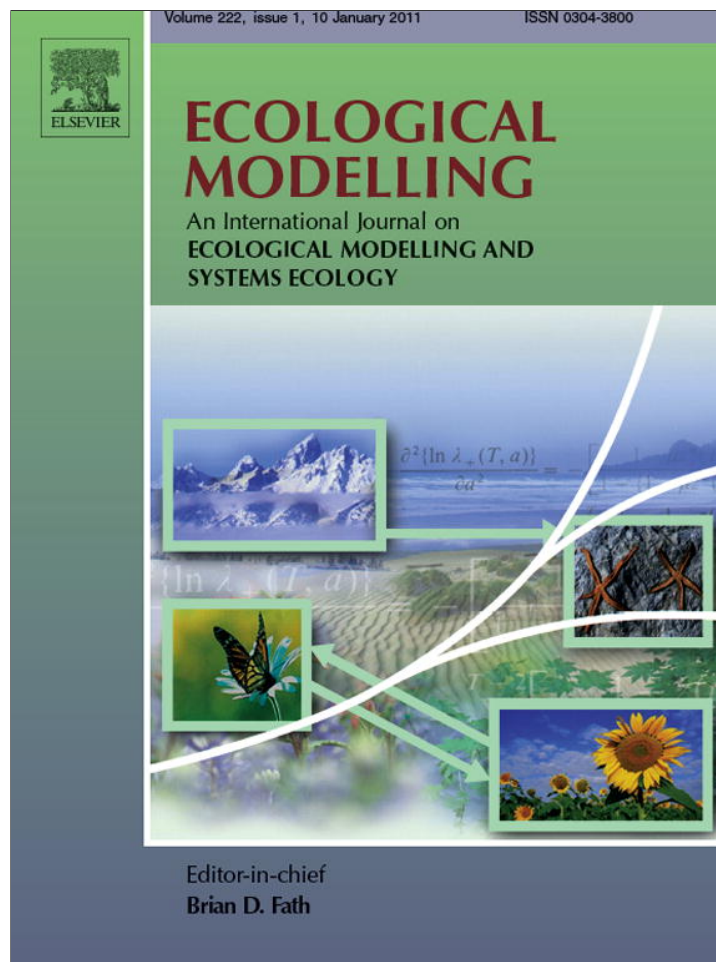


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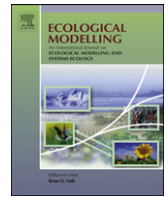
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Describing interactive growth using vector universalities

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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.

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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

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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 pre-existing 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 $y(t)$,

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

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

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

(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 $a(t)$,

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

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),

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

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 $A[Y(t)]$

can be expressed as a power series expansion in the operator A itself, which we truncate to order N ,

$$\dot{A}(t) = \sum_{m=1}^N \alpha_m A^m. \quad (5)$$

Eqs. (4) and (5) form a differential equation system whose initial conditions are $Y(0) = Y_0$ and $A(0) = A_0$. To solve this system, we start by integrating Eq. (5). The first step is to diagonalize the matrix A_0 through a similarity transformation,

$$B_0 = PA_0Q, \quad (6)$$

with $QP = 1$. This transformation always exists if the eigenvalues λ_j of A_0 are nondegenerate. B_0 is a diagonal matrix whose entries are the λ_j 's. Crucially, it can be shown (Barberis et al., 2011) that the same transformation that diagonalizes the system at time $t = 0$ diagonalizes it for all $t \geq 0$. Eq. (5) can thus be transformed into a new diagonal system,

$$\dot{B}(t) = \sum_{m=1}^N \alpha_m B^m. \quad (7)$$

Since B is a diagonal matrix whose components have the form $B_{ij}(t) = b_N(\lambda_j; t)\delta_{ij}$ (δ_{ij} is Kronecker's symbol), Eq. (7) can be decomposed into a set of n uncoupled differential equations,

$$\dot{b}_N(\lambda_j; t) = \sum_{m=1}^N \alpha_m [b_N(\lambda_j; t)]^m, \quad (8)$$

with the initial condition $b_N(\lambda_j; 0) = \lambda_j$. These equations are easily integrated for $N = 0, 1$, and 2 , yielding $b_0(\lambda_j; t) = \lambda_j$, $b_1(\lambda_j; t) = \lambda_j \exp(\alpha_1 t)$, and $b_2(\lambda_j; t) = \lambda_j \alpha_1 [(\alpha_1 + \lambda_j \alpha_2) \exp(-\alpha_1 t) - \lambda_j \alpha_2]^{-1}$, respectively. The transformed growth vector $Z(t) = QY(t)$ satisfies the uncoupled system,

