Does structural sensitivity alter complexity–stability relationships?

Clement Aldebert, David Nerini, Mathias Gauduchon, J.C. Poggiale

HAL Id: hal-01827263

https://hal.science/hal-01827263

Submitted on 11 Dec 2018

Does structural sensitivity alter complexity-stability relationships?

C. Aldebert[a,*], D. Nerini[a], M. Gauduchon[a], JC. Poggiale[a]

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

* corresponding author, +33 (0)4 860 90 640

E-mails:

- clement.aldebert@univ-amu.fr,

- david.nerini@univ-amu.fr,

- mathias.gauduchon@univ-amu.fr,

- jean-christophe.poggiale@univ-amu.fr

Keywords

food webs ; dynamical systems ; structural sensitivity ; complexity-stability relationships ; functional response

Highlights

- We study food webs of varying trophic complexity (number of species, connectance)

- Food web dynamics is modeled using either Holling's or Ivlev's functional response

- Community persistence is mainly driven by trophic complexity

- Occurrence of fluctuating dynamics is mainly driven by the functional response

- Conclusions are robust to some changes in parameter values and model assumptions

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.

1 Introduction

Predictions made by mathematical models can be sensitive to model formulation (Anderson *et al.*, 2010; Fulton *et al.*, 2003b; Fussmann & Blasius, 2005, among others). However, this sensitivity hass rarely been tested in theoretical and operational ecosystem models (Arhonditsis & Brett, 2004; Fulton *et al.*, 2003a). 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 behaviours as well as physiological processes involved in predation are collapsed into one function, the functional response (Gentleman *et al.*, 2003; Jeschke *et al.*, 2002). 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 (Cordoleani *et al.*, 2011; Mullin *et al.*, 1975). Moreover, some of these functions may have the same mathematical properties (pointwise properties, monotonicity, convexity, ...). 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 (Adamson & Morozov, 2012, 2014; Fussmann & Blasius, 2005; Gross *et al.*, 2004; Myerscough *et al.*, 1996). 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 (Loreau, 2010; May, 1999; McCann, 2000). 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 empirically consistent structural properties and a desired trophic complexity can be

built by simple random models (Cattin *et al.*, 2004; Williams & Martinez, 2000, among others). These models have been used to statistically investigate complexity-stability relationships in food web models based on different ecological phenomena (Brose *et al.*, 2006; Heckmann *et al.*, 2012; Kartascheff *et al.*, 2009, 2010; Plitzko *et al.*, 2012; Stouffer & Bascompte, 2010, 2011; Uchida & Drossel, 2007; Williams, 2008; Williams & Martinez, 2004).

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 modelling 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 & 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 (Allesina *et al.*, 2008; Cattin *et al.*, 2004; Williams & Martinez, 2000). 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 (Plitzko *et al.*, 2012; Yodzis & Innes, 1992, 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:

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

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 $R_i = \varnothing$ and top-predators have $C_i = \varnothing$. 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 $G_{i,j}^\phi$. For simplicity, all species are assumed to have the same formulation. This one is either Holling's disc equation (1959; 1965) denoted as $G_{i,j}^H$ or Ivlev's functional response (1955) denoted as $G_{i,j}^I$ (later called Holling's FR and Ivlev's FR):

$$G_{i,j}^H = \frac{a_i^H f_{i,j} B_j}{1 + h_i^H a_i^H T_i}, \ G_{i,j}^I = \frac{1}{h_i^I} \left(1 - \exp\left(-h_i^I a_i^I T_i\right)\right) \frac{f_{i,j} B_j}{T_i} \text{ with } T_i = \sum_{j \in R_i} f_{i,j} B_j.$$

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 $G^\phi_{i,j} = 0$ if $j \notin R_i$). This means that the total functional response of a predator $G^{\phi,tot}_i(T_i) = \sum_{j \in R_i} G^\phi_{i,j}$ is a function of T_i (figure 1) and that $G^\phi_{i,j} = G^{\phi,tot}_i f_{i,j} B_j / T_i$. Both functional responses also fulfills properties:

$$G^{\phi,tot}_i \in \mathcal{C}^2,\ G^{\phi,tot}_i(0) = 0,\ G^{\phi,tot}_i(T_i) \geq 0,\ G^{\phi,tot}_i{}'(T_i) > 0,\ G^{\phi,tot}_i{}''(T_i) < 0,\ \lim_{T_i \to +\infty} G^{\phi,tot}_i(T_i) < +\infty,$$

with $\mathcal{C}^2$ being the class of twice continuously differentiable functions. Other properties means that $G^{\phi,tot}$ 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:

$$G^{\phi,tot}_i{}'(0) = a^\phi_i,\ \lim_{T_i \to +\infty} G^{\phi,tot}_i(T_i) = \frac{1}{h^\phi_i}.$$

Thus, a^ϕ_{pred} gives the slope of the functional response at the origin, and $1/h^\phi_{pred}$ gives the asymptotic value of the functional response when it saturates at high prey biomass.

The term of primary productivity q^ϕ_i has the same equation as the functional response $G^\phi_{i,j}$ with a constant pool of resources B_{res}:

$$q^H_i = \begin{cases} \dfrac{a^H_i B_{res}}{1 + h^H_i a^H_i B_{res}} & \text{if } i \in P_I \\ 0 & \text{otherwise} \end{cases},\ q^I_i = \begin{cases} \dfrac{1}{h^I_i}\left(1 - \exp\left(-h^I_i a^I_i B_{res}\right)\right) & \text{if } i \in P_I \\ 0 & \text{otherwise.} \end{cases}$$

This term vanishes for predators, with P_I being the set of primary producers. Setting a constant pool of resource implies two assumptions. First, the time scale of the resource dynamics is such that it is always at quasi-equilibrium in comparison to the time scale of population dynamics. Second, the equilibrium value is independent of the food web dynamics, it only depends on the environment, which is supposed to be constant.

