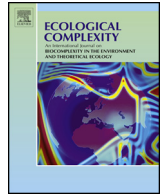




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Original Research Article

Does structural sensitivity alter complexity–stability relationships?

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ABSTRACT

Structural sensitivity, namely the sensitivity of a model dynamics to slight changes in its mathematical formulation, has already been studied in some models with a small number of state variables. The aim of this study is to investigate the impact of structural sensitivity in a food web model. Especially, the importance of structural sensitivity is compared to that of trophic complexity (number of species, connectance), which is known to strongly influence food web dynamics. Food web structures are built using the niche model. Then food web dynamics are modeled using several type II functional responses parameterized to fit the same predation fluxes. Food web persistence was found to be mostly determined by trophic complexity. At the opposite, even if food web connectance promotes equilibrium dynamics, their occurrence is mainly driven by the choice of the functional response. These conclusions are robust to changes in some parameter values, the fitting method and some model assumptions. In a one-prey/one-predator system, it was shown that the possibility that multiple stable states coexist can be highly structural sensitive. Quantifying this type of uncertainty at the scale of ecosystem models will be both a natural extension to this work and a challenging issue.

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1. Introduction

Predictions made by mathematical models can be sensitive to model formulation (Fulton et al., 2003b; Fussmann and Blasius, 2005; Anderson et al., 2010, among others). However, this sensitivity has rarely been tested in theoretical and operational ecosystem models (Fulton et al., 2003a; Arhonditsis and Brett, 2004). In ecological models with multiple interacting populations, phenomena observed at the community scale are usually represented by simplifying smaller scale processes. For instance, collective and individual behaviors as well as physiological processes involved in predation are collapsed into one function, the functional response (Jeschke et al., 2002; Gentleman et al., 2003). Numerous mathematical formulations of a given biological phenomenon are relevant in the sense that: (i) their properties and assumptions about underlying processes are consistent with the knowledge of the system to model, (ii) they equivalently fit empirical data (Mullin et al., 1975; Cordoleani et al., 2011). Moreover, some of these functions may have the same mathematical properties (pointwise properties, monotonicity, convexity,

etc.). However, the choice of a particular function among relevant ones can affect the dynamics predicted by the same model. Differences occur in predicted steady-state values, equilibrium vs. oscillating dynamics and in the system response to external disturbances (Aldebert et al., 2016). Uncertainty due to this choice of a function is coined as “structural sensitivity” (*sensu* Cordoleani et al., 2011).

Structural sensitivity has been theoretically studied in simple models with a few state variables, mainly predator–prey and food chain models (Myerscough et al., 1996; Gross et al., 2004; Fussmann and Blasius, 2005; Adamson and Morozov, 2012, 2014). The aim of this study is to extend these results to more complex models such as food webs. Previous results on predator–prey models may suggest that food web models are sensitive to the choice of type II functional response. We propose to compare food web dynamics under changes in both functional response formulation and trophic complexity (number of trophic species and trophic links).

Trophic complexity is known to affect food web dynamics and stability. Complexity–stability relationships have been conceptually studied by MacArthur (1955) and then more formally by May (1972, 1973). May’s work has led to a long-standing debate which is still open after decades of field and theoretical researches (May, 1999; McCann, 2000; Loreau, 2010). Food webs exhibit a huge number of different structures. A relevant analysis of their common properties requires to reproduce their diversity. Numerous food webs with

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empirically consistent structural properties and a desired trophic complexity can be built by simple random models (Williams and Martinez, 2000; Cattin et al., 2004, among others). These models have been used to statistically investigate complexity–stability relationships in food web models based on different ecological phenomena (Kartascheff et al., 2009, 2010; Stouffer and Bascompte, 2010, 2011; Plitzko et al., 2012; Williams and Martinez, 2004; Brose et al., 2006; Uchida and Drossel, 2007; Williams, 2008; Heckmann et al., 2012).

The questions we address in this paper are: (i) are dynamics predicted by a food web model more impacted by structural sensitivity or by trophic complexity? (ii) Does structural sensitivity alter complexity–stability relationships?

Next section presents the studied food web model. It is an extension of a predator–prey model in which structural sensitivity has already been explored (Aldebert et al., 2016). Structural sensitivity in this model is compared to the impact of trophic complexity in Section 3.1. Observed results are then explained from the knowledge of predator–prey models (Section 3.2) and their robustness to changes in the method used to fit functional responses is tested (Section 3.3). Then, the relative importance of trophic complexity, functional response formulation and parameter values is estimated (Section 3.4). Next, robustness to changes in model assumptions is assessed, and complexity–stability relationships are compared to empirical findings (Section 3.5). Paper ends with a more general discussion about structural sensitivity and modeling of biological systems (Section 3.6).

2. Models

2.1. Food web structure

Food webs are composed by S species (*sensu* trophic species) and one resource. Species are linked by L trophic interactions, so that food web connectance is $C = L/S^2$ (directed connectance, Martinez, 1991). The niche model (Williams and Martinez, 2000) is used to randomly build numerous food webs with the desired number of species and connectance. The niche model generates quickly numerous food webs with patterns that are consistent with empirical data (Williams and Martinez, 2000; Cattin et al., 2004; Allesina et al., 2008). It is based on the principle of ecological niche (Hutchinson, 1957). A species i is characterized by a niche value n_i uniformly drawn in the interval $[0, 1]$, the niche axis.

