

# Approaching predator-prey Lotka-Volterra equations by simplicial linear differential equations

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## Abstract

Predator-prey Lotka-Volterra equations was one of the first models reflecting interaction of different species and modeling evolution of respective populations. It considers a large population of hares (preys) which is depredated by an also large population of lynxes (predators). It proposes an increasing/decreasing law of the number of individuals in each population thus resulting in an apparently simple system of ordinary differential equations. However, the Lotka-Volterra equation, and most of its modifications, is non-linear and its generalization to a larger number of species is not trivial. The present aim is to study approximations of the evolution of the proportion of species in the Lotka-Volterra equations using some simple model defined in the simplex.

Calculus in the simplex has been recently developed on the basis of the Aitchison geometry and the simplicial derivative. Evolution of proportions in time (or other parameters) can be represented as simplicial ordinary differential equations from which the simpler models are the linear ones. Simplicial Linear Ordinary Differential Equations are not able to model the evolution of the total mass of the population (total number of predators plus preys) but only the evolution of the proportions of the different species (ratio predators over preys). This way of analysis has been successful showing that the compositional growth of a population in the Malthusian exponential model and the Verhulst logistic model were exactly the same one: the first order simplicial linear differential equation with constant coefficients whose solution is a compositional straight-line. This strategy of studying the total mass evolution and the compositional evolution separately is used to get a simplicial differential equation whose solutions approach suitably the compositional behavior of the Lotka-Volterra equations. This approach has additional virtues: it is linear and can be extended in an easy way to a number of species larger than two.

## 1 Introduction

Systems of ordinary differential equations have been frequently used to model the behaviour of populations, understanding populations in a wide sense: biological, human, resources, epidemia, etc. (Bacaër, 2011). The population is partitioned into classes of individuals and the number of individuals in each class is treated as a continuous real variable. This continuous number of individuals of a class will be called mass of the class. Elementary models express the derivative of the mass of a class as a simple function of the number of all masses. Solutions of this kind of differential equations are generically known as growth curves (Odum, 1971). The simplest and older model is the exponential growth model which appear in bacteria growth, human communities (Euler, 1760), radioactive decay, etc. and it can be formulated as

$$Dm_i(t) = k_i m_i(t) , \quad i = 1, 2, \dots, n , \quad (1)$$

where  $m_i(t)$  represents the mass of the  $i$ -th class as a function of time  $t$ ;  $D$  is the ordinary derivative operator with respect to  $t$  and  $n$  is the number of classes. Model (1) can be complemented with new classes of individuals without changing the meaning of the equations. For instance, the traditional Euler-Malthus model is  $Dm_1 = k_1 m_1$  being  $m_1$  the individuals of a human population and  $k_1 > 0$ . If  $m_1(0)$  is the initial mass, the solution of the differential equation is  $m_1(t) = m_1(0) \exp(k_1 t)$ ,  $t \geq 0$ . We can redefine the population as made of resources cells: some of them,  $m_1(t)$ , occupied by individuals; and those cells which are available,  $m_2(t)$ . Assuming that  $m_2(t)$  is a constant it satisfies the differential equation  $Dm_2 = 0$ . Solving for the system (1), with  $n = 2$ ,  $k_1 > 0$ ,  $k_2 = 0$ , the solution of the mass  $m_1(t)$  is exactly the previous one.

An apparently more complex model is the logistic one (Verhulst, 1838). It can be written as

$$Dm_1(t) = k_1 m_1(t) (m_1^\infty - m_1(t)) , \quad k_1 > 0 , \quad (2)$$

which is a non linear-Ricatti equation whose solution is the well known logistic curve, and  $m_1^\infty$  is the asymptotic mass of population. Again equation (2) can be complemented with an equation for the available resource cells. An option is  $m_2 = M - m_1$ ,  $M > 0$ , or equivalently  $Dm_2 = -k_1 m_1 (m_1^\infty - m_1)$  which maintains the solution for  $m_1(t)$  unaltered.