Let $M_i = 10^{xn_i}$ be the body mass of species i, with a scale parameter x. We assume that some parameter values scale allometrically across species (Brown $et\ al.$, 2004):
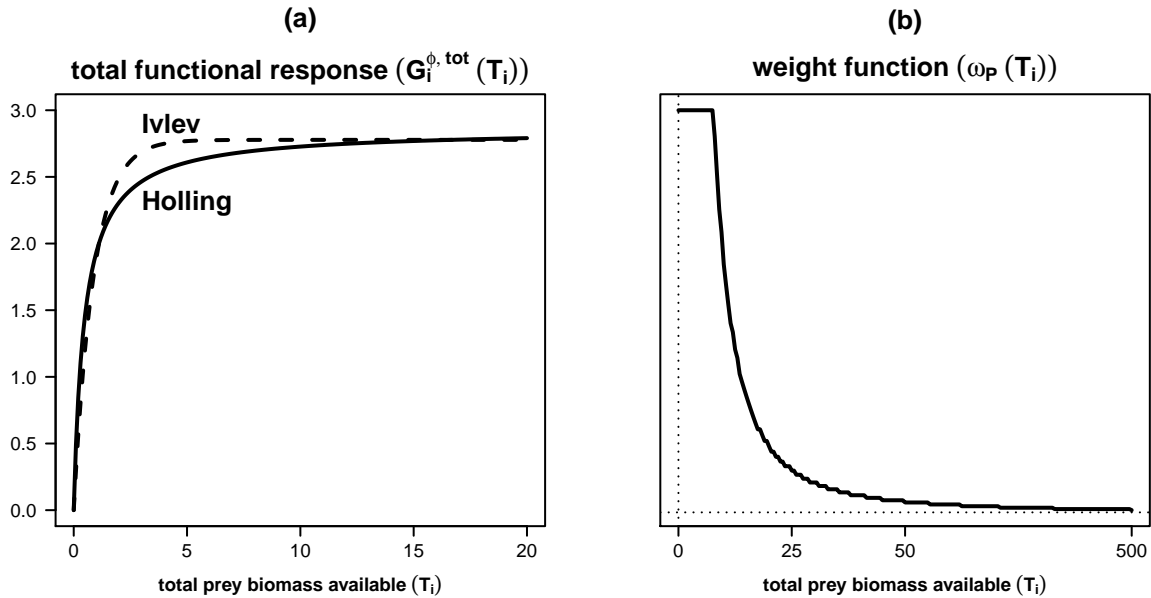
Figure 1. Functional responses used in the model. a: total functional response of species i (total amount of preys eaten by predator and by time unit) calculated as a function of its total prey biomass available, using Holling's disc equation (solid) or Ivlev's functional response (dashed). The latter is parameterized in order to minimize the weighted Euclidean distance between the two formulations. For the sake of visibility, only a part of the fitting range is shown. b: weighting function used to calculate the distance between formulations. See section 2.2 for formulations and section 2.3 for parameterization.

$$a_i^\phi = a^\phi M_i^{-1/4}, \ h_i^\phi = h^\phi M_i^{1/4}, \ \alpha_i = \alpha M_i^{-1/4}, \ \beta_i = \beta M_i^{-1/4}.$$

As species abundance is quantified in terms of biomass, the scaling exponent $-1/4$ corresponds to an increase of individual metabolic rate with body mass power $3/4$, divided by individual body mass. The $3/4$ exponent is controversial. Empirical data and theoretical studies indicate values between $2/3$ and 1 (Kooijman, 2010). Nevertheless, the exact value of this exponent has a limited impact on species extinctions in similar food web models (Kartascheff *et al.*, 2010).

Note that if two species have the same trophic interactions and parameter values, model (1) is sensitive to the aggregation of these identical species as no direct inter-specific competition is considered. It has no impact on our numerical results as identical (or infinitely close) species are infinitely rare in food webs built by the niche model. This problem in model consistency can be solved by considering an inter-specific competition term, with a competition strength that decreases with a measure of distance between species.

Table 1. Parameter values used in the food web model. Parameter values from Heckmann *et al.* (2012) were estimated from empirical data sets (up to > 700 organisms from unicellular eukaryotes to plants and mammals, which span 20 orders of magnitude in body mass, Brose *et al.*, 2006; Brown *et al.*, 2004) using allometric scaling or set to values similar to other studies for comparison (like Kartascheff *et al.*, 2009, 2010).

biological meaning	parameter	value	source	unit
mortality rate	α	0.3	(Heckmann *et al.*, 2012)	time^{-1}
per-capita competition rate	β	0.5	(Heckmann *et al.*, 2012)	biomass^{-1}time^{-1}
assimilation efficiency	λ	0.65	(Heckmann *et al.*, 2012)	-
resource biomass	B_{res}	500	(Heckmann *et al.*, 2012)	biomass
magnitude of body mass range	x	8	(Plitzko *et al.*, 2012)	-
Holling's disc equation:				
attack rate	a^H	6	(Heckmann *et al.*, 2012)	biomass^{-1}time^{-1}
handling time	h^H	0.35	(Heckmann *et al.*, 2012)	time
Ivlev's functional response:				
maximal consumption rate	$1/h^I$	$1/0.36$	see text	time^{-1}
satiation coefficient	$a^I h^I$	3.17×0.36	see text	biomass^{-1}

2.3 Parameterization and numerical study

Parameter values are displayed in table 1. The range of trophic complexity (20 to 60 species, connectance of 0.10 to 0.30) is set to include values used in previous studies (Gross *et al.*, 2009; Kartascheff *et al.*, 2009, 2010; Plitzko *et al.*, 2012, among others) for comparison. The number of simulations is limited by assuming that a species i has the same feeding preference $f_{i,j} = 1/|R_i|$ for all its prey species $j \in R_i$ (with $|R_i|$ being the number of prey species of species i). This choice implies that T_i is the average biomass of prey species $\sum_{j \in R_i} B_j / |R_i|$ (weak generalist model, *sensu* Williams, 2008).

Parameters in Ivlev's FR are chosen to minimize the weighted Euclidean distance between both functional responses:

$$S_{A,\omega}\left(a^I, h^I\right) = d^2_{A,\omega}\left(G_i^{H,tot}, G_i^{I,tot}\right) = \int_A \omega(T_i)\left(G_i^{H,tot}(T_i) - G_i^{I,tot}(T_i)\right)^2 dT_i, \qquad (2)$$

with a weighting function $\omega(T_i)$ on a fitting range A of T_i values. Total prey biomass ranges from 0 to constant resource biomass for primary producers, so we set $A = [0, B_{res}]$. For a fixed amount of total prey biomass $\sum_{j \in R_i} B_j$, the resulting T_i depends on $|R_i|$. To balance this effect *a priori*, the distance is

8

weighted by (figure 1):

$$\omega_{\mathcal{P}}(T_i) = \frac{1}{S_{max} T_{max}} \sum_{n=1}^{N} n \text{ with } N = \min\left(\lfloor T_{max}/T_i \rfloor, S_{max}\right) \text{ and } T_{max} = \max(A), \qquad (3)$$

which is the frequency distribution of T_i values for $\sum_{j \in R_i} B_j \in A$ and for a predator's number of prey species which ranges between one and $S_{max} = 60$. Minimizing the cost function $S_{[0, B_{res}], \omega_{\mathcal{P}}}$ using the simplex method by Nelder & Mead (1965) give values $a^I = 3.17$ and $h^I = 0.36$. The sensitivity of our results to choices in A and $\omega(T_i)$ is discussed in section 3.3.

Let us recall that, when an equilibrium is reached, the right-hand side of equation (1) vanishes for all species, with $B_1^*, B_2^*, ..., B_S^*$ being the species biomass at an equilibrium (and T_i^* the total prey biomass available of species i at equilibrium). The jacobian matrix J^ϕ of system (1) is presented in appendix S1.

