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# FAST OSCILLATING MIGRATIONS IN A PREDATOR-PREY MODEL

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The aim of this paper is to give a method which permits us to describe how individual properties can emerge at the population level, in population dynamics. We consider interacting populations. In order to take into account the spatial or behavioral heterogeneity, we subdivide each population into subpopulations. A given subpopulation corresponds to those individuals having the same behavior and who are in a homogeneous environment. Furthermore, we assume that the migration process is faster than the growth and interaction processes. Therefore, we must study models with many variables coupled together into large scaled differential systems. Firstly, our method permits us to reduce these complex systems into simpler ones, which will be called reduced systems. Secondly, these reduced systems give the population dynamics and contains informations about individuals' behavior. that is we can explain how individual dynamics emerge in the population dynamics. We already investigated the case where the fast dynamics reach an equilibrium in previous works. In this paper, we are interested in those models where the fast dynamics oscillates because it is ecologically relevant.

## 1. Introduction

Many authors have proposed reduction methods for complex systems in population dynamics (Refs. 2, 3, 5, 7, 11 and 12). Our approach is the same as the approach of Auger and Roussarie (Ref. 3). but in our case, the fast dynamics are assumed to reach a limit cycle instead of an equilibrium. In their paper, Auger and Roussarie use a central manifold theorem to reduce the complex global dynamics to a simpler one. Their model is of the same type as the model used in our paper: fast dynamics for the individual processes (change of environment or behavior) and slow dynamics for growth and interaction. These assumptions mean for instance that we consider populations where individuals change their behavior or their environment many times in a day, but the effect of growth and interaction (predation, competition, ...) are noticeable after a few weeks.

In many cases, the migrations are periodic. We can find examples in Ref. 14 about spatial distribution of fish and their prey: the authors explain that many species of aquatic animals undergo regular daily vertical movements in the water column. There are also examples for small mammals. Furthermore, the periodicity of migrations could be forced by the sun periodicity for instance. This means that we must consider models which depend explicitly on time (nonautonomous systems). We study in this paper both cases: autonomous and nonautonomous systems.

In the next section, we describe the reduction method. We apply it in Sec. 3, for a predator-prey model. In the last section, we show how our method permits individual properties to emerge to the population level. In order to see this emergence, we have chosen to construct a complex functional response from a Lotka–Volterra's one, in the same way as has been done in Ref. 15, in which the migrations reached an equilibrium.

## 2. Reduction Method

### 2.1. *The model*

We use the following notations: $n_i^\alpha$ is the density of subpopulation $i$ of population $\alpha$, $n^\alpha$ is the density of population $\alpha$, $A$ is the number of populations, and for $\alpha \in [1,\ldots,A]$, $N^\alpha$ is the number of subpopulations in $\alpha$. The general model that we use in this paper has the following form:

$$\frac{dn_i^\alpha}{dt} = Rf_i^\alpha(n_1^1,\cdots,n_{N^A}^A,t) + F_i^\alpha(n_1^1,\cdots,n_{N^A}^A), \tag{2.1}$$

where $R \gg 1$ is the scale factor, that is the part of Eq. (2.1) just near $R$ is the fast model (change of behavior or environment). The functions $f_i^\alpha$ and $F_i^\alpha$ are assumed $C^2$.

In order to reduce this global system, we will use theorems of perturbation theory, then we transform this system (2.1) in another form which is adapted to those theorems. First, we consider the frequencies of subpopulations:

$$u_i^\alpha = \frac{n_i^\alpha}{n^\alpha},\ i \in [1,\ldots,N^\alpha].\ \alpha \in [1,\ldots,A]. \tag{2.2}$$

For each population $\alpha$, we omit to consider the frequency $u_{N^\alpha}^\alpha$ because when we know $N^\alpha - 1$ frequencies, we know all of them. In this way, we only consider $k_N$ frequencies, with

$$k_N = \sum_{\alpha=1}^{A}(N^\alpha - 1).$$

Finally, putting $\varepsilon = 1/R$ and considering the new time $\tau$ such that $t = \varepsilon\tau$, we can rewrite system (2.1) with the new variables. We use vectorial notations. Let $\mathrm{n} = (n^1,\ldots,n^A)$ be the vector of global densities, and let $\mathrm{u} = (u_1^1,\ldots,u_{N^1-1}^1,\cdots,$

