



Is structural sensitivity a problem of oversimplified biological models? Insights from nested Dynamic Energy Budget models



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ABSTRACT

Many current issues in ecology require predictions made by mathematical models, which are built on somewhat arbitrary choices. Their consequences are quantified by sensitivity analysis to quantify how changes in model parameters propagate into an uncertainty in model predictions. An extension called structural sensitivity analysis deals with changes in the mathematical description of complex processes like predation. Such processes are described at the population scale by a specific mathematical function taken among similar ones, a choice that can strongly drive model predictions. However, it has only been studied in simple theoretical models. Here, we ask whether structural sensitivity is a problem of oversimplified models. We found in predator–prey models describing chemostat experiments that these models are less structurally sensitive to the choice of a specific functional response if they include mass balance resource dynamics and individual maintenance. Neglecting these processes in an ecological model (for instance by using the well-known logistic growth equation) is not only an inappropriate description of the ecological system, but also a source of more uncertain predictions.

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1. Introduction

Facing current socio-environmental issues, such as species extinctions and loss of ecosystem services, requires to make ecological predictions with a level of accuracy that is not yet achieved (Morozov, 2017; Mouquet et al., 2015; Pennekamp et al., 2017). Uncertainty arises in predictions made by mathematical models, which are perceived as objective tools but remain simplified representations built on somewhat arbitrary choices (Anderson, 2005; 2010). Among these choices, two types can be distinguished. The first ones are the processes and components (e.g. species, nutrients) to include, which are often a consensus between scientists from different ecology-related disciplines (animal and plant biology, microbiology, chemistry, physics, Demongeot et al., 2009). Those choices are assumptions that can be discussed, and testing their consequences on predictions helps to improve ecological theories. The second type of choices is still an open issue and is the mathematical function selected to model a given process (Lafferty et al., 2015). A process can be described by many functions that fit available data with the same accuracy but that

are based on different assumptions. Whereas different assumptions about the emerging process shape (e.g. density-dependence, group behaviour) have been widely considered in the literature, the choice between similar functions (i.e. mechanisms) to model the same process shape (e.g. process rate increases with population abundance) has received only little attention in ecology. However, this attention has increased in the past decade since the preliminary work by Myerscough et al. (1996) and Wood and Thomas (1999), followed by Gross et al. (2004) and Fussmann and Blasius (2005). Recent studies indicate that this choice can deeply affect both qualitative and quantitative predictions (Cordoleani et al., 2011), including those at the food web level or about system resilience (Aldebert et al., 2016a, 2016b). This concept extends the idea of parameter sensitivity, as it becomes the sensitivity of model predictions to any change in parameter values and/or model formulation (see Cordoleani et al., 2011, for a proper mathematical formulation). This more general concept has been coined structural sensitivity.

Structural sensitivity emerges if several scales of organization, space and/or time are entangled in a complex process. Such a process is for instance predation. Predation involves individual to population level mechanisms that are often summarized at the population scale by one function, the functional response (Solomon, 1949). Many functional responses can be derived de-

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pending on the mechanisms considered (Jeschke et al., 2002). A mechanism underlying a formulation (e.g. prey handling) might be relevant, but additional assumptions that translate it into mathematics (e.g. space homogeneity, no individual variability) are almost always violated. Thus, the best formulation from a theoretical point of view might not be the best quantitative description of data. As this uncertainty propagates into model predictions, Gross and Feudel (2006) and Adamson and Morozov (2012) proposed approaches based on generic (partially-specified) models. These generalized models avoid the issue of structural sensitivity and are useful to draw widely applicable conclusions in theoretical studies (Gross et al., 2009). However, such models hardly consider non-equilibrium dynamics (Kuehn and Gross, 2013) and tell nothing about the existence of alternative stable states, two important characteristics of living systems (Fussmann et al., 2000; Scheffer et al., 2012) that can be affected by structural sensitivity (Aldebert et al., 2016b).

In this study, we suggest an alternative way to deal with structural sensitivity that applies to systems with non-equilibrium dynamics and alternative stable states. Structural sensitivity has only been studied in theoretical population models, where population growth is logistic for the prey and proportional to the feeding rate for the predator. So, one may think that structural sensitivity is a problem of oversimplified models. We test this hypothesis by presenting the first study on structural sensitivity in ecosystem models (*sensu* with explicit resource dynamics) that include various level of details to describe individual metabolism.

Modelling individual metabolism requires to add processes and create model sensitivity to their formulation. Mechanistic formulations of metabolic processes can be derived from Dynamic Energy Budget (DEB) theory (Jusup et al., 2017; Kooijman, 2010). This reductionist theory focuses on the individual level, as it allows to make easy mass and energy budgets. As a consequence, the formulation of metabolic processes is constrained by the laws of thermodynamics. Another advantage of DEB theory is that it provides a level of abstraction that allows generalization to many living organisms.