The algorithm presented in section 2 of SOM (with a discussion about its limits) is used to automatically determine the kind of asymptotic dynamics reached by a food web. The proposed algorithm classifies asymptotic dynamics in three types: dynamics in which at least one species goes extinct, equilibrium in which all species coexist, fluctuating dynamics (e.g. limit cycle, torus, strange attractor) in which all species coexist. The proportion of food webs in which all species coexist (at equilibrium or with fluctuating dynamics) is a measure of food web persistence. The proportion of persistent food webs (i.e. food webs in which all species coexist) which exhibit a fluctuating dynamics is a measure of food web variability. Food webs construction and simulation were achieved by C++ programs using GNU Scientific Library for C/C++ (Galassi *et al.*, 2013). Post-simulation analysis and figures were performed using R language (R Core Team, 2013).

3 Results and Discussion

3.1 Structural sensitivity vs. trophic complexity

Both functional responses predict similar patterns of food web persistence as a function of trophic complexity (figure 2a,c). Within this range, Ivlev's FR predicts less extinctions than Holling's FR does (from -11 % to $+1$ % food webs with at least one species extinction). With both functional responses, the proportion of non-persistent food webs increases with trophic complexity. This increase is higher with the number of species ($\times 1.4$ with Holling's FR and $\times 1.5$ with Ivlev's FR) than with connectance ($\times 1.2$

9

and ×1.3). Functional responses are parameterized to predict quantitatively close predation fluxes, which explains their similar predictions of food web persistence.

Conversely, food web variability is mainly driven by functional response formulation within the tested range of trophic complexity (figure 2b,d). Ivlev's FR predicts 2.3 times more equilibrium dynamics (from 98 % to 99 % of persistent food webs reach an equilibrium) than Holling's FR does (from 25 % to 80 %). The proportion of equilibrium dynamics increases more with connectance (on average ×3.2 with Holling's FR and +1 % with Ivlev's FR) than with the number of species (×1.1 with Holling's FR, no trend with Ivlev's FR). Even if the effect of trophic complexity can change with other measures of food web persistence and variability, the latter is still higher with Ivlev's FR (section 5 in SOM).

3.2 Understanding structural sensitivity in food webs

Model (1) applied to a one-predator/one-prey system owns an equibrium which is stable with Ivlev's FR and unstable with Holling's FR in 26 % to 49 % of the parameter space explored in Aldebert *et al.* (2016). With Holling's FR, dynamics converge on a stable limit cycle. Equilibrium stability is different because the slope of Holling's FR at equilibrium is lower. The slope of the functional response at equilibrium in food webs can be described by its elasticity:

$$\gamma_i := g_i^{\phi'}(1) \in [0,1] \text{ with } t_i := \frac{T_i}{T_i^*} \text{ and } g_i^\phi(t_i) := \frac{G_i^{\phi,tot}(t_i T_i^*)}{G_i^{\phi,tot}(T_i^*)},$$

where the normalized functional response equals 1 at equilibrium ($g_i^\phi(1) = 1$). A high elasticity γ_i stabilizes equilibria in predator-prey (Aldebert *et al.*, 2016; Yeakel *et al.*, 2011) and food web models (section 6 of SOM).

The elasticity depends on prey biomass at equilibrium, which has a similar distribution between functional responses (figure 3). However, Ivlev's FR has a higher elasticity than Holling's FR for low prey biomass values (figure 4b). As a consequence, the realized γ_i distribution in food web simulations is 1.6 times higher with Ivlev's FR ($\bar{\gamma} = 0.60$) than with Holling's FR ($\bar{\gamma} = 0.37$, figure 4a). With the latter, one can expect that stable equilibria are closer to a bifurcation threshold (with respect to γ_i). Thus, more food webs are likely to be on the unstable side of this bifurcation with Holling's FR. This can explain why this function leads more frequently to fluctuating dynamics. This reasoning extends the previous mechanism found in predator-prey models (Fussmann & Blasius, 2005) to the scale of complex

