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Collective observables in repeated experiments of population dynamics

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Abstract. We here discuss the outcome of an hypothetical experiments of populations dynamics, where a set of independent realizations is made available. The importance of ensemble average is clarified with reference to the registered time evolution of key collective indicators. The problem is here tackled for the logistic case study. Theoretical prediction are compared to numerical simulations.

1. Introduction

The problem of explaining the emergence of self-organized, macroscopic, patterns from a limited set of rules governing the mutual interaction of a large assembly of microscopic actors, is often faced in several domains of physics and biology. This challenging task defines the realm of complex systems, and calls for novel paradigms to efficiently intersect distinct expertise.

Population dynamics has indeed attracted many scientists [1] and dedicated models were put forward to reproduce *in silico* the change in population over time as displayed in real ecosystems (including humans). Two opposite tendencies are in particular to be accommodated for. On the one hand, microscopic agents do reproduce themselves with a specific rate r , an effect which translates into a growth of the population size P . On the other, competition for the available resources (and death) yields a compression of the population. In a seminal work by Verhulst [2], these ingredients were formalized in the differential equation:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K}\right). \quad (1)$$

K is the so called carrying capacity and identifies the maximum allowed population for a selected organism, under specific environmental conditions. The above model predicts an early exponential growth, which is subsequently antagonized by the quadratic contribution, responsible for the asymptotic saturation. The adequacy of the Verhulst's model was repeatedly tested versus laboratory experiments: Colonies of bacteria, yeast or other simple organic entities were grown, while monitoring the time evolution of the population amount. In some cases, an excellent agreement [3, 4] with the theory was reported, thus supporting the biological validity of Eq. (1). Conversely, the match with the theory was definitely less satisfying for e.g. fruit flies, flour beetles and in general for other organisms that rely on a more complex life cycle. For those latter, it is necessary to invoke a somehow richer modelling scenario which explicitly includes age structures and time delayed effects of overcrowding population [4]. For a more detailed account on these issues the interested reader can refer to the review paper [3] and references therein.

Clearly, initial conditions are crucial and need to be accurately determined. An error in assessing the initial population, might reflect in the estimates of the parameters r and K , which are tuned so to adjust theoretical and experimental data. In general, the initial condition relative to one specific experimental realization could be seen as randomly extracted from a given distribution. This, somehow natural, viewpoint is elaborated in this paper and its implications for the analysis of the experiments thoroughly explored.

In particular we shall focus on the setting where N independent population communities are (sequentially or simultaneously) made to evolve. The experiment here consists in measuring collective observables, as the average population and associated momenta of the ensemble distribution. As anticipated, sensitivity to initial condition do

play a crucial role and so need to be properly addressed when aiming at establishing a link with (averaged) ensemble measurements, or, equivalently, drawing reliable forecast. To this end, we will here develop two analytical approaches which enable us to reconstruct the sought distribution. The first, to which section 2 is devoted, aims at obtaining a complete description of the momenta, as e.g. the mean population amount. This is an observable of paramount importance, potentially accessible in real experiments. The second, discussed in section 4, introduces a master equation which rules the evolution of the relevant distribution. It should be remarked that this latter approach is a priori more general than the former, as the momenta can in principle be calculated on the basis of the recovered distribution. However, computational difficulties are often to be faced which make the analysis rather intricate. In this perspective the two proposed scenarios are to be regarded as highly complementary.

In the following, for practical purposes, we shall assume each population to evolve as prescribed by a Verhulst type of equation. The methods here developed are however not limited to this case study but can be straightforwardly generalized to settings where other, possibly more complex, dynamical schemes are put forward.

2. On the momenta evolution

Imagine to label with x_i the population relative to the i -th realization, belonging to the ensemble of N independent replicas. As previously recalled, we assume each x_i to obey a first order differential equation of the logistic type, namely:

$$\frac{dx_i}{dt} = x_i(1 - x_i), \quad (2)$$

that can be straightforwardly obtained from (1) by setting $x = P/K$ and renaming the time $t \rightarrow rt$. The initial condition will be denoted by x_i^0 .

