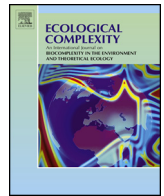




Contents lists available at [ScienceDirect](#)

Ecological Complexity

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



Original Research Article

Structural sensitivity and resilience in a predator–prey model with density-dependent mortality

C. Aldebert*, D. Nerini, M. Gauduchon, J.C. Poggiale

Mediterranean Institute of Oceanography, Aix-Marseille University, Toulon University, CNRS/INSU, IRD, MIO, UM 110, 13288 Marseille, Cedex 09, France

ARTICLE INFO

Article history:

Received 8 July 2015
Received in revised form 18 May 2016
Accepted 25 May 2016
Available online xxx

Keywords:

Structural sensitivity
Functional response
Bifurcations
Generalized modelling
Multiple stable states
Hysteresis

ABSTRACT

Numerous formulations with the same mathematical properties can be relevant to model a biological process. Different formulations can predict different model dynamics like equilibrium vs. oscillations even if they are quantitatively close (structural sensitivity). The question we address in this paper is: does the choice of a formulation affect predictions on the number of stable states? We focus on a predator–prey model with predator competition that exhibits multiple stable states. A bifurcation analysis is realized with respect to prey carrying capacity and species body mass ratio within range of values found in food web models. Bifurcation diagrams built for two type-II functional responses are different in two ways. First, the kind of stable state (equilibrium vs. oscillations) is different for 26.0–49.4% of the parameter values, depending on the parameter space investigated. Using generalized modelling, we highlight the role of functional response slope in this difference. Secondly, the number of stable states is higher with Ivlev's functional response for 0.1–14.3% of the parameter values. These two changes interact to create different model predictions if a parameter value or a state variable is altered. In these two examples of disturbance, Holling's disc equation predicts a higher system resilience. Indeed, Ivlev's functional response predicts that disturbance may trap the system into an alternative stable state that can be escaped from only by a larger alteration (hysteresis phenomena). Two questions arise from this work: (i) how much complex ecological models can be affected by this sensitivity to model formulation? and (ii) how to deal with these uncertainties in model predictions?

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

The choice of a model formulation in biology is often associated to uncertainties. Uncertainties arise from intrinsic data variability and simplified assumptions chosen to represent complex processes. Numerous mathematical formulations of a process are relevant in the sense that: (i) they fit empirical data, (ii) their properties and assumptions are consistent with the knowledge of the studied system (Mullin et al., 1975; Cordoleani et al., 2011). Even if these functions are quantitatively close, they can predict very different model dynamics (Myerscough et al., 1996; Wood and Thomas, 1999; Gross et al., 2004; Fussmann and Blasius, 2005; Poggiale et al., 2010; Adamson and Morozov, 2012, 2014). This change in model dynamics can be both quantitative and qualitative, a phenomenon coined “structural sensitivity” (Cordoleani et al., 2011).

Structural sensitivity has been mainly explored in models of predator–prey interactions. Predation emerges from the interplay between physiological, individual and collective processes. Depending on which processes are considered, predation can be modelled using numerous functional responses (amount of prey eaten per predator and per time unit, see Jeschke et al., 2002; Gentleman et al., 2003, for a review). Functional responses are classified by their main mathematical properties that define different types, such as Holling-types (1959a) or with vs. without predator interference (Beddington, 1975; DeAngelis et al., 1975). Two functions of different type create different dynamics (Cantrell and Cosner, 2001; Oaten and Murdoch, 1975; Scheffer and de Boer, 1995). But different dynamics are also generated by functions that belong to the same type. A model is thus structurally sensitive to the functional response formulation. For example, different type-II functional responses predict either a stable equilibrium or oscillations in predator–prey and food chain models. These models are also more sensitive to functional response formulation than to parameter values (Myerscough et al., 1996; Gross et al., 2004; Fussmann and Blasius, 2005; Cordoleani et al., 2011; Adamson and Morozov, 2012, 2014).

