Ecological Modelling 227 (2012) 56–63

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Describing interactive growth using vector universalities

L. Barberis*, C.A. Condat

IFEG-CONICET and FaMAF-Universidad Nacional de Córdoba, X5016LAE Córdoba, Argentina

ARTICLE INFO

Article history:
Received 7 October 2011
Received in revised form
12 December 2011
Accepted 15 December 2011
Available online 9 January 2012

Keywords:
Growth phenomena
Cooperation
Competition
Nonlinear dynamics

ABSTRACT

The Phenomenological Universalities are a formal way to classify growth. We apply this concept to investigate interactive growth phenomena in biological and ecological systems. Using a vector formulation of these Universalities without any *ad hoc* assumptions on the nature of the interactions, we are able to characterize the joint growth of two or more interacting organisms and assess the direct mutual influences between them, as well as the indirect influences that operate through environment modifications. Various interactions, such as cooperation, parasitism, and mutual hindrance can be suitably described. We present several illustrative examples, including an examination of the growth dynamics in a mixed-species plantation and compare the predictions of our method with the conclusions obtained by biologists through direct observation.

1. Introduction

Organisms have evolved to grow at rates adapted to their location in an ecological niche. Although the variety of organisms and niches is immense, many studies have been devoted to find general laws describing the growth rates of biological systems. These descriptions have often been based on simple dataset fitting, without attempting to correlate the fits to the underlying biophysical processes. However, some thought-provoking explanations have emerged: In their seminal work, West et al. (2001) and Zuo et al. (2008) described the observed uniformity in the ontogenetic growth rates of a multiplicity of organisms on the basis of energy conservation and the assumed fractality of the energy distribution networks. They showed that these assumptions lead to von Bertalanffian growth with a well-determined metabolic rate scaling exponent (with some caveats such as that this procedure cannot account simultaneously for the childhood and adulthood data in humans (Dingli and Pacheco, 2007)). Less well known is the work of Calderón and Kwembe (1991), who explained Gompertzian tumor growth in terms of entropy maximization. This work was later extended by the use of non-extensive thermodynamics (González and Rondón, 2006). Research in this field has been recently reinvigorated by careful studies of the properties of supply and collection networks (Dodds, 2010; Corson, 2010; Katifori et al., 2010).

The influence of competition between species and individuals has been the object of numerous studies since the pioneering works of Lotka (1925), Volterra (1926), and Gause (1934) and is now regularly discussed in population biology and population ecology textbooks (May, 1973; Murray, 2003; Edelstein-Keshet, 2005; Turchin, 2003). Our approach, however, is weakly related to population ecology because we look for data fitting functions in the spirit of model-selection (Burnham and Anderson, 2002; Zucchini, 2000): if the model that we can think of is too complex to be described in every detail from the information available or if no model exists, we still can extract information about the system by analyzing a suitable family of functions that fits the data.

A possible systematization of biological growth phenomena, which provides a suitable family of fitting functions, was achieved by Delsanto's group (Castorina et al., 2006), which developed the concept of Phenomenological Universalities (PUN) to classify some well-known growth laws. This PUN approach can be applied to unbiasedly extract information from a given experimental or observational dataset, and could be especially useful if no a priori model is available. It has been successfully applied to the analysis of problems in various disciplines (Castorina et al., 2006; Pugno et al., 2008; Delsanto et al., 2008, 2009; Gliozzi et al., 2009, 2010). Recently, we presented a PUN-based method to identify possible correlations between variations in the physical features of an organism. The method describes allometric growth with the use of a time-dependent complex function whose real and imaginary parts quantify two phenotypic traits of the same organism (Barberis et al., 2010; Delsanto et al., 2011).

A challenging field of study is that of the growth of resource-sharing interacting organisms. Such organisms can affect each other either through direct interactions or through indirect interactions mediated by the modifications introduced by the other actors in their environment. Twins in a womb, trees in a copse, and

* Corresponding author.
E-mail addresses: lbarberi@famaf.unc.edu.ar (L. Barberis), condat@famaf.unc.edu.ar (C.A. Condat).

0304-3800/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2011.12.011

cancer cell subpopulations in a tumor are obvious examples. In the case of plants it is an established fact that they nonadditively integrate information about resource and neighbor-based cues in the environment (Cahill et al., 2010).

The purpose of this paper is to develop a general framework to describe the growth dynamics of a given trait (height, weight, biomass, limb length, *etc.*) in a set of n agents undergoing interactive growth. By *agent* we mean any animal or vegetal organism or even an ecological population. This last case may encompass, for instance, cell subpopulations in a tumor or joint plantations of two or more tree species. A distinctive feature of these ecological problems is the presence of simultaneous intraspecific and interspecific competition for resources and space.

The results of the work presented in this paper provide a description of joint growth phenomena in a purely phenomenological way, *i.e.* for each growth-related dataset containing information about n agents, the Vector Universalities of class N (VUN) machinery gives n growth functions that may fit the data with great accuracy. These functions can be particularly advantageous when there is no preexisting theory to support the data. They could also be used to give an analytical approximation to data points obtained from the numerical integration of a mathematical model, such as a population dynamics or an evolutionary game theory model, which has no analytical solution. As we shall see, additional information can be obtained from the functions themselves concerning the nature of the interactions and the growth potential of the involved agents.

