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Synchrony in slow-fast metacommunities

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Synchrony in slow-fast metacommunities

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Abstract

The synchronization of metacommunities due to dispersal among patches is analyzed in the case of slow-fast populations. The analysis is performed by studying a standard model with the fast population dispersing when special meteorological conditions are present. This assumption fits very well with the peculiar nature of slow-fast systems and implies that metacommunities synchronize if the slow population accelerates during the outbreak of the fast population. This result has great potentials for the study of marine and fresh-water plankton communities as well as for the study of synchronization of insect-pest outbreaks in forests.

1 Introduction

Synchrony has been observed in metapopulations and metacommunities representing virtually all major taxa and ecological roles [Liebhold *et al.*, 2004]. It is the consequence of two independent factors: the dispersal of populations among patches and the existence of common meteorological driving forces (Moran effect). The theory is well established: see [Pecora & Carroll, 1998; Blasius *et al.*, 1999; Jansen & Lloyd, 2000] for dispersal, [Royama, 2005] for the Moran effect, and [Ranta *et al.*, 1995; Haydon & Steen, 1997; Colombo *et al.*, 2008] for the mixed case. Since the theory predicts that the rate of convergence to synchrony should be of the order of the dispersal rate, which is known to be small (for many, if not all, populations), and local noise tends to desynchronize patches, it is surprising that synchrony has been so often observed in the field. Here the puzzle is solved by showing that in the quite frequent case of slow-fast populations characterized by recurrent crashes and outbreaks of the fast populations [Rinaldi & Scheffer, 2000] (e.g. pest outbreaks, plankton blooms, and fires in Mediterranean forests) the rate of convergence to synchrony can be large.

Synchrony of slow-fast systems has already been studied in neuroscience, where the synchronization of spiking neurons is a central problem. Indeed, in a series of contributions, Kopell and coauthors (see , for all, [Somers & Kopell, 1993]) have shown through specific models that synchronization can be very quick and almost independent upon the coupling strength if the fast variable is responsible for the coupling. Here we give an almost intuitive support to this conclusion by studying a standard prey-predator model.

Our method is based on the analysis of the so-called singular case, obtained by imagining that the prey population is infinitely faster than the predator population. In such a limit case, the prey-predator cycle can be easily identified and is composed of four alternate slow and fast phases [Rinaldi & Scheffer, 2000]. The two fast phases correspond to the sudden outbreak and crash of the fast population. The analysis shows that deliberate or accidental introductions or removals of the fast population do not influence the time of the next crash if they are performed when the fast population is abundant, while they accelerate or delay the next outbreak in the opposite case. This simple property allows one to point out sharp conditions for the synchronization of coupled communities under realistic assumptions on the dispersal processes.

2 Slow-fast Prey-predator Dynamics

Let us consider the prey-predator model with fast prey (x) and slow predator (y)

$$\varepsilon \dot{x} = x f(x, y), \quad \dot{y} = y g(x, y) \quad (1)$$

where ε is a small positive parameter. For generic values of x and y , the absolute value of \dot{x} is high. This means that prey abundance varies quickly unless the state (x, y) of the system evolves along the trivial prey isocline ($x = 0$) or along the non-trivial prey isocline ($f(x, y) = 0$).

In the absence of prey, i.e., for $x = 0$, the predator abundance varies slowly, in accordance with the equation $\dot{y} = y g(0, y)$ and the predator goes extinct if $g(0, y) < 0$, as shown in Fig. 1a. However, the prey net growth rate $f(0, y)$ is in general negative for high predator

densities but positive in the opposite case. That is to say, there exists, in general, a critical value y_0 of predator abundance at which $f(0, y_0) = 0$. Thus, in the vicinity of the y axis, i.e., after the introduction of a small amount of prey, the state of the system quickly evolves to the left if $y > y_0$ and to the right if $y < y_0$, as shown in Fig. 1a. For decreasing values of ε the trajectories become more and more horizontal until the singular case $\varepsilon = 0$ is obtained, as shown in Fig. 1b. Figure 1b points out that the outbreak of the prey occurs when the predator abundance reaches a value y_{out} which is uniquely determined, through a suitable function Ψ , by the abundance of the predator at the time of prey introduction, i.e.,

$$y_{out} = \Psi(y_{in}). \quad (2)$$

The function Ψ can be determined as follows ([Rinaldi & Muratori, 1992] and references therein). First write eqs. (1) in the form

$$\varepsilon \frac{dx}{x} = f(x, y) dt, \quad dt = \frac{1}{yg(x, y)} dy, \quad (3)$$