* Corresponding author.

E-mail addresses: clement.aldebert@univ-amu.fr (C. Aldebert), david.nerini@univ-amu.fr (D. Nerini), mathias.gauduchon@univ-amu.fr (M. Gauduchon), jean-christophe.poggiale@univ-amu.fr (J.C. Poggiale).

To overcome both parameter and structural sensitivity, Gross and Feudel (2006) proposed a method called generalized modelling. The local stability of positive equilibria is studied in a class of models without specifying their exact formulation and parameter values (see Yeakel et al., 2011, for a review in ecology). New parameters are defined to describe system dynamics near an equilibrium. As a drawback, this method is local and cannot explore global situations as a whole, like multiple stable states.

Multiple stable states can be important to investigate how a system behaves when facing some disturbances. Thus, the study of multiple stable states is of growing interest in ecology (Beisner et al., 2003; Knowlton, 2004; Scheffer et al., 2009, 2012). Despite this interest, studies on structural sensitivity focused on qualitative change (equilibrium vs. limit cycle) of a single stable state (except a short note in Fussmann and Blasius, 2005). The number of stable states can be modified by a quantitatively small change in model formulation in theory (as discussed by Adamson and Morozov (2014)), but such possibility has not been investigated so far. However, multiple stable states can coexist in predator–prey models like Bazykin’s model (Bazykin et al., 1985, in Metzler and Wischniewsky, 1985; Kuznetsov, 2004).

Bazykin’s model is equivalent to Rosenzweig and MacArthur’s model (1963) with density-dependent mortality for the predator. The predator has no density-dependent mortality in previous studies on structural sensitivity and generalized predator–prey models (Kuehn and Gross, 2011; Yeakel et al., 2011). However, density-dependent mortality represents the effects of diseases and/or competition and can be relevant for a wide range of predator species (Loreau, 2010). Furthermore, a density-dependent mortality is often used for the top-most predator in applied ecological models as a closure term to implicitly represent higher trophic levels (Fulton et al., 2003a,b). Predator competition modelled with quadratic mortality implicitly involves other limiting resource than the prey. In case of predator interference, the functional response may be predator-dependent (Ivlev, 1955; Beddington, 1975; DeAngelis et al., 1975; Arditi and Ginzburg, 1989; DeAngelis, 2013). However, different predator-dependent functional responses exist and structural sensitivity can also be studied in models based on this type of functions.

The question we want to address in this paper is: what is the impact of structural sensitivity on the number of stable states? We focus on Bazykin’s model which can exhibit multiple stable states. This predator–prey model can be a building block of some food web models (Aldebert et al., submitted for publication; Plitzko et al., 2012, and references therein) and its study may help to understand those more complex models. The next section presents Bazykin’s model and the functional response formulations that we test. Then a bifurcation analysis is conducted for two functional response formulations. In the fourth section, we derive a generalized predator–prey model in order to identify stabilizing factors independently of a specific formulation. This provides an additional understanding of the local stability of equilibria found in the previous section. Finally, results are discussed using examples where system resilience predicted by the model is tested using different functional response formulations.

2. Predator–prey model

We modelled predator–prey dynamics with Bazykin’s model. We wrote the model in a form that can easily be extended to more complex food webs. Population dynamics are modelled using the following differential system:

$$\begin{cases} \frac{dB_{prey}}{dt} = [\lambda q^\phi - \alpha_{prey} - \omega \beta_{prey} B_{prey}] B_{prey} - G^\phi(B_{prey}) B_{pred} \\ \frac{dB_{pred}}{dt} = [\lambda G^\phi(B_{prey}) - \alpha_{pred} - \beta_{pred} B_{pred}] B_{pred}, \end{cases} \quad (1)$$