$u_1^A, \ldots, u_{N^A-1}^A$) be the vector of frequencies. System (2.1) can be written in the following form:

$$\begin{cases} \dfrac{d\mathbf{u}}{d\tau} = f(\mathbf{u}, \mathbf{n}, \varepsilon, \tau), \\ \dfrac{d\mathbf{n}}{d\tau} = \varepsilon g(\mathbf{u}, \mathbf{n}, \varepsilon), \\ \dfrac{d\varepsilon}{d\tau} = 0, \end{cases} \tag{2.3}$$

$\mathbf{u} \in \mathbb{R}^{k_1}$ and $\mathbf{n} \in \mathbb{R}^A$. Furthermore, $f$ and $g$ are at least $C^2$. We assume that for $\varepsilon = 0$, and for each $\mathbf{n}$, there is a limit cycle $\gamma_{\mathbf{n}}$ which is a strong attractor, in a way that will be precised later.

In a first step, we assume that $f$ does not explicitly depend on $\tau$, that is (2.3) has the following form:

$$\begin{cases} \dfrac{d\mathbf{u}}{d\tau} = f(\mathbf{u}, \mathbf{n}, \varepsilon), \\ \dfrac{d\mathbf{n}}{d\tau} = \varepsilon g(\mathbf{u}, \mathbf{n}, \varepsilon), \\ \dfrac{d\varepsilon}{d\tau} = 0. \end{cases} \tag{2.4}$$

In this case, we assume that for $\varepsilon = 0$, $\gamma_{\mathbf{n}}$ is hyperbolic and stable, that is the linear part of the Poincaré map defined near the limit cycle has eigenvalues such that each eigenvalue has a real part strictly less than 1. Using the following theorem (Ref. 18):

**Theorem 2.1.1.** *Let* $(\mathbf{u}_0, \mathbf{n}_0)$ *be an initial condition near* $\gamma_{\mathbf{n}_0}$, *the solution* $(\mathbf{u}(\tau), \mathbf{n}(\tau))$ *of system* (2.4) *stay in a* $\varepsilon$*-neighborhood of* $\gamma_{\mathbf{n}(\varepsilon\tau)}$ *after a time* $\tau_0 = O(|\ln(\varepsilon)|)$, *that is* $t_0 = O(\varepsilon|\ln(\varepsilon)|)$.

In a second step, we consider functions $f$ explicitly depending on $\tau$. In this case, we assume that:

- the limit cycle of the fast part ($\varepsilon = 0$) does not explicitly depend on time.
- each trajectory through an initial condition in a given compact is in a $\varepsilon$-neighborhood of a limit cycle $\gamma_{\mathbf{n}}$ after $\tau = O(\ln(\varepsilon))$.

Finally, in both autonomous and nonautonomous cases, trajectories starting in a given compact are in a $\varepsilon$-neighborhood of a limit cycle $\gamma_{\mathbf{n}}$ after a short time $t = O(\varepsilon \ln(\varepsilon))$.

## 2.2. *Reduction*

The reduction method is firstly founded on an averaging theorem. In order to apply this theorem, we need to transform systems (2.3) and (2.4), but the transformation is available in a neighborhood of the limit cycles $\gamma_{\mathbf{n}}$. As a consequence, we use the fact that in both autonomous and nonautonomous cases, trajectories are quick in such a neighborhood. Now, we describe explicitly the transformation. Let $\varphi \in [0, 2\pi]$ be a parametrization of $\gamma_{\mathbf{n}}$ for each $\mathbf{n}$ and let $\mathbf{z} \in \mathbb{R}^{k_1-1}$ be the transversal coordinates.

The limit cycle is $\{\mathbf{z}=\mathbf{0}\}$. After the substitution $\mathbf{u} \mapsto (\varphi, \mathbf{z})$, the system (2.3) becomes (Ref. 17):

$$\begin{cases} \dfrac{d\mathbf{z}}{d\tau} = a(\varphi, \mathbf{n}, \tau) \cdot \mathbf{z} + O(\|\mathbf{z}\|^2) + O(\varepsilon), \\ \dfrac{d\varphi}{d\tau} = \omega(\mathbf{n}) + O(\|\mathbf{z}\|) + O(\varepsilon), \\ \dfrac{d\mathbf{n}}{d\tau} = \varepsilon \cdot \bar{g}(\mathbf{z}, \varphi, \mathbf{n}, \varepsilon), \end{cases} \tag{2.5}$$

where $\omega(\mathbf{n}) \neq 0$.