then integrate along the trajectory from point (ε, y_{in}) to point (ε, y_{out}) (see Fig. 1a), and finally let $\varepsilon \rightarrow 0$ by substituting x with 0, thus obtaining

$$\int_{y_{in}}^{y_{out}} \frac{f(0, y)}{yg(0, y)} dy = 0. \quad (4)$$

In general, eq. (4) cannot be solved analytically with respect to y_{out} , so that the function Ψ cannot be derived in closed form. A typical graph of the function is reported in Fig. 2. It shows that if the introduction of prey occurs when $y = y_{in} > y_0$, the outbreak occurs when the predator density reaches the value $y_{out} = \Psi(y_{in}) < y_0$. The time $T_{i,o}$ separating the introduction of prey from their outbreak can be evaluated by integrating eq. (3) along the y axis from y_{in} to y_{out} , i.e.,

$$T_{i,o} = \int_{y_{in}}^{y_{out}} \frac{1}{yg(0, y)} dy. \quad (5)$$

By contrast, if the introduction of prey occurs when $y = y_{in} < y_0$, then the outbreak is immediately triggered, since $f(0, y) > 0$ for $y < y_0$, so that $\dot{x} > 0$.

The case of two introductions is depicted in Fig. 3, where it is evident that any new introduction of individuals of the fast population accelerates the outbreak. One can use the same argument to show that a removal of prey occurring after the last introduction has the effect of delaying the outbreak. By contrast, if the net growth rate of the prey is decreasing with density (i.e., $\partial f / \partial x < 0$) introductions or removals of prey when abundant (i.e., when the system slowly evolves along the non-trivial prey isocline $f(x, y) = 0$) are immediately compensated because the fast population is stable in these conditions. This implies that perturbations of the prey when abundant do not impact on the time of their next crash.

3 The Rosenzweig-MacArthur Model

We now focus on the most popular prey-predator model, namely the Rosenzweig-MacArthur model [Rosenzweig & MacArthur, 1963]

$$\dot{x} = r^* x \left(1 - \frac{x}{K}\right) - a^* \frac{x}{x+b} y, \quad \dot{y} = c \frac{x}{x+b} y - dy \quad (6)$$

where x and y are prey and predator abundances, r^* and K are net growth rate and carrying capacity of the prey, a^* is maximum predation rate of the predator, b half-saturation constant of the predator functional response, c prey / predator conversion factor, and d predator death rate.

We assume that $c > d$ since, otherwise, the predator population cannot persist. We also assume that the per-capita net growth rate of the prey r^* and the maximum predation rate a^* are high because this guarantees that the prey population is fast. Letting $r^* = r/\varepsilon$ and $a^* = a/\varepsilon$ with ε positive and small, we can write model (6) in the standard form (1) with

$$f(x, y) = r\left(1 - \frac{x}{K}\right) - a\frac{y}{x + b}, \quad g(x, y) = c\frac{x}{x + b} - d.$$

If $K > b(c + d)/(c - d)$ (in the following we assume $K \gg b$) the non-trivial prey isocline $f(x, y) = 0$ (a parabola) and the non-trivial predator isocline $g(x, y) = 0$ (a vertical straight line) intersect at an equilibrium point E on the left of the vertex of the parabola, as shown in Fig. 4. This equilibrium is unstable and surrounded (for any $\varepsilon > 0$) by a globally stable limit cycle which is not known in closed form. However, if the prey population is fast, the limit cycle is well approximated by the singular cycle $ABCD$ shown in Fig.4 (see [Rinaldi & Muratori, 1992]), which is composed of four phases:

- (i) A slow transition from A to B (the vertex of the parabola) during which prey and predator vary at comparable speeds;
- (ii) A fast (rigorously infinitely fast) transition from B to C during which the prey population collapses to zero (in practice to very low densities, if $\varepsilon > 0$);
- (iii) A slow transition from C to D during which prey are absent (scarce if $\varepsilon > 0$) and predator decay in accordance with eq. (6) with $x = 0$;
- (iv) A fast transition from D to A corresponding to a sudden prey outbreak.

The maximum predator density y_{max} along the slow-fast cycle is the y -coordinate of the vertex of the parabola, namely $y_{max} = r(K + b)^2/(4Ka)$, while the minimum predator density y_{min} can be obtained using the method described above. In fact, when predator decay in the absence of prey, point C in Fig. 4 can be considered as the point of the last introduction of prey, while D is the point of the corresponding outbreak, so that (see eq. (2)) $y_{min} = \Psi(y_{max})$.

