

Does structural sensitivity alter complexity–stability relationships?

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

▶ To cite this version:

Clement Aldebert, David Nerini, Mathias Gauduchon, J.C. Poggiale. Does structural sensitivity alter complexity–stability relationships?. Ecological Complexity, 2016, 28, pp.104 - 112. 10.1016/j.ecocom.2016.07.004 . hal-01827263

HAL Id: hal-01827263 https://hal.science/hal-01827263

Submitted on 11 Dec 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Does structural sensitivity alter complexity-stability relationships?

- ³ C. Aldebert^{a,*}, D. Nerini^a, M. Gauduchon^a, JC. Poggiale^a
- ⁴ a Mediterranean Institute of Oceanography, Aix-Marseille University, Toulon University, CNRS/INSU,
- 5 IRD, MIO, UM 110, 13288, Marseille, Cedex 09, France.
- ⁶ * corresponding author, +33 (0)4 860 90 640

7 E-mails:

- clement.aldebert@univ-amu.fr,
- david.nerini@univ-amu.fr,
- mathias.gauduchon@univ-amu.fr,
- jean-christophe.poggiale@univ-amu.fr

12 Keywords

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

15 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

²¹ Abstract

Structural sensitivity, namely the sensitivity of a model dynamics to slight changes in its mathematical 22 formulation, has already been studied in some models with a small number of state variables. The 23 aim of this study is to investigate the impact of structural sensitivity in a food web model. Especially, 24 the importance of structural sensitivity is compared to that of trophic complexity (number of species, 25 connectance), which is known to strongly influence food web dynamics. Food web structures are built 26 using the niche model. Then food web dynamics are modeled using several type II functional responses 27 parameterized to fit the same predation fluxes. Food web persistence was found to be mostly determined 28 by trophic complexity. At the opposite, even if food web connectance promotes equilibrium dynamics, 29 their occurrence is mainly driven by the choice of the functional response. These conclusions are robust to 30 changes in some parameter values, the fitting method and some model assumptions. In a one-prey/one-31 predator system, it was shown that the possibility that multiple stable states coexist can be highly 32 structural sensitive. Quantifying this type of uncertainty at the scale of ecosystem models will be both a 33 natural extension to this work and a challenging issue. 34

35 1 Introduction

Predictions made by mathematical models can be sensitive to model formulation (Anderson et al., 2010; 36 Fulton et al., 2003b; Fussmann & Blasius, 2005, among others). However, this sensitivity has rarely been 37 tested in theoretical and operational ecosystem models (Arhonditsis & Brett, 2004; Fulton et al., 2003a). 38 In ecological models with multiple interacting populations, phenomena observed at the community scale 39 are usually represented by simplifying smaller scale processes. For instance, collective and individual 40 behaviours as well as physiological processes involved in predation are collapsed into one function, the 41 functional response (Gentleman et al., 2003; Jeschke et al., 2002). Numerous mathematical formulations 42 of a given biological phenomenon are relevant in the sense that: (i) their properties and assumptions about 43 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 45 have the same mathematical properties (pointwise properties, monotonicity, convexity, ...). However, the 46 choice of a particular function among relevant ones can affect the dynamics predicted by the same model. 47 Differences occur in predicted steady-state values, equilibrium vs. oscillating dynamics and in the system 48 response to external disturbances (Aldebert et al., 2016). Uncertainty due to this choice of a function is 49 coined as "structural sensitivity" (sensu Cordoleani et al., 2011). 50

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 ⁶⁴ built by simple random models (Cattin *et al.*, 2004; Williams & Martinez, 2000, among others). These
⁶⁵ models have been used to statistically investigate complexity-stability relationships in food web models
⁶⁶ based on different ecological phenomena (Brose *et al.*, 2006; Heckmann *et al.*, 2012; Kartascheff *et al.*,
⁶⁷ 2009, 2010; Plitzko *et al.*, 2012; Stouffer & Bascompte, 2010, 2011; Uchida & Drossel, 2007; Williams,
⁶⁸ 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 complexitystability relationships?

Next section presents the studied food web model. It is an extension of a predator-prey model in 72 which structural sensitivity has already been explored (Aldebert et al., 2016). Structural sensitivity in 73 this model is compared to the impact of trophic complexity in section 3.1. Observed results are then 74 explained from the knowledge of predator-prey models (section 3.2) and their robustness to changes 75 in the method used to fit functional responses is tested (section 3.3). Then, the relative importance 76 of trophic complexity, functional response formulation and parameter values is estimated (section 3.4). 77 Next, robustness to changes in model assumptions is assessed, and complexity-stability relationships are 78 compared to empirical findings (section 3.5). Paper ends with a more general discussion about structural 79 sensitivity and modelling of biological systems (section 3.6). 80

$_{\scriptscriptstyle 81}$ 2 Models

$_{82}$ 2.1 Food web structure

Food webs are composed by S species (*sensu* trophic species) and one resource. Species are linked by Ltrophic 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.