10
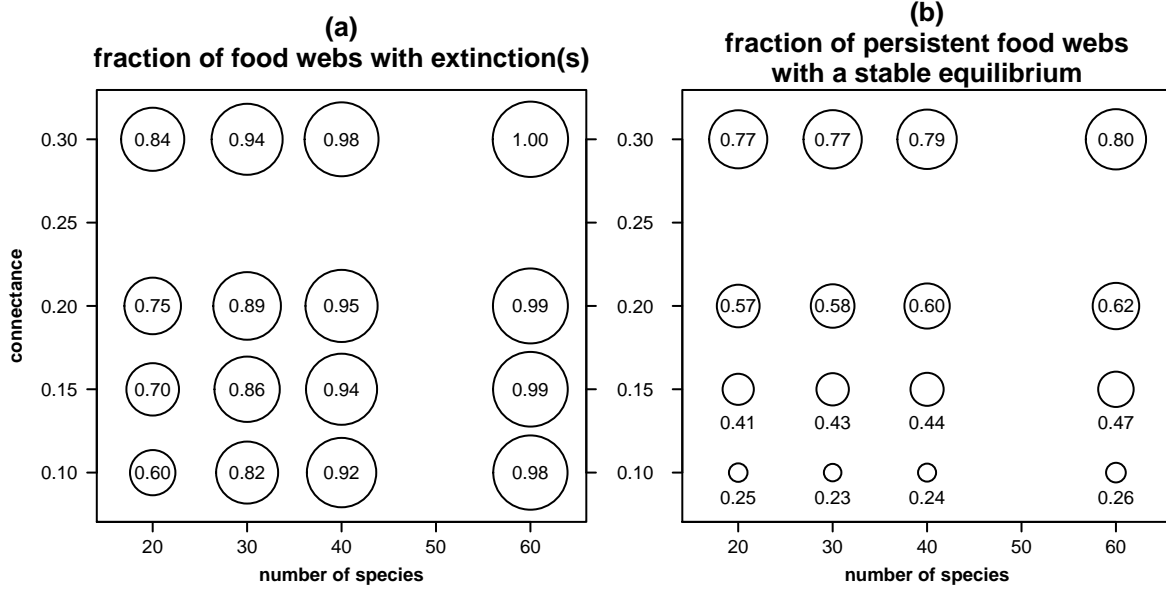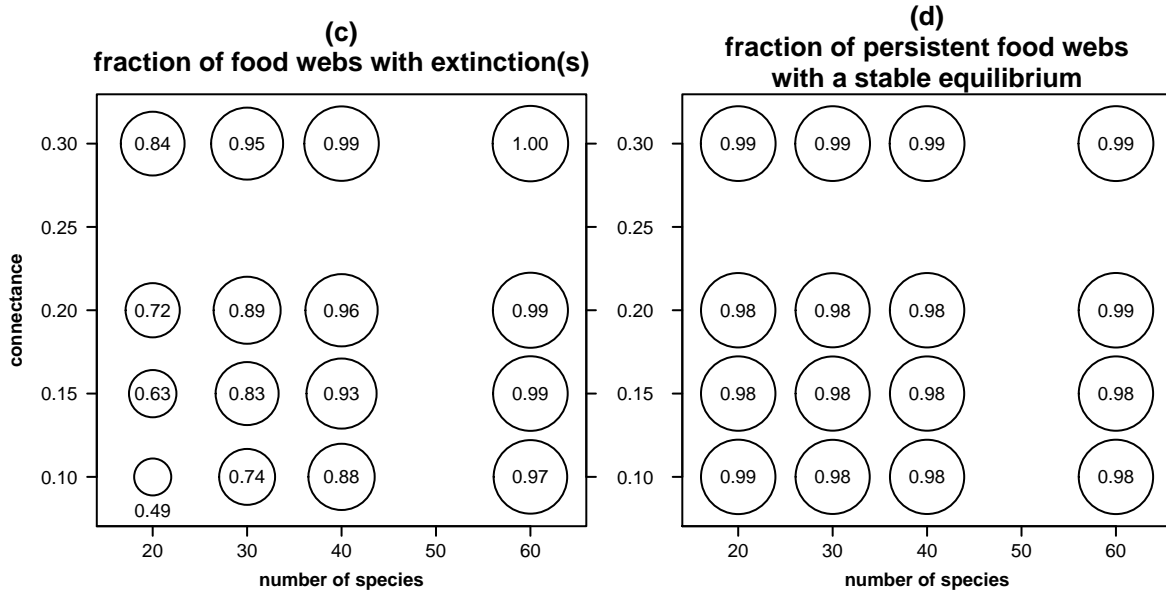
Figure 2. Food web dynamics as a function of trophic complexity predicted by Holling's (a, b) and Ivlev's functional responses (c, d). a, c: proportion of food webs with at least one species extinction. b, d: proportion of persistent food webs with a stable positive equilibrium. The number of food webs studied for each pair of parameters is enough to obtain 10 000 food webs with a stable positive equilibrium.
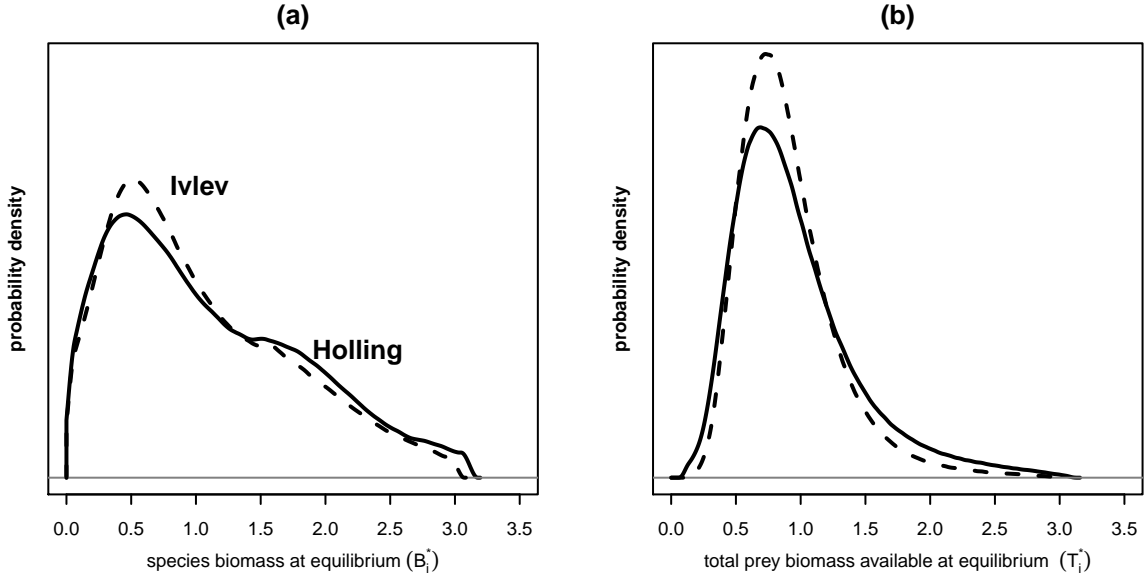
food webs.

Figure 3. Estimated densities of species biomass (a) and total prey biomass available for predator species (b) in food webs reaching a positive equilibrium with Holling's (plain) or Ivlev's (dashed) functional response. Computed from 160 000 food webs of varying complexity (4 levels of connectance and 4 numbers of species, 10 000 food webs by pair of values). Density estimates are realized using non-parametric kernel methods (Simonoff, 1996).

3.3 Structural sensitivity and the method used to fit the functional responses

As the slope of the functional response drives food web variability, one can think about different ways to parameterize Ivlev's FR. The relevance of these different approaches from a biological point of view is discussed in section 3.6. Here, we focus on robustness to changes in parameter values estimated for Ivlev's FR. Different parameter sets are estimated by minimizing the weighted distance (2): (i) over different ranges of T_i values, and (ii) using either the weighting function $\omega_{\mathcal{P}}$ (3) (figure 1) or a uniform weighting function $\omega_{\mathcal{U}}(T_i)$. One last parameter set is estimated using the empirical distribution of total prey biomass observed in persistent food webs at equilibrium with Holling's FR (figure 3b).

Parameter sets that give a better fit to Holling's FR at low prey biomass (closer a^{ϕ} value) predict a closer value of food web variability between functional responses (table 2 and figure 5). However, they also predict more distant primary productivity ($\approx 1/h^{\phi}$ value) and predicted value of food web persistence. Furthermore, equilibrium dynamics are still more frequent with Ivlev's FR within the tested range of
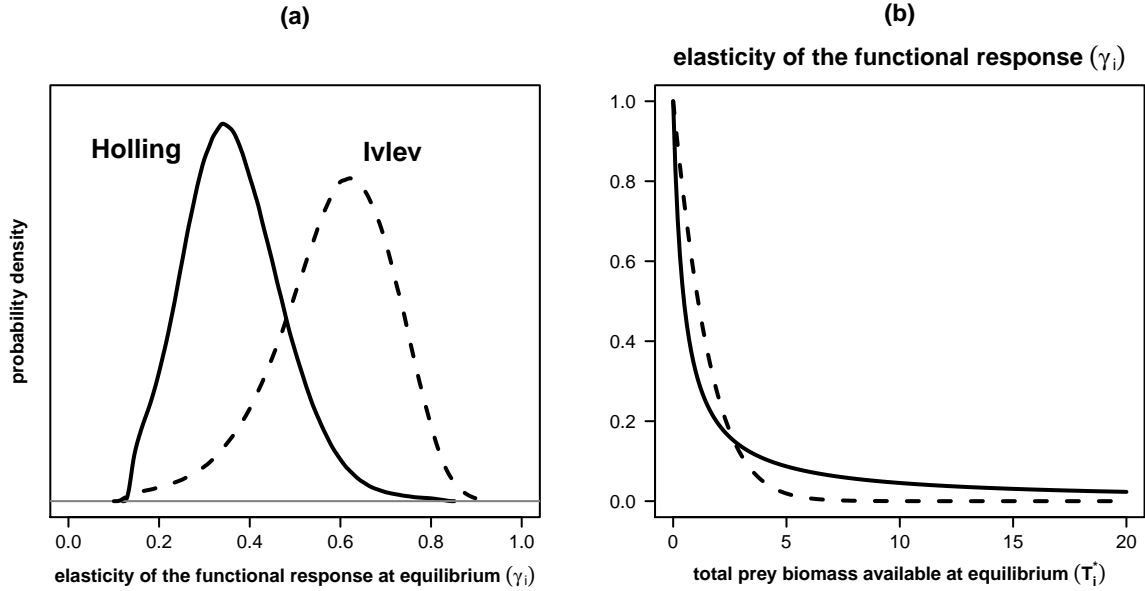
Figure 4. Elasticity of the functional response: estimated density in food webs reaching a positive equilibrium (a) and as a function of total prey biomass available (b) with Holling's (plain) or Ivlev's (dashed) functional response. Computed for predator species from 160 000 food webs of varying complexity (4 levels of connectance and 4 numbers of species, 10 000 food webs by pair of values). Density estimates are realized using non-parametric kernel methods (Simonoff, 1996).