$$\dot{Z}(t) = B(t)Z(t). \quad (9)$$

Since B is diagonal, the components of $Z(t)$ are easily calculated; they have the form $z_j = z_{0j} f_N(\lambda_j; t)$, where the $f_N(\lambda_j; t)$ are the universal functions obtained by Castorina et al. (2006). We can thus immediately find the time-dependent growth vector by inverting the transformation, i.e., by writing $Y(t) = PZ(t)$. Its components have the form,

$$y_i(t) = \sum_{j,k=1}^n P_{ij} Q_{jk} y_{0k} f_N(\lambda_j; t), \quad i = 1, \dots, n \quad (10)$$

Here the truncation order N determines the *Vector Universality Class* VUN, whose elements are linear combinations of the functions $f_N(\lambda_j; t)$. The lowest truncation orders yield,

$$f_0(\lambda_j; t) = \exp(\lambda_j t), \quad (11)$$

$$f_1(\lambda_j; t) = \exp\left[\frac{\lambda_j}{\alpha_1} [\exp(\alpha_1 t) - 1]\right], \quad (12)$$

$$f_2(\lambda_j; t) = \left\{ \frac{\alpha_2 \lambda_j}{\alpha_1} [1 - \exp(\alpha_1 t)] + 1 \right\}^{\frac{1}{\alpha_2}}. \quad (13)$$

2.3. Interpretation

The solutions (11)–(13), which depend on the eigenvalues λ_j of the dynamical operator, correspond, respectively, to joint Malthusian (VU0), joint Gompertzian (VU1), and joint von Bertalanffian (VU2) growth processes. They apply to n interacting agents and are natural generalizations of the functions obtained in Castorina et al. (2006) for the single-agent problem.

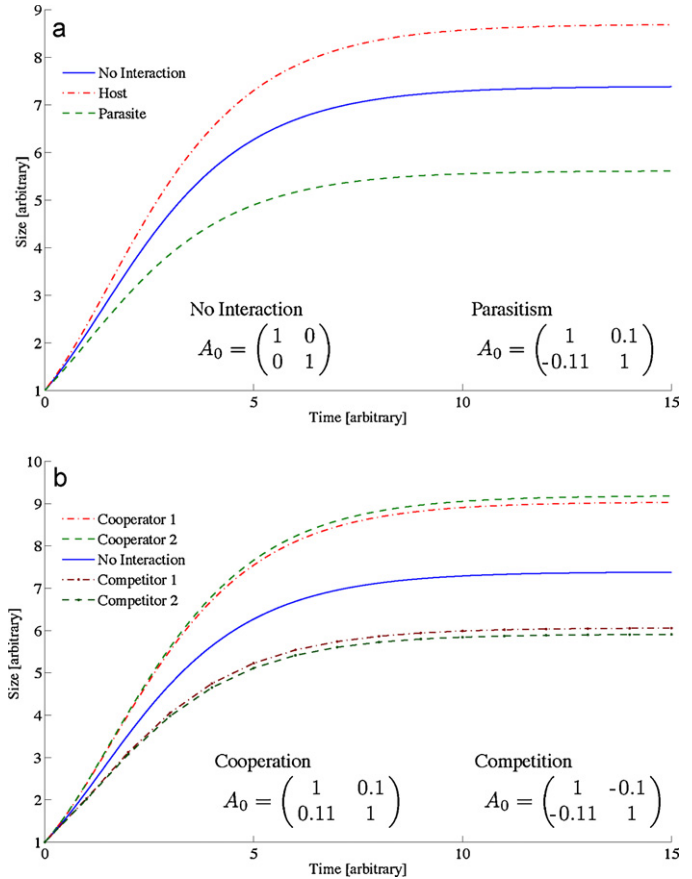


Fig. 1. Three examples of two-agent interaction-influenced growth characterized by the A_0 matrix. For simplicity, the two diagonal elements (the IGP) and the initial values have been chosen to be identical. In (a) we represent a parasite–host relation (off-diagonal elements have different signs), while in (b) we represent the enhanced growth of cooperators (off diagonal elements positive) and the depressed growth of mutually hindered competitors (off diagonal elements negative).