⁹⁶ 2.2 Food web dynamics

1 1

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:

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

Right terms of model (1) handle respectively a gain in biomass by primary production, sum of gains 101 by predation, sum of losses by predation, linear mortality and respiration, density-dependent mortality 102 (intra-specific competition, diseases). Species i possesses a set of prey (predator) species denoted as R_i 103 (C_i) . By definition, primary producers have $R_i = \emptyset$ and top-predators have $C_i = \emptyset$. The parameter 104 λ is the assimilation efficiency. For the sake of simplicity, λ is assumed to be the same for all species. 105 Parameter α_i is the linear mortality rate and parameter β_i is the per-capita intra-specific competition 106 rate of species i. The letter ϕ indicates the specific formulation used for the Holling-type II functional 107 response $G_{i,j}^{\phi}$. For simplicity, all species are assumed to have the same formulation. This one is either 10 Holling's disc equation (1959; 1965) denoted as $G_{i,j}^H$ or Ivlev's functional response (1955) denoted as $G_{i,j}^I$ 109 (later called Holling's FR and Ivlev's FR): 110

$$G_{i,j}^{H} = \frac{a_{i}^{H} f_{i,j} B_{j}}{1 + h_{i}^{H} a_{i}^{H} T_{i}}, \ G_{i,j}^{I} = \frac{1}{h_{i}^{I}} \left(1 - \exp\left(-h_{i}^{I} a_{i}^{I} T_{i}\right)\right) \frac{f_{i,j} B_{j}}{T_{i}} \text{ with } T_{i} = \sum_{j \in R_{i}} f_{i,j} B_{j}.$$

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

¹¹⁹ functional responses also fulfills properties:

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

with 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:

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

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.

The term of primary productivity q_i^{ϕ} has the same equation as the functional response $G_{i,j}^{\phi}$ with a constant pool of resources B_{res} :

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

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 <i>et al.</i> , 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 <i>et al.</i> , 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 imes 0.36	see text	$biomass^{-1}$

¹⁴⁴ 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:

$$S_{A,\omega}\left(a^{I},h^{I}\right) = d_{A,\omega}^{2}\left(G_{i}^{H,tot},G_{i}^{I,tot}\right) = \int_{A}\omega(T_{i})\left(G_{i}^{H,tot}(T_{i}) - G_{i}^{I,tot}(T_{i})\right)^{2}dT_{i},$$

$$(2)$$

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 ¹⁵⁶ weighted by (figure 1):

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

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 161 species, with $B_1^*, B_2^*, ..., B_S^*$ being the species biomass at an equilibrium (and T_i^* the total prey biomass 162 available of species i at equilibrium). The jacobian matrix J^{ϕ} of system (1) is presented in appendix S1. 163 The algorithm presented in section 2 of SOM (with a discussion about its limits) is used to auto-164 matically determine the kind of asymptotic dynamics reached by a food web. The proposed algorithm 165 classifies asymptotic dynamics in three types: dynamics in which at least one species goes extinct, equi-166 librium in which all species coexist, fluctuating dynamics (e.g. limit cycle, torus, strange attractor) in 167 which all species coexist. The proportion of food webs in which all species coexist (at equilibrium or 168 with fluctuating dynamics) is a measure of food web persistence. The proportion of persistent food webs 169 (i.e. food webs in which all species coexist) which exhibit a fluctuating dynamics is a measure of food 170 web variability. Food webs construction and simulation were achieved by C++ programs using GNU 171 Scientific Library for C/C++ (Galassi *et al.*, 2013). Post-simulation analysis and figures were performed 172 using R language (R Core Team, 2013). 173

¹⁷⁴ 3 Results and Discussion

¹⁷⁵ 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 (×1.4 with Holling's FR and ×1.5 with Ivlev's FR) than with connectance (×1.2 and $\times 1.3$). Functional responses are parameterized to predict quantitatively close predation fluxes, which explains their similar predictions of food web persistence.