Another class of models of population growth is the so called SIR-models (and generalisations). Let  $m_1 \equiv S$ ,  $m_2 \equiv I$ ,  $m_3 \equiv R$  the mass of susceptible to a disease, the mass of infected people, and the mass of recovered people, respectively. Whenever the latent evolution of the population is neglected the SIR-model (Kermack and McKendrick, 1927) is

$$Dm_1(t) = -\alpha m_1(t)m_2(t) , \quad Dm_2(t) = \alpha m_1(t)m_2(t) - \gamma m_2(t) , \quad Dm_3(t) = \gamma m_2(t) , \quad (3)$$

for some positive constants  $\alpha$ ,  $\gamma$ . This model has been successfully used in prediction of epidemics evolution.

Also predator-prey Lotka-Volterra equations, and their sequels, corresponds to the same type of equations. If  $m_1$  represents the mass of predators,  $m_2$  the mass of preys then Lotka-Volterra equations are

$$Dm_1(t) = -a_1 m_1(t) + a_2 m_1(t)m_2(t) , \quad Dm_2(t) = b_1 m_2(t) - b_2 m_1(t)m_2(t) , \quad (4)$$

where the coefficients  $a_1$ ,  $a_2$ ,  $b_1$ ,  $b_2$  are assumed positive. Despite of the apparent simplicity of these equations, their solution is not explicit although the orbit  $(m_1(t), m_2(t))$  is easily obtained. Figure 1 (left) shows predator-prey (lynx-hare) data used in Section 4 as an example and at the right panel one cycle orbit described by observed data (blue) and the orbit of the solution of Lotka-Volterra equations fitted to the data set.

All cited examples can be viewed in two different ways: the traditional representation using masses of each class as in equations (1), (2), (3), (4); an alternative consisting of representing the system as an equation for the total mass  $m(t) = \sum_i m_i(t)$  and a simplicial differential equation for the composition containing the proportion of masses, i.e.  $\mathbf{x}(t) = \mathcal{C}(m_1(t), m_2(t), \dots, m_n(t)) \in \mathcal{S}^n$  where  $\mathcal{C}$  is the closure to unit and  $\mathcal{S}^n$  the  $n$ -part simplex. The difference between these two representations is the metric of the space where the solutions are defined. In the traditional case, masses evolve in  $\mathbb{R}_+^n$  assuming that the metric is inherited from the Euclidean space  $\mathbb{R}^n$ . In the second case, the representation, total mass and composition, is a curve in the space  $\mathbb{R}_+ \times \mathcal{S}^n$  which is also a  $n$ -dimensional Euclidean space (Pawlowsky-Glahn and Egozcue, 2001). This strategy separating the compositional model from the total mass evolution has been successful proving that the compositional differential equation for the Euler-Malthus Eq. (1), with  $n = 2$ ,  $k_1 > 0$ ,  $k_2 = 0$ , and the logistic Verhulst model (2) are just equal, and they only differ in the behaviour of the total mass (Jarauta-Bragulat and Egozcue, 2008, 2010). Moreover, in the case of the logistic model (2), the compositional equation is a first order linear equation which is simpler than the Eq. (2) itself. This previous results suggest that, in some cases, models expressed in mass may be simplified or approached studying their compositional and total mass models separately.

Attention is now focussed in the Lotka-Volterra system (4). The main idea is that these equations can be approached by simple compositional and total mass models. These simple models have been chosen to be harmonic oscillators (Section 4) for the total mass and for the compositional part being the natural frequency equal in both equations.

## 2 Linear differential equations in $\mathcal{S}^n$ and $\mathbb{R}_+$

### Derivatives on the simplex

Simplicial derivatives have been defined in Aitchison (1986) (postscript 2003 printing) and also in Aitchison et al. (2002), Egozcue et al. (2008). A more detailed development is found in Egozcue et al. (2011). If  $\mathbf{f} : \mathbb{R} \rightarrow \mathcal{S}^n$  is a function of a real variable (time) on the simplex (proportions of masses), the simplicial derivative of  $\mathbf{f}$  at  $t$  is defined as

$$D^\oplus \mathbf{f}(t) = \lim_{h \rightarrow 0} \left( \frac{1}{h} \odot (\mathbf{f}(t+h) \ominus \mathbf{f}(t)) \right) , \quad (5)$$

