Angular velocity variations and stability of spatially explicit prey-predator systems

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Population oscillations in prey predator systems, as predicted by the Lotka-Volterra equations [1], are known to be unstable with respect to additive and multiplicative noise. This instability must lead to the extinction of one of the interacting species, a fact that has been confirmed in various experiments for well-mixed populations [2]. The persistence of natural prey-predator and host-parasitoid systems, thus, is commonly attributed to their spatial structure, such that migration between desynchronized patches yields an inward flow toward the coexistence fixed point and is responsible for the sustainability of the oscillations [3]. In fact, spatially extended systems tend to support finite amplitude oscillation [4]. The stabilization of such oscillations is considered to be a major factor affecting species conservation and ecological balance [5].

The main challenge, thus, is to understand the conditions for the appearance of desynchronization in diffusively coupled patches, since diffusion tends to synchronize these patches so after a while the whole system flows to the well mixed, unstable limit [6]. One of the solutions to that problem was presented by Jansen [7, 8, 9]. It turns out that the trajectories far from the fixed point become unstable if the inter-patch migration rate of the predator is much larger than that of the prey. Jansen used Floquet analysis to show that instability. In this paper, we try to elucidate the underlying mechanism that yields Jansen’s instability, to generalize it in the framework of the recently presented coupled oscillator model, and to discuss the conditions under which one may observe the stabilizing effect of Jansen’s mechanism, like oscillation amplitude that grows under noise until it reaches the first unstable orbit.

The Lotka-Volterra predator-prey system is a paradigmatic model for oscillations in population dynamics [1]. It describes the time evolution of two interacting populations: a prey (b) population that grows with a constant birth rate σ in the absence of a predator (the energy resources consumed by the prey are assumed to be inexhaustible), while the predator population (a) decays with death rate μ, in the absence of a prey. Upon encounter, the predator may consume the prey with a certain probability. Following a consumption event, the predator population grows and the prey population decreases. For a well-mixed population, the corresponding partial differential equations are,

\[ \frac{\partial a}{\partial t} = -\mu a + \lambda_1 ab \]
\[ \frac{\partial b}{\partial t} = \sigma b - \lambda_2 ab, \]

where \( \lambda_1 \) and \( \lambda_2 \) are the relative increase (decrease) of the predator (prey) populations due to the interaction between species, correspondingly.

The system admits two unstable fixed points: the absorbing state \( a = b = 0 \) and the state \( a = 0, b = \infty \). There is one marginally stable fixed point at \( \bar{a} = \sigma/\lambda_2, \bar{b} = \mu/\lambda_1 \). Local stability analysis yields the eigenvalues \( \pm i\sqrt{\mu \sigma} \) for the stability matrix. Moreover, even beyond the linear regime there is neither convergence nor repulsion. Using logarithmic variables \( z = \ln(a) \), \( q = \ln(b) \) eqs. [1] take the canonical form \( \dot{z} = \partial H/\partial q, \dot{q} = -\partial H/\partial z \), where the conserved quantity \( H \) (in the \( ab \) representation) is,

\[ H = \lambda_1 b + \lambda_2 a - \mu \ln(a) - \sigma \ln(b). \]

The phase space, thus, is segregated into a collection of nested one-dimensional trajectories, where each one is characterized by a different value of \( H \), as illustrated in Figure 3. Given a line connecting the fixed point to one of the "walls" (e.g., the dashed line in the phase space portrait, Figure 3), \( H \) is a monotonic function on that line, taking its minimum \( H_{\text{min}} \) at the marginally stable fixed point (center) and diverging on the wall. Without loss of generality, we employ hereon the symmetric parameters \( \mu = \sigma = \lambda_1 = \lambda_2 = 1 \). The corresponding phase space, along with the dependence of \( H \) on the distance from the center and a plot of the oscillation period vs. \( H \), are represented in Figure 3. 
FIG. 1: The Lotka-Volterra phase space (left panel) admits a marginally stable fixed point surrounded by close trajectories (three of these are plotted). Each trajectory corresponds to single $H$ defined in Eq. (2), where $H$ increases monotonically along the (dashed) line connecting the center with the $a = 0$ wall, as shown in the lower right panel. In the upper right panel, the period of a cycle $T$ is plotted against $H$, and is shown to increase almost linearly from its initial value $T = 2\pi/\sqrt{\mu\sigma}$ close to the center.