¹⁸³ Conversely, food web variability is mainly driven by functional response formulation within the tested ¹⁸⁴ range of trophic complexity (figure 2b,d). Ivlev's FR predicts 2.3 times more equilibrium dynamics (from ¹⁸⁵ 98 % to 99 % of persistent food webs reach an equilibrium) than Holling's FR does (from 25 % to ¹⁸⁶ 80 %). The proportion of equilibrium dynamics increases more with connectance (on average $\times 3.2$ with ¹⁸⁷ Holling's FR and +1 % with Ivlev's FR) than with the number of species ($\times 1.1$ with Holling's FR, no ¹⁸⁸ trend with Ivlev's FR). Even if the effect of trophic complexity can change with other measures of food ¹⁸⁹ web persistence and variability, the latter is still higher with Ivlev's FR (section 5 in SOM).

¹⁹⁰ 3.2 Understanding structural sensitivity in food webs

¹⁹¹ Model (1) applied to a one-predator/one-prey system owns an equibrium which is stable with Ivlev's FR ¹⁹² and unstable with Holling's FR in 26 % to 49 % of the parameter space explored in Aldebert *et al.* (2016). ¹⁹³ With Holling's FR, dynamics converge on a stable limit cycle. Equilibrium stability is different because ¹⁹⁴ the slope of Holling's FR at equilibrium is lower. The slope of the functional response at equilibrium in ¹⁹⁵ 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 199 functional responses (figure 3). However, Ivlev's FR has a higher elasticity than Holling's FR for low 200 prey biomass values (figure 4b). As a consequence, the realized γ_i distribution in food web simulations 201 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 202 latter, one can expect that stable equilibria are closer to a bifurcation threshold (with respect to γ_i). 203 Thus, more food webs are likely to be on the unstable side of this bifurcation with Holling's FR. This 204 can explain why this function leads more frequently to fluctuating dynamics. This reasoning extends the 205 previous mechanism found in predator-prev models (Fussmann & Blasius, 2005) to the scale of complex 206



Holling's disc equation

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.

0.15

0.10

0.99

0.97

60

0.98

0.99

20

0.98

0.98

30

0.98

0.98

40

number of species

50

0.98

0.98

60

0.83

0.74

30

0.63

0.49 1 20

0.15

0.10

0.93

0.88

40

number of species

50

207 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).

²⁰⁸ 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 prev 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).

trophic complexity (section 3 in SOM). The parameter set that leads to the closer food web variability 220 $(\omega_{\mathcal{P}} \text{ within } [0, 3.5])$ does not lead to the best fit of functional responses within the range of prey biomass 221 observed (column $S_{\omega_{\mathcal{U}},[0,3,5]}$ in table 2), as it is optimized for even smaller biomass values. In other 222 words, this parameter set optimizes only the slope at the origin (a^{ϕ}) , as we know that the functional 223 response slope drives food web variability. Only one parameter set is usually considered in previous 224 studies on structural sensitivity in predator-prey models (Aldebert et al., 2016; Cordoleani et al., 2011; 225 Fussmann & Blasius, 2005; Myerscough et al., 1996). We checked here with different parameter sets that 226 functional response formulation influences food web variability, even if this influence is lower with some 227 fitting methods. 228

²²⁹ 3.4 Structural sensitivity vs. parameter sensitivity

Even with the simplifying assumption that parameter values scale allometrically, a full parameter sensitivity analysis requires a high computational effort. Indeed, to be reasonably exhaustive it is necessary 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 $(a^{\phi} \text{ and } h^{\phi})$ 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}	$S_{\omega_{u},[0,3.5]}$	$S_{\omega_{\mathcal{U}},[3.5,500]}$	$\operatorname{extinction}(s)$	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	ı fig. 3b	4.50	0.44	0.015	0.327	0.91	0.80
Holling's disc equat	ion	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



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).

²⁴⁵ correspond to a quantitatively similar variation measured between the functional responses (Adamson ²⁴⁶ & Morozov, 2012, 2014; Cordoleani *et al.*, 2011; Wood & Thomas, 1999). Indeed, for a quantitatively ²⁴⁷ similar variation, a change of formulation may affect the function shape and lead to a higher change in ²⁴⁸ functional response slope near equilibrium, i.e. in equilibrium stability.

²⁴⁹ 3.5 Model assumptions, complexity-stability relationships and biological sys-

250 tems

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 detailled 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.