From the second equality in (2.5), if $\|\mathbf{z}\| = O(\varepsilon)$ and if $\tau << \frac{1}{\varepsilon}$, then

$$\varphi(\tau) = \varphi_0 + \omega(\mathbf{n})\tau + O(\varepsilon).$$

As a consequence, if $\varphi_0 = 0$, we can consider the following change of variables:

$$\tau = \frac{\varphi}{\omega(\mathbf{n})} + O(\varepsilon).$$

It means that the time $\tau$ is proportional to the parameter $\varphi$ more or less a term near $\varepsilon$. Finally, we can now consider the nonautonomous case as the autonomous one.

Using $|\mathbf{z}| = O(\varepsilon)$, we can write (2.5) as follows:

$$\begin{cases} \dfrac{d\varphi}{d\tau} = \omega(\mathbf{n}) + \varepsilon \cdot f(\varphi, \mathbf{n}, \varepsilon). \\ \dfrac{d\mathbf{n}}{d\tau} = \varepsilon \cdot g(\varphi, \mathbf{n}, \varepsilon) + O(\varepsilon^2). \end{cases} \tag{2.6}$$

We will use an averaging theorem, that we can find in Ref. 1, and which is given below:

**Theorem 2.2.1.** *Assume the following perturbated differential system:*

$$\begin{cases} \dot{\varphi} = \omega(\mathbf{n}) + \varepsilon f(\mathbf{n}, \varphi, \varepsilon), \\ \dot{\mathbf{n}} = \varepsilon g(\mathbf{n}, \varphi, \varepsilon), \end{cases} \tag{2.7}$$

*where $f$ and $g$ are $2\pi$-periodic with respect to $\varphi$, and $\mathbf{n} \in D \subset \mathbb{R}^A$ and let the averaged equation be:*

$$\dot{\mathbf{p}} = \varepsilon G(\mathbf{p}) \text{ with } G(\mathbf{p}) = \frac{1}{2\pi} \int_0^{2\pi} g(\varphi, \mathbf{p}, 0) d\varphi. \tag{2.8}$$

*Assume that $\omega$ does not vanish in $\mathcal{D}$, and that the solution $\mathbf{p}(\tau)$ for the averaged equation stays in $\mathcal{D}$ during the time $t = T << 1$. With these assumptions, the distance between the solution of the averaged equation $\mathbf{p}(\tau)$ and the $\mathbf{n}$-coordinate of the solution of the perturbated differential system (2.7), with an initial condition $\mathbf{n}(0) = \mathbf{p}(0)$ stays near 0 during $\tau \in [0, \frac{T}{\varepsilon}]$, if $\varepsilon$ is small enough:*

$$\| \mathbf{n}(\tau) - \mathbf{p}(\tau) \| \leq C\varepsilon,$$

*where $C$ is independent of $\varepsilon$.*

In order to apply this theorem, we define the following function:

$$G(\mathbf{p}) = \frac{1}{2\pi}\int_0^{2\pi} g(\varphi, \mathbf{p}, 0)d\varphi \tag{2.9}$$

on a domain $\mathcal{D} \subset \mathbb{R}^A$. Now, we consider the system:

$$\frac{d\mathbf{p}}{d\tau} = \varepsilon G(\mathbf{p})\,. \tag{2.10}$$

From Theorem 2.2.1, there exist $T << 1$ and a constant $C$ such that:

$$\forall \tau \in [0, T/\varepsilon],\ \|\mathbf{n}(\tau) - \mathbf{p}(\tau)\| \leq C\varepsilon\,.$$

Finally, we have reduced the global system. The approximation for the solutions for both perturbated and averaged equations is available during a finite time. We explain now a method which permits to reduce the global dynamics, without the time limitation. This second process is founded on a central manifold theorem, and the dynamics obtained on the central manifold is exact: the problem of time limitation disappears.

As we have assumed that for each $\mathbf{n}$ when $\varepsilon = 0$, there exists a limit cycle $\gamma_{\mathbf{n}}$, we can define a Poincaré map $P_{\mathbf{n}}$ on a section $\Sigma_{\mathbf{n}}$ transversal with respect to $\gamma_{\mathbf{n}}$. Let $\Sigma$ be defined by:

$$\Sigma = \bigcup_{\mathbf{n}\in\Delta} \Sigma_{\mathbf{n}}\,,$$

where $\Delta$ is compact in $\mathbb{R}^A$. We can choose the transversal sections $\Sigma_{\mathbf{n}}$ such that $\Sigma$ is a smooth submanifold of $\mathbb{R}^{k_1} \times \mathbb{R}^A$, and the map $P : \Sigma \to P(\Sigma)$ is defined by: $P(\mathbf{u}, \mathbf{n}) = P_{\mathbf{n}}(\mathbf{u})$ for each $\mathbf{n} \in \Delta$.