4 Synchronization of Coupled Patches through Blinking Dispersal

Let us now consider two identical patches coupled through migration of the fast prey population (the addition of predator migration would not be influential). In the absence of migration, the two patches would behave on the same slow-fast cycle and would remain out of phase forever. In most theoretical studies, the migration process is assumed to be a continuous process with net migration flow proportional (through a constant dispersal coefficient

D) to the unbalance of population densities. Under this assumption, a two-patch system is described by eqs.(6) with x_1 and y_1 for patch 1 and x_2 and y_2 for patch 2, and with the addition of a prey migration flow $D(x_j - x_i)$ in the two prey equations. This model is perfectly suited for applying the general methods of analysis of the stability of the synchronous state [Pecora & Carroll, 1998; Jansen & Lloyd, 2000]. However, here we follow a different approach by assuming that migration is a blinking process [Belykh *et al.*, 2004], namely that the dispersal coefficient D is almost always zero but very high from time to time. That is to say, migration episodes are due to rare and short particular meteorological conditions, such as high winds or strong water currents, but occur relatively frequently during each slow phase of the cycle. The assumption of blinking dispersal not only has the advantage of being more realistic in many cases but, as shown in the following, it allows one to discuss the synchronization of slow-fast systems very effectively. Moreover the general theory of synchronization through blinking dispersal [Belykh *et al.*, 2004] guarantees that if a system synchronizes under blinking dispersal it also synchronizes for a suitable constant dispersal coefficient.

Let us then consider the effect of blinking dispersal. If both patches are in the slow phase (iii), migration cannot be relevant because the patches are practically empty. On the other hand, if both patches are in the slow phase (i) the masses of migrating prey can be relevant but they cannot have serious consequences since the introduction or removal of a mass of prey in a densely populated patch would be immediately compensated (notice that the right branch of the parabola of Fig. 4 is the stable manifold of the prey population). Thus, the only migrations that can have important consequences are those that transfer prey from a densely populated patch to an empty patch. In order to determine if these migrations can synchronize the outbreaks, we now limit our discussion to the local stability of the synchronous state, i.e., we consider patches which are only slightly out of phase. Assume, then, that both patches are in the slow phase (i) and that patch 2 is delayed with respect to patch 1 of τ units of time (with τ small). Immediately after the prey collapse in the leading patch, the predator of patch 1 decrease exponentially (as $y_{max} \exp(-dt)$) while the predator in the delayed patch continue to grow until they reach the value y_{max} at which their prey collapse. At that point the density of the predator is y_{max} in patch 2 and $y_{max} \exp(-d\tau)$ in patch 1. Moreover, from the hypothesis we made on the frequency of migration events, we can assume that shortly before that moment there has been a consistent migration of prey from patch 2 to patch 1. Thus, the next prey outbreak in the leading patch occurs when the predator reach the density $\Psi(y_{max} \exp(-d\tau))$. At that time, patch 2 has predator at a slightly higher density, namely $\exp(d\tau)\Psi(y_{max} \exp(-d\tau))$ and has shortly after, a prey outbreak triggered by an introduction of prey coming from patch 1. After this last outbreak both patches are in the slow phase (i) (patch 2 is now leading) and their predator densities are $\Psi(y_{max} \exp(-d\tau))$ in patch 1 and $\exp(d\tau)\Psi(y_{max} \exp(-d\tau))$ in patch 2. But in phase (i), immediately after the outbreaks, the predator increase exponentially because their dynamics can be approximated by $\dot{y} = (c-d)y$ (see eq. (6) and recall that $x \cong K \gg b$). Thus, the new delay τ' between the two patches satisfies the relationship $(\exp((c-d)\tau')\Psi(y_{max} \exp(-d\tau)) = \exp(d\tau)\Psi(y_{max} \exp(-d\tau))$ from which it follows that $\tau'/\tau = d/(c-d)$.

The delay τ has therefore been changed into τ' after one population cycle and $\tau' < \tau$ if

the *compression factor* $(c - d)/d$ [Somers & Kopell, 1993] is greater than 1, i.e., if

$$c > 2d. \tag{7}$$

This result shows that the convergence to the synchronous state can be very quick, so that synchrony is also guaranteed in the field [Liebhold *et al.*, 2004]. It is worth noticing that the two patches synchronize if the slow population accelerates during the outbreak of the fast one, while what happens during the rest of the cycle does not matter. Moreover, results obtained for two patches obviously hold for longer chains of patches provided relatively frequent meteorological conditions favour prey migration between pairs of contiguous patches.