A natural question concerns the expected output of an hypothetical set of experiments constrained as above. More concretely, can we describe the distribution of possible solutions, once the collection of initial data is entirely specified?

The m -th momentum associated to the discrete distribution of N repeated measurements acquired at time t reads:

$$\langle x^m \rangle (t) = \frac{(x_1(t))^m + \dots + (x_N(t))^m}{N}, \quad (3)$$

To reach our goal, we introduce the *time dependent moment generating function*, $G(\xi, t)$,

$$G(\xi, t) := \sum_{m=1}^{\infty} \xi^m \langle x^m \rangle (t). \quad (4)$$

This is a formal power series whose Taylor coefficients are the momenta of the distribution that we are willing to reconstruct, task that can be accomplished using the following relation:

$$\langle x^m \rangle (t) := \frac{1}{m!} \left. \frac{\partial^m G}{\partial \xi^m} \right|_{\xi=0}. \quad (5)$$

By exploiting the evolution's law for each x_i , we shall here obtain a partial differential equation governing the behavior of G . Knowing G will eventually enables us to calculate any sought momentum via multiple differentiation with respect to ξ as stated in (5).

Deriving (3) and making use of Eq. (2) immediately yields:

$$\begin{aligned} \frac{d}{dt} \langle x^m \rangle (t) &= \frac{1}{N} \sum_{i=1}^N \frac{dx_i^m}{dt} = \frac{m}{N} \sum_{i=1}^N x_i^{m-1} \frac{dx_i}{dt} \\ &= \frac{m}{N} \sum_{i=1}^N x_i^{m-1} x_i (1 - x_i) = m (\langle x^m \rangle - \langle x^{m+1} \rangle) , \end{aligned} \quad (6)$$

On the other hand, by differentiating (4) with respect to time, one obtains :

$$\frac{\partial G}{\partial t} = \sum_{m \geq 1} \xi^m \frac{d \langle x^m \rangle}{dt} = \sum_{m \geq 1} m \xi^m (\langle x^m \rangle - \langle x^{m+1} \rangle) , \quad (7)$$

where used has been made of Eq. (6). We can now re-order the terms so to express the right hand side as a function of G ‡ and finally obtain the following non-homogeneous linear partial differential equation:

$$\partial_t G - (\xi - 1) \partial_\xi G = \frac{G}{\xi} . \quad (10)$$

Such an equation can be solved for ξ close to zero (as in the end of the procedure we shall be interested in evaluating the derivatives at $\xi = 0$, see Eq. (5)) and for all positive t . To this end we shall specify the initial datum:

$$G(\xi, 0) = \sum_{m \geq 1} \xi^m \langle x^m \rangle (0) = \Phi(\xi) , \quad (11)$$

i.e. the initial momenta or their distribution.

Before turning to solve (10), we first simplify it by introducing

$$G = e^g \quad \text{namely} \quad g = \log G , \quad (12)$$

‡ Here the following algebraic relations are being used:

$$\xi \partial_\xi G(\xi, t) = \xi \sum_{m \geq 1} m \xi^{m-1} \langle x^m \rangle = \sum_{m \geq 1} m \xi^m \langle x^m \rangle , \quad (8)$$

and

$$\begin{aligned} \xi \partial_\xi \frac{G(\xi, t)}{\xi} &= \xi \partial_\xi \sum_{m \geq 1} \xi^{m-1} \langle x^m \rangle = \xi \sum_{m \geq 1} (m-1) \xi^{m-2} \langle x^m \rangle \\ &= \sum_{m \geq 1} (m-1) \xi^{m-1} \langle x^m \rangle \end{aligned}$$

