Phase Space Formulation of Population Dynamics in Ecology

Jesús Martínez-Linares
Departamento de Física Aplicada II. Universidad de Sevilla.
41012-Seville, Spain.
(Dated: May 26, 2007)

A phase space theory for population dynamics in Ecology is presented. This theory applies for a certain class of dynamical systems, that will be called $\mathcal{M}$-systems, for which a conserved quantity, the $\mathcal{M}$-function, can be defined in phase space. This $\mathcal{M}$-function is the generator of time displacements and contains all the dynamical information of the system. In this sense the $\mathcal{M}$-function plays the role of the hamiltonian function for mechanical systems. In analogy with Hamilton theory we derive equations of motion as derivatives over the resource function in phase space. A $\mathcal{M}$-bracket is defined which allows one to perform a geometrical approach in analogy to Poisson bracket of hamiltonian systems. We show that the equations of motion can be derived from a variational principle over a functional $J$ of the trajectories. This functional plays for $\mathcal{M}$-systems the same role than the action $S$ for hamiltonian systems. Finally, three important systems in population dynamics, namely, Lotka-Volterra, self-feeding and logistic evolution, are shown to be $\mathcal{M}$-systems.

Conservation of energy modeled by differential geometry is the cornerstone of the phase space formulation of classical mechanics [1]. There exist a wide machinery of analytical methods developed during the past two centuries for such systems [2]. For instance, the Hamilton formalism resorts on a Hamiltonian function defined on phase space which contains all the dynamical information of the system. Once specified, we can generate upon differentiation equations of motion for the system.

The situation is much more precarious in population dynamics in Ecology. Ecological systems are overwhelmingly complex systems [3]. However, in some cases they can be described by simplified phenomenological rate equations that describes the net effect of the environment and the interaction between densities of species [4]. However, a systematic approach allowing one to derive equations of motion from general principles is still lacking. The present paper is a step towards this goal. In fact, in some cases a mutual resource function is conserved and keep constant during the evolution of the interacting species. The question is then, can be developed a phase space formalism that expresses the conservation of this quantity?

We show in this paper that there exist a wide class of systems in ecology, that will be called $\mathcal{M}$-systems, for which population dynamics can be described by a phase space theory analogous to the hamiltonian formulation of classical mechanics. We exploit this analogy in order to use the elaborated analytical methods developed for the latter. Hamilton function, Poisson bracket, variational principles, action functional and Lagrangian, all of them useful tools for hamiltonian systems will find their counterparts in the theory.

Finally, we show that three important system in population ecology are $\mathcal{M}$-systems. They are the Lotka-Volterra predator-prey system, the self-feeding interaction and the logistic evolution. These systems are also applied in many other disciplines outside ecosystems, which sets forth the wide range of applications of the $\mathcal{M}$-system formalism.

We start with the definition of $\mathcal{M}$-systems. A $\mathcal{M}$-system is a dynamical system defined by a given resource function $\mathcal{M}(q,p,t)$, and equations of motions given by

\begin{align}
\dot{q} &= qp \frac{\partial \mathcal{M}}{\partial p}, \\
\dot{p} &= -qp \frac{\partial \mathcal{M}}{\partial q}.
\end{align}

Not every conceivable motion in phase space $\Gamma = (q,p)$ is a $\mathcal{M}$-dynamical system. In order to obtain a necessary condition let us consider the generic dynamical system

\begin{align}
\dot{q} &= g_1(q,p), \\
\dot{p} &= g_2(q,p),
\end{align}

where $g_1, g_2 \in \mathcal{F}(\Gamma)$ are two arbitrary functions in phase space. The existence of a continuous $\mathcal{M}$-function requires

\[ \frac{\partial^2 \mathcal{M}}{\partial q \partial p} = \frac{\partial^2 \mathcal{M}}{\partial p \partial q}. \]

Eq. (3), together with (1) and (2) yields

\[ g_1 \frac{1}{q} + g_2 \frac{1}{p} = \frac{\partial g_1}{\partial q} + \frac{\partial g_2}{\partial p}, \]

which is a necessary condition for the dynamical system (2) to be a $\mathcal{M}$-system. If this is the case we say that $g_1, g_2$ are the components of a $\mathcal{M}$-vector field.

