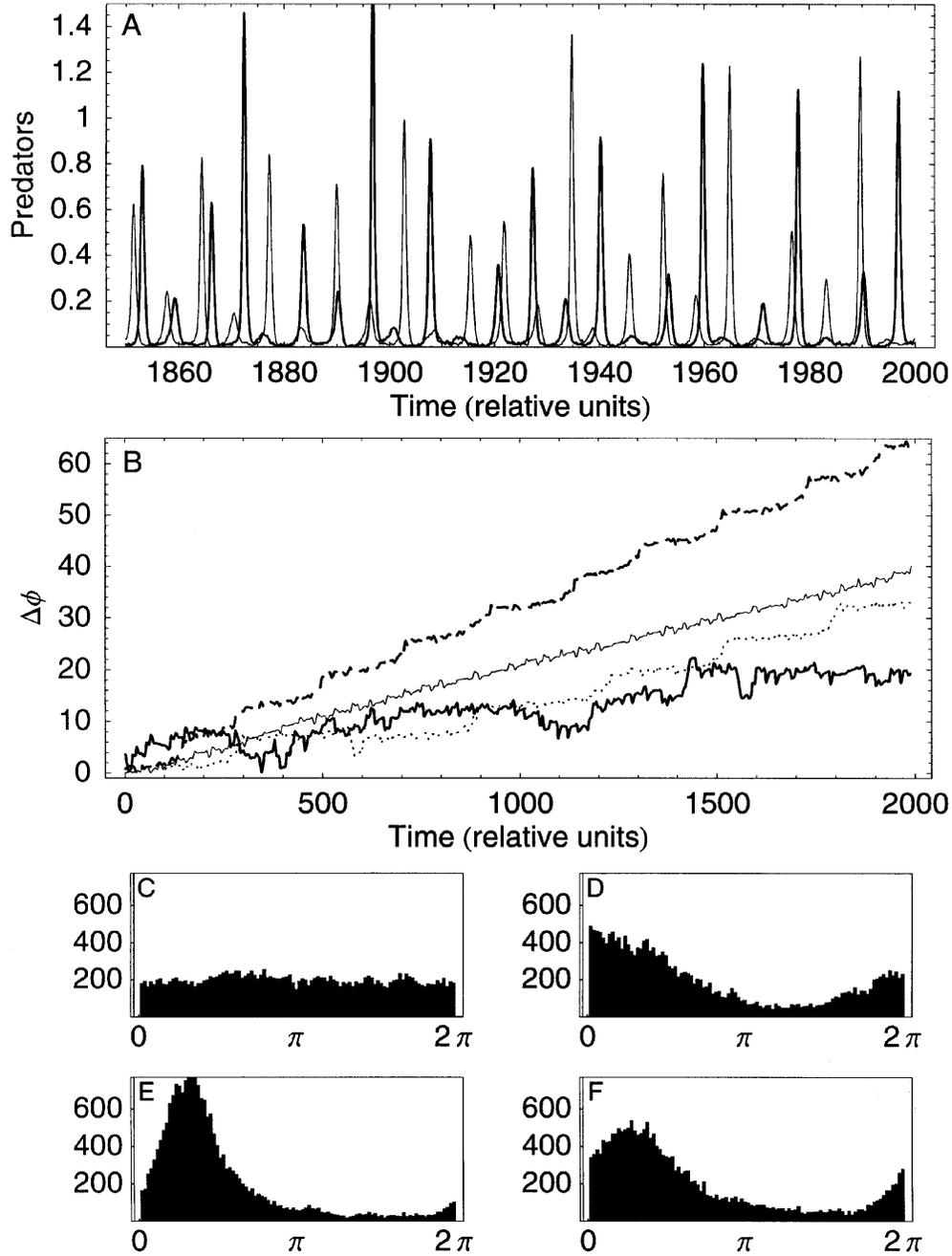


Figure 3: Phase synchronization in nonlinked chaotic populations. The parameter values are $a = 1$, $c = 10$, $\alpha_1 = 0.2$, $\alpha_2 = 1$, $k_1 = 0.05$, $k_2 = 0$, $w^* = 0.006$, but the two patches have different herbivore mortality rates: $b_1 = 1.1$, $b_2 = 1.055$. *A*, Phase synchronization in the time series of predator populations in two nonlinked patches in presence of noisy periodic forcing ($\omega = 0.5$, $A_j = 0.025$, $\sigma = 10^{-2}$; thin line, patch 1, and thick line, patch 2). *B*, Difference of phases ($\Delta\phi$) between the predator populations of the two patches computed by the phase analysis method of Blasius et al. (1999), for different types of forcing: in absence of environmental forcing (*thin line*, $A_j = 0$, $\sigma = 0$); with global periodic forcing contaminated by Gaussian noise (*thick line*, $\omega = 0.5$, $A_j = 0.025$, $\sigma = 10^{-2}$); global periodic forcing plus red noise (*dotted line*, $\omega = 0.95$, $A_j = 0.030$, $\sigma = 10^{-3}$, and $\rho = 0.30$); and global forcing plus local but correlated noise (*thick dashed line*, $\omega = 0.95$, $A_j = 0.025$, $\sigma = 10^{-2.5}$, and $\rho = 0.50$). *C–F*, Distribution of the cyclic phase difference ($\psi = \Delta\phi \bmod 2\pi$) for 10 runs over 2,000 relative time units for different types of forcing definitions: *C*, in absence of environmental forcing (*thin line*, $A_j = 0$, $\sigma = 0$); *D*, with global periodic forcing contaminated by Gaussian noise ($\omega = 0.5$, $A_j = 0.025$, $\sigma = 10^{-2}$); *E*, global periodic forcing plus red noise ($\omega = 0.95$, $A_j = 0.030$, $\sigma = 10^{-3}$, and $\rho = 0.30$); *F*, global forcing plus local but correlated noise ($\omega = 0.95$, $A_j = 0.025$, $\sigma = 10^{-2.5}$, and $\rho = 0.50$). The χ^2 tests have shown significant differences between the ψ distributions with and without noisy periodic forcing (P values $\ll 10^{-3}$).

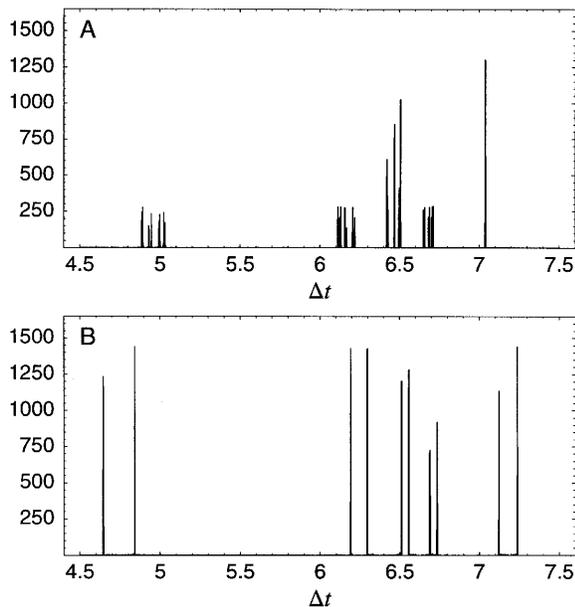


Figure 4: Distribution of time (Δt) between predator peaks. The parameter values used are $a = 1$, $c = 10$, $\alpha_1 = 0.2$, $\alpha_2 = 1$, $k_1 = 0.05$, $k_2 = 0$, $w^* = 0.006$, and $b_1 = 1.1$. A, Without forcing, $A_j = 0$; B, with periodic forcing, $\omega = 1$, $A_j = 0.025$.