Renaming the summation index, $m-1 \rightarrow m$, one finally gets (note the sum still begins with $m=1$):

$$\xi \partial_\xi \frac{G(\xi, t)}{\xi} = \sum_{m \geq 1} m \xi^m \langle x^{m+1} \rangle . \quad (9)$$

then for any derivative

$$\partial_* G = G \partial_* g, \quad (13)$$

where $*$ = ξ or $*$ = t , thus (10) is equivalent to

$$\partial_t g - (\xi - 1) \partial_\xi g = \frac{1}{\xi}, \quad (14)$$

with the initial datum

$$g(\xi, 0) = \phi(\xi) \equiv \log \Phi(\xi). \quad (15)$$

This latter equation can be solved using the *method of the characteristics*, here represented by:

$$\frac{d\xi}{dt} = -(\xi - 1), \quad (16)$$

which are explicitly integrated to give:

$$\xi(t) = 1 + (\xi(0) - 1)e^{-t}, \quad (17)$$

where $\xi(0)$ denotes $\xi(t)$ at $t = 0$. Then the function $u(\xi(t), t)$ defined by:

$$u(\xi(t), t) := \phi(\xi(0)) + \int_0^t \frac{1}{1 + (\xi(0) - 1)e^{-s}} ds, \quad (18)$$

is the solution of (14), restricted to the characteristics. Observe that $u(\xi(0), 0) = \phi(\xi(0))$, so (18) solves also the initial value problem.

Finally the solution of (15) is obtained from u by reversing the relation between $\xi(t)$ and $\xi(0)$, i.e. $\xi(0) = (\xi(t) - 1)e^t + 1$:

$$g(\xi, t) = \phi((\xi - 1)e^t + 1) + \lambda(\xi, t), \quad (19)$$

where $\lambda(\xi, t)$ is the value of the integral in the right hand side of (18).

This integral can be straightforwardly computed as follows (use the change of variable $z = e^{-s}$):

$$\lambda = \int_0^t \frac{1}{1 + (\xi(0) - 1)e^{-s}} ds = \int_1^{e^{-t}} \frac{-dz}{z} \frac{1}{1 + (\xi(0) - 1)z}, \quad (20)$$

which implies

$$\begin{aligned} \lambda &= - \int_1^{e^{-t}} dz \left(\frac{1}{z} - \frac{\xi(0) - 1}{1 + (\xi(0) - 1)z} \right) = - \log z + \log(1 + (\xi(0) - 1)z) \Big|_1^{e^{-t}} \\ &= t + \log(1 + (\xi(0) - 1)e^{-t}) - \log \xi(0). \end{aligned} \quad (21)$$

According to (19) the solution g is then

$$g(\xi, t) = \phi((\xi - 1)e^t + 1) + t + \log \xi - \log((\xi - 1)e^t + 1), \quad (22)$$

from which G straightforwardly follows:

$$G(\xi, t) = \Phi((\xi - 1)e^t + 1) \frac{\xi e^t}{(\xi - 1)e^t + 1}. \quad (23)$$

As anticipated, the function G makes it possible to estimate any momentum (5). As an example, the mean value correspond to setting $m = 1$, reads:

$$\begin{aligned} \langle x \rangle (t) &= \partial_\xi G \Big|_{\xi=0} = \left[\Phi' (1 + (\xi - 1)e^t) e^t \frac{\xi e^t}{(\xi - 1)e^t + 1} \right. \\ &\quad \left. + \Phi (1 + (\xi - 1)e^t) e^t \frac{(\xi - 1)e^t + 1 - \xi e^t}{(1 + (\xi - 1)e^t)^2} \right] \Big|_{\xi=0} \\ &= \frac{e^t}{1 - e^t} \Phi(1 - e^t). \end{aligned} \quad (24)$$

In the following section we shall turn to considering a specific application and test the adequacy of the proposed scheme.