FIG. 2: The survival probability $Q(t)$ is plotted versus time for a single-patch, noisy LV system. Eqs. (1) (with the symmetric parameters) were integrated numerically (Euler integration with time step 0.001), where the initial conditions are at the fixed point $a = b = 1$. At each time step, a small random number $\eta(t)\Delta t$ was added to each population density, where $\eta(t) \in [-\Delta, \Delta]$. A typical phase space trajectory, for $\Delta = 0.5$, is shown in the inset. The system "dies" when the trajectory hits the walls $a = 0$ or $b = 0$. Using 300 different noise histories, the survival probability is shown here for $\Delta = 0.5$ (full line), $\Delta = 0.3$ (dotted line) and $\Delta = 0.25$ (dashed line). Clearly, the survival probability decays exponentially at long times, $Q(t) \sim \exp(-t/\tau)$. As expected for a random walk with absorbing boundary conditions, $1/\tau$ scales with $\Delta^2$.

Given the integrability of that system, the effect of noise is quite trivial: if $a$ and $b$ randomly fluctuate in time (e.g., by adding or subtracting small amounts of population during each time step), the system wanders between trajectories, thus performing some sort of random walk in $H$ with "repelling boundary conditions" at $H_{\text{min}}$ and "absorbing boundary conditions" on the walls (as negative densities are meaningless, the "death" of the system is declared when the trajectory hits the zero population state for one of the species). This result was emphasized by Gillespie [10] for the important case where intrinsic stochastic fluctuations are induced by the discrete character of the reactants. In that case, the noise is multiplicative (proportional to the number of particles), and the system flows away from the center and eventually hits one of the absorbing states at 0, 0 or 0, $\infty$. The corresponding situation for a single patch Lotka-Volterra system with additive noise is demonstrated in Figure 4, where the survival probability $Q(t)$ (the probability that a trajectory does not hit the absorbing walls within time $t$) is shown for different noise amplitudes.

The Lotka-Volterra system on spatial domains has been investigated, usually in a form of diffusively coupled patches, during the last decades. Any patch is assumed to be well mixed, and the flow of the reactants from one patch to its neighbors is governed by the density gradient. Clearly, any system of that type, independent of its spatial topology (either regular lattice of some dimensionality or some sort of network without isolated nodes) admits an infinite number of solutions that correspond to synchronous oscillations of the whole system along one of the $H$ trajectories, where the diffusion has no role as there are no population gradients. The simplest example is the two-patch system,
described by:

\[
\begin{align*}
\frac{\partial a_1}{\partial t} &= -\mu a_1 + \lambda_1 a_1 b_1 + D_a (a_2 - a_1) \\
\frac{\partial a_2}{\partial t} &= -\mu a_2 + \lambda_1 a_2 b_2 + D_a (a_1 - a_2) \\
\frac{\partial b_1}{\partial t} &= \sigma b_1 - \lambda_2 a_1 b_1 + D_b (b_2 - b_1) \\
\frac{\partial b_2}{\partial t} &= \sigma b_2 - \lambda_2 a_2 b_2 + D_b (b_1 - b_2).
\end{align*}
\] (3)

Here the invariant manifold is the two dimensional subspace \( a_1 = a_2, \ b_1 = b_2 \). The diffusion, of course, suppresses fluctuations and stabilizes the invariant manifold; one may expect, thus, that the single-patch dynamics also capture the main features of the extended system, and that the system behaves like a random walker in the invariant manifold (with a rescaled noise) and hits the absorbing walls after some characteristic time \( \tau \), where \( \tau \) scales linearly with the noise strength \( \Delta^2 \).

As a first hint for a stabilizing mechanism, let us consider the total \( H_T \),

\[
H_T \equiv H_1 + H_2 = a_1 + a_2 + b_1 + b_2 - \ln(a_1 a_2 b_1 b_2).
\] (4)

With the deterministic dynamics (3), \( H_T \) is a monotonously decreasing quantity in the non-negative population regime:

\[
\frac{dH_T}{dt} = -D_a \left( \frac{(a_1 - a_2)^2}{a_1 a_2} \right) - D_b \left( \frac{(b_1 - b_2)^2}{b_1 b_2} \right) < 0.
\] (5)

Accordingly, if an orbit on the invariant manifold becomes unstable, the flow will be inward and the population oscillations stabilizes.