phase of the predators to different types of “weak” periodic forcing (i.e., periodic forcing with “weak” amplitude that only slightly modifies the dynamics). Figure 3A shows the evolution of the predators of the two patches in the absence of dispersal, when a global noisy periodic forcing is added. Although the herbivores of the different patches have different mortality rates and thus different average instantaneous frequencies (see, e.g., Blasius and Stone 2000), the common environmental disturbances tend to synchronize the phase of the two populations. This occurs even though the chaotic dynamics of the populations tend to magnify the differences between the two populations.

Figure 3B displays results of phase analysis adopting the method used by Blasius et al. (1999) and shows that in the presence of different types of noisy forcing, the phase difference evolves quasi-erratically. However, for adequate amplitude, the difference of phase between the predators of the two patches shows several epochs with plateaus of synchronization where the phase difference growth is minimal, interrupted by phase slips where the phase difference growth jumps. In these cases the synchronization is difficult to detect “by eye”; nevertheless, it is detectable (fig. 3D–3F) and can be understood in a statistical sense by examining the frequency distribution of the cyclic phase differences when analyzed over a long period of time. The existence of sharp peaks in this distribution clearly indi-

cates a preferred phase difference (Schäfer et al. 1998; Tass et al. 1998; Blasius and Stone 2000). Cyclic phase difference fluctuates around some preferred values; phase slips change this quantity only by $\pm 2\pi$, with little influence on the dominating peaks of the distribution (fig. 3D–3F). Thus, in the presence of noisy periodic forcing, phase synchronization may be understood as the existence of the general tendency to bring the phase of the population into synchrony. This weak form of synchronization is obtained for “weak” periodic forcing, a relatively high noise component and frequency that can take different multiple or submultiple values of a common intrinsic frequency ($\omega_0 \approx 1$) estimated by the averaged instantaneous frequency (fig. 3D–3F).