3. Uniform distributed initial conditions

In this section we will focus on a particular case study in the aim of clarifying the potential interest of our findings. The initial data (i.e. initial population amount) are assumed to span uniformly a bound interval $[a, b]$. No prior information is hence available which favours one specific choice, all accessible initial data being equally probably. To fix the ideas we shall here set $a = 0$ and $b = 1/2$. The probability distribution $\psi(x)$ clearly reads §:

$$\psi(x) = \begin{cases} 2 & \text{if } x \in [0, 1/2] \\ 0 & \text{otherwise} \end{cases}, \quad (25)$$

and cosequently the initial momenta are:

$$\langle x^m \rangle (0) = \int_0^1 \xi^m \psi(\xi) d\xi = \int_0^{1/2} 2\xi^m d\xi = \frac{1}{m+1} \frac{1}{2^m}. \quad (26)$$

Hence the function Φ as defined in (11) takes the form:

$$\Phi(\xi) = \sum_{m \geq 1} \frac{1}{m+1} \frac{\xi^m}{2^m}. \quad (27)$$

A straightforward algebraic manipulation allows us to re-write (27) as follows:

$$\sum_{m \geq 1} \frac{y^m}{m+1} = \frac{1}{y} \int_0^y \sum_{m \geq 1} z^m dz = \frac{1}{y} \int_0^y \frac{z}{1-z} dz = -1 - \frac{1}{y} \log(1-y), \quad (28)$$

thus

$$\Phi(\xi) = -1 - \frac{2}{\xi} \log \left(1 - \frac{\xi}{2} \right). \quad (29)$$

We can now compute the time dependend moment generating function, $G(\xi, t)$, given by (23) as:

$$G(\xi, t) = \frac{\xi e^t}{(\xi - 1)e^t + 1} \left[-1 - \frac{2}{(\xi - 1)e^t + 1} \log \left(1 - \frac{(\xi - 1)e^t + 1}{2} \right) \right], \quad (30)$$

§ We hereby assume to sample over a large collection of independent replica of the system under scrutiny (N is large). Under this hypothesis one can safely adopt a continuous approximation for the distribution of allowed initial data. Conversely, if the number of realizations is small, finite size corrections need to be included.

and thus recalling (5) we get

$$\begin{aligned} \langle x \rangle (t) &= \frac{e^t}{e^t - 1} - \frac{2e^t}{(e^t - 1)^2} \log \left(\frac{e^t + 1}{2} \right) \\ \langle x^2 \rangle (t) &= \frac{e^{2t}}{(e^t - 1)^2} + \frac{4e^{2t}}{(e^t - 1)^3} \log \left(\frac{e^t + 1}{2} \right) + \frac{2e^{2t}}{(e^t - 1)^2(e^t + 1)}. \end{aligned} \quad (31)$$

For large enough times, the distribution of the experiments' outputs is in fact concentrated around the asymptotic value 1 with an associated variance (calculated from the above momenta) which decreases monotonously with time. In Fig. 1 direct numerical simulations are compared to the analytical solution (31a), returning a good agreement. A naive approach would suggest interpolating the averaged numerical profile with a solution of the logistic model whose initial datum \hat{x}^0 acts as a free parameter to be adjusted to its best fitted value. As testified by visual inspection of Fig. 1 this procedure yields a significant discrepancy, which could be possibly misinterpreted as a failure of the underlying logistic evolution law. For this reason, and to avoid drawing erroneous conclusions when ensemble averages are computed, attention has to be paid on the role of initial conditions.

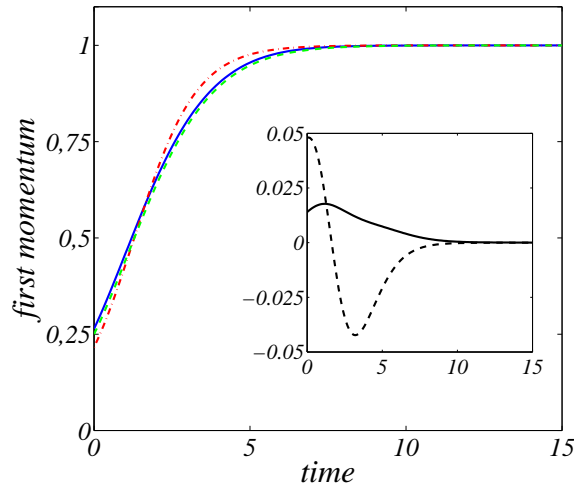


Figure 1. Main panel: Time evolution of the first moment $\langle x \rangle (t)$. The (blue) solid line stands for direct simulations averaged over $N = 100$ independent realizations. The (green) dashed line represents the analytical solution (31a). The (red) dot-dashed line is the solution of the logistic Eq. (2), where the initial datum is being adjusted to the best fit value $\hat{x}^0 = 0.216$. Inset: the solid (resp. dashed) line represents the difference between the analytical (resp. fitted) and numerical curves.