The niche model is described in section 1 of Supporting Online Material (SOM). Food webs are made of distinct species, that are either a primary producer or a predator. Attribution of trophic links allows for cannibalism and trophic loops. We added a rejection step after food webs construction to avoid unrealistic patterns. We only studied food webs with a realized connectance that deviated at most by 0.01 of the expected one, that are connected (no disconnected parts), and in which all predators feed (as a prey or through a food chain) upon at least one primary producer.

2.2. Food web dynamics

Food web dynamics is modeled using a dynamical system of S differential equations. It is a bio-energetic model extended for a multi-species system (Yodzis and Innes, 1992; Plitzko et al., 2012, among others). This deterministic model is continuous in time with unstructured populations. Each species i is described by its biomass B_i , with dynamics given by the ordinary differential equation:

$$\frac{dB_i}{dt} = \lambda q_i^\phi B_i + \sum_{j \in R_i} G_{ij}^\phi B_j - \sum_{j \in C_i} G_{ji}^\phi B_j - \alpha_i B_i - \beta_i B_i^2 \quad i = 1, \dots, S. \quad (1)$$

Right terms of model (1) handle respectively a gain in biomass by primary production, sum of gains by predation, sum of losses by predation, linear mortality and respiration, density-dependent mortality (intra-specific competition, diseases). Species i possesses a set of prey (predator) species denoted as R_i (C_i). By definition, primary producers have $R_i = \emptyset$ and top-predators have $C_i = \emptyset$. The parameter λ is the assimilation efficiency. For the sake of simplicity, λ is assumed to be the same for all species. Parameter α_i is the linear mortality rate and parameter β_i is the per-capita intra-specific competition rate of species i . The letter ϕ indicates the specific formulation used for the Holling-type II functional response G_{ij}^ϕ . For simplicity, all species are assumed to have the same formulation. This one is either Holling's disc equation (1959, 1965) denoted as G_{ij}^H or Ivlev's functional response (1955) denoted as G_{ij}^I (later called Holling's FR and Ivlev's FR):

$$G_{ij}^H = \frac{a_i^H f_{ij} B_j}{1 + h_i^H a_i^H T_i},$$

$$G_{ij}^I = \frac{1}{h_i^I} (1 - \exp(-h_i^I a_i^I T_i)) \frac{f_{ij} B_j}{T_i} \quad \text{with } T_i = \sum_{j \in R_i} f_{ij} B_j.$$

Both functional responses are extended for a predator with multiple prey species by assuming that it does not switch between preys (Gentleman et al., 2003). For Holling's FR, parameters a_i^H and h_i^H are respectively the attack rate and the handling time of the predator. For Ivlev's FR, parameter $1/h_i^I$ is the maximal digestion rate and a_i^I/h_i^I is the satiation coefficient of the predator. The total amount of prey available for species i is the weighted sum of its prey species biomass T_i . The weighting parameter $f_{i,j}$ is constant and it can be considered as the foraging effort or the feeding preference of predator i for its prey species j (obviously, $f_{i,j} = 0$ and $G_{ij}^\phi = 0$ if $j \notin R_i$). This means that the total functional response of a predator $G_i^{\phi, tot}(T_i) = \sum_{j \in R_i} G_{ij}^\phi$ is a function of T_i (Fig. 1) and that $G_{ij}^\phi = G_i^{\phi, tot} f_{ij} B_j / T_i$. Both functional responses also fulfills properties:

$$G_i^{\phi, tot} \in C^2, \quad G_i^{\phi, tot}(0) = 0, \quad G_i^{\phi, tot}(T_i) \geq 0, \quad G_i^{\phi, tot}'(T_i) > 0,$$

$$G_i^{\phi, tot}''(T_i) < 0, \quad \lim_{T_i \rightarrow +\infty} G_i^{\phi, tot}(T_i) < +\infty,$$

with C^2 being the class of twice continuously differentiable functions. Other properties means that $G_i^{\phi, tot}$ is null in absence of prey, increases with prey biomass, is concave and saturates at high prey biomass.

Functional response's parameters have the same mathematical meaning in both formulations:

$$G_i^{\phi, tot}'(0) = a_i^\phi, \quad \lim_{T_i \rightarrow +\infty} G_i^{\phi, tot}(T_i) = \frac{1}{h_i^\phi}.$$

Thus, a_i^ϕ gives the slope of the functional response at the origin, and $1/h_i^\phi$ gives the asymptotic value of the functional response when it saturates at high prey biomass.

The term of primary productivity q_i^ϕ has the same equation as the functional response G_{ij}^ϕ with a constant pool of resources B_{res} :

$$q_i^H = \begin{cases} \frac{a_i^H B_{res}}{1 + h_i^H a_i^H B_{res}} & \text{if } i \in P_I \\ 0 & \text{otherwise} \end{cases},$$

$$q_i^I = \begin{cases} \frac{1}{h_i^I} (1 - \exp(-h_i^I a_i^I B_{res})) & \text{if } i \in P_I \\ 0 & \text{otherwise.} \end{cases}$$

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