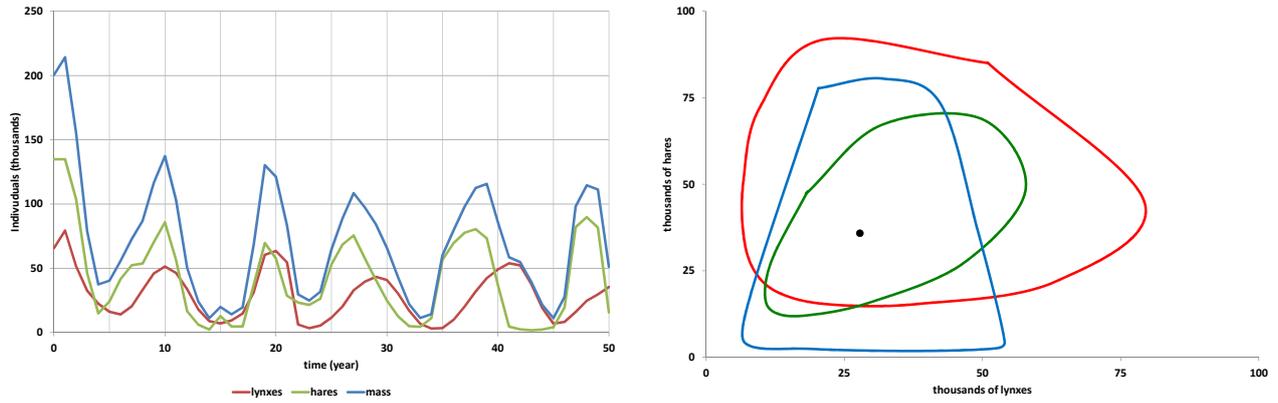


Figure 1: Left, observed number (in thousands) of hares and lynxes 1885-1935 (Odum, 1971). Right, periodic orbits of  $(m_2, m_1)$  as observed (blue), for fitted Lotka-Volterra equations (LV, red) and the proposed harmonic oscillator (HO, green) fitted to data. The central dot is the equilibrium value estimated for both LV and HO.

if the limit exists. In Equation (5), standard notation of operations in the simplex is adopted:  $\oplus$  is perturbation and  $\ominus$  is the opposite of perturbation;  $\odot$  denotes powering by real scalars. Computation of the derivative is easily carried out using logarithmic derivatives,

$$D^{\oplus} \mathbf{f}(t) = \mathcal{C} \exp(D \log(\mathbf{f}(t))) = \mathcal{C} \exp\left(\frac{Df_1(t)}{f_1(t)}, \dots, \frac{Df_n(t)}{f_n(t)}\right), \quad (6)$$

where functions (exp, log, ...) operate componentwise on vectors. Moreover,  $\mathbf{f}$  is not necessarily closed to unit because any equivalent (proportional) function gives the same result. A further simplification consists of expressing the compositional function in coordinates with respect to any orthonormal basis. If  $\text{ilr} : \mathcal{S}^n \rightarrow \mathbb{R}^{n-1}$  assigns orthonormal coordinates to any composition (Egozcue et al., 2003; Egozcue and Pawlowsky-Glahn, 2005, 2006), then

$$D^{\oplus} \mathbf{f}(t) = \text{ilr}^{-1}(D(\text{ilr}(\mathbf{f}))), \quad (7)$$

where again  $D$  denotes derivative with respect to the real variable (time).

Using expressions Eq. (6) and (7),  $K$ -order simplicial linear (ordinary) differential equations (SLODE) expressed in the simplex are

$$\bigoplus_{k=0}^K a_k \odot (D^{\oplus})^k \mathbf{x}(t) = \varphi(t),$$

being  $(D^{\oplus})^k$  the  $k$ -th simplicial derivative ( $(D^{\oplus})^0$  is the identity) and  $\varphi$  a forcing compositional term. Once an orthonormal basis of the simplex is selected, the compositional functions  $\mathbf{x}(t)$  and  $\varphi(t)$  can be expressed using their coordinates, i.e.  $\mathbf{x}^*(t) = (x_1^*(t), x_2^*(t), \dots, x_{n-1}^*(t)) = \text{ilr}(\mathbf{x}(t))$  (analogously for  $\varphi(t)$ ), given rise to a system of  $n - 1$  linear ordinary differential equations

$$\sum_{k=0}^K a_k \cdot D^k \mathbf{x}^*(t) = \varphi^*(t).$$

Methods for solving this kind of differential equations are well-known and can be applied without any restriction. Once a solution for the coordinates  $\mathbf{x}^*$  is known it can be immediately translated into the compositional solution as  $\mathbf{x} = \text{ilr}^{-1}(\mathbf{x}^*)$ .