Remarkably, the diagonalization of the dynamic operator A_0 at a fixed time results in the uncoupling of the system at all subsequent times. This indicates that the interaction dynamics can always be characterized by its elements at all times. The diagonal elements of A_0 determine the maximum size corresponding to the noninteracting agents and thus its trace characterizes the global potential growth of the n independent agents. We can say that each diagonal element defines the individual growth potential (IGP) of the corresponding agent in a given environment. Agent–agent interactions not only generate nonzero off-diagonal elements (the *direct* interactions), but may also modify the diagonal elements. This would occur if there are *indirect* influences among the agents, as it would be the case if the agents themselves modify the growth environment and, consequently, change their own IGP. We can thus describe various kinds of n -agent growth processes with n^2 real numbers, which allows us to quantify and classify various ecological-like interactions. Some representative situations in the VU1 class are depicted in Fig. 1 for the case of two agents. As a benchmark, we have chosen a trait that would evolve identically in each of the agents in the absence of interactions. For simplicity, we will assume here that the agents only influence each other directly, i.e., without modifying the environment. Then, all the interaction effects are represented by off-diagonal matrix elements. For a *parasitic* interaction, the trait of one of the agents grows at the expense of the other, while for a *cooperative* (synergistic) interaction both agents benefit and for a *mutual hindrance* (antagonistic) interaction

both agents are negatively affected. The signs of the off-diagonal matrix elements determine how much an agent may gain (positive elements) or lose (negative elements) from the direct interaction. Note that the reciprocal of α_1 defines a time scale that characterizes the joint growth rate.

3. Applications

Next we provide three examples to illustrate the use of the VUN to obtain information about the relevant interactions in a given system. The first is a heuristic population model that has not been obtained from a physically meaningful hypothesis but provides reasonable numerical solutions. The second is a macroscopic model for the joint growth of two cell phenotypes in a tumor. The third example refers to real experimental data obtained from mixed plantations of Acacia and Eucalyptus trees, which had not been mathematically modeled. In the three examples we fit the given datasets with VUN equations and provide an interpretation of the resulting A_0 matrix.

3.1. A Gompertzian population dynamics: a VU1 application

Our first example is the generalized Gompertz model for two species (1 and 2) as was postulated in Kar (2004). This is a heuristic population dynamics model, which is defined by the following equations for the populations N_1 and N_2 :

$$\frac{dN_1}{dt} = N_1[k_1 - h_{11} \ln(N_1) - h_{12} \ln(N_2)], \quad (14)$$

$$\frac{dN_2}{dt} = N_2[k_2 - h_{21} \ln(N_1) - h_{22} \ln(N_2)], \quad (15)$$

where the k_i and h_{ij} are, respectively, the growth and competition rates. The diagonal h_{ii} rates stand for intraspecific negative interactions, while the nondiagonal h_{ij} rates stand for negative influences between the populations. This set of equations does not have an analytical solution, but we will show that the VUN approach gives a very good analytical approximation to the real solution. To do this we build two datasets by the numerical integration of Eqs. (14) and (15). Each dataset describes the evolution of the populations N_1 and N_2 , which we fit using the VU1 class (Fig. 2).

For the first dataset (Fig. 2a), we assume that population 1 parasitizes (or preys on) population 2 ($h_{21} = 0.0001$), while population 2 does not directly influence population 1 ($h_{12} = 0$). In order to isolate the effects of the interspecific (predation/parasitic) interaction, we set the same initial population sizes, growth rates and intraspecific interactions for both populations ($N_i = 1$, $k_i = 0.1$ and $h_{ii} = 0.01$, $i = 1, 2$). The VU1 method fits this dataset with excellent precision, with coefficients of determination $R_{VU1}^2 \simeq 0.9995$. These coefficients are defined in the usual way as the normalized measure of the distances between the data points $y_i^*(t)$ and their respective predicted values $y_i(t)$. A VU2 fitting, on the other hand, yields $\alpha_2 \rightarrow 0$, and $R_{VU2}^2 \rightarrow R_{VU1}^2$, i.e. VU2 reduces to VU1 (a Gompertzian-like model is recovered). Here and in what follows the nonlinear fits were performed using the “Trust-Region-Reflective” algorithm in the MATLAB environment. This procedure allowed us to obtain accurate values for the parameters. The high R^2 values confirm the suitability of the VUN classification as was pointed out in Delsanto et al. (2008). The A_0 matrix obtained from this fit yields the following information: the parasite population obtains some benefit ($a_{12} = 0.00062 > 0$) from its host population, which loses ($a_{21} = -0.00054 < 0$) growth capability as the outcome of the parasitic (or predatory) interaction. Since we chose $h_{11} = h_{22}$ and relatively weak interspecific interactions, it is not surprising that the IGP's turn out to be quite close to each other. From this example, we conclude that the assumed benefits (or disadvantages) of the interspecific interaction are closely reproduced by the A_0 matrix.