Remark 3.1 (Best parameters estimates). *In the preceding discussion the role of initial condition was elucidated. In a more general setting one might imagine r , the logistic parameter, to be an unknown entry to the model (see Eq. (2)). One could therefore imagine to proceed with a fitting strategy which adjusts both \hat{x}^0 and r so to match the (averaged) data. Alternatively, and provided the distribution of initial conditions is*

assigned (here assumed uniform), one could involve the explicit solution (31a) where time is scaled back to its original value:

$$\langle x \rangle (t) = \frac{e^{rt}}{e^{rt} - 1} - \frac{2e^{rt}}{(e^{rt} - 1)^2} \log \left(\frac{e^{rt} + 1}{2} \right). \quad (32)$$

and let the sole parameter r to run freely so to search for the optimal agreement with the data. As an example, we performed $N = 100$ repeated numerical simulations of the logistic model with parameter $r = 1.5$ and initial data uniformly distributed in $[0, 1/2]$. Using the straightforward solution of the logistic equation where \hat{x}^0 and r are adjusted, returns $r = 1.2123$. The analysis based on (32) leads to $r = 1.5662$, which is definitely closer to the true value.

Remark 3.2 (On the case of a normal distribution). *The above discussion is rather general and clearly extends beyond the uniform distribution case study. The analysis can be in fact adapted to other settings, provided the distribution of initially allowed population amount is known. We shall here briefly discuss the rather interesting case where a normal distribution is to be considered. Let us assume that x_i^0 are random normally distributed values with mean $1/4$ and standard deviation σ^2 , one can compute all the initial momenta $\langle x^m \rangle (0)$ as:*

$$\langle x^m \rangle (0) = \int \xi^m \frac{1}{\sigma^2 \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{\xi - 1/4}{\sigma} \right)^2} d\xi. \quad (33)$$

Assuming σ^k , $k \geq 3$ to be negligible with respect to σ^2 , the function $\Phi(\xi)$ specifying the initial datum in Eq. (11) reads:

$$\Phi(\xi) = \sum_{m \geq 1} \langle x^m \rangle \xi^m = \frac{\xi}{4} + \frac{\xi^2}{4^2} + \sigma^2 \xi^2 + \sum_{m \geq 3} \left[\left(\frac{\xi}{4} \right)^m + \frac{m(m-1)}{2} \left(\frac{\xi}{4} \right)^{m-2} \sigma^2 \xi^2 \right]. \quad (34)$$

Collecting together the terms $(\xi/4)^m$ for $m \geq 1$ we obtain:

$$\sum_{m \geq 1} \left(\frac{\xi}{4} \right)^m = \frac{\xi}{4 - \xi}, \quad (35)$$

while the remaining terms read:

$$\sigma^2 \xi^2 + \sum_{m \geq 3} \frac{m(m-1)}{2} \left(\frac{\xi}{4} \right)^m 4^2 \sigma^2 = \sum_{m \geq 2} \frac{m(m-1)}{2} \left(\frac{\xi}{4} \right)^m 4^2 \sigma^2. \quad (36)$$

It is then easy to verify that their contribution to the required Φ function results in

$$\Phi(\xi) = \frac{\xi}{4 - \xi} + \frac{(4\sigma)^2}{2} \frac{2(\xi/4)^2}{(1 - \xi/4)^3} = \frac{\xi}{4 - \xi} + \frac{4^3 \xi^2 \sigma^2}{(4 - \xi)^3}. \quad (37)$$

To proceed further we again calculate the derivatives of G (defined through the function Φ), evaluate them at $\xi = 0$, and eventually get the evolution of $\langle x^m \rangle$ in time, for all $m \geq 1$.