## Derivatives in $\mathbb{R}_+$

Whenever a relative scale in  $\mathbb{R}_+$  is assumed, differences are no longer measured by ordinary differences but logarithmic differences (Pawlowsky-Glahn and Egozcue, 2001). Therefore, a derivative of a

function  $f : \mathbb{R} \rightarrow \mathbb{R}_+$  needs a re-definition. The idea is that  $\mathbb{R}_+$  is a one-dimensional Euclidean space, where the group operation (addition, also denoted  $\oplus$ ) is the ordinary product and the external operation (denoted  $\odot$ ) is powering. Similarly to the simplex, a basis can be defined so that any element in  $\mathbb{R}_+$  can be represented by its coordinate with respect to the basis. A simple choice of a basis in  $\mathbb{R}_+$  is the number  $e = \exp(1)$  which allows the coordinate expression  $x = \exp(\log x)$  for any  $x \in \mathbb{R}_+$ . Therefore,  $\log x \in \mathbb{R}$  is the coordinate of  $x \in \mathbb{R}_+$  when the selected basis is  $e$ . After these concepts, the derivative for the coordinates of functions in  $\mathbb{R}_+$  is

$$D(\log f(t)) = \lim_{h \rightarrow 0} \frac{\log f(t+h) - \log f(t)}{h},$$

which translated back to  $\mathbb{R}_+$  gives the desired derivative

$$D^+ f(t) = \exp(D(\log f(t))),$$

which clearly recalls derivatives in the simplex (5-7).

Differential equations in  $\mathbb{R}_+$  can be equivalently written using  $D^+$  or using coordinates. For instance, a  $K$ -order linear differential equation in  $\mathbb{R}_+$  is

$$\bigoplus_{k=0}^K a_k \odot (D^+)^k x(t) = \varphi(t),$$

where, for  $x, y \in \mathbb{R}_+$ ,  $\alpha \in \mathbb{R}$ ,  $x \oplus y = \exp(\log x + \log y) = xy$ ,  $\alpha \odot x = \exp(\alpha \log x) = x^\alpha$ ;  $x(t)$  is the unknown positive function and  $\varphi(t)$  represents a positive forcing term. This equation can be written in coordinates

$$\sum_{k=0}^K a_k \cdot D^k x^*(t) = f^*(t), \quad x^*(t) = \log x(t), \quad \varphi^*(t) = \log \varphi(t),$$

which is a linear ordinary differential equation in  $\mathbb{R}$ .

### Total mass and compositional models

An important point is how to get the total mass and the compositional evolution equations from the differential equations for masses of the classes. There are essentially two ways to do it. The first one is to solve the system in masses; then, compute proportions and their representation in coordinates; and finally, obtain the simplicial differential equations from the solution in coordinates. Although apparently simple, this way is plenty of difficulties: the solution in mass should be explicit and also the solution in coordinates; and afterwards, the identification of the differential equation should be feasible. A second way, which may be considered standard, starts transforming the derivatives of the differential equation in mass into logarithmic derivatives, and then, expressing the remaining term in a compositional way. Even simple equations in mass can exhibit unexpected links between the compositional part of the equation and the total mass equation. If this is the case, little benefit is obtained from expressing the equations of the system as compositional and total mass equations. However, if the compositional and total mass equations are not coupled, then the interpretation of the model is simplified.

### 3 Lotka-Volterra equations

The predator-prey Lotka-Volterra equations (4) are

$$Dm_1(t) = -a_1 m_1(t) + a_2 m_1(t) m_2(t) \quad , \quad Dm_2(t) = b_1 m_2(t) - b_2 m_1(t) m_2(t) \quad , \quad (8)$$

where  $m_1(t)$  is the mass of predators,  $m_2(t)$  is the mass of preys and  $m(t) = m_1(t) + m_2(t)$  is the total mass. It is interesting to pay attention to the reasoning that leads to both equations in (8). It can be summarised as: *the mass of predators decreases proportionally to the predator mass because predator individuals compete for their territory; and the mass of predators increases proportionally to*

the number of encounters between predators and preys which is the way of feeding predators; moreover, the number of predator-prey encounters is proportional to the product of masses of predators and preys. Similarly, the mass of preys increases proportionally to preys mass, provided there is enough vegetal food for preys; and decreases proportionally to the number of predator-prey encounters because some of them conclude with the dead of the prey. This kind of reasoning has three remarkable characteristics: (a) there is no mention of the total mass of predators and preys and it is not sensible to the mass of individuals; (b) it implicitly assumes that the way of measuring change of mass is the ordinary derivative for real functions with the ordinary way of measuring differences; (c) when it is said that the increase/decrease of the mass is proportional to two quantities, the two proportionality effects on the change are assumed additive.