where B_{prey} and B_{pred} are the respective biomass of unstructured prey and predator populations. In model (1), the prey grows using an implicit constant resource with a rate q^ϕ . The predator feeds on the prey with a functional response $G^\phi(B_{prey})$. We assume that both populations have the same conversion efficiency λ . Each population has intrinsic losses due to (i) linear mortality with a mortality rate α_{prey} (resp. α_{pred}) and (ii) competition with a per-capita density-dependent mortality rate β_{prey} (resp. β_{pred}). Prey competition is proportional to an environmental parameter ω , so prey carrying capacity is proportional to $1/\omega$. Predation is modelled using a type-II functional response G^ϕ which does not depend on predator biomass and fulfills the following properties:

$$\begin{aligned} G^\phi \in \mathcal{C}^2, \quad G^\phi(0) = 0, \quad G^\phi(B_{prey}) \geq 0, \quad G^{\phi'}(B_{prey}) > 0, \\ G^{\phi''}(B_{prey}) < 0, \quad \lim_{B_{prey} \rightarrow +\infty} G^\phi(B_{prey}) < +\infty, \end{aligned} \quad (2)$$

where \mathcal{C}^2 is the class of twice continuously differentiable functions. Other properties means that G^ϕ is null in absence of prey, increases with prey biomass, is concave and saturates at high prey biomass.

As examples of functions with properties (2), we consider Holling’s disc equation (1959b, 1965) G^H and Ivlev’s functional response (1955) G^I (Fig. 1):

$$\begin{aligned} G^H(B_{prey}) &= \frac{a_{pred}^H B_{prey}}{1 + h_{pred}^H a_{pred}^H B_{prey}}, \\ G^I(B_{prey}) &= \frac{1}{h_{pred}^I} (1 - \exp(-h_{pred}^I a_{pred}^I B_{prey})). \end{aligned} \quad (3)$$

For the first formulation, parameters a_{pred}^H and h_{pred}^H are respectively the attack rate and the handling time of the predator. For the second formulation, parameter $1/h_{pred}^I$ is the maximal consumption rate and $a_{pred}^I h_{pred}^I$ is the satiation coefficient of the predator. Parameters are defined in order to have a consistent mathematical meaning across formulations (4):

$$G^{\phi'}(0) = a_{pred}^\phi, \quad \lim_{B_{prey} \rightarrow +\infty} G^\phi(B_{prey}) = \frac{1}{h_{pred}^\phi}. \quad (4)$$

Thus, a_{pred}^ϕ gives the slope of the functional response at the origin, and $1/h_{pred}^\phi$ gives the asymptotic value of the functional response when it saturates at high prey biomass.

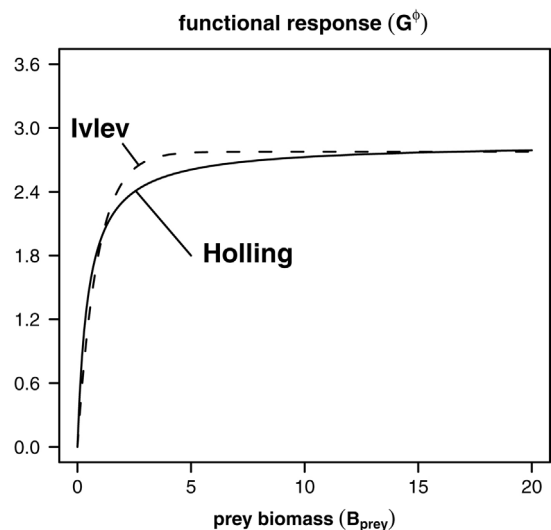


Fig. 1. Functional responses used in the model: Holling’s disc equation (solid) and best fitted Ivlev’s functional response (dashed). The former is used as “data” to parameterize the latter (Section 1 in supplementary material). Parameter values are given in Table 1. For the sake of visibility, only a part of the fitting range ($[0, B_{res}] = [0, 500]$) is shown.

Download English Version:

<https://daneshyari.com/en/article/8844893>

Download Persian Version:

<https://daneshyari.com/article/8844893>

[Daneshyari.com](https://daneshyari.com)