If condition (7) is not satisfied, i.e., if

$$d < c < 2d \tag{8}$$

then the delay τ' after one population cycle is greater than τ , so that the synchronous state is unstable. This means that under condition (8) the two patches will either tend toward a periodic asynchronous solution or to a quasi-periodic or intermittently chaotic attractor [Cazelles *et al.*, 2001; Harrison *et al.*, 2001; Jansen, 2001]. This result disproves a common belief, namely that dispersal synchronizes the oscillations of Rosenzweig-MacArthur prey-predator communities [Jansen, 1999].

5 Application to Fresh-water Plankton Communities

The study of synchronization of fresh-water plankton communities becomes possible through our condition. In fact the values of the parameters suggested for algae-zooplankton interactions [Rose *et al.*, 1988] are $c = 0.6 - 0.7$ and $d = 0.20 - 0.23$ so that condition (7) is satisfied (compression factor roughly equal to 2). Since also condition $b \ll K$ is satisfied (suggested ratio $b/K = 0.05$) and algae grow slightly faster than zooplankton, we can expect that chains of shallow lakes connected from time to time through small channels could have synchronous algae outbreaks and crashes, i.e., synchronous clear water episodes. Moreover, the seasonal forcing of the water body reinforces this result through the Moran effect. Indeed, a long and detailed survey [Ravera, 1977] of the main characteristics of Lake Lugano (CH), a narrow lake composed of a chain of four weakly connected pools (see Fig. 5), has pointed out a remarkable synchrony of the clear water episodes in the four pools. This is perfectly illustrated in Fig. 6 (extracted from [Ravera, 1977]) where the four graphs report the transparency (measured through Secchi depth) in each pool in the period 1972-75. The sharp raises of each curve (see, in particular, the end of February 1974) indicate a transition from transparent to turbid water due to an algae bloom (i.e. to a prey outbreak).

Our result might also be used for studying the patchiness of oceanic plankton populations, a well documented phenomenon [Hillary & Bees, 2004]. Another promising line of application of the ideas presented here is the study of synchronization of insect-pest outbreaks in forests, which has been largely debated but not yet fully understood [Johnson *et al.*, 2005].

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Figure captions

Figure 1

Trajectories of a prey-predator model with fast prey and slow predator when prey are very scarce: (a) $\varepsilon > 0$ small; (b) singular case $\varepsilon = 0$. Double arrows indicate fast motion.

Figure 2

The graph of the function Ψ given by (2) for the model analyzed in the text. The function is defined for $y_{in} \geq y_0$.

Figure 3

When there are two introductions of prey (the first when $y = y'_{in}$ and the second when $y = y''_{in}$) the outbreak occurs at y''_{out} , i.e., it is accelerated with respect to the outbreak that would be produced by the first introduction alone.

Figure 4

Prey and predator isoclines of model (6) and singular cycle $ABCD$ for the following parameter values $r = 2$, $K = 1.1$, $a = 3$, $b = 0.25$, $c = 0.75$, $d = 0.2$.

Figure 5

The four pools of Lake Lugano (CH) and their maximum depths. Along the dotted lines the lake is only one meter deep.

Figure 6

Transparency in the four pools (measured in Secchi depth) in the period 1972-75. Sharp raises of the curves indicate algae blooms.