While if \( D_a = D_b \) the stability properties of an orbit on the invariant manifold are identical to the stability properties of the corresponding single-patch orbit [11], if the diffusion of both species is different, there is a possibility for unstable orbits on the homogenous plane. This option was materialized by Jansen [7], who considered the set of Equations 3 in the limit \( D_b = 0 \), so that only the predator undergoes diffusion. With the transformation:

\[
\begin{align*}
A &= \frac{a_1 + a_2}{2} & B &= \frac{b_1 + b_2}{2} \\
\delta &= \frac{a_1 - a_2}{2} & \theta &= \frac{b_1 - b_2}{2},
\end{align*}
\] (6)

one recognizes the homogenous \( AB \) manifold and that the \( \delta \theta \) coordinates measure the deviation from that manifold (the heterogeneity of the population). In these coordinates the system satisfies,

\[
\begin{align*}
\frac{\partial A}{\partial t} &= -\mu A + \lambda_1 A B + \lambda_1 \delta \theta \\
\frac{\partial B}{\partial t} &= \sigma B - \lambda_2 A B + \lambda_2 \delta \theta \\
\frac{\partial \delta}{\partial t} &= -\mu \delta + \lambda_1 A \theta + \lambda_1 B \delta - 2D_a \delta \\
\frac{\partial \theta}{\partial t} &= \sigma \delta - \lambda_2 A \theta - \lambda_2 B \delta - 2D_b \theta.
\end{align*}
\] (7)

Linearizing around the homogenous manifold, The \( AB \) dynamic is equivalent to that of a single patch,

\[
\begin{align*}
\dot{A} &= -\mu A + \lambda_1 A B \\
\dot{B} &= \sigma B - \lambda_2 A B
\end{align*}
\] (8)

and the \( \delta - \theta \) linearized dynamic is

\[
\frac{\partial}{\partial t} \begin{pmatrix} \delta \\ \theta \end{pmatrix} = \begin{pmatrix} -\mu + \lambda_1 B - 2D_a \\ -\lambda_2 B \end{pmatrix} \begin{pmatrix} \lambda_1 A \\ \sigma - \lambda_2 A - 2D_b \end{pmatrix} \begin{pmatrix} \delta \\ \theta \end{pmatrix}.
\] (9)
FIG. 3: Stability diagram for phase space orbits (ordered by their conserved quantity $H$) for different values of predator diffusion $D_a$, where $D_b=0$.

FIG. 4: The angular velocity along some orbits of the Lotka-Volterra dynamic. Fast regions marked in red, slow regions are blue. Clearly, the dynamics is slowest when the populations of both species are diluted, and fastest along the dense region in the upper-right "shoulder." Note that the velocity gradient along an orbit increases with $H$.

One may thus calculate the eigenvalues of the Floquet operator for one period along an orbit of the homogenous manifold. The resulting stability diagram, first obtained by [7], is shown in Figure 3.

Our first mission is to intuitively explain Jansen’s results. First, we notice that the angular velocity along a single Lotka-Volterra orbit is not fixed. Figure 4 emphasizes the angular velocity gradient along an orbit. While the inner trajectories (close to the fixed point) are almost harmonic with constant angular velocity, the eccentric large $H$ orbits admit large variations. In particular, the motion in the dilute population region [close to the unstable empty fixed point $(0,0)$] is very slow, while in the dense population region the angular velocity is large.

Following the caricature of an orbit in Fig. 5, we can explain the source of the instability. For a two-patch system, if one patch is at point A along the orbit and the other patch at B, since the A patch is moving faster along the line it will get closer and closer to B during their flow toward the slow region. The diffusion of the prey plays no role along this branch, since the prey density is almost equal, while the predator diffusion may only strengthen that effect. Thus, the two patches must (almost) synchronize along this branch.

The situation is completely different in the exit from the slow region. The patch at D moves much faster than that at C, so they will desynchronize. As the predator density along this branch is almost constant, the only factor that may avoid desynchronization is the prey migration. In the absence of prey migration, the two patches reach the points C’ and D’, where the predator migration produces an inward flow. Figure 6 is now well understood: the inward flow happens when the desynchronization interferes with the predator diffusion, as explained.

Let us consider, now, Jansen’s instability in the framework of the coupled nonlinear oscillator toy model, recently presented [12] as a generic tool for the investigation of oscillation stability in diffusively coupled metapopulations.
FIG. 5: An orbit of the LV dynamics and its fast and slow regions. As explained in the text, with no prey migration the two patches desynchronize in the CD region, thus predator diffusion causes a flow toward the fixed point and stabilizes the oscillations.