Suppose we have measurements of the size of a given trait taken on two or more agents that are known (or suspected) to have interacted during development. If we wish to investigate how the interaction affects growth, the usual strategy is to write down the growth equations for the separate specimens and, in some cases, postulate *ad hoc* interaction terms. Examples of such strategy are the separate Gompertz functions used to model protein growth in competing prawn populations (Sara et al., 2009) and population growth in microbial cocultures (Buchanan and Bagi, 1999). If a separate Gompertzian fit is performed on each dataset, the mutual interactions, the influence of the environment, and the intraspecific interactions, if any, will all be inextricably mixed in the Gompertz parameters of each agent, and the fits will not provide useful information on the strength and nature of the possible interactions. There are also theoretical models for competing Gompertzian (Yu et al., 2007; Kar, 2004) and θ-logistic (Gilpin and Ayala, 1973) populations, but in all these cases the couplings are introduced phenomenologically in such a way that they can describe the desired behavior. Since these models postulate the interaction terms, the fitted parameters that characterize the interaction will inform us only about its strength. The method is satisfactory if we know *a priori* the nature of the interaction, but this is often precisely what we want to identify. Often, we would like to predict what happens if two or more organisms are forced to cooperate or compete for resources in the same environment, *i.e.* we wish to develop rational predictions for the outcome of the interacting growth process in the absence of precise evidence about the form of the interaction. Preferably, the formalism should also help us to obtain information about the nature of the interactions. The VUN formalism we introduce here has no underlying model beyond the universality class scheme; the interaction effects emerge naturally and can be quantified. In summary, we put the PUN concept developed in references Castorina et al. (2006), Pugno et al. (2008), Delsanto et al. (2008, 2009), Gliozzi et al. (2009, 2010) in a vector context in such a way that each vector component represents the size of a trait in a given agent. The resulting formalism can be used to obtain simultaneous fits to the datasets corresponding to the different agents and separates the intraspecific and interspecific interactions.

The outline of this paper is as follows. In the following section we briefly review the PUN formulation and describe the VUN formalism, providing an interpretation of the results. In Section 3 we discuss three very different applications that illustrate the possible uses of the method. Finally, some potential applications of the method are briefly referred to in Section 4.

2. Vector Universalities

2.1. Scalar growth equations

A clear and comprehensive characterization of the growth functions of populations was presented by de Vladar (2006), who described growth using two first order differential equations, one for the population size $y(t)$,

$$\dot{y}(t) = a(t)y(t), \tag{1}$$

(the *growth* equation) and another for the growth rate $a(t)$,

$$\dot{a}(t) = [\theta a(t) - \rho]a(t), \tag{2}$$

(the *rate* equation) where θ and ρ are two real parameters. Various combinations of these parameters reproduce, among others, the θ-logistic, von Bertalanffy, Gompertz, and potential growth equations. De Vladar indicates that the size of the dimensionless parameter θ defines the density scale at which the reproduction rate of an individual is affected by its interaction with the population, while ρ^{-1} is a characteristic time over which the individual downregulates its reproduction rate.

In the work of Castorina et al. (2006), the right-hand side of Eq. (2) is replaced by a power series expansion in the rate $a(t)$,

$$\dot{a}(t) = \sum_{m=0}^{\infty} \alpha_m a^m(t). \tag{3}$$

Of course, by truncation and a suitable choice of the parameters α_m, Eq. (3) reduces to the different possibilities generated by Eq. (2), but Castorina et al. (2006) suggest that the concept of Phenomenological Universalities may be used in conjunction with Eqs. (1) and (3) as a tool for the classification and interpretation of observed data in the context of cross-disciplinary research. In fact, they have applied this concept to fields as diverse as those of elastodynamics (Pugno et al., 2008), human growth (Delsanto et al., 2008), and cell proliferation in cancer (Gliozzi et al., 2010).

In Barberis et al. (2010), the use of complex variables $y(t)$ and $a(t)$ made it possible to investigate the simultaneous variations of two phenotypic features of an individual. This procedure showed the existence of correlations between changes in the fat distribution of the human body. We are now interested in the description of the correlations between variations in the same trait of different agents. As in the original case, our generalization of the Phenomenological Universalities formulation is especially useful in those cases for which no reliable model is available.

2.2. Vector formalism

We describe the time evolution of a given phenotypic feature observed in n interacting agents through an n-component *growth vector* $Y(t)$, and postulate that the evolution of this vector is determined by a generalization of the autonomous growth equation proposed by Castorina et al. (2006),

$$\dot{Y}(t) = AY(t), \tag{4}$$

where t, the time, is a real continuous parameter, $Y(t) \in \mathbb{R}^n$, and the dynamic operator $A[Y(t)] \in \mathbb{R}^{n\times n}$. According to the PUN formulation, we assume that the rate of change of the functional $A[Y(t)]$