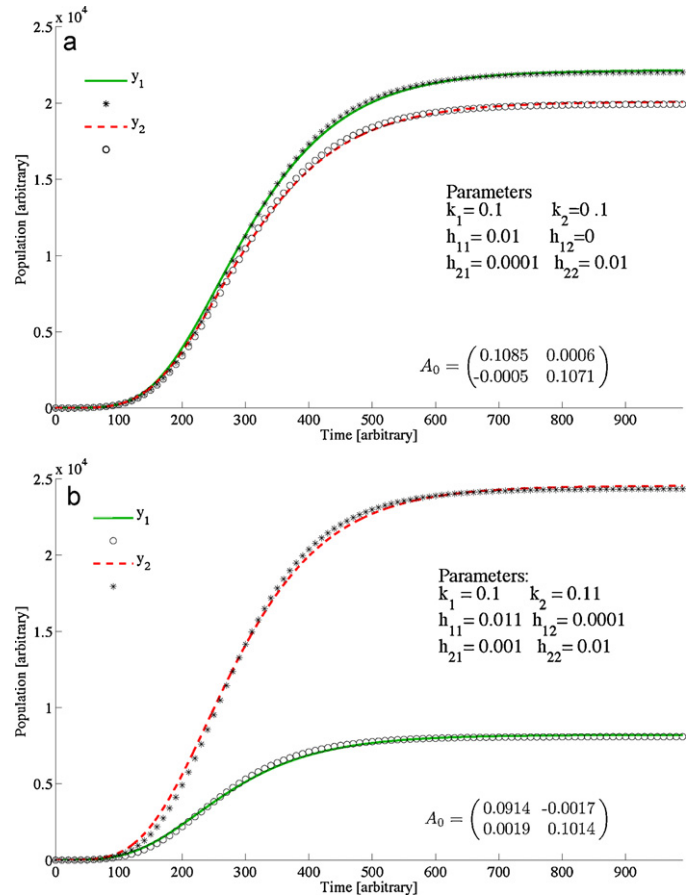


Fig. 2. Two examples of VU1 fits to Kar's model (Kar, 2004): (a) In the absence of a direct action of population 2 on 1 ($h_{21} = 0$), the A_0 matrix confirms that species 1 must be either a parasite or a predator ($a_{12} > 0$), while $a_{21} (< 0)$ quantifies the losses suffered by the parasitized (or predated) species. Here $R_1^2 = 0.99964$ and $R_2^2 = 0.99959$. (b) Starting with arbitrary values of the model parameters, VU1 not only provides a very good fit but also helps us to interpret the data (see text). Here $R_1^2 = 0.99848$ and $R_2^2 = 0.99902$.

The second illustrative dataset corresponds to an arbitrary parameter setting: $k_1 = 0.1$; $k_2 = 0.11$; $h_{11} = 0.011$; $h_{12} = 0.0001$; $h_{21} = 0.001$; $h_{22} = 0.01$, $y_{01} = 1$; $y_{02} = 1.1$. Since in this set-up both populations have advantages and disadvantages, it is not easy to see, at first glance, what the outcome of their interaction will be. But the results of the VU1 fits, shown in Fig. 2b, help us to interpret what happens in the system: the IGP's are of the order of the k_i but not equal to them. The IGP's are not simply Gompertzian growth rates, but they must account for the environmental contributions to growth and for the intraspecific interactions. The opposite signs of the Direct Interaction Factors (DIFs) a_{12} and a_{21} reveal a parasitic (or predatory) behavior. These DIFs represent the net effect of complex interactions on each population, in such a way that the parasite–host (or predator–prey) interpretation of the interaction is clear-cut only if both populations have similar IGP's. Otherwise, it is difficult to assign precise roles to each population.

These examples show how the VU1 method can not only fit data points generated by a population model with no analytical solution, but also help us to interpret the data.