Characteristic (a) points out the compositional character that should be present in the equation. However, Eq. (8) is not scale invariant and the influence of encounters depends on the masses and not only on their proportions. Point (b) assumes, e.g., that the difference in mass of 100 and 1,000 individuals is exactly the same as between 1 million and 1 million plus 900 individuals, against the appreciation of an ecologist that probably feels that 100 is a critical number of individuals for a population near of extinction; 1000 individuals is dangerous but not critical; and 1,000,000 and 1,000,900 individuals in two populations are very similar masses. Probably, the ecologist would better understand that for measure these differences is better to compare the numbers using ratios,  $1,000/100 = 10$ ,  $(10^6 + 900)/10^6 \approx 1$ . A little step further is to measure the ratio differences taking their logarithm so that symmetrizing the role of numerator and denominator: in the first case  $\log(10^3/10^2) \simeq 2.3$  and the second one  $\log((10^6 + 9 \cdot 10^2)/10^6) \simeq 8 \cdot 10^{-4}$ . Characteristic (c) is a little bit mysterious. Reasoning mainly mentions proportionality and additivity does not take place. One can think this was introduced to get a simple equation, but many aspects of Lotka-Volterra equations (8) are not simple, and finally the equations must be solved numerically.

Proportion of predators and preys over the total is denoted  $\mathbf{x} = (x_1, x_2) = \mathcal{C}(m_1, m_2)$ . Transforming Eq. (8) to express it using logarithmic derivatives, this is

$$D \log m_1(t) = -a_1 + a_2 m_2(t) \quad , \quad D \log m_2(t) = b_1(t) - b_2 m_1(t) .$$

Since  $\mathbf{x}$  is a composition of two parts, it is represented by a single coordinate  $x^* = 2^{-1/2} \log(x_1/x_2)$ . The derivative  $Dx^*$  is the coordinate expression of the simplicial derivative

$$D^{\oplus} \mathbf{x} = \mathcal{C} \exp(D \log(m_1, m_2)) = \mathcal{C} \exp(D \log(x_1, x_2)) .$$

After some algebra

$$Dx^* = \frac{1}{\sqrt{2}} \left( -(a_1 + b_1) + e^{m^*} (a_2 x_2 + b_2 x_1) \right) \quad , \quad Dm^* = -(a_1 x_1 - b_1 x_2) + e^{m^*} (a_2 - b_2) x_1 x_2 \quad , \quad (9)$$

where the proportions  $\mathbf{x} = (x_1, x_2)$  can be expressed as a function of the coordinate (balance)  $x^*$  and the coordinate of  $m$  in  $\mathbb{R}_+$ ,  $m^* = \log m$  (Pawlowsky-Glahn and Egozcue, 2001). The expressions for  $x_1$  and  $x_2$  are

$$x_1 = \frac{\exp(\sqrt{2} x^*)}{1 + \exp(\sqrt{2} x^*)} \quad , \quad x_2 = \frac{1}{1 + \exp(\sqrt{2} x^*)} \quad ,$$

which is the  $\text{ilr}^{-1}$  transformation into  $\mathcal{S}^2$ , and also the inverse logit transform up to the constant  $\sqrt{2}$ . Although Equations (9) are numerically tractable, they are coupled and they do not offer any advantage over the original Lotka-Volterra equations (8).

After these equations using coordinates in  $\mathbb{R}_+ \times \mathcal{S}^2$  and the criticisms to the underlying ideas to Lotka-Volterra equations, to approach these equations with a simple total mass-compositional model seems advisable.

## 4 A simple model approaching Lotka-Volterra equations

Lotka-Volterra equations have periodic solutions (Fig. 1, right). This means that the approaching equations should have solutions for coordinate in  $\mathcal{S}^2$  and coordinate in  $\mathbb{R}_+$  which must be also periodic.