FIG. 6: Phase portrait of the inward flow in the homogenous manifold (average prey density vs. average predator density) for two-patch LV system with no prey diffusion and $D_{\text{predators}} = 1$. Clearly, the inward flow happens in the $C' - D'$ region of Figure 5 where the desynchronization along the CD branch interferes with the predator diffusion. There is almost no inward motion along the rest of the orbit.

With the intuition gathered from the above example, we want to consider diffusively coupled orbits where the angular velocity depends on the radial angle and the diffusing species density is changing along the slowing branch. The following equations,

$$\frac{\partial x_1}{\partial t} = \omega(\theta_1)y_1 + D_x(x_2 - x_1)$$  \hspace{1cm} (10)
$$\frac{\partial x_2}{\partial t} = \omega(\theta_2)y_2 + D_x(x_1 - x_2)$$
$$\frac{\partial y_1}{\partial t} = -\omega(\theta_1)x_1 + D_y(y_2 - y_1)$$
$$\frac{\partial y_2}{\partial t} = -\omega(\theta_2)x_2 + D_y(y_1 - y_2),$$

will satisfy these conditions for $D_x = D, D_y = 0$ and

$$\omega = \omega_0 + \omega_1 \cos(\theta - \frac{\pi}{4}).$$  \hspace{1cm} (11)
each of the species) at the coexistence fixed point is $1/\lambda$ of the last stable orbit and is way too large to allow amplitude desynchronization (see [12]).

No such instability is present. Both cases were simulated for two opposite cases: no predator migration (where one should expect angular instability), and no prey diffusion, where via a noise term proportional to the square root of the population size. The results are presented in Figure 9, for the effect of amplitude-induced instability is suppressed by patches synchronization.

The amplitude synchronization prediction is that the oscillation radius scales like $D$ for large and small migration rates and is not based on a linear instability of an orbit. One may ask, thus, how to make a distinction of the angular velocity (see the upper right panel of Figure 1), works as well for system of equal prey and predator populations, so the "rod" completes its cycle in opposite "phase" (see Figure 7, right panel).

We now turn to our last point, a comparison of this stabilizing mechanism with the nonlinear, noise induced mechanism recently presented by us [12]. The stability mechanism of [12] involved with the amplitude dependence of the angular velocity (see the upper right panel of Figure 1), works as well for system of equal prey and predator migration rates and is not based on a linear instability of an orbit. One may ask, thus, how to make a distinction between these two mechanisms in real systems.

In order to make a distinction between amplitude-induced stability [12] and angular-induced stability [12] one should compare the corresponding radius of oscillations, where the dominant mechanism corresponds to the smaller radius. The amplitude synchronization prediction is that the oscillation radius scales like $D/(\omega')^2$, where $\omega' \equiv \partial \omega / \partial r$ is the frequency gradient along the oscillations amplitude (See Figure 1, upper right panel). This result should be compared with the instability radius of [12], and for small migration rates ($D \sim 0.01$) it is smaller in few orders of magnitude. It seems, thus, that the angular induced instability will be relevant only for relatively large diffusivities, where the effect of amplitude-induced instability is suppressed by patches synchronization.

In order to observe the phase instability, we have simulated the two-patch LV system, where the effect of demographic stochasticity, an intrinsic noise that should appear in any system independent of environmental factors, was introduced via a noise term proportional to the square root of the population size. The results are presented in Figure 9 for the two opposite cases: no predator migration (where one should expect angular instability), and no prey diffusion, where no such instability is present. Both cases were simulated for $\mu = \sigma = 1$, so the population (number of individuals in each of the species) at the coexistence fixed point is $1/\lambda$. The diffusion $D = 1$ corresponds to the smallest amplitude of the last stable orbit and is way too large to allow amplitude desynchronization (see [12]).

Fig. 9 clearly shows the stabilizing effect of angular-induced desynchronization. For small populations at the fixed point (large $\lambda$) the prey diffusion systems reach the absorbing state, while only predator diffusion stabilizes the inner
FIG. 7: An illustration of the trajectories of two diffusively-coupled patches, with slightly different initial conditions, projected on the invariant manifold. In the strong coupling case, (left panel) the strong predator diffusion forces the two points to be on the same vertical line (same predator concentration) along the orbit, hence the phase of the Floquet eigenvalue inverted twice along the trajectory, yielding a positive eigenvalue. In the small diffusion limit, the patches possess equal predator density only in the slow portion of the orbit, when the intra-patch dynamics is slow with regard to the migration. This leads to trajectories like those illustrated in the right panel (points connected by "rod" stand for the population density in equal times), where only one sign change happens and the Floquet eigenvalue is positive.

orbits. Large populations, though, may be stable in both regimes, but the instability cuts the tail of the distribution, leaving only a peak close to the "reflecting boundary."