According to Eq. (1), the resource function $\mathcal{M}$ characterizes the dynamics of the system. The $\mathcal{M}$-systems are not hamiltonian systems, since they do not obey the hamiltonian canonical equations of motion. However, they possess a close relationship with each other. In fact, consider the change of variables

\begin{align}
q' &= \ln(q/\sigma), \\
p' &= \ln(p/\xi),
\end{align}

PACS numbers: 87.23.Cc 87.10.+e 87.23.-n
where \( \sigma, \xi \) are two positive constants. Using Eqs. \([1]\) it is easy to check that they obey the hamilton canonical equations \([1]\)

\[
\dot{q}' = \frac{\partial H}{\partial p'}, \\
\dot{p}' = -\frac{\partial H}{\partial q'},
\]

where \( H(q', p') = M(q(q'), p(p')) \) is the hamiltonian function. Thus, Eqs. \([6]\) allows one to construct an associated \( M \)-system starting from a generic hamiltonian system. Conversely, note that these relations comprise the Hamilton phase space \( \Lambda = \mathbb{R}^2 \) into the first octant \( \mathbb{R}^2_+ = (q, p, q, p \geq 0) \). Thus, the class of \( M \)-system on \( \Gamma = \mathbb{R}^2 \) has an associated hamiltonian system on \( \Lambda \). We will discuss later the importance of this system subclass in ecology and game theory.

For many dynamical systems \( H \) gives their mechanical energy \( E \). The resource function \( M \) play for \( M \)-systems the same role than the function \( H \) for hamiltonian systems. In order to see this, we introduce a geometrical approach analogous to the Poisson bracket of hamiltonian system. The Poisson bracket (PB) is defined as \([1]\)

\[
\{f, g\}_{PB} = (\partial_j f) \Omega^{jk}(\partial_k g)
\]

where \( f, g \in \mathcal{F}(\Gamma) \) are two arbitrary functions on phase space, \( \Omega \) is the symplectic matrix

\[
\Omega = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix},
\]

and we have defined the derivative operators \( \partial_i \equiv \frac{\partial}{\partial q^i} \), \( \partial_i q \). We follow the Einstein rule of summation over repeated indexes. In terms of the PB, Eqs. \([6]\) can be written as

\[
\dot{\eta}_i = \{\eta_i, H\}_{PB}.
\]

Moreover, the evolution of any dynamical variable \( f(q, p; t) \in \Gamma \) is given by

\[
\frac{df}{dt} = \{f, H\}_{PB} + \frac{\partial f}{\partial t}.
\]

According to \([10]\), \( H \) is the generator of time displacements of the system. Due to the antisymmetry of the PB, the time evolution of the hamiltonian is \( \dot{H} = \frac{\partial H}{\partial t} \). This reflects the conservation of energy for time-independent hamiltonian systems.

We now define the \( M \)-bracket (MB) as

\[
[f, g]_{MB} = (\partial_j f) \Omega^{jk}(\partial_k g),
\]

where we have defined the derivative operators \( \partial_j \equiv \frac{\partial}{\partial M(q)} \). It can be shown that MB (as the PB) is bilinear, antisymmetric and satisfies the Jacobi identity. These are the defining properties of a Lie algebra \([5]\). The function space \( \mathcal{F}(\Gamma) \) is a Lie algebra under the action of the MB. MB also satisfies the product rule

\[
[f, gh]_{MB} = [f, g]_{MB}h + g[f, h]_{MB}.
\]

Thus, MB is a kind of derivative operator \([6]\). As a matter of fact, Eqs. \([1]\) can be recast in terms of the MB as

\[
\dot{\eta}_i = \{\eta_i, M\}_{MB}.
\]

The function \( M \in \mathcal{F}(\Gamma) \) is the generator of time displacements on the system, since the time derivative of any dynamical variable \( f \) along the motion is

\[
\frac{df}{dt} = [f, M]_{MB} + \frac{\partial f}{\partial t}.
\]

In particular, choosing \( M = f \) we obtain \( \dot{M} = \frac{\partial M}{\partial t} \), i.e., the resource function of the system is conserved if it does not depend explicitly on time. The equation \( M(q, p) = R \) for \( M \)-systems plays the same role than the equation \( H(q, p) = E \) for hamiltonian systems.