4. Monitoring the time evolution of the probability distribution function of expected measurements

As opposed to the above procedure, one may focus on the distribution function of expected outputs, rather than computing its momenta. The starting point of the analysis relies on a generalized version of the celebrated Liouville theorem. This latter asserts that the phase-space distribution function f is constant along the trajectory of the system. For a non Hamiltonian system this condition results in the following equation (for convenience derived in the Appendix Appendix A) for the evolution of the probability density function under the action of a generic ordinary differential equation, here represented by the vector field \vec{X} :

$$\frac{\partial f}{\partial t} + \nabla f \cdot \vec{X} + f \operatorname{div} \vec{X} = 0, \quad (38)$$

where $\operatorname{div} \vec{X} = \sum \partial X_i / \partial x_i$.

For the case under inspection the 1-dim vector field reads $\vec{X}(x) = x(1-x)$ and hence $\operatorname{div} \vec{X} = (1-2x)$. Thus, introducing $F = \log f$ Eq. (38) can be cast in the form:

$$\frac{\partial F}{\partial t} + x(1-x) \frac{\partial F}{\partial x} + (1-2x) = 0. \quad (39)$$

To solve this equation we use once again the methods of characteristics, which are now solutions of $\dot{x} = x(1-x)$, namely:

$$x(t) = \frac{x(0)e^t}{1 - x(0) + x(0)e^t}, \quad (40)$$

The solution of (39) is hence:

$$F(x, t) = F_0(x(0)) - \int_0^t (1 - 2x(s)) ds, \quad (41)$$

where $F_0 = \log \psi$ is related to the probability distribution function at $t = 0$ and must be evaluated at $x(0)$, seen as a function of $x(t)$. The integral can be computed as follows:

$$\int_0^t (1 - 2x(s)) ds = \int_0^t \left(1 - 2 \frac{x(0)e^s}{1 - x(0) + x(0)e^s} \right) ds = t + 2 \log (1 - x(0) + x(0)e^t). \quad (42)$$

Such an expression has to be introduced into (41) once we explicit $x(0)$ for $x(t) = x$ as:

$$x(0) = \frac{xe^{-t}}{1 - x + xe^{-t}}. \quad (43)$$

Hence:

$$F(x, t) = F_0 \left(\frac{xe^{-t}}{1 - x + xe^{-t}} \right) - t - 2 \log (1 - x + xe^{-t}), \quad (44)$$

and finally back to the original f :

$$f(x, t) = \psi \left(\frac{xe^{-t}}{1 - x + xe^{-t}} \right) \frac{e^{-t}}{(1 - x + xe^{-t})^2}, \quad (45)$$

which stands for the probability density function which describes for all t the expected distribution of x 's. In Fig. 2 we compare the analytical solutions (45) with the numerical