To conclude, it has been shown that systems where only the predator admits the ability to migrate (a canonical examples include herbivore - plant or parasite insect - plant systems, like in the famous example of biological control of the Prickly Pear cactus by the moth Cactoblastis cactorum in eastern Australia [13]) may support sustained oscillations in noisy environments. This phenomenon has been explained here, and its cause was traced to the dependence of the angular velocity on the azimuthal angle along an orbit lying in the homogenous manifold. This insight allows us to incorporate that phenomenon into a generic framework of coupled nonlinear oscillators and to compare that mechanism with other stabilizing effects. In a separate publication [14], we intend to put forward a general classification scheme for stable population oscillations, a scheme that may be used to typify the observed desynchronization-induced stable manifold according to its underlying mechanism.

[1] Lotka A.J. Proc. Natl. Acad. Sci. USA 6, 410 (1920); Volterra V. Lecon sur la Theorie Mathematique de la Latte pour le vie, Gauthier-Villars, Paris, 1931; Murray J.D., Mathematical Biology (Springer, New-York, 1983).
[2] Gause G.F. The struggle for existence. William and Wilkins, Baltimore (1934); Pimentel D., Nagel W.P. and Madden J.L., American Naturalist, 97, 141 (1963); Huffaker C.B. Hilgardia 27 343 (1958).
[3] Nicholson, A.J., J. Anim. Ecol. 2, 132 (1933).
[4] Luckinbill L.S. Ecology 1142 (1974); Kerr B. et. al. Nature 442, 75 (2006); Holyoak M. & Lawler S.P. Ecology 77, 1867 (2000).
[5] Earn D.J.D., Levin S.A. and Rohani P. (2000) Science 290, 1360-1363; Blasius B., Huppert A. and Stone L. (1999) Nature 399, 354-359.
[6] See a recent review by Briggs C.J. and Hoopes M.F. Theoretical Population Biology 65, 299 (2004).
FIG. 8: Stability diagram in the $\omega_1 - D_x$ plane for the Floquet operator (same as Figure 3) for the coupled oscillator system described by Eqs. (10) with $D_y = 0$. The two unstable regions correspond to different signs of the Floquet unstable eigenvalue, as explained in the text.

FIG. 9: Histograms of the probability density as a function of $H$, for a two-patch LV system with only prey diffusion ($D_b = 1$, $D_a = 0$)(b) and only predator diffusion ($D_a = 1$, $D_b = 0$)(a). Both systems were subject to demographic stochasticity, modeled by a multiplicative noise proportional to the square root of the population density. In both cases, the probability density is concentrated around $H = 0$; however, Jansen’s instability manifests itself in the peak at the instability radius at the left panel, caused by the “reflection” from the unstable manifold (note the arrow that indicates the first unstable orbit). The log-log plots of that histogram (insets) show that the tail of the distribution is continuous at the right panel, but the probability to find the system with $H$ above the instability limit is practically zero. The LV parameters are $\mu = \sigma = 1$ and $\lambda = 10^{-5}$.

[7] Jansen, V.A.A. *Oikos* **74**, 384 (1995).
[8] Jansen V.A.A and de Roos A.M. In: *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, eds. Dieckmann U., Law R and Metz J.A.J., pp. 183 Cambridge University Press, (2000).
[9] Jansen V.A.A. and Sigmund K., Theo. Pop. Bio. **54**, 195 (1998).
[10] Gillespie D. T. *Jour. Phys. Chem.* **81**, 2340 (1977).
[11] See, e.g., Abarbanel H.D.I. *Analysis of observed chaotic data* Springer, Berlin (1995), p. 87.
[12] Abta R., Schiffer M. and Shnerb N.M., [cond-mat/0608108](http://arxiv.org/abs/cond-mat/0608108).
[13] Freeman D.B., Geographical Review **82**, 413 (1992).
[14] Abta R., Ben-Ishay A., Schiffer M. and Shnerb N.M., in preparation.