3.2. Growth of a heterogeneous tumor spheroid: a VU2 application

Multicellular tumor spheroids (MTS) are spherical aggregations of tumor cells that may be grown *in vitro* under strictly controlled conditions (Hamilton, 1998; Mueller-Kliesler, 2000). Since oxygen

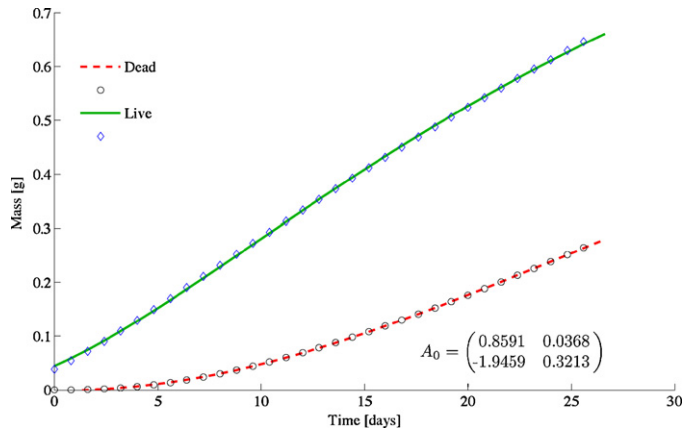


Fig. 3. VU2 fitting for a growth model of an implanted tumor spheroid. The dataset starts at the onset of necrosis. The A_0 matrix describes how the necrotic subspecies benefits from the living cell population, which is negatively affected by the necrosis and limited in its growth by necrotic cell generated inhibitors. We set $\alpha_2 = -1/3$ in agreement with the assumptions of Condat and Menchón (2006) for diffusion-mediated feeding. Here $R_1^2 = 0.99997$ and $R_2^2 = 0.99981$.

and nutrients cannot diffuse beyond a viable outer shell, spheroids whose diameters exceed a few tenths of a millimeter develop a necrotic core. Due to their simple geometries and the possibility to produce them in large quantities, MTS have become popular model systems for cancer research. It was shown by Guiot and coworkers that the growth of a homogeneous spheroid can be described in terms of the ideas proposed in West et al. (2001) by a von Bertalanfian growth equation (Guiot et al., 2003; Delsanto et al., 2004). This description was later generalized to spheroids containing a necrotic core by Condat and Menchón (2006) and Menchón and Condat (2007). The time evolution of the live (m_{live}), necrotic (m_{dead}) and total ($M = m_{live} + m_{dead}$) spheroid masses is given by the equations,

$$\frac{dM}{dt} = cM^{\frac{2}{3}} - b[M - (M^{\frac{1}{3}} - \tilde{m}^{\frac{1}{3}})^3], \quad (16a)$$

$$\frac{dm_{dead}}{dt} = M^{-\frac{2}{3}}(M^{\frac{1}{3}} - \tilde{m}^{\frac{1}{3}})^2 \frac{dM}{dt}, \quad (16b)$$

$$\frac{dm_{live}}{dt} = \frac{dM}{dt} - \frac{dm_{dead}}{dt}, \quad (16c)$$

where \tilde{m} is the MTS mass at the time the first dead cell appears, and b and c are the metabolic rates defined in West et al. (2001). The key assumptions used to obtain Eqs. (16b) and (16c) are the validity of the growth description in West et al. (2001) and the constancy of the thickness Δ of the outer live cancer cell shell, a feature first predicted by Burton (1966) and then discussed by Groebe and Mueller-Klieser (1996). This equation has been shown to provide a precise fit to Steel's experimental data on implanted spheroids (Steel, 1977) as reported by Guiot et al. (2006). In Fig. 3 we present synthetic datasets for the live and necrotic MTS masses obtained using the constant Δ assumption and Eq. (16b) with the parameters given by Menchón and Condat (2007). From the fit of experimental data: $m = 0.03496$ g, $c = 0.2812$ g^{1/3}/day and $b = 0.3515$ 1/day. The data obtained by this procedure were then fitted by using VU2. In the figure, the time $t = 0$ corresponds to the onset of necrosis (at earlier times a single species was present). The excellent values of the coefficients of determination R^2 bear witness to the quality of the fit. The resulting A_0 matrix reveals that the necrotic cells (species 1) benefit from the presence of the live cancer cells (species 2), while the increase in the number of the latter is handicapped by their transformation into necrotic cells ($a_{12} > 0$ and $a_{21} < 0$). This asymmetry results in a decrease in the slope of the live cell population (the large initial slope of this population results from a preceding period without necrosis, i.e. without interspecies competition).