²²⁰ trophic complexity (section 3 in SOM). The parameter set that leads to the closer food web variability

²²¹ ($\omega_{\mathcal{P}}$ within $[0, 3.5]$) does not lead to the best fit of functional responses within the range of prey biomass

²²² observed (column $S_{\omega_{\mathcal{U}}, [0,3.5]}$ in table 2), as it is optimized for even smaller biomass values. In other

²²³ words, this parameter set optimizes only the slope at the origin (a^{ϕ}), as we know that the functional

²²⁴ response slope drives food web variability. Only one parameter set is usually considered in previous

²²⁵ studies on structural sensitivity in predator-prey models (Aldebert *et al.*, 2016; Cordoleani *et al.*, 2011;

²²⁶ Fussmann & Blasius, 2005; Myerscough *et al.*, 1996). We checked here with different parameter sets that

²²⁷ functional response formulation influences food web variability, even if this influence is lower with some

²²⁸ fitting methods.

²²⁹ 3.4 Structural sensitivity vs. parameter sensitivity
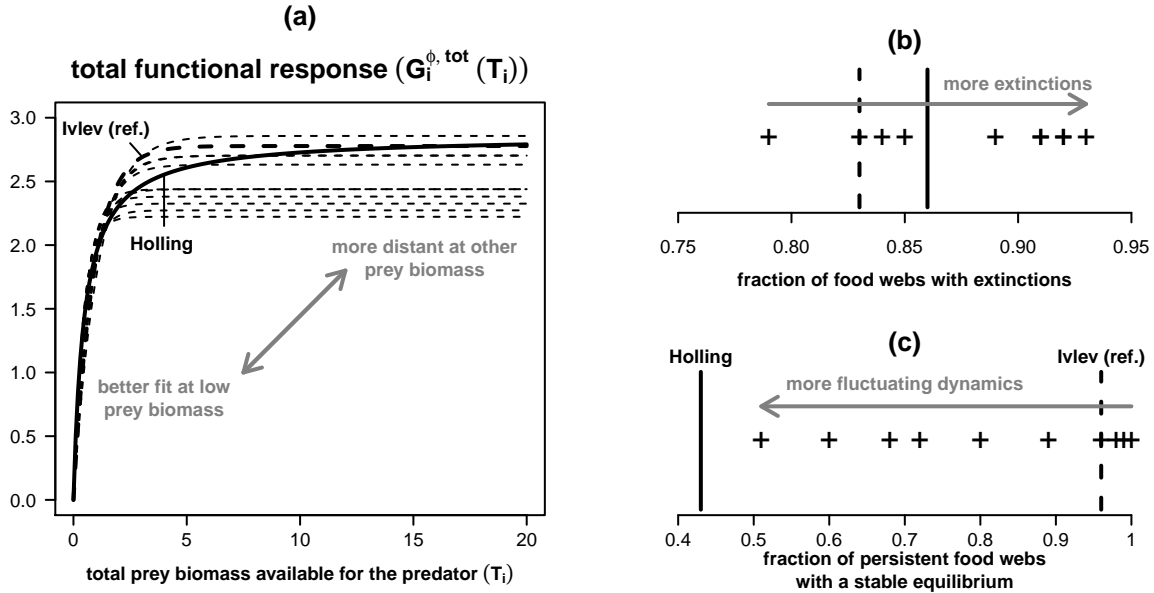
²³⁰ Even with the simplifying assumption that parameter values scale allometrically, a full parameter sensi-

²³¹ tivity analysis requires a high computational effort. Indeed, to be reasonably exhaustive it is necessary

²³² to study thousands of food webs with different numbers of species and connectance levels for each pa-

Table 2. Impact of the method used to fit the functional responses. The columns indicate respectively: the weighting function used, the range of T_i values within which the weighted distance between functions is minimized, the pair of parameters values obtained (a^ϕ and h^ϕ) for Ivlev's functional response, the corresponding distance (computed with the same weighting function for comparison) between functions at low ($[0, 3.5]$) and high ($[3.5, 500]$) total prey biomass available, the predicted dynamics (proportion of food webs with extinction(s), proportion of persistent food webs reaching an equilibrium) in 30-species food webs with a connectance of 0.15. The number of food webs studied for each pair of parameters is enough to obtain 1 000 food webs with a stable positive equilibrium. The bold line corresponds to the parameters values used in the rest of the study. In addition, one parameter set for Ivlev's functional response has been estimated using the empirical distribution of T_i observed in persistent food webs at equilibrium with Holling's disc equation (figure 3b). Dynamics predicted by Holling's disc equation are indicated for comparison.

weighting function	$T_i \in A$	a^ϕ	h^ϕ	$S_{\omega_{\mathcal{U}},[0,3.5]}$	$S_{\omega_{\mathcal{U}},[3.5,500]}$	extinction(s)	equilibrium
	$[0, 500]$	2.70	0.35	0.049	< 0.001	0.79	1.00
	$[0, 20]$	3.12	0.37	0.026	0.021	0.83	0.99
$\omega_{\mathcal{U}}$	$[0, 15]$	3.22	0.37	0.025	0.021	0.84	0.98
	$[0, 10]$	3.39	0.38	0.017	0.046	0.85	0.96
	$[0, 3.5]$	4.03	0.41	0.004	0.165	0.89	0.89
	$[0, 500]$	**3.17**	**0.36**	**0.036**	**0.005**	**0.83**	**0.98**
	$[0, 20]$	4.67	0.41	0.007	0.165	0.91	0.72
$\omega_{\mathcal{P}}$	$[0, 15]$	4.82	0.42	0.007	0.215	0.92	0.68
	$[0, 10]$	4.98	0.43	0.010	0.269	0.92	0.60
	$[0, 3.5]$	5.31	0.45	0.023	0.387	0.93	0.51
T_i distribution from fig. 3b		4.50	0.44	0.015	0.327	0.91	0.80
Holling's disc equation		6	0.35			0.86	0.43

rameter set. However, we investigate the robustness of our results to the functional response parameter values. We vary the parameter values used for Holling's FR (a^H and h^H) within a range $[-20\ \%, +20\ \%]$ (discretized by steps of 10 %) and re-estimate the parameters for Ivlev's FR by fitting the two functions. The relative variation considered is comparable to uncertainties in parameter estimation from empirical data (Cordoleani *et al.*, 2011). Food webs with the same numbers of species and connectance levels as in figure 2 are studied for each parameter set and each functional response for a total amount of $\approx 6.10^7$ food webs studied.