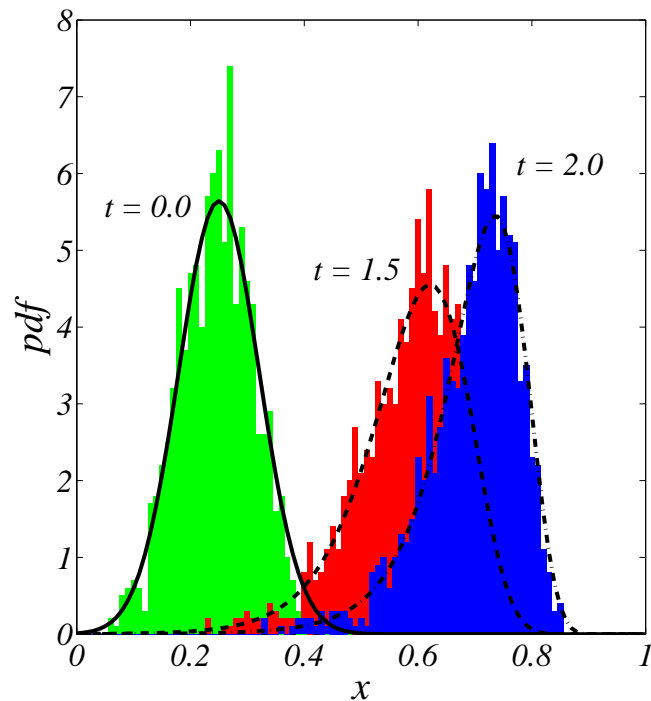


Figure 2. Time evolution of the probability distribution function. Histograms refers to numerical simulation and are calculated at different time: $t = 0$ (green online), $t = 1.5$ (red, online), $t = 2.0$ (blue online). The lines represent the corresponding analytical solution

simulation of the logistic model (2) under the assumption of $N = 1000$ initial data normally distributed with mean $1/2$ and variance 0.005 .

Notice that having calculated the distribution f will enable in turn, at least in principle, to calculate all the associated momenta.

5. Conclusion

Forecasting the time evolution of a system which obeys to a specific governing differential equation and is initialized as follows a specific probability distribution, constitutes a central problem in several domains of applications. Assume for instance a set of independent measurements to return an ensemble average which is to be characterized according to a prescribed model. Biased conclusion might result from straightforward fitting strategies which do not correctly weight the allowed distribution of initial condition.

In this paper we address this problem by providing an exact formula for the time evolution of momenta and probability distribution function of expected measurements, which is to be invoked for a repeated set of independent experiments. Though general, the method is here discussed with reference to a simple, demonstrative problem of population dynamics.

6. Acknowledgments

We wish to thank M. Villarini for several discussion and, in particular, for suggesting Eq. (A.5).

Appendix A. The generalized Liouville theorem

Let $\vec{X}(x)$ be a vector field to which we associate the ordinary differential equation:

$$\dot{x} = \vec{X}(x) \quad \forall x \in \Omega, \quad (\text{A.1})$$

where Ω is the phase space. Suppose to define a probability density function of the initial data on Ω . Namely we have a function ψ defined in the phase space Ω , such that for all $B \subset \Omega$, $\int_B \psi(x) dx$ denotes the probability that a randomly drawn initial datum will belong to B and $\int_{\Omega} \psi(x) dx = 1$.

We are interested in determining for any $t > 0$, the probability that a solution of (A.1) will fall in a open set $B' \subset \Omega$. Let us call $f(x, t)$ such probability, by continuity we must have $f(x, 0) = \psi(x)$ and $\int_{\Omega} f(x, t) dx = 1$ for all $t > 0$.

For any $B \subset \Omega$, $P(B) = \int_B f(x, t) dx$ denotes the probability to find a point in B at time t . We can then assume that this probability does not change if the set B' is transported by the flow of (A.1), $P(B) = P(A)$ where $A = \Phi^s(B)$, being Φ^s the flow at time s of the vector field. Namely

$$\int_{A=\Phi^s(B)} f(y, t+s) dy = \int_B f(x, t) dx, \quad (\text{A.2})$$

the change of coordinates $y = \Phi^s(x)$ allows to rewrite the previous relation as follows:

$$\int_{A=\Phi^s(B)} f(y, t+s) dy = \int_B f(\Phi^s(x), t+s) \det D\Phi^s(x) dx = \int_B f(x, t) dx, \quad (\text{A.3})$$

being $D\Phi^s(x)$ the Jacobian of the change of variables.

The relation (A.3) should be valid for any set B , thus:

$$f(x, t) = f(\Phi^s(x), t+s) \det D\Phi^s(x), \quad (\text{A.4})$$

for all $x \in \Omega$ and for all t, s . Deriving with respect to s and evaluating the derivative at $s = 0$ we get the required relation (recall $D\Phi^0(x) = \text{identity}$):

$$\frac{\partial f}{\partial t}(x, t) + \nabla_x f(x, t) \cdot \vec{X}(x) + f(x, t) \text{div} \vec{X}(x) = 0. \quad (\text{A.5})$$

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