Table 1

VU1 simultaneous fittings to diameter datasets of mixed populations of *E. globulus* (species 1) and *A. mearnsii* (species 2) trees (Forrester et al., 2004). The a_{ij} are the elements of the dynamic matrix A_0 . The absolute value of α_1 is the inverse of a joint characteristic growth time. The y_{0j} are the (extrapolated) initial diameters. The R_j^2 ($j = 1, 2$) are the respective coefficients of determination.

	100E:0A	75E:25A	50E:50A	25E:75A	0E:100A
a_{11}	0.5566	0.5831	0.6923	0.5951	–
a_{22}	–	0.7538	0.7328	0.6370	0.4877
a_{12}	–	–0.0029	–0.0078	–0.0092	–
a_{21}	–	–0.8056	–0.5910	–0.5295	–
y_{01}	1.1603	1.1447	1.123	1.2444	–
y_{02}	–	3.4779	3.1280	3.2797	2.8627
α_1	–0.2421	–0.2460	–0.2685	–0.2276	–0.3517
R_1^2	0.9950	0.9905	0.99637	0.9904	–
R_2^2	–	0.9891	0.9884	0.9867	0.9858

The results are exceedingly good: the VU2 fitting has a remarkable regression parameter ($R^2 > 0.9998$) for both datasets. The smaller value of a_{22} as compared to a_{11} may be at least partially attributed to the generation of growth inhibitors by the necrotic cells; these inhibitors modify the environment of the live cells, constraining their growth.

Incidentally, Fig. 3 shows that the VU2 functions can adequately fit points located approximately along a straight segment.

3.3. Dynamics of mixed plantations: an empirical case study

As a final example, we use the VUN formalism to analyze the growth dynamics of mixed plantations of *Eucalyptus globulus* and *Acacia mearnsii*, which have been exhaustively studied by Forrester et al. (2004, 2005b, 2006) and Richards et al. (2010). It was observed that *E. globulus* heights, diameters and above-ground biomass are higher in mixtures than in monocultures. Indeed, the diameters and heights of both species increase nearly monotonically with the degree of admixture. Since there is no obvious *a priori* mathematical model to describe the relevant tree-tree interactions, the VUN appear to be especially well-suited to investigate them.

In the preceding examples, the Kar and spheroid models are, by construction, in the VU1 and VU2 classes, respectively. In particular, the spheroid growth equations are based on the ideas of West and co-workers, so that they are directly in VU2. Since there is no *a priori* choice for the mixed plantations, the Occam's razor criterion suggests the use of VU1, which has one parameter less. Furthermore, according to our experience with the use of these functions, VU1 generally works better when there are strong variations at intermediate times.

The experimental values of tree diameters for three degrees of admixture are depicted in Fig. 4, together with the corresponding VU1 fits, as functions of time. As it is shown in Table 1, the R^2 coefficients have very good values; indeed the p -value (the probability of having a value of R^2 at least as good as the one obtained) is lower than 0.001 in all cases, confirming the robustness of the fitting method.

The A_0 elements a_{ij} resulting from VU1 fits to diameter data are presented in Table 1. The analysis of the matrix elements corresponding to the various mixtures yields the following qualitative features:

- The *E. globulus* IGP (a_{11}) grows with the addition of *A. mearnsii* (which we interpret as an environment-mediated enhancement), reaching a maximum for the 50:50 admixture; for higher admixtures it decreases. Thus, the 50:50 admixture appears to provide the optimal conditions for *E. globulus* growth, although observation indicates that at the 11th year *E. globulus* diameters are