Within the tested range of trophic complexity, food web persistence is strongly correlated (0.76) to the number of species, whereas food web variability is strongly correlated (0.82) to functional response formulation (3). Both persistence and variability are also correlated (0.37 and 0.36) to connectance. In comparison, food web dynamics are weakly correlated to parameter values. A change in parameter values has a weaker impact on model dynamics than a change in model formulation, even if both changes

14

(a)

total functional response ($G_i^{\phi,\,tot}(T_i)$)

Ivlev (ref.)

Holling

more distant at other prey biomass

better fit at low prey biomass

total prey biomass available for the predator (T_i)

(b)

more extinctions

fraction of food webs with extinctions

(c)

Holling

Ivlev (ref.)

more fluctuating dynamics

fraction of persistent food webs with a stable equilibrium

Figure 5. Impact of the method used to fit the functional responses. a: Holling's disc equation (plain), Ivlev's functional response with the parameter set used in the study (bold dashed) and with parameter sets obtained with different fitting methods (thin dashed, see table 2). b and c: food web dynamics (30 species, connectance of 0.15) predicted for these parameter sets. Gray labels and arrows summarize the main trend of results: a better fit at low prey biomass (a) leads to a closer predicted food web variability (c), but also to more distant functions at other prey biomass values (a) and more distant predicted food web persistence (b).

correspond to a quantitatively similar variation measured between the functional responses (Adamson & Morozov, 2012, 2014; Cordoleani *et al.*, 2011; Wood & Thomas, 1999). Indeed, for a quantitatively similar variation, a change of formulation may affect the function shape and lead to a higher change in functional response slope near equilibrium, i.e. in equilibrium stability.

3.5   Model assumptions, complexity-stability relationships and biological systems

Different combinations of model assumptions are made by recent studies on food webs, often for simplifying reasons (Brose *et al.*, 2006; Gross *et al.*, 2009; Heckmann *et al.*, 2012; Kartascheff *et al.*, 2010; Plitzko *et al.*, 2012; Stouffer & Bascompte, 2010, 2011; Williams, 2008). The impact of these assumptions is detailed in section 4 of SOM and summarized in table 4. In all cases, equilibrium dynamics are more frequent with Ivlev's FR than with Holling's FR. In addition, both functional responses show the same qualitative effect of each assumption.

15

Table 3. Correlations between food web dynamics, trophic complexity, the functional response used and its parameterization. We simulated food webs of varying complexity (4 numbers of species times 4 connectance levels) with different functional response formulation (Holling's or Ivlev's FRs) and parameterization (5 values of a^ϕ times 5 values of h^ϕ), leading to $n = 800$ combinations. For each one, food web dynamics is summarized by the proportion of food webs with extinction(s) and the proportion of persistent food webs reaching a stable equilibrium. A positive correlation with the functional response corresponds to an increase with Ivlev's FR. NS means that the corresponding p-value is higher than 0.01 (Student's test on the regression coefficient). For each combination, the number of food webs studied is enough to obtain 1 000 food webs with a stable positive equilibrium. The total number of food webs simulated is $\approx 6.10^7$.

	number of species	connectance	a^ϕ	h^ϕ	functional response
extinction(s)	**0.76**	0.37	0.12	0.07	-0.17
equilibrium	NS	0.36	-0.22	0.07	**0.82**

Table 4. Model assumptions and complexity-stability relationships. Three changes in model assumptions are tested: studying food webs with a fixed number of five primary producer species (PP), setting the body mass of primary producers to 1 and deleting cannibalistic links. For each changes, results (proportion of food webs with extinction(s) and proportion of persistent food webs that reach an equilibrium) are summarized for Holling's and Ivlev's functional responses. Trophic complexity (number of species S and connectance C) is varied within the same range as in figure 2. The obtained range of results and the mean impact of trophic complexity are shown. The "-" indicates that the impact of the number of species is not discussed because the number of persistent food webs studied has been decreased for computational reasons.

assumption	functional response	extinction(s) range	S	C	equilibrium range	S	C
number of PP	Holling	$[0.48, 1.00]$	$\times 1.6$	$\times 0.8$	$[0.15, 0.78]$	-	$\times 4.3$
	Ivlev	$[0.47, 1.00]$	$\times 1.7$	$\times 0.9$	$[0.92, 0.99]$	-	$\times 1.03$
body mass of PP	Holling	$[0.48, 0.99]$	$\times 1.6$	$\times 1.2$	$[0.38, 0.86]$	$\times 1.02$	$\times 2.2$
	Ivlev	$[0.43, 1.00]$	$\times 1.7$	$\times 1.3$	1.00	$=$	$=$
body mass of PP	Holling	$[0.60, 1.00]$	$\times 1.4$	$\times 1.2$	$[0.35, 0.81]$	$\times 1.05$	$\times 2.2$
+ no cannibalism	Ivlev	$[0.51, 1.00]$	$\times 1.5$	$\times 1.3$	1.00	$=$	$=$

These changes in model assumptions show that food web persistence decreases with connectance due to a decrease of the proportion of primary producer species in food webs made by the niche model (SOM, figure 2). However, persistence is increased by the connectance *per se*, i.e. the number of pathways where energy can flow. Furthermore, connectance increases the occurrence of equilibrium dynamics and improves species survival by keeping their dynamics far from the extinction threshold. More equilibrium dynamics occur at high connectance because it increases the number of weak trophic links. Weak links stabilize equilibria by dampening predator-prey oscillations (McCann *et al.*, 1998).

The impact of the number of species on system dynamics can be related to general questions on the effect of biodiversity on ecosystem functioning (May, 1999; McCann, 2000). Jiang & Pu (2009) have made a meta-analysis of empirical studies on the effect of biodiversity. Both observational and experimental studies on multi-trophic communities indicate that the temporal variability of state variables (biomasses, processes, etc.) decreases at the population level (15 studies), and even more at the community level (25 studies). These trends are predicted by the model, which predicts more equilibrium dynamics (figure 2 and table 4) and a lower temporal variability of population biomass (section 5 in SOM) in larger persistent food webs. In addition, larger food webs have a lower variability of their predicted total biomass (data not shown). Note that in the model we used, there is no feedback of population dynamics on the trophic structure, which is set *a priori*. Thus, the link between diversity and ecosystem persistence can be better explored using evolutionary models that build persistent networks of interaction based on population dynamics (Drossel *et al.*, 2001; Loeuille & Loreau, 2005; Rossberg *et al.*, 2006).