Hamiltonian systems admit a variational formulation. In fact, dynamical systems in classical mechanics minimize the action functional \([11]\)

\[
S = \int_{t_o}^{t_1} L(q(t), \dot{q}(t), t) \, dt
\]

where \( L \) is the Lagrangian function of the system

\[
L = p' \dot{q}' - H
\]

It can be shown \([11]\) that Hamilton canonical equations given in \([6]\) can be derived from the variational principle \( \delta S = 0 \). With the help of Eqs. \([5]\), we can now construct a variational principle for the associated \( M \)-system. To this end we define the \( M \)-Lagrangian

\[
\mathcal{L} = \frac{\dot{q}}{q} \ln(p/\xi) - M,
\]

and the \( M \)-Action

\[
\mathcal{J} = \int_{t_o}^{t_1} \mathcal{L} \, dt.
\]

It is easy to check \([11]\) that the imposition of the extreme condition to the \( M \)-Action, i.e., \( \delta \mathcal{J} = 0 \), renders the canonical equations of motion for \( M \)-systems given in Eqs. \([1]\). Thus, among all the possible trajectories that a \( M \)-system could undertake, the actual motion \( (q(t), p(t)) \) is the one that makes Eq. \([18]\) minimal, i.e., \( \delta \mathcal{J} = 0 \), where \( \delta \mathcal{J} \) is the variation of \( \mathcal{J} \) over different trajectories connecting \( (q(t_o), p(t_o)) \) and \( (q(t_1), p(t_1)) \).
amount of ambiguity [8]. As a matter of fact, we can construct \( \mathcal{L} \) in the form
\[
\mathcal{L} = \dot{q} \alpha + \dot{p} \beta - \mathcal{M},
\]
where \( \alpha(q, p), \beta(q, p) \) are generic functions in phase space (dynamical variables) satisfying
\[
\frac{\partial \beta}{\partial q} = -\frac{1}{qp} + \frac{\partial \alpha}{\partial p}.
\]

The main goal of population dynamics is to describe the evolution of the population of different species interacting in an ecological system. We show now that \( \mathcal{M} \)-systems comprises a wide class of important system in ecology. Let us start with the Lotka-Volterra (LV) model [9] describing an ecological predator-prey (or parasite-host) system. The LV two-species model is given by the equations
\[
\begin{align*}
\frac{dU}{dt} &= (a_1 - b_1 V) U, \\
\frac{dV}{dt} &= (-a_2 + b_2 U) V,
\end{align*}
\]
where \( a_1 \) is the the growth rate of prey \( U \), \( b_1 \) the rate at which predators \( V \) destroy the prey, \( a_2 \) the the death rate of predators and \( b_2 \) the rate at which predators increase by consuming prey. We take the adimensional variables proposed by Hsu [11]
\[
q = \frac{b_2}{a_2} U, \quad p = \frac{b_1}{a_2} V, \quad \tau = a_2 t, \quad \xi = \frac{a_1}{a_2},
\]
to reduce the Lotka-Volterra (LV) system to
\[
\begin{align*}
\frac{dq}{d\tau} &= (\xi - p) q, \\
\frac{dp}{d\tau} &= (q - 1) p.
\end{align*}
\]

In spite of non-linearity of the equations of motion given in (23) an analytical solution is possible, namely,
\[
q p^\xi = e^{R + \tau + p},
\]
where \( R \) is an integration constant. This takes us to define
\[
\mathcal{M} = \xi \ln p - p + \ln q - q,
\]
which \( \mathcal{M} \) is \( R \) a constant of motion. Moreover, it can be rapidly checked that the insertion of (25) into Eqs. (1) yields the LV equations given in (23). Thus LV is a \( \mathcal{M} \)-dynamical system.

This ecological interpretation of the \( \mathcal{M} \)-function as a mutual abstract resource shared by the interacting species is enforced by considering a simple self-feeding system, modeled by the equations of motion
\[
\begin{align*}
\dot{q} &= qp, \\
\dot{p} &= -qp.
\end{align*}
\]
consider direct disease transmission [11] in a total population of \( q + p \) individuals where \( q \) are the number of infected individuals and \( p \) the number of individuals who are susceptible of infection. In this simple system there is an obvious conserved quantity: the total population given by the initial condition \( R = q_o + p_o \). \( R \) can be interpreted as a mutual global resource being distributed between the "interacting species" \( q \) and \( p \) that remains conserved during the process. The corresponding \( \mathcal{M} \)-function is then
\[
\mathcal{M} = q + p.
\]
In fact, it can be checked rapidly that the equations of motion (26) are obtained by inserting (27) into Eqs. (1).