Let $\varepsilon_0$ be a positive real in a 0-neighborhood. We take note of the time $\tilde{T}_{\varepsilon_0}(\mathbf{u}, \mathbf{n})$ for it to return to $\Sigma$ when starting from $\Sigma$. We consider the following diffeomorphism:

$$\begin{aligned} F : \Sigma \dot{\times} [-\varepsilon_0, \varepsilon_0] &\longrightarrow F(\Sigma \times [-\varepsilon_0, \varepsilon_0])\,, \\ (\mathbf{u}_0, \mathbf{n}_0, \varepsilon) &\longmapsto (\mathbf{u}(\tilde{T}_\varepsilon(\mathbf{u}_0, \mathbf{n}_0)), \mathbf{n}(\tilde{T}_\varepsilon(\mathbf{u}_0, \mathbf{n}_0)), \varepsilon)\,. \end{aligned} \tag{2.11}$$

As we have seen before, all trajectories starting in a given compact of $\mathbb{R}^{k_1} \times \mathbb{R}^A$ early jump in a $\varepsilon$-neighborhood $\mathcal{U}$ of the union of limit cycles $\gamma_{\mathbf{n}}$ for all $\mathbf{n} \in \Delta$. In $\mathcal{U}$, we consider again the change of coordinates $\mathbf{u} \mapsto (\mathbf{z}, \varphi)$. With the new coordinates, we can assume that the equation of $\Sigma$ is $\{\varphi = 0\}$.

It is clear that $\mathcal{M} = \{\mathbf{0}\} \times \mathbb{R}^A \times \{0\}$ is a set of fixed points of $F$. For each $\mathbf{n} \in \mathbb{R}^A$, we define $DF(\mathbf{n})$ as the linear part of $F$ at $(\mathbf{0}, \mathbf{n}, 0) \in \mathcal{M}$. We have assumed that $\gamma_{\mathbf{n}}$ is hyperbolic and stable, then $DF(\mathbf{n})$ has $k_1 - 1$ eigenvalues of modulus less than 1, and 1 is an eigenvalue with multiplicity $A + 1$. We define $E^c_{\mathbf{n}}$ as the eigenspace associated with 1 (it is called the central space). With these notations, we use the following theorem (Refs. 4, 6, 10 and 13):

**Theorem 2.2.2.** *For all compact $\Delta \subset \mathbb{R}^A$ and for all natural integers $K$, there exists a positive real $\varepsilon_0$ and a $C^K$-map $\mathbf{h} : \Delta \times [-\varepsilon_0, \varepsilon_0] \to \mathbb{R}^{k_1}$, such that:*

(i) $\mathbf{h}(\mathbf{n}, 0) = \mathbf{0}$,
(ii) *the graph* $\mathcal{W}$ *of* $\mathbf{h}$ *is tangent to* $E^c_{\mathbf{n}}$, *for all* $\mathbf{n} \in \mathcal{M}$
(iii) $\mathcal{W}$ *is invariant by* $F$.

In the new system of coordinates $(\mathbf{z}, \varphi)$, it is easy to see that the diffeomorphism $F$ can be written as follows:

$$F : \Sigma \times [-\varepsilon_0, \varepsilon_0] \longrightarrow F(\Sigma \times [-\varepsilon_0, \varepsilon_0]),$$

$$(\mathbf{z}_0, \mathbf{n}_0, \varepsilon) \longmapsto (\mathbf{z}(\bar{T}_\varepsilon(\mathbf{z}_0, \mathbf{n}_0)), \mathbf{n}_0 + O(\varepsilon), \varepsilon),$$

where $\bar{T}_\varepsilon$ is the composition of the change of coordinates $\mathbf{u} \mapsto (\mathbf{z}, \varphi)$ and $\tilde{T}_\varepsilon$. The linear part of $F$ is:

$$DF(\mathbf{n}_0) = \begin{pmatrix} \frac{DF}{D\mathbf{z}}(0, \mathbf{n}_0, 0) & * & * \\ \mathbf{0} & 1 & * \\ 0 & 0 & 1 \end{pmatrix}. \tag{2.12}$$