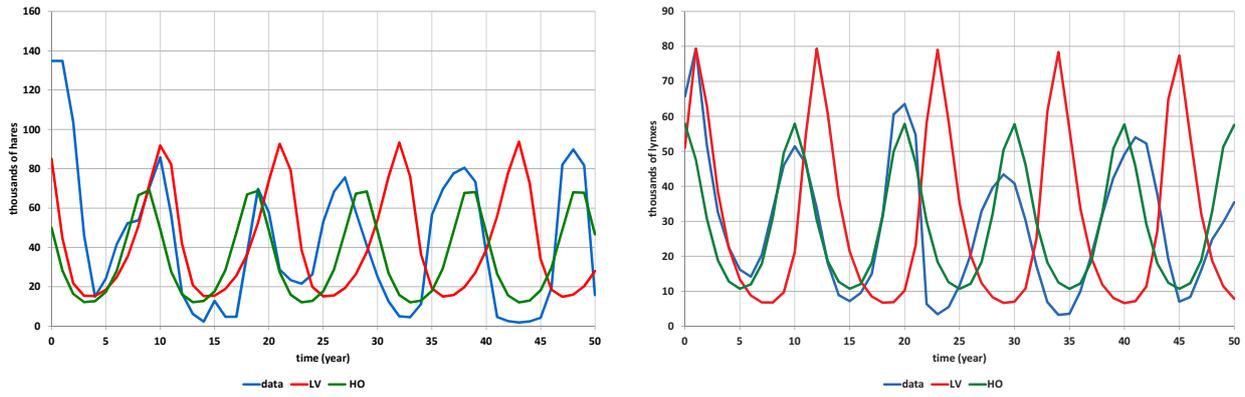


Figure 2: Mass, in thousands, of hares (left) and lynxes (right). Observed 1885-1935 (Odum, 1971) (blue); for fitted Lotka-Volterra equations (red) and the proposed harmonic oscillator (green).

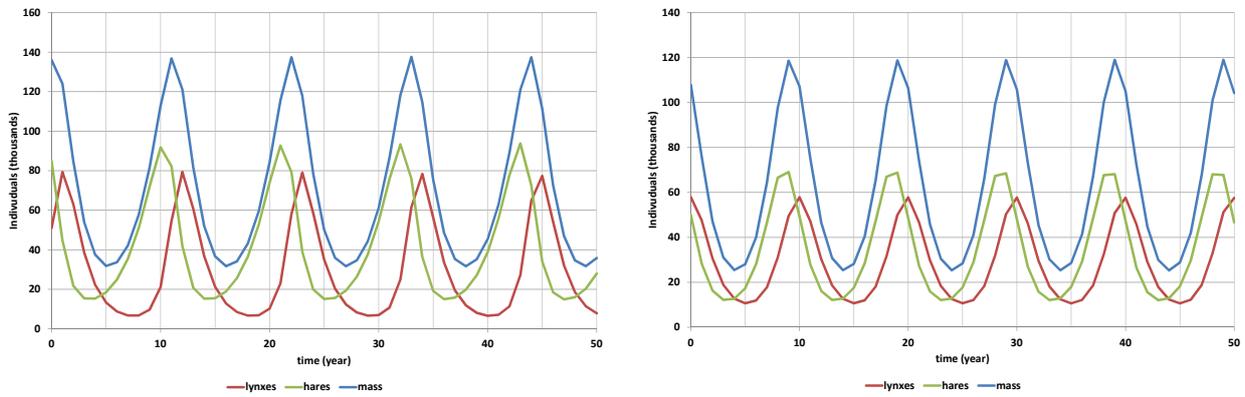


Figure 3: Comparison in time (1885-1935) of number (in thousands) of lynxes, hares and total individuals for the fitted Lotka-Volterra equations (LV, left) and for the fitted harmonic oscillator (HO, right).