To test whether structural sensitivity is a result of model oversimplification, we focus on a predator–prey system of dividing unicellular organisms living in a chemostat-like environment (Fig. 1(a)). This system is modelled using different functional responses (Fig. 1(b)) and levels of metabolic details (Fig. 1(c)). For the metabolism, we consider a predator–prey model based on DEB theory (Kooi and Kooijman, 1994) that describes chemostat experiments and includes two buffers between feeding and population growth: an energy reserve and maintenance costs. These two features are neglected at limit cases of this model, leading to three simpler models: Droop (1973), Marr–Pirt (Marr et al., 1963) and Monod (1942) models. Thus, these four models are nested within the framework of DEB theory.

Next section presents the nested predator–prey models. Then, their predictions are analyzed and discussed in the light of the general question: Is structural sensitivity a problem of oversimplified biological models? Discussion ends with a synthesis of research on structural sensitivity that leads to a guidance for ecologists in their modelling choices.

2. Models

2.1. Functional responses to model predation

To model predation, we consider the next three functions (Fig. 1(b)):

$$F^H(X) = \frac{j_{XAm}^H X}{X + K^H}, \quad F^I(X) = j_{XAm}^I (1 - \exp(-X/K^I)),$$

$$F^t(X) = j_{XAm}^t \tanh(X/K^t), \quad (1)$$

where X is prey biomass, j_{XAm} is the maximum assimilation rate and j_{XAm}/K is the function slope at 0. The classical Holling functional response F^H assumes that a predator splits its activity between searching and handling prey (Holling, 1965). It is equivalent to Michaelis–Menten function for enzyme kinetics. Ivlev functional response F^I is based on digestion (Ivlev, 1955). Conversely, the hyperbolic tangent function F^t has no theoretical basis, but it happens to be an appropriate description of data (Jassby and Platt, 1976) and it is used in some population models (Cordoleani et al., 2011; Fussmann and Blasius, 2005). The three prey-dependent functions (1) are type-II functional responses (they vanish at zero, are strictly increasing, concave and saturating). However, the same exercise can be performed with more complex functions like type-III (sigmoid) or ratio-dependent functional responses.

2.2. Predator–prey models

Starting from a DEB model for unicellular dividing individuals (Appendix A), Kooi and Kooijman (1994) proposed the following model (referred as DEB model) to describe a predator–prey system living an environment described by a chemostat:

$$\begin{cases} \frac{de_1}{dt} = k_E^1 (f_1(X_0) - e_1) \\ \frac{de_2}{dt} = k_E^2 (f_2(X_1) - e_2) \\ \frac{dX_0}{dt} = h(X_r - X_0) - F_1(X_0)X_1 \\ \frac{dX_1}{dt} = \left(\frac{k_E^1 e_1 - k_M^1 g_1}{e_1 + g_1} - h \right) X_1 - F_2(X_1)X_2 \\ \frac{dX_2}{dt} = \left(\frac{k_E^2 e_2 - k_M^2 g_2}{e_2 + g_2} - h \right) X_2. \end{cases} \quad (2)$$

The prey (structure X_1 and scaled reserve density e_1) feeds on an inorganic resource (concentration X_0) and is eaten by a predator (structure X_2 and scaled reserve density e_2), with $f_i(X_{i-1}) := F_i(X_{i-1})/j_{XAm}^i$, $i = 1, 2$ being scaled functional responses. The biological parameters k_E^i (in h^{-1}), k_M^i (in h^{-1}) and g_i (no unit) are the specific energy conductance, somatic maintenance rate and energy investment rate of species i respectively. Two environmental parameters describe the chemostat, its dilution rate h (in h^{-1}) and the resource concentration in the feed X_r . This model assumes that the predator digests only prey structure, as adding reserve digestion does not improve the fit to data (Kooijman, 2010, p357).

Marr–Pirt model is a specific case of the DEB model (2) where reserve dynamics is assumed to be infinitely fast ($k_E^i \rightarrow +\infty$). It implies that the scaled reserve density is a function of the available food ($e_i(t) = f_i(X_{i-1}(t))$) at the same time. Taking also $g_i \rightarrow +\infty$, the growth rate of structure becomes $\mu_i f_i(X_{i-1}) - k_M^i$, where $\mu_i = k_E^i/g_i$. The new parameter μ_i (in h^{-1}) is the maximum growth rate of the population. Then, the DEB model (2) simplifies into the following three-dimensional system based on Marr–Pirt model:

$$\begin{cases} \frac{dX_0}{dt} = h(X_r - X_0) - f_1(X_0)j_{XAm}^1 X_1 \\ \frac{dX_1}{dt} = (\mu_1 f_1(X_0) - k_M^1 - h)X_1 - f_2(X_1)j_{XAm}^2 X_2 \\ \frac{dX_2}{dt} = (\mu_2 f_2(X_1) - k_M^2 - h)X_2. \end{cases} \quad (3)$$

Droop and Monod models are specific cases of the DEB and Marr–Pirt models respectively, where $k_M^1 = k_M^2 = 0$, i.e. maintenance costs are neglected for both species.

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