Discussion

Here we have shown that noisy periodic disturbances, probably related to environmental fluctuations, can induce a weak form of population synchrony in two nonlinked tritrophic communities with nonidentical chaotic dynamics. Our results thus provide new insight into the synchronization of population fluctuations: even if environmental forcings only weakly influence complex (chaotic) population dynamics, they can bring into synchrony the phases of nonlinked populations. These results concur with those of recently published field studies dealing with the effect of environmental fluctuations on population dynamics (Grenfell et al. 1998; Stenseth et al. 1999; Pascual et al. 2000; Sæther et al. 2000; Sillett et al. 2000). In particular, Grenfell et al. (1998) reported synchronized, irregular fluctuations of sheep population dynamics on two separated islands in the Saint Kilda archipelago. Because in this example the two islands are completely separated by the sea, the observed population synchrony indicates a strong influence that originates from external environ-

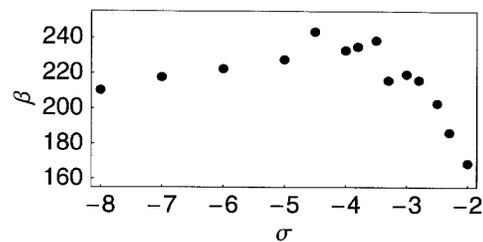


Figure 5: Evolution of the ratio β with additive noise intensity. By analogy to the signal to noise ratio, β is the ratio of the distribution height of ψ , the cyclic phase difference, to the variance of the distribution of ψ . Parameter values are $a = 1$, $c = 10$, $\alpha_1 = 0.2$, $\alpha_2 = 1$, $k_1 = 0.05$, $k_2 = 0$, $w^* = 0.006$, $b_1 = 1.1$, $b_2 = 1.055$, $\omega = 0.95$, and $A_j = 0.016$, and 30 runs over 2,000 relative time units are used for each noise intensity.

mental fluctuations. Our findings are supported by this convincing example of the Moran effect on these isolated island populations characterized by irregular fluctuations.

The synchronization of chaotic oscillators by common noise is a subject of intense activity (e.g., Pikovsky 1992). However, the influence of external periodic forcing on chaotic oscillators has been less investigated (Stone 1992; Pikovsky et al. 1997). Pikovsky et al. (1997) systematically studied the entrainment of the phase of chaotic systems by external forcing, using two prototypic models of nonlinear dynamics, the Rössler and the Lorenz models. They showed that external periodic forcing can lead to phase synchronization. The synchronization properties depend on the amplitude of the forcing but also on the coherence of the attractor considered. Periodic external force with frequency close to the frequency of cycles embedded in the attractor (stable and unstable cycles) leads to phase locking of these cycles. Pikovsky et al. (1997) stressed that phase synchronization by external periodic forcing can also be understood in terms of instantaneous periods. In synchronous state, the return time to a Poincaré secant of the attractor becomes equal, in average, to the period of the external forcing. Similar behavior has been observed with Blasius et al.'s model (Blasius et al. 1999). Figure 4 shows that periodic forcing induces a more coherent distribution of the time between two predator peaks. This coherence of the attractor of the tritrophic model explicates the entrainment of the phases of the predator population by the external forcing and thus the possibility of phase synchronization of two populations by two identical or correlated external forcings.

From an ecological point of view, a pure periodic forcing appears unrealistic, and we have used noisy periodic forcing on systems with two different frequencies (fig. 3). But the noise components used did not destroy the coherence of the dynamics, and phase synchronization has been observed (fig. 3D–3F). Nonintuitive results are obtained in the presence of noisy periodic forcing. A particularly interesting result concerns the existence, for low-amplitude forcing, of an optimal level of noise intensity that optimizes the relative coherence between the phases of predator populations in the two patches (fig. 5). We define an equivalent “signal to noise ratio” β as the ratio of the height over the variance of the cyclic phase difference (ψ) distribution seen in the graphs of figure 3. The dependence of this ratio β on noise level is summarized in figure 5. If the intensity of the noise is too small, the results are identical to those in the absence of noise. If the intensity of the noise is too great, the noise reduced the phase coherence. But just as in stochastic resonance, there exists an optimal level of noise that enhances the coherence of the phases (Roy and Amrirkar 1997; Kádár et al. 1998; Neiman et al. 1998, 1999a).

These results emphasize the complex relations between the synchronizing effects of environmental stochasticity and the desynchronizing effects of nonlinear dynamics. These results also demonstrate that stochasticity has a major role to play in nonlinear dynamics and its influence is becoming increasingly recognized in ecological theory.

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