The hypothesis of Theorem 2.2.2 can be verified. As a consequence, there exists a central manifold, on which the dynamics is exact, and is given by the following formula:

$$\phi : \Delta \times [-\varepsilon_0, \varepsilon_0] \longrightarrow \phi(\Delta \times [-\varepsilon_0, \varepsilon_0]),$$
$$(\mathbf{n}_0, \varepsilon) \longmapsto (\mathbf{n}(\bar{T}_\varepsilon(\mathbf{h}(\mathbf{n}_0, \varepsilon), \mathbf{n}_0), \varepsilon). \tag{2.13}$$

This diffeomorphism leaves the variable $\varepsilon$ invariant, we then write it as $\phi_\varepsilon$, that is we have a family of diffeomorphisms with one parameter $\varepsilon$. Finally, we have:

$$\begin{aligned} \phi_\varepsilon(\mathbf{n}) &= \mathbf{n} + \int_0^{\bar{T}_\varepsilon(\mathbf{h}(\mathbf{n},\varepsilon),\mathbf{n})} \frac{d\mathbf{n}}{d\tau} d\tau \\ &= \mathbf{n} + \varepsilon \int_0^{T_\varepsilon(\mathbf{n})} \bar{g}(\mathbf{h}(\mathbf{n}(\tau), \varepsilon), \varphi(\tau), \mathbf{n}(\tau), 0) d\tau + O(\varepsilon^2) \\ &= \mathbf{n} + \varepsilon \int_0^{T_\varepsilon(\mathbf{n})} \bar{g}(\mathbf{0}, \varphi(\tau), \mathbf{n}(\tau), 0) d\tau + O(\varepsilon^2). \end{aligned} \tag{2.14}$$

By construction, we also have

$$\omega(\mathbf{n}) \cdot T_\varepsilon(\mathbf{n}) = 2\pi$$

and (2.14) gives

$$\phi_\varepsilon(\mathbf{n}) = \mathbf{n} + \varepsilon \int_0^{2\pi} \frac{g(\varphi, \mathbf{n}, 0)}{\omega(\mathbf{n})} d\varphi + O(\varepsilon^2). \tag{2.15}$$

This diffeomorphism gives the global dynamics for every time. The problem is that now we have to study discrete dynamics, and it is more difficult than the study of continuous dynamics.

We will now compare both methods, in order to show that in some cases, the averaging method is available for every time. It is necessary to discretize the dynamics obtained by the averaging method. This discretization gives:

$$\begin{aligned}\bar{\phi}_\varepsilon(\mathbf{n}) &= \mathbf{n} + \varepsilon \int_0^{T_\varepsilon(\mathbf{n})} G(\mathbf{n}(\tau))d\tau + O(\varepsilon^2) \\ &= \mathbf{n} + \frac{\varepsilon}{2\pi} \int_0^{T_\varepsilon(\mathbf{n})} \int_0^{2\pi} g(\varphi, \mathbf{n}(\tau), 0)d\varphi d\tau + O(\varepsilon^2)\,. \end{aligned} \tag{2.16}$$

For all $\mathbf{n} \in \Delta$, $T_\varepsilon(\mathbf{n})$, which is the period of $\gamma_{\mathbf{n}_0}$, is much less than $1/\varepsilon$, and then, for all $\tau \in [0, T_\varepsilon(\mathbf{n}(0))]$, we have:

$$\mathbf{n}(\tau) = \mathbf{n}(0) + O(\varepsilon)$$

and we note $\mathbf{n} = \mathbf{n}(0)$. From (2.16), we have:

$$\begin{aligned}\bar{\phi}_\varepsilon(\mathbf{n}) &= \mathbf{n} + \frac{\varepsilon}{2\pi} \int_0^{T_\varepsilon(\mathbf{n})} \int_0^{2\pi} g(\varphi, \mathbf{n}, 0)d\varphi d\tau + O(\varepsilon^2) \\ &= \mathbf{n} + \frac{\varepsilon}{2\pi} \left(\int_0^{T_\varepsilon(\mathbf{n})} d\tau\right)\left(\int_0^{2\pi} g(\varphi, \mathbf{n}, 0)d\varphi\right) + O(\varepsilon^2) \\ &= \mathbf{n} + \frac{\varepsilon}{2\pi} \left(\int_0^{2\pi} \frac{1}{\omega(\mathbf{n})} d\varphi\right)\left(\int_0^{2\pi} g(\varphi, \mathbf{n}, 0)d\varphi\right) + O(\varepsilon^2) \\ &= \mathbf{n} + \frac{\varepsilon}{\omega(\mathbf{n})} \int_0^{2\pi} g(\varphi, \mathbf{n}, 0)d\varphi + O(\varepsilon^2)\,. \end{aligned}$$