3.6   Structural sensitivity and modelling biological systems

We have shown that quantitatively close mathematical functions can lead to qualitatively different food web dynamics. However, the amount of differences in dynamics depends on the way the functions were parameterized. In general, parameterization is realized by either fitting the functions to data on the process itself (Anderson *et al.*, 2010; Cordoleani *et al.*, 2011; Fussmann *et al.*, 2000; Poggiale *et al.*, 2010), or fitting the full model predictions (other parameters can be optimized at the same time) to data on the temporal evolution of the system (Canale *et al.*, 1973; Kooi & Kooijman, 1994).

Here, we used the first method in different ways. The most classical ones, namely a fit with a uniform weight over the range of biomass observed or a fit using the empirical biomass distribution, lead to significant differences in model dynamics between functional responses. These differences become lower

17

only if the fit is done so that functions are close in term of property that drives model dynamics (here the functional response slope at the origin). So, model dynamics have to be known *a priori* to be able to use this approach, which is in fact more similar to the second method of fit.

The second method focuses on the dynamics predicted by the model. Different functions can be parameterized in order to predict close dynamics. However, these dynamics are specific to the set of environmental conditions (i.e. other parameter values) used. If these conditions are changed (e.g. resource availability, mortality due to external factors), the different functions are likely to predict different dynamics as they are outside the range of optimization. The underlying idea is similar to the method of generalized modelling (Gross & Feudel, 2006) and the approach proposed by Adamson & Morozov (2012). These approaches do not specify model formulation and describe only the local properties of the model (like the slope of a function) near an equilibrium. So, results on equilibrium stability are independent of a specific formulation. However, these approaches provide no information on the system dynamics far from this equilibrium, like the existence of alternative stable states. In conclusion, if different functions are parameterized to predict similar dynamics in a given situation, this is likely to work only in the vicinity of this given situation (e.g. a given equilibrium). Choosing to do so or to use the first method depends on the purpose of the study.

Stable equilibria and limit cycles can coexist in the food web model applied to a one-predator/one-prey system, due to density-dependent mortality (Aldebert *et al.*, 2016). Density-dependent mortality allows the coexistence of different asymptotic states that depend on functional response formulation. As a consequence, functional response formulation drives model predictions in situations where external disturbances and recovery policies are applied (resilience, hysteresis phenomena). Such situations have not been investigated in food webs in this study, as we did one dynamical simulation per food web. Multiple simulations with different initial conditions are required for each food web to try to detect different asymptotic dynamics. Indeed, the existence of such dynamics cannot be fully determined using bifurcation analysis in systems with tens of state variables like food webs. However, quantifying uncertainties in food web model predictions in situations with external disturbances would be an important step toward more accurate model predictions.

4 Conclusion

We investigated the sensitivity of a food web model to the choice of functional response formulation (Holling's or Ivlev's FRs). We found a little effect of functional response formulation on food web persistence, whereas food web variability is significantly lower with Ivlev's functional response. Functional response slope at equilibrium explains this lower variability. In addition, food web variability is more driven by functional response formulation than by its parameter values and the tested range of trophic complexity (number of species, connectance). However, complexity-stability relationships are not qualitatively affected by functional response formulation. These conclusions are robust both to different combinations of model assumptions (cannibalism, primary production) and to different fitting methods to parameterize functional responses.

Because of intrinsic data variability and because model formulation is always a simplified representation of complex biological processes, the choice of functional response may remain uncertain for many species. The results demonstrate that this uncertainty in the formulation of a food web model can lead to uncertainties in the type of asymptotic dynamics it predicts. In addition, uncertainties in predicted system resilience in case of external disturbances are known to arise in some predator-prey models, and so are likely to occur in food web models. The quantification of these potential uncertainties in food web resilience may be a challenging way of research toward more accurate model predictions.

Acknowledgments

References

Adamson, MW, Morozov, AY. 2012. When can we trust our model predictions? Unearthing structural sensitivity in biological systems. *Proceedings of the Royal Society of London A*, **469**(2149).

Adamson, MW, Morozov, AY. 2014. Defining and detecting structural sensitivity in biological models: developing a new framework. *Journal of Mathematical Biology*, **69**, 1815–1848.

Aldebert, C, Nerini, D, Gauduchon, M, Poggiale, JC. 2016. Structural sensitivity and resilience in a predator-prey model with density-dependent mortality. *Ecological Complexity*. http://dx.doi.org/10.1016/j.ecocom.2016.05.004.

Allesina, S, Alonso, D, Pascual, M. 2008. A general model for food web structure. *Science*, **320**, 658–661.

Anderson, TR, Gentleman, WC, Sinha, B. 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global ocean general circulation model. *Progress in Oceanography*, **87**, 201–213.

Arhonditsis, GB, Brett, MT. 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. *Marine Ecology Progress Series*, **271**, 13–26.

Brose, U, Williams, RJ, Martinez, ND. 2006. Allometric scaling enhances stability in complex food webs. *Ecology Letters*, **9**, 1228–1236.

Brown, JH, Gillooly, JF, Allen, AP, Savage, VM, West, GB. 2004. Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Canale, RP, Lustig, TD, Kehrberger, PM, Salo, JE. 1973. Experimental and mathematical modeling studies of protozoan predation on bacteria. *Biotechnology and Bioengineering*, **15**, 707–728.

Cattin, MF, Bersier, LF, Banasek-Richter, C, Baltensperger, R, Gabriel, JP. 2004. Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**, 835–839.

Cordoleani, F, Nerini, D, Gauduchon, M, Morozov, A, Poggiale, JC. 2011. Structural sensitivity of biological models revisited. *Journal of Theoretical Biology*, **283**, 82–91.

Drossel, B, Higgs, PG, McKane, AJ. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology*, **208**, 91–107.

Fulton, EA, Smith, ADM, Johnson, CR. 2003a. Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series*, **253**, 1–16.

20

Fulton, EA, Smith, ADM, Johnson, CR. 2003b. Mortality and predation in ecosystem models: is it important how these are expressed? *Ecological Modelling*, **169**, 157–178.

Fussmann, GF, Blasius, B. 2005. Community response to enrichment is highly sensitive to model structure. *Biology Letters*, **1**(1), 9–12.

Fussmann, GF, Ellner, SP, Shertzer, KW, Hairston Jr, NG. 2000. Crossing the Hopf bifurcation in a live predator-prey system. *Science*, **290**, 1358–1360.

Galassi, M, Davies, J, Theiler, J, Gough, B, Jungman, G, Alken, P, Booth, M, Rossi, F, Ulerich, R. 2013. *GNU Scientific Library Reference Manual (3rd eds), version 1.16.* ISBN 0954612078, `http://www.gnu.org/software/gsl/`.

