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Density-dependence as a size-independent regulatory mechanism

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Abstract

The growth function of populations is central in biomathematics. The main dogma is the existence of density-dependence mechanisms, which can be modelled with distinct functional forms that depend on the size of the population. One important class of regulatory functions is the θ-logistic, which generalizes the logistic equation. Using this model as a motivation, this paper introduces a simple dynamical reformulation that generalizes many growth functions. The reformulation consists of two equations, one for population size, and one for the growth rate. Furthermore, the model shows that although population is density-dependent, the dynamics of the growth rate does not depend either on population size, nor on the carrying capacity. Actually, the growth equation is uncoupled from the population size equation, and the model has only two parameters, a Malthusian parameter ρ and a competition coefficient θ. Distinct sign combinations of these parameters reproduce not only the family of θ-logistics, but also the van Bertalanffy, Gompertz and Potential Growth equations, among other possibilities. It is also shown that, except for two critical points, there is a general size-scaling relation that includes those appearing in the most important allometric theories, including the recently proposed Metabolic Theory of Ecology. With this model, several issues of general interest are discussed such as the growth of animal population, extinctions, cell growth and allometry, and the effect of environment over a population.

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1. Introduction

The logistic equation is a paradigm for population biology. This simple model, in its continuous (Verhulst, 1838; Pearl, 1927) or discrete (May, 1976) versions describe two fundamental properties of population biology, which are (i) the initial exponential rates of growth, and (ii) density-dependent effects, like competition under limited resources, indicated by saturation values. The discrete logistic equation, in itself opened a new and broad field in biology related to chaotic behaviours, and for which some experimental evidences exist (Hanski et al., 1993; González et al., 2003b). The continuous version of logistic growth, although sharing properties with its discrete analogue, differs in some

aspects. It does not show intrinsic bifurcations as the discrete version does, and is much more simple to treat analytically.

Gilpin and Ayala (1973) and Gilpin et al. (1976) introduced a model that "slightly" generalizes the popular logistic equation. Their model, consists on modifying the term corresponding to the density-dependence with an exponent θ

$$\dot{x} = \rho x \left[1 - \left(\frac{x}{x_\infty} \right)^\theta \right], \tag{1}$$

where x is population size, the notation $\dot{x}$ corresponds to time derivative dx/dt, and ρ, θ, and x_∞ are parameters of the model. Compared to the logistic equation, their "global model" describes a population that converges in time to the same size as the logistic growth, i.e. to the carrying capacity x_∞. However, the exponent θ gives new interpretations to this sigmoid model of growth. If

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Table 1
Common regulation functions for different population growth models

Model	Growth rate	Malthusian parameter	Interaction parameter	Initial rate
Exponential	$r(x) = \alpha$	$\rho = 0$	$\theta = 0$	$\alpha(0) = \alpha \neq 0$
Logistic	$r(x) = \rho(1 - \alpha x)$	$\rho > 0$	$\theta = 1$	$\alpha(0) > 0$
θ-Logistic	$r(x) = \frac{\rho}{\theta}(1 - \alpha x^\theta)$	$\rho > 0$	$\theta > 0$	$\alpha(0) > 0$
Gompertzian	$r(x) = -\rho \log(\alpha x)$	$\rho > 0$	$\theta = 0$	$\alpha(0) > 0$
Potential	$r(x) = \alpha x^\theta$	$\rho = 0$	$\theta \neq 0$	$\alpha(0) \neq 0$
von Bertalanffy	$r(x) = -3\rho(1 - \alpha x^{-1/3})$	$\rho > 0$	$\theta = -\frac{1}{3}$	$\alpha(0) > 0$
West et al. (2001)	$r(x) = -4\rho(1 - \alpha x^{-1/4})$	$\rho > 0$	$\theta = -\frac{1}{4}$	$\alpha(0) > 0$

In all these equations x is the size of the population, ρ is the Malthusian parameter, θ is the competition coefficient, and α is a parameter determined from environmental conditions. When populations grow to a saturation, α is related to the carrying capacity.

$\theta > 1$ then intra-specific competition is high, and the population takes more time to reach its asymptotic value, termed carrying capacity. If $0 < \theta < 1$ then competition is lower and the carrying capacity is reached earlier than in the corresponding logistic dynamics (Gilpin and Ayala, 1973; Gilpin et al., 1976).

The θ-logistic model, as it has been termed afterwards, introduced a new concept on population ecology that is the θ-selection strategies (Gilpin and Ayala, 1973; Gilpin et al., 1976). Originally, they proposed the model to explain data from competing *Drosophila* systems after failure to use a Lotka–Volterra-like model (Ayala et al., 1973). Afterwards, non-competitive versions of the system (i.e. one "allele" or one "species" model) have been used in conservation ecology to model avian population dynamics and calculate extinction times (Saether et al., 2000), and also to estimate the effects of environmental stochasticity on population growth (Saether and Engen, 2002). Other population models have included stochasticity to aid parameter estimation and study the effect of environmental changes in caprine populations (Saether et al., 2002). This model has also been employed in community ecology to estimate species abundance (Diserud and Engen, 2000). The θ-logistic equation is a "slightly more complicated model [that] yields significantly more accurate results", using the original words of Gilpin and Ayala (1973).

There are, however, other kinds of regulation terms that have been successfully employed to model other kinds of populations and growth. Sigmoid curves in particular are attractive for biologists, but are not necessarily described by θ-logistic equations. The von Bertalanffy (1966) equation, for example, is a sigmoid curve that is frequently used in allometric modelling, as well as the recently proposed (and controversial) curve derived from bioenergetic considerations by West et al. (2001). Another kind of sigmoid is given by the Gompertz equation (Gompertz, 1825), which was originally formulated to model human demographic data. The Gompertz equation has become an important tool in modelling tumour growth (Norton et al., 1976), although applications include a wider range of topics.

All of these sigmoid share the property of reaching carrying capacity, although they have different functional forms (Table 1), which confere distinct dynamical properties: inflection points, critical behaviours near $x = 0$, or rate of convergence to equilibrium.

However, not all populations obey saturated growth. Among non-saturated growths the first classical example is exponential growth, typically employed to describe bacterial cloning (Hershey, 1939), or simply as descriptors for non-regulated conditions of growth. A "general version" of the exponential is potential growth—which actually shows some kind regulation but does not reach a carrying capacity. Potential growth appears in tumour biology (Hart et al., 1998), early-life evolution (Szathmary and Demeter, 1987), lifehistory theory (Calder, 1984; Roff, 1986; Day and Taylor, 1997; Stearns, 2004), as well as in allometry (Peters, 1983; Calder, 1984; Brown and West, 2000). Potential growth functions is typically a consequence of complex systems where there are several levels of organization having a direct consequence on growth (e.g. Szathmary and Demeter (1987); West et al. (1997)).

Motivated by the θ-logistic equation, this paper introduces an alternative way to interpret and formulate population dynamics models. The description explained through out this paper reduces *exactly* to most common population models, including the above-mentioned growth dynamics (resumed in Table 1). With this new formalism general scaling laws are derived, using initial population size and carrying capacities. These scaling laws, include the heuristic scaling introduced by West et al. (2001) in allometry.

2. "Mechanics" of self-regulation

One of the central issues in population dynamics is to determine the growth function that describes a particular population. Growth dynamics in general can be expressed in the form

$$\dot{x} = x r(x). \tag{2}$$