We can now conclude that

$$\bar{\psi}_\varepsilon = \psi_\varepsilon + O(\varepsilon^2)\,.$$

It means that the diffeomorphism obtained by discretization of the averaged dynamics is a perturbation of the dynamics obtained on the central manifold. As a consequence, if the dynamics obtained on the central manifold is structurally stable, then the dynamics obtained by the averaging method is available for every time.

## 3. Application

We consider in this section, a predator-prey system in which each population is subdivided into two subpopulations. Each subpopulation for a given population is associated to a spatial patch. We assume that individuals migrate quickly between the patches. The interactions predators-preys are assumed to follow the Mass Action Law (Ref. 16) in each patch, that is the interaction is proportional to the number of encounters. It is relevant because the subpopulations are assumed to be

homogeneous. We propose the following model:

$$\begin{cases} \dfrac{dn_1}{d\tau} = k_{12}^N n_2 - k_{21}^N n_1 + \varepsilon r.n_1\left[1 - b_1.p_1\right], \\ \dfrac{dn_2}{d\tau} = k_{21}^N n_1 - k_{12}^N n_2 + \varepsilon r.n_2\left[1 - b_2.p_2\right], \\ \dfrac{dp_1}{d\tau} = k_{12}^P p_2 - k_{21}^P p_1 - \varepsilon p_1\left[\mu - e.b_1.n_1\right], \\ \dfrac{dp_2}{d\tau} = k_{21}^P p_1 - k_{12}^P p_2 - \varepsilon p_2\left[\mu - e.b_2.n_2\right], \end{cases} \tag{3.1}$$

where $k_{ij}^N$ and $k_{ij}^P$ are functions defined as follows:

$$\begin{cases} k_{12}^N = a - (r_1\omega + r_2)\sin(\omega\tau) + (r_1 - r_2\omega)\cos(\omega\tau), \\ k_{21}^N = 1 - a + (r_1\omega + r_2)\sin(\omega\tau) - (r_1 - r_2\omega)\cos(\omega\tau), \\ k_{12}^P = b - (r_1\omega - r_2)\sin(\omega\tau) + (r_1 + r_2\omega)\cos(\omega\tau), \\ k_{21}^P = 1 - b + (r_1\omega - r_2)\sin(\omega\tau) - (r_1 + r_2\omega)\cos(\omega\tau), \end{cases} \tag{3.2}$$

and $a$, $r_i$ and $\omega$ could be functions of the global densities $(n, p)$. $k_{ij}^\alpha$ is the rate of subpopulation $j$ of population $\alpha$ going in subpopulation $j$ of population $\alpha$ at any moment. Expressions (3.2) mean that the fast process oscillates, that is individuals change their behavior or their environment regularly in the day. $\omega$ is then the frequency of these changes. We can calculate the solutions of the fast dynamics defined by (3.1) and $\varepsilon = 0$. These solutions are:

$$\begin{cases} u_1(\tau) = a + r_1\cos(\omega\tau) - r_2\sin(\omega\tau) + R_1(\tau), \\ v_1(\tau) = b + r_1\cos(\omega\tau) + r_2\sin(\omega\tau) + R_2(\tau), \end{cases} \tag{3.3}$$

$R_i(\tau)$ exponentially reach to 0, that is if $\tau > |\ln(\varepsilon)|$ then there exist constants $M_i$ such that: $R_i(\tau) < M_i\varepsilon$ for $i = 1, 2$.

This means that the frequencies $(u_1 = \dfrac{n_1}{n_1 + n_2}, v_1 = \dfrac{p_1}{p_1 + p_2})$ quickly reach an ellipse which is centered at $(a^2, b^2)$.