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.

		extinction(s)			equilibrium		
assumption	functional response	range	S	C	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 264 effect of biodiversity on ecosystem functioning (May, 1999; McCann, 2000). Jiang & Pu (2009) have made 265 a meta-analysis of empirical studies on the effect of biodiversity. Both observational and experimental 266 studies on multi-trophic communities indicate that the temporal variability of state variables (biomasses, 267 processes, etc.) decreases at the population level (15 studies), and even more at the community level (25 268 studies). These trends are predicted by the model, which predicts more equilibrium dynamics (figure 2 269 and table 4) and a lower temporal variability of population biomass (section 5 in SOM) in larger persistent 270 food webs. In addition, larger food webs have a lower variability of their predicted total biomass (data 271 not shown). Note that in the model we used, there is no feedback of population dynamics on the trophic 272 structure, which is set a priori. Thus, the link between diversity and ecosystem persistence can be better 273 explored using evolutionary models that build persistent networks of interaction based on population 274 dynamics (Drossel et al., 2001; Loeuille & Loreau, 2005; Rossberg et al., 2006). 275

²⁷⁶ 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 ²⁸⁶ only if the fit is done so that functions are close in term of property that drives model dynamics (here ²⁸⁷ the functional response slope at the origin). So, model dynamics have to be known *a priori* to be able ²⁸⁸ 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 289 parameterized in order to predict close dynamics. However, these dynamics are specific to the set of 290 environmental conditions (i.e. other parameter values) used. If these conditions are changed (e.g. re-291 source availability, mortality due to external factors), the different functions are likely to predict different 292 dynamics as they are outside the range of optimization. The underlying idea is similar to the method of 293 generalized modelling (Gross & Feudel, 2006) and the approach proposed by Adamson & Morozov (2012). 294 These approaches do not specify model formulation and describe only the local properties of the model 295 (like the slope of a function) near an equilibrium. So, results on equilibrium stability are independent of a 296 specific formulation. However, these approaches provide no information on the system dynamics far from 297 this equilibrium, like the existence of alternative stable states. In conclusion, if different functions are 298 parameterized to predict similar dynamics in a given situation, this is likely to work only in the vicinity 299 of this given situation (e.g. a given equilibrium). Choosing to do so or to use the first method depends 300 on the purpose of the study. 301

Stable equilibria and limit cycles can coexist in the food web model applied to a one-predator/one-302 prey system, due to density-dependent mortality (Aldebert et al., 2016). Density-dependent mortality 303 allows the coexistence of different asymptotic states that depend on functional response formulation. 304 As a consequence, functional response formulation drives model predictions in situations where external 305 disturbances and recovery policies are applied (resilience, hysteresis phenomena). Such situations have not 306 been investigated in food webs in this study, as we did one dynamical simulation per food web. Multiple 30 simulations with different initial conditions are required for each food web to try to detect different 308 asymptotic dynamics. Indeed, the existence of such dynamics cannot be fully determined using bifurcation 309 analysis in systems with tens of state variables like food webs. However, quantifying uncertainties in food 310 web model predictions in situations with external disturbances would be an important step toward more 311 accurate model predictions. 312

313 4 Conclusion

We investigated the sensitivity of a food web model to the choice of functional response formulation 314 (Holling's or Ivlev's FRs). We found a little effect of functional response formulation on food web per-315 sistence, whereas food web variability is significantly lower with Ivlev's functional response. Functional 316 response slope at equilibrium explains this lower variability. In addition, food web variability is more 317 driven by functional response formulation than by its parameter values and the tested range of trophic 318 complexity (number of species, connectance). However, complexity-stability relationships are not qual-319 itatively affected by functional response formulation. These conclusions are robust both to different 320 combinations of model assumptions (cannibalism, primary production) and to different fitting methods 321 to parameterize functional responses. 322

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.

330 Acknowledgments

The authors thank four anonymous reviewers for their very constructive comments on earlier versions of the manuscript. We also thank Bastien Bellemin-Noel for language proof-reading. The authors acknowledge the staff of the "Cluster de calcul intensif HPC" Platform (OSU Institut Pythéas, Aix-Marseille Université, INSU-CNRS) for providing computing facilities. The PhD scholarship of C.A. was funded by the French Ministry for Education and Research.

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 re silience 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.
- ³⁵⁴ Canale, RP, Lustig, TD, Kehrberger, PM, Salo, JE. 1973. Experimental and mathematical modeling
 ³⁵⁵ 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 con straints and adaptation explain food-web structure. *Nature*, 427, 835–839.
- ³⁵⁸ Cordoleani, F, Nerini, D, Gauduchon, M, Morozov, A, Poggiale, JC. 2011. Structural sensitivity of
 <sup>biological models revisited. Journal of Theoretical Biology, 283, 82–91.
 </sup>
- ³⁶⁰ Drossel, B, Higgs, PG, McKane, AJ. 2001. The influence of predator-prey population dynamics on the
 ³⁶¹ long-term evolution of food web structure. *Journal of Theoretical Biology*, **208**, 91–107.
- ³⁶² Fulton, EA, Smith, ADM, Johnson, CR. 2003a. Effect of complexity on marine ecosystem models. Marine
- 363 Ecology Progress Series, 253, 1–16.