Gentleman, W, Leising, A, Frost, B, Strom, S, Murray, J. 2003. Functional responses for zooplancton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep-Sea Research II*, **50**, 2847–2875.

Gross, T, Feudel, U. 2006. Generalized models as a universal approach to the analysis of nonlinear dynamical systems. *Physical Review E*, **73**(1), 016205.

Gross, T, Ebenhöh, W, Feudel, U. 2004. Enrichment and foodchain stability: the impact of different forms of predator-prey interaction. *Journal of Theoretical Biology*, **227**, 349–358.

Gross, T, Rudolf, L, Levin, SA, Dieckmann, U. 2009. Generalized models reveal stabilizing factors in food webs. *Science*, **325**, 747–750.

Heckmann, L, Drossel, B, Brose, U, Guill, C. 2012. Interactive effects of body-size structure and adaptative foraging on food-web stability. *Ecology Letters*, **15**, 243–250.

Holling, CS. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**(7), 385–398.

Holling, CS. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, **45**, 3–60.

Hutchinson, GE. 1957. *Concluding remarks.* Cold Spring Harbor symposium on quantitative biology. **22**, 415-427.

Ivlev, VS. 1955. *Experimental ecology of the feeding of fishes.* Pischepromizdat, Moscow. 302 pp. (translated from Russian by D. Scott, Yale University Press, New Haven, 1961).

Jeschke, JM, Kopp, M, Tollrian, R. 2002. Predator functional response: discriminating between handling and digesting prey. *Ecological Monographs*, **72**(1), 95–112.

Jiang, L, Pu, Z. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist*, **174**(5), 651–659.

Kartascheff, B, Guill, C, Drossel, B. 2009. Positive complexity-stability relations in food web models without foraging adaptation. *Journal of Theoretical Biology*, **259**, 12–23.

Kartascheff, B, Heckmann, L, Drossel, B, Guill, C. 2010. Why allometric scaling enhances stability in food web models. *Theoretical Ecology*, **3**, 195–208.

Kooi, BW, Kooijman, SALM. 1994. The transient behaviour of food chains in chemostat. *Journal of Theoretical Biology*, **170**, 87–94.

Kooijman, SALM. 2010. *Dynamic energy budget theory for metabolic organisation.* 3rd edn. Cambridge University Press, Cambridge. 514 pp.

Loeuille, N, Loreau, M. 2005. Evolutionary emergence of size-structure food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**(16), 5761–5766.

Loreau, M. 2010. *From populations to ecosystems: theoretical foundations for a new ecological synthesis.* Princeton University Press, Princeton. 297 pp.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of commmunity stability. *Ecology*, **36**(3), 533–536.

Martinez, ND. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, **61**(4), 367–392.

May, RM. 1972. Will a large complex system be stable? *Nature*, **238**, 413–414.

May, RM. 1973. Qualitative stability in model ecosystems. *Ecology*, **54**(3), 638–641.

May, RM. 1999. Unanswered questions in ecology. *Philosophical Transactions of the Royal Society of London B*, **354**, 1951–1959.

22

McCann, K, Hastings, A, Huxel, GR. 1998. Weak trophic interaction and the balance of nature. *Nature*, **395**, 794–798.

McCann, KS. 2000. The diversity-stability debate. *Nature*, **405**, 228–233.

Mullin, MM, Stewart, EF, Fuglister, FJ. 1975. Ingestion by planktonic grazers as a function of food concentration. *Limnology and Oceanography*, **20**(2), 259–262.

Myerscough, MR, Darwen, MJ, Hogarth, WL. 1996. Stability, persistence and structural stability in a classical predator-prey model. *Ecological Modelling*, **89**, 31–42.

Nelder, JA, Mead, R. 1965. A simplex method for function minimization. *Computer journal*, **7**(4), 308–313.

Plitzko, SJ, Drossel, B, Guill, C. 2012. Complexity-stability relations in generalized food-web models with realistic parameters. *Journal of Theoretical Biology*, **306**, 7–14.

Poggiale, JC, Baklouti, M, Queguiner, B, Kooijman, SALM. 2010. How far details are important in ecosystem modelling: the case of multi-limiting nutrients in phytoplankton-zooplankton interactions. *Philosophical Transactions of the Royal Society of London B*, **365**, 3495–3507.

R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. `http://www.R-project.org/`.

Rossberg, AG, Matsuda, H, Amemiya, T, Itoh, K. 2006. Food webs: experts consuming families of experts. *Journal of Theoretical Biology*, **241**, 552–563.

Simonoff, JS. 1996. *Smoothing methods in statistics*. Springer, New York. 338 pp.

Stouffer, DB, Bascompte, J. 2010. Understanding food-web persistence from local to global scales. *Ecology Letters*, **13**, 154–161.

Stouffer, DB, Bascompte, J. 2011. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, **108**(9), 3648–3652.

Uchida, S, Drossel, B. 2007. Relation between complexity and stability in food webs with adaptive behavior. *Journal of Theoretical Biology*, **247**, 713–722.

441 Williams, RJ. 2008. Effects of network and dynamical model structure on species persistence in large

442   model food webs. *Theoretical Ecology*, **1**(3), 141–151.

443 Williams, RJ, Martinez, ND. 2000. Simple rules yield complex food webs. *Nature*, **404**, 180–183.

444 Williams, RJ, Martinez, ND. 2004. Stabilization of chaotic and non-permanent food-web dynamics. *The*

445   *European Physical Journal B*, **38**, 297–303.

446 Wood, SN, Thomas, MB. 1999. Super–sensitivity to structure in biological models. *Proceedings of the*

447   *Royal Society of London B*, **266**, 565–570.

448 Yeakel, JD, Stiefs, D, Novak, M, Gross, T. 2011. Generalized modeling of ecological population dynamics.

449   *Theoretical Ecology*, **4**, 179–194.

450 Yodzis, P, Innes, S. 1992. Body size and consumer-resource dynamics. *The American Naturalist*, **139**(6),

451   1151–1175.

452 # Appendix S1: the jacobian matrix

$$
\begin{aligned}
J_{i,i}^{\phi} &= \lambda \left[q_i^{\phi} + G_i^{\phi,tot} + B_i \frac{\partial G_i^{\phi,tot}}{\partial B_i} \right] - G_{i,i}^{\phi} - \sum_{k \in C_i} B_k \frac{\partial G_{k,i}^{\phi}}{\partial B_i} - \alpha_i - 2\beta_i B_i \quad i = 1, ..., S \\
J_{i,j}^{\phi} &= \lambda B_i \frac{\partial G_i^{\phi,tot}}{\partial B_j} - G_{j,i}^{\phi} + \sum_{k \in C_i} \frac{\partial G_{k,i}^{\phi}}{\partial B_j} \qquad\qquad\qquad\qquad\quad i, j = 1, ..., S, \ j \neq i
\end{aligned}
$$