Consider now the \( \mathcal{M} \)-function for a two-species Malthusian system
\[
\mathcal{M} = -\gamma \ln q + k \ln p,
\]
where \( q = q_o e^{k t}, \) \( p = p_o e^{\gamma t} \). Consider now the coupling
\[
\mathcal{M} = -\gamma \ln q + k \ln p - \mu q \ln \frac{p}{p_s},
\]
where \( p_s \geq p_o \) is a saturation constant. The canonical equations of motion given in Eqs. (1) equipped with (29) yield
\[
\begin{align*}
\dot{q} &= kq - \mu q^2, \\
\dot{p} &= \gamma p + \mu qp \ln \left( \frac{p}{p_s} \right).
\end{align*}
\]
Eq. (30) defines logistic evolution, where \( k \) is the growing rate for the population \( q \). The mortality rate \( \mu q \) is density dependent, making the logistic evolution a simple model to describe the phenomena of saturation of population growth in time [15 16].

Now we turn to the analysis of Eq. (31). Remarkably, Eqs. (30) and (31) have both analytical solutions. \( p \) is the amount of food supply feeding the system, and thus being depleted by \( q \). We take \( \gamma = 0 \) and the change of variables \( q = \overline{q} e^{kt}, \) \( p = p_o e^{\gamma t} \), and \( \overline{q} = q/q_o \) where \( q_o \) is the saturation value \( q_o = k/\mu \). Eqs. (30)-(31) reads now
\[
\begin{align*}
\frac{d\overline{q}}{d\tau} &= \overline{q}(1 - \overline{q}), \\
\frac{d\overline{p}}{d\tau} &= \overline{q} \overline{p} \ln \overline{p}.
\end{align*}
\]
An analytical solution of Eqs. (32)-(33) can be found in the form
\[
\begin{align*}
\overline{q} &= \frac{e^\tau}{e^\tau - 1 + \frac{1}{q_o}}, \\
\overline{p} &= \exp \left[ \alpha \left( e^\tau - 1 + \frac{1}{q_o} \right) \right],
\end{align*}
\]
where \( \alpha \leq 0 \) is an integration constant fixing \( \overline{p}_o = e^{\alpha/q_o} \). Therefore, \( \alpha \) depends on the distance between \( p_o \) and \( p_s \).
It is easy to check that the solutions obtained make \( M \) constant in time.

The solution \([35]\) has two stationary limits, \( p = p_s \) and the asymptotic limit \( p = 0 \), since both limits make the right hand side of Eq. \([33]\) vanish. They correspond to \( \alpha = 0 \) and \((\alpha < 0, \tau \to \infty)\), respectively. The parameter \( \alpha \) measures how fast the food supply is depleted; giving the width of the decay as \( \Delta = \ln(1 - 1/\alpha) \). This is shown in Fig. 1 where Eqs. \([34]\) and \([35]\) are plotted for \( \alpha = -0.03 \).

An explicit form of \( \bar{p} \) as a function of \( \bar{q} \) can be obtained after elimination of the time variable between Eqs. \([34]\) and \([35]\), namely

\[
\bar{p} = e^{-D/(1-\bar{q})},
\]

where \( D = \alpha(1-1/\bar{q}_0) \). The above equation provide us of the phase space of the system.

The analogy between \( M \)-systems and hamiltonian systems can be exploited further. In this paper, a geometrical approach has been developed based in the introduction of a \( M \)-bracket which, as the Poisson bracket of hamiltonian systems, has the structure of a Lie algebra. The \( M \)-bracket establishes a bridge than can be used to generalize the breadth of analytical methods in phase space developed for the Poisson bracket \([2]\) (Noether theorem connecting symmetry and conservation laws, Liouville theorem establishing conservation in time of phase space volume for ensembles, etc).

The author thanks ecologists Antonio Pérez and F. García Novo for pointing out some helpful bibliography. J.M-L is supported by a Return Program from the Consejería de Educación y Ciencia de la Junta de Andalucía in Spain.

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