In order to apply the method described in Sec. 2, we perform a change of coordinates: $(u_1, v_1) \mapsto (z, \varphi)$, that is we consider:

$$\begin{cases} u_1 = a + r_1\cos(\varphi) - r_2\sin(\varphi). \\ v_1 = b + r_1\cos(\varphi) + r_2\sin(\varphi). \end{cases} \tag{3.4}$$

The functions $a$, $b$, $r_i$ and $\omega$ must then be chosen such that the expressions given by (3.4) are available, that is $u_1 \in [0, 1]$ and $v_1 \in [0, 1]$.

If $\varepsilon \neq 0$, it is clear that:

$$\begin{cases} \cos(\varphi) = \cos(\omega\tau) + O(\varepsilon). \\ \sin(\varphi) = \sin(\omega\tau) + O(\varepsilon). \end{cases} \tag{3.5}$$

Furthermore, a straightforward computation gives:

$$\begin{cases} \dfrac{dn}{d\tau} = \varepsilon r.n\left[1 - (b_1u_1v_1 + b_2u_2v_2)p\right] = \varepsilon g_1(\varphi, n, p, \varepsilon), \\ \dfrac{dp}{d\tau} = -\varepsilon p\left[\mu - e(b_1u_1v_1 + b_2u_2v_2)n\right] = \varepsilon g_2(\varphi, n, p, \varepsilon), \end{cases} \tag{3.6}$$

with $u_2 = 1 - u_1$ and $v_2 = 1 - v_1$. We will now apply the averaging theorem. Let us consider:

$$G_i(n,p) = \frac{1}{2\pi}\int_0^{2\pi} g_i(\varphi, n, p, 0)d\varphi\,.$$

Using (3.6) and the following formulas, obtained with (3.4) and (3.5), we get the reduced dynamics.

$$\begin{cases} u_1 = a + r_1\cos(\varphi) - r_2\sin(\varphi) + O(\varepsilon)\,, \\ v_1 = b + r_1\cos(\varphi) + r_2\sin(\varphi) + O(\varepsilon)\,. \end{cases} \tag{3.7}$$

Finally, the global dynamics are the following:

$$\begin{cases} \dfrac{dn}{dt} = rn(1 - \tilde{b}p)\,, \\ \dfrac{dp}{dt} = -p(\mu - e\tilde{b}n)\,, \end{cases} \tag{3.8}$$

with

$$\tilde{b} = b_2(1 - (a+b)) + (b_1 + b_2)\Big(ab + \frac{(r_1)^2 - (r_2)^2}{2}\Big)\,.$$

## 4. Functional Response: An Example

We easily observe that the last system is a Lotka–Volterra system if $\tilde{b}$ is a constant. On the other hand, if $\tilde{b}$ is $(n,p)$-dependent, which is possible because $a$, $b$, $r_i$ and $\omega$ could be $(n,p)$-dependent, then the global dynamics are not a Lotka–Volterra system: there emerge properties from the individuals' level to the population level.

In the previous application, we have assumed that the local dynamics follow the Mass Action Law, and it results in new dynamics at the global level. We use this example to construct a functional response which is not of Lotka–Volterra type.

We recall that the functional response for a predator-prey system (Refs. 8, 9 and 15) is the number of preys catched per predator and per unit time. This means that the local functional response of our model is proportional to $n$ (a Lotka–Volterra's functional response), on each patch. If the migration rates are $(n,p)$-dependent, then we show that the global functional response is more complex than the Lotka–Volterra's one. Let us assume that patch 2 is a refuge for the prey, that is $b_2 = 0$, and for the sake of simplicity, we also assume that $r_1 = r_2$, which is relevant in an ecological point of view. In this case, we can simplify the expression for $\tilde{b}$:

$$\tilde{b} = b_1(ab)\,.$$

If $a$ and $\omega$ are constant, and $b = \frac{1}{1+\alpha n}$, then the functional response of the global system is of the following form:

$$FR(n) = \frac{\beta n}{1 + \alpha n}\,.$$

It is known as the Holling functional response (Ref. 9). The main goal of our work is to bring to light that the method permits us to use local properties to give a global description of the population dynamics. However, we give a quick interpretation of the theoretical example of this Holling functional response: if $n$ increases then $b$ decreases, this means that the number of predators foraging (on patch 1) decreases. We can for instance interpret this fact as a physiological saturation of the predator.

We can also remark that a small change of $\omega$ (which could be modified by the slow dynamics because it could be $(n,p)$-*dependent*) is translated in a big change of $\tilde{b}$. It would be interesting to investigate in this direction from a biological viewpoint. It would explain what is the effect of the fast frequency on the global dynamics. It will be the aim of future work.

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