- 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.
- ³⁶⁶ Fussmann, GF, Blasius, B. 2005. Community response to enrichment is highly sensitive to model struc-
- $_{367}$ ture. Biology Letters, $\mathbf{1}(1)$, 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/.
- 373 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.

- ³⁹⁰ Ivlev, VS. 1955. Experimental ecology of the feeding of fishes. Pischepromizdat, Moscow. 302 pp.
 ³⁹¹ (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.
- ³⁹⁶ Kartascheff, B, Guill, C, Drossel, B. 2009. Positive complexity-stability relations in food web models
 ³⁹⁷ 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*
- ⁴⁰⁵ National Academy of Sciences of the United States of America, **102**(16), 5761–5766.
- ⁴⁰⁶ Loreau, M. 2010. From populations to ecosystems: theoretical foundations for a new ecological synthesis.
- ⁴⁰⁷ Princeton University Press, Princeton. 297 pp.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community 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.
- 412 May, RM. 1972. Will a large complex system be stable? Nature, 238, 413–414.
- ⁴¹³ 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.

- ⁴¹⁶ McCann, K, Hastings, A, Huxel, GR. 1998. Weak trophic interaction and the balance of nature. *Nature*,
 ⁴¹⁷ **395**, 794–798.
- ⁴¹⁸ McCann, KS. 2000. The diversity-stability debate. *Nature*, **405**, 228–233.
- ⁴¹⁹ Mullin, MM, Stewart, EF, Fuglister, FJ. 1975. Ingestion by planktonic grazers as a function of food ⁴²⁰ concentration. *Limnology and Oceanography*, **20**(2), 259–262.
- ⁴²¹ Myerscough, MR, Darwen, MJ, Hogarth, WL. 1996. Stability, persistence and structural stability in a
 ⁴²² classical predator-prey model. *Ecological Modelling*, 89, 31–42.
- ⁴²³ Nelder, JA, Mead, R. 1965. A simplex method for function minimization. *Computer journal*, 7(4),
 ⁴²⁴ 308–313.
- 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.
- ⁴²⁷ Poggiale, JC, Baklouti, M, Queguiner, B, Kooijman, SALM. 2010. How far details are important in
 ⁴²⁸ ecosystem modelling: the case of multi-limiting nutrients in phytoplankton-zooplankton interactions.
 ⁴²⁹ Philosophical Transactions of the Royal Society of London B, 365, 3495–3507.
- ⁴³⁰ R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for
- 431 Statistical Computing, Vienna, Austria. http://www.R-project.org/.
- ⁴³² Rossberg, AG, Matsuda, H, Amemiya, T, Itoh, K. 2006. Food webs: experts consuming families of
 ⁴³³ experts. *Journal of Theoretical Biology*, **241**, 552–563.
- 434 Simonoff, JS. 1996. Smoothing methods in statistics. Springer, New York. 338 pp.
- ⁴³⁵ Stouffer, DB, Bascompte, J. 2010. Understanding food-web persistence from local to global scales. *Ecology* ⁴³⁶ *Letters*, 13, 154–161.
- 437 Stouffer, DB, Bascompte, J. 2011. Compartmentalization increases food-web persistence. Proceedings of
 438 the National Academy of Sciences of the United States of America, 108(9), 3648–3652.
- ⁴³⁹ Uchida, S, Drossel, B. 2007. Relation between complexity and stability in food webs with adaptive
 ⁴⁴⁰ behavior. *Journal of Theoretical Biology*, 247, 713–722.

- Williams, RJ. 2008. Effects of network and dynamical model structure on species persistence in large
 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
- European Physical Journal B, **38**, 297–303.
- Wood, SN, Thomas, MB. 1999. Super-sensitivity to structure in biological models. Proceedings of the *Royal Society of London B*, 266, 565–570.
- Yeakel, JD, Stiefs, D, Novak, M, Gross, T. 2011. Generalized modeling of ecological population dynamics.
 Theoretical Ecology, 4, 179–194.
- Yodzis, P, Innes, S. 1992. Body size and consumer-resource dynamics. The American Naturalist, 139(6),
 1151–1175.

452 Appendix S1: the jacobian matrix

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