For simplicity, linear differential equations are preferred as approaching equations, but periodic solutions are only attained with linear differential equations of order 2 or higher. The simplest model in  $\mathbb{R}_+ \times \mathcal{S}^2$ , stated in coordinates, and with periodic solutions is the free oscillating, uncoupled harmonic oscillator

$$D^2\mu^* + \omega^2\mu^* = 0 \quad , \quad D^2y^* + \omega^2y^* = 0 \quad , \quad (10)$$

with a single parameter  $\omega$  which represents the natural angular frequency of oscillation around the point  $\mu^* = 0, y^* = 0$ . Since orbits of Lotka-Volterra equations are centered on a point which is determined by the coefficients  $a_1, a_2, b_1, b_2$  (8), a shift of the oscillator (10) adapts the oscillator to the Lotka-Volterra system. This can be done defining  $m^* = m_0^* + \mu^*$  and  $x^* = x_0^* + y^*$ , where  $m_0^* = \log m_0$ ,  $x_0^* = 2^{-1/2} \log(x_{10}/x_{20})$  represents a shift in coordinates of  $\mathbb{R}_+ \times \mathcal{S}^2$ ;  $m_0$  is a multiplicative change in total mass and  $(x_{10}, x_{20})$  is a perturbation (shift) in  $\mathcal{S}^2$ . This completes a three parameter model which are  $\omega, m_0^*$ , and  $x_0^*$

The general solution of the oscillator (10) is explicit

$$m^*(t) = m_0^* + A_m \sin(\omega t) + B_m \cos(\omega t) \quad , \quad x^*(t) = x_0^* + A_x \sin(\omega t) + B_x \cos(\omega t) \quad , \quad (11)$$

where the constants  $m_0^*, x_0^*$ , correspond to mean values and  $A_m, B_m, A_x, B_x$  are determined by initial or boundary conditions.

To show the effectiveness of the proposed approach, a demonstration data set for the Lotka-Volterra equation have been used (Odum, 1971). It corresponds to 1845-1935 year record of the mass of lynxes (predators  $m_1$ ) and mass of hares (preys  $m_2$ ). Only data for years 1885-1935 are used in the present example as measurements are more reliable. Masses are measured in thousands of individuals. Parameters of Lotka-Volterra (LV) and the harmonic oscillator (HO) in Equation 11 have been fitted

Table 1: Parameters for Lotka-Volterra (LV) equations and the harmonic oscillator (HO) fitted to data.  $T$  is the estimated period in year corresponding to  $\omega$ .

Lotka-Volterra	
$a_1 = 0.842$	$a_2 = 0.019$
$b_1 = 0.473$	$b_2 = 0.016$
harmonic oscillator	
eq. coordinates	eq. $\mathbb{R}^+ \times \mathcal{S}^n$
$m_0^* = 4.276$	$m_0 = 71.953$ thousands
$x_0^* = -0.273$	$x_{10} = 0.405$
	$x_{20} = 0.595$
$\omega = 0.631$ (years) $^{-1}$	
$T = 9.957$ years	

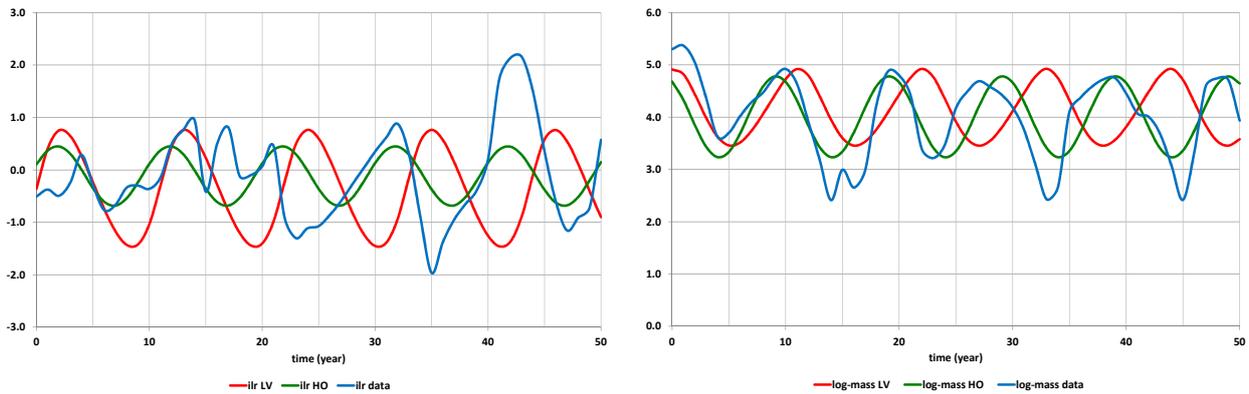


Figure 4: Comparison of the coordinates (ilr) of composition (lynxes, hares) and the log-total mass of lynxes (red), hares (green) and total mass (blue) along 1885-1935. Left: ilr-coordinate  $x^*$ ; right: log-total mass (thousands)  $m^*$ .