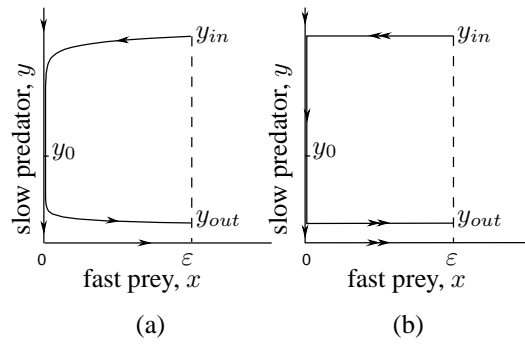


Figure 1

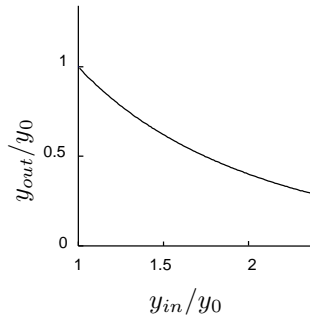


Figure 2

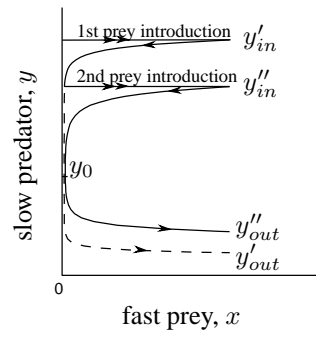


Figure 3

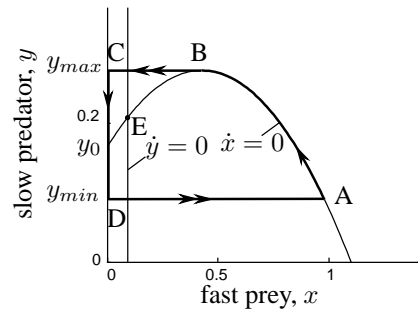


Figure 4

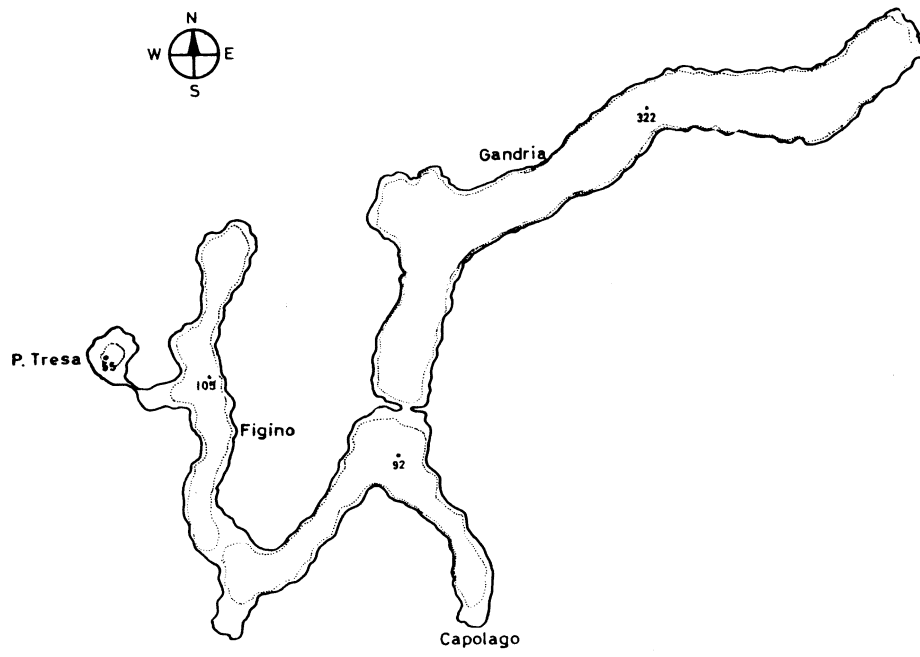


Figure 5

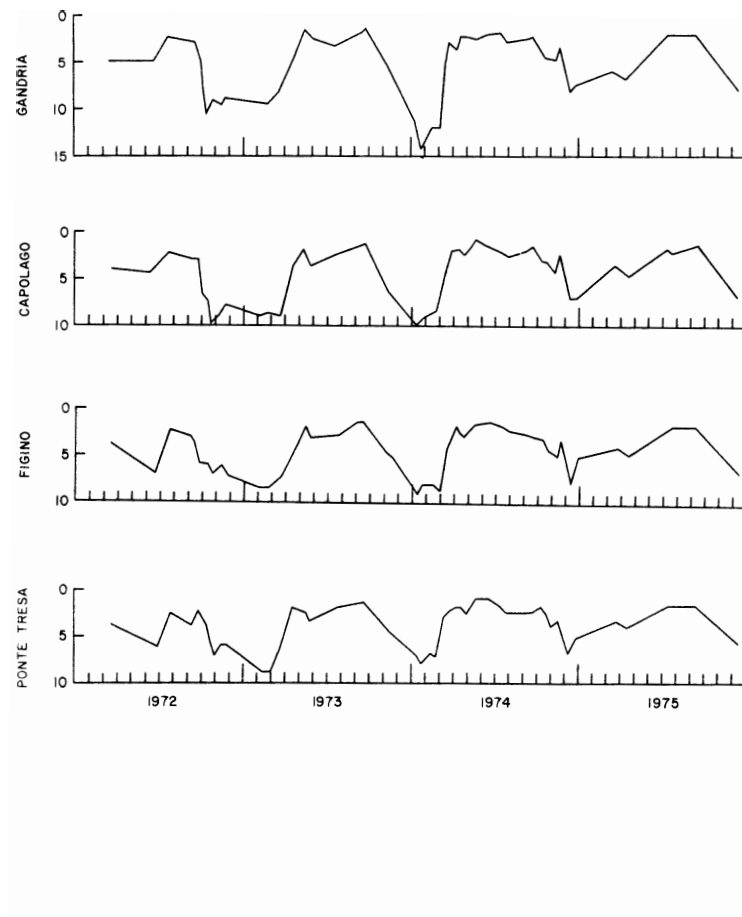


Figure 6