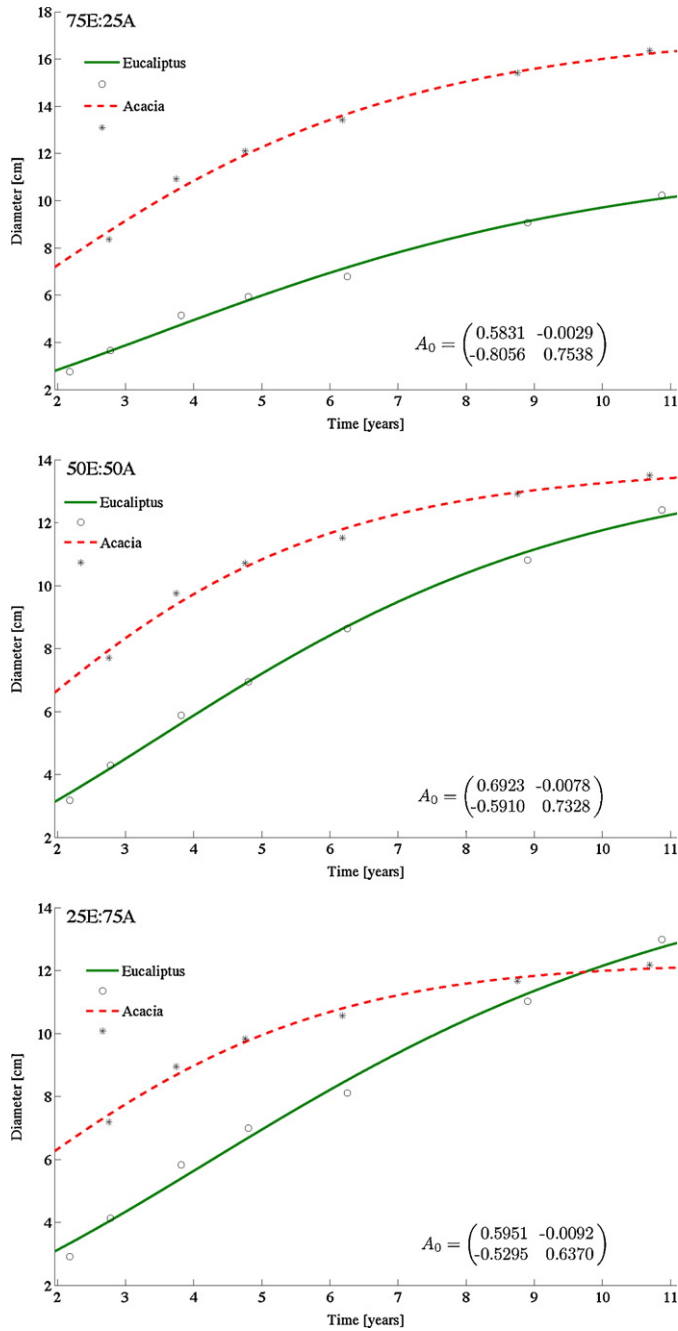


Fig. 4. VU1 simultaneous fits to diameter datasets of mixed populations of *E. globulus* (species 1) and *A. mearnsii* (species 2) trees (Forrester et al., 2004). The species proportions and the corresponding A_0 matrices are specified in the figure. Other parameters and the regression coefficients are given in Table 1. Note the strong increase in *E. globulus* diameters for the acacia-rich mixtures (*A. mearnsii* also benefits from growing in mixture). Here R_1^2 and R_2^2 are given in Table 1.

slightly larger for 25:75 admixtures. *A. mearnsii* not only dilutes the *E. globulus* concentration but also affects other growth-related factors. For example *A. mearnsii* increases nutrient availability via accelerated rates of nitrogen and phosphorus cycling (Forrester et al., 2005a) and symbiotic nitrogen fixation (Forrester et al., 2007).

- The *A. mearnsii* IGP (a_{22}) increases monotonically when the *E. globulus* admixture increases. This result indicates that the main effect of *E. globulus* is to decrease the intraspecific competition between acacia trees.

Table 2

U1 (Gompertzian) fittings to diameter datasets taken separately for populations of *E. globulus* (gray) and *A. mearnsii* (white) inside a mixture.

	100E:0A	75E:25A	50E:50A	25E:75A	0E:100A
a_{0E}	0.5566	0.5470	0.6540	0.5503	–
a_{0A}	–	0.5700	0.6021	0.6200	0.4877
α_E	–0.2421	–0.2370	–0.2610	–0.2180	–
α_A	–	–0.3350	–0.3823	–0.3994	–0.3517
y_{0E}	1.1603	1.1996	1.1590	1.2965	–
y_{0A}	–	3.0952	2.8337	2.6608	2.8627
R_E^2	0.9950	0.9900	0.9960	0.9905	–
R_A^2	–	0.9900	0.9872	0.9898	0.9858

- As noted before, the negative values of a_{12} and a_{21} can be interpreted as representing a negative direct influence of the presence of one species on the growth of the other. Since the increase in the *A. mearnsii* IGP is bigger than that of *E. globulus* IGP, they compensate their bigger DIF losses ($|a_{12}| < |a_{21}|$). The large negative value of a_{21} is probably responsible for the fact that the *E. globulus* diameter eventually overtakes that of *A. mearnsii* for the 75% acacia admixtures.
- The absolute value of the parameter α_1 , which is the inverse of a joint characteristic growth time, does not change much with the degree of admixture. It has a weak maximum for the 50:50 admixture and then decays, in accordance with the observation that the diameters of 25:75 Eucalyptus trees take longer to reach their maximum asymptotic value. However, we notice that α_1 is only slightly bigger than the α_E values resulting from a U1 (purely Gompertzian) fit to the *E. globulus* data (see Table 2). The value of α_1 is always determined by the slowest-growing species.