using least squares. The procedure consists of the following steps: (a) express the data in coordinates  $m^*(t_i)$  and  $x^*(t_i)$  for the sampling times  $t_i$ ; (b) determine the equilibrium values  $m_0^*$ ,  $x_0^*$  as the mean values along the coordinates; (c) determine the angular frequency  $\omega$  using Pisarenko harmonic analysis (Pisarenko, 1973) on the coordinates computed in (a); (d) using the estimated values of  $m_0^*$ ,  $x_0^*$ ,  $\omega$ , determine  $a_1$ ,  $a_2$ ,  $b_1$ ,  $b_2$  and solve numerically the Lotka-Volterra equations (8) using observed initial conditions; (e) using the estimated values of  $m_0^*$ ,  $x_0^*$ ,  $\omega$ , determine the values  $A_m$ ,  $B_m$ ,  $A_x$ ,  $B_x$  in Equation (11) using least squares. The resulting parameters are shown in Table 1.

Figure 1 (left) shows the evolution of the mass of hares (blue) and lynxes (red) as observed along 50 years (1885-1935); also the total mass is reported. In Figure 1 (right) the orbit described by data in one cycle is represented in blue. Also in Figure 1 (right), orbits for the fitted Lotka-Volterra (LV, red) and harmonic oscillator (HO, green) are represented. They go around the equilibrium point  $m_{01} = m_0 x_{01}$  (lynxes),  $m_{02} = m_0 x_{02}$  (hares). The represented orbits appear quite different. However, one should take into account the inconvenient scale of this representation where relative scale is ignored. The size of the cycle of observed data corresponds to the first cycle which has an amplitude larger than the rest of the signal; other cycles would appear smaller than the represented one. Further comparisons of data, LV and HO are shown in time in Figure 2. An overestimation of the amplitude in LV is apparent. Also LV appears to be slightly shifted in its maxima-minima with respect to data. This is mainly due to the procedure of solving Lotka-Volterra equations (8) which is based on initial conditions and, consequently, the obtained solution will be sensible to the initial point and not to the rest of the time-series. Here, an inconvenient of non-simple model clearly appear: solution cannot be easily fitted to data and initial conditions are used instead. This is not the case of HO because the solution is explicit (11).

Figure 3 shows the joint behaviour of mass of lynxes (red), of hares (green) and total mass (blue) for

LV (right) and HO (left). Qualitative comparison of left and right figures reveals a similar behaviour of the two models thus justifying the approach using the harmonic oscillator. Figure 4 shows the behaviour of coordinates of total mass,  $m^*(t)$  (right), and the composition (lynxes, hares),  $x^*(t)$  (left), for the data, LV and HO. Again the qualitative behaviour of LV (red) and HO (sinusoidal) (green) appears to be quite similar. Particularly, log-total mass is almost sinusoidal for LV. Figure 4 also shows that the model fits the data poorly for both LV and HO. It appears that there are changes in the oscillating period and in amplitude. This may suggest that introducing forcing terms in Equations (10) may be convenient to model interactions of the system with the environment.

## 5 Conclusions

Many models of population evolution have been formulated as systems of ordinary differential equations for the number of individuals of each considered class. An alternative formulation is proposed: modelling the evolution of the total of individuals as a function of time in  $\mathbb{R}_+$ , and the evolution of the proportions of individuals as a function of time in the simplex. Both functions can be represented in coordinates of the respective spaces using ordinary differential equations for these coordinates.

The predator-prey Lotka-Volterra equations have been examined. Despite of reasoning leading to the equations are mainly compositional, the equations themselves are not scale invariant thus putting forward some criticism on the model. Following the idea of modelling total mass and composition in coordinates of  $\mathbb{R}_+ \times \mathcal{S}^n$  and using differential equations, a simple uncoupled harmonic oscillator is proposed to approach the dynamics of a predator-prey population which solutions satisfactorily approach those of the corresponding Lotka-Volterra equations.

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