A completely similar analysis can be carried out for the height data from (Forrester et al., 2004). After noting that the diameters of both tree species increase due to the admixture, Forrester et al. (2004) interpreted this as meaning that the weakening of the intraspecific interaction (due to the reduction in the tree density of each species) dominates the direct interspecific effect. A similar observation had been previously made by Debelle et al. (1997), who explained the increase in height and diameter of *Eucalyptus saligna* when mixed with *Albizia falcataria* by the reduction in intraspecific competition between *E. saligna* trees and nutrient status enhancement. This interpretation is also consistent with theoretical results indicating that when species coexist competition is stronger within than between forest tree species (Clark, 2010). This is all in agreement with the VUN interpretation of the experiment.

The advantages of the VUN can be put into perspective if we compare Table 1 with the data shown in Table 2. In this Table we present the results of separate, species specific U1 (Gompertzian) fittings for each species to the same datasets as used for Table 1. The monocultures (columns 1 and 5) have the same parameter values as in Table 1 because the VUN reduce to separate UN equations in this limit. The corresponding solutions have the form,

$$y_j(t) = y_{0j} \exp \left[-\frac{a_{0j}}{\alpha_j} \left(\exp \left(\frac{t}{\alpha_j} \right) - 1 \right) \right], \quad (17)$$

where the index j stands for *E. globulus* or *A. mearnsii*. Because there are no crossed terms in these fittings, the modifications introduced by changing the degree of admixture are collected in the individual parameters for each species. All the results presented in Table 2 are compatible with observation. For instance, the inverse characteristic time $|\alpha_E|$ is smaller than $|\alpha_A|$, in agreement with the observation that *E. globulus* grows over longer periods than *A. mearnsii*. However, these results do not reveal anything new about the system, because the simple U1 model does not allow

us to discriminate the origin of the interactions. If VU1 fittings are performed instead, as in Table 1, the interspecific interactions are separated from the intraspecific ones, and new, useful information can be extracted.

4. Possible extensions

In the preceding section we have worked out examples where two agents are jointly growing, but it is possible to describe in detail interactions between three or more agents. In the case of an n -agent system, we can obtain $3^{n(n-1)}$ possible interaction combinations by modifying the signs of the nondiagonal elements of the dynamic matrix, or taking some of them equal to zero. For instance, if all nondiagonal matrix elements are positive, we will have a completely synergistic interaction where all agents benefit from the presence of the other agents. The possible applications of the many agent system deserve a more detailed study.

Although the main goal of the UN formalism is to classify joint growth using a universal framework, the natural emergence of interaction parameters could be useful to understand other biology-related problems. An intriguing possibility is to apply the method developed here to those problems in evolutionary biology and ecology where an outcome can be influenced by the interactions involved in the competition for resources in a given ecosystem. For instance, both Life History Theory (LHT) (Stearns, 2000) and Evolutionary Game Theory (EGT) (Argasinski, 2006) address the problem of evolution by following the adaptation of a (physiological, morphological or strategic) trait to the environmental conditions. The populations involved in such studies might grow until they reach a stable state in which the coexistence of the best strategies is possible. But LHT does not say what happens during the fixation process for the involved traits. Indeed, in Stearns (2000), the author writes: "One limitation of optimality theory is that it provides no opportunity to consider what happens when two or more life history phenotypes compete with each other within a population". If a given trait in LHT becomes fixed, it could be due to an (interspecific) advantage over the others or because it weakens some intraspecific competition process. In EGT, the pay-off matrix, which determines the interaction between (intraspecific and interspecific) strategies, remains constant in time, while the A_0 matrix contains the initial conditions for the temporal evolution of the interaction. Since the VUNs are adequate to make predictions on the outcome of the interactions between specimens sharing an environment, it could evolve into a useful tool to work in the framework of LHT and EGT.

In summary, the vector version of the Phenomenological Universalities formalism presented here is an adequate framework for studying the joint growth of interacting agents, admitting direct and indirect, *i.e.*, environment mediated, influences. It leads to a natural generalization of the usual ontogenetic growth laws whose power and convenience have been exhibited through several examples, including the characterization and interpretation of a concrete ecological system.

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