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# Does structural sensitivity alter complexity-stability relationships?

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## 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

## 21 **Abstract**

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

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).

69 The questions we address in this paper are: (i) are dynamics predicted by a food web model more im-  
70 pacted by structural sensitivity or by trophic complexity? (ii) Does structural sensitivity alter complexity-  
71 stability relationships?

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

## 81 2 Models

### 82 2.1 Food web structure

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

90 The niche model is described in section 1 of Supporting Online Material (SOM). Food webs are made  
91 of distinct species, that are either a primary producer or a predator. Attribution of trophic links allows for

92 cannibalism and trophic loops. We added a rejection step after food webs construction to avoid unrealistic  
 93 patterns. We only studied food webs with a realized connectance that deviated at most by 0.01 of the  
 94 expected one, that are connected (no disconnected parts), and in which all predators feed (as a prey or  
 95 through a food chain) upon at least one primary producer.

## 96 2.2 Food web dynamics

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

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

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

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

111 Both functional responses are extended for a predator with multiple prey species by assuming that it  
 112 does not switch between preys (Gentleman *et al.*, 2003). For Holling's FR, parameters  $a_i^H$  and  $h_i^H$  are  
 113 respectively the attack rate and the handling time of the predator. For Ivlev's FR, parameter  $1/h_i^I$  is the  
 114 maximal digestion rate and  $a_i^I h_i^I$  is the satiation coefficient of the predator. The total amount of prey

115 available for species  $i$  is the weighted sum of its prey species biomass  $T_i$ . The weighting parameter  $f_{i,j}$   
 116 is constant and it can be considered as the foraging effort or the feeding preference of predator  $i$  for its  
 117 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  
 118 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  
 119 functional responses also fulfills properties:

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

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

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

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

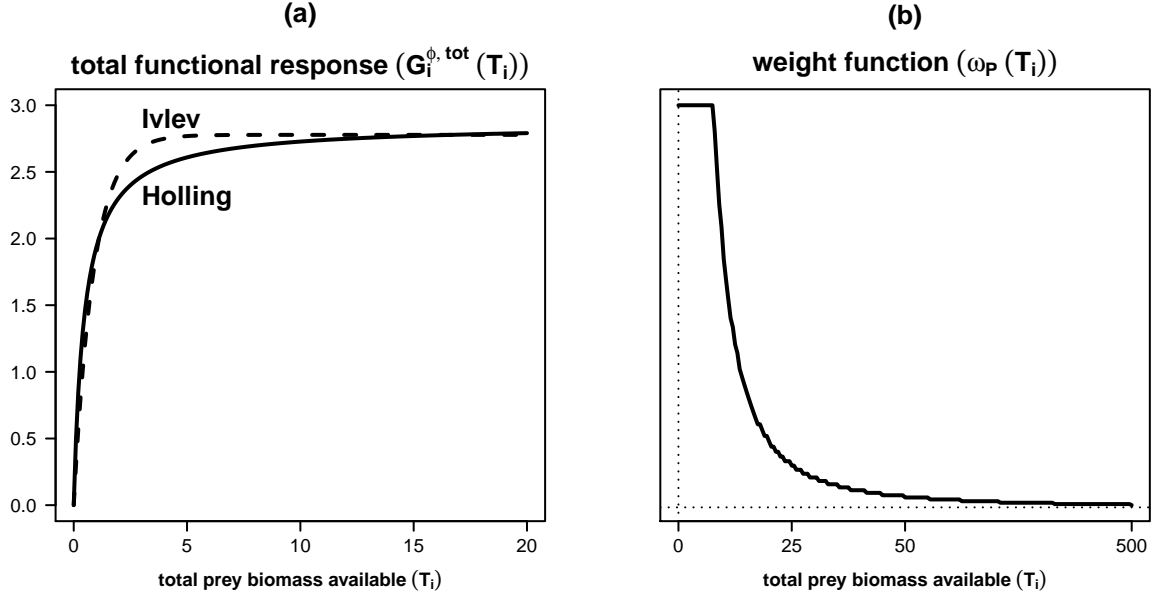
123 Thus,  $a_{pred}^\phi$  gives the slope of the functional response at the origin, and  $1/h_{pred}^\phi$  gives the asymptotic  
 124 value of the functional response when it saturates at high prey biomass.

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

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

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

132 Let  $M_i = 10^{x m_i}$  be the body mass of species  $i$ , with a scale parameter  $x$ . We assume that some  
 133 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.

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

134 As species abundance is quantified in terms of biomass, the scaling exponent  $-1/4$  corresponds to an  
 135 increase of individual metabolic rate with body mass power  $3/4$ , divided by individual body mass. The  
 136  $3/4$  exponent is controversial. Empirical data and theoretical studies indicate values between  $2/3$  and  
 137  $1$  (Kooijman, 2010). Nevertheless, the exact value of this exponent has a limited impact on species  
 138 extinctions in similar food web models (Kartascheff *et al.*, 2010).

139 Note that if two species have the same trophic interactions and parameter values, model (1) is sensitive  
 140 to the aggregation of these identical species as no direct inter-specific competition is considered. It has  
 141 no impact on our numerical results as identical (or infinitely close) species are infinitely rare in food webs  
 142 built by the niche model. This problem in model consistency can be solved by considering an inter-specific  
 143 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	$\alpha$	0.3	(Heckmann <i>et al.</i> , 2012)	$\text{time}^{-1}$
per-capita competition rate	$\beta$	0.5	(Heckmann <i>et al.</i> , 2012)	$\text{biomass}^{-1}\text{time}^{-1}$
assimilation efficiency	$\lambda$	0.65	(Heckmann <i>et al.</i> , 2012)	-
resource biomass	$B_{res}$	500	(Heckmann <i>et al.</i> , 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 <i>et al.</i> , 2012)	$\text{biomass}^{-1}\text{time}^{-1}$
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	$\text{time}^{-1}$
satiation coefficient	$a^I h^I$	$3.17 \times 0.36$	see text	$\text{biomass}^{-1}$

### 144 2.3 Parameterization and numerical study

145 Parameter values are displayed in table 1. The range of trophic complexity (20 to 60 species, connectance  
146 of 0.10 to 0.30) is set to include values used in previous studies (Gross *et al.*, 2009; Kartascheff *et al.*,  
147 2009, 2010; Plitzko *et al.*, 2012, among others) for comparison. The number of simulations is limited by  
148 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  
149  $|R_i|$  being the number of prey species of species  $i$ ). This choice implies that  $T_i$  is the average biomass of  
150 prey species  $\sum_{j \in R_i} B_j / |R_i|$  (weak generalist model, *sensu* Williams, 2008).

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

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

153 with a weighting function  $\omega(T_i)$  on a fitting range  $A$  of  $T_i$  values. Total prey biomass ranges from 0 to  
154 constant resource biomass for primary producers, so we set  $A = [0, B_{res}]$ . For a fixed amount of total  
155 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):

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

157 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  
158 species which ranges between one and  $S_{max} = 60$ . Minimizing the cost function  $S_{[0, B_{res}], \omega_{\mathcal{P}}}$  using the  
159 simplex method by Nelder & Mead (1965) give values  $a^I = 3.17$  and  $h^I = 0.36$ . The sensitivity of our  
160 results to choices in  $A$  and  $\omega(T_i)$  is discussed in section 3.3.

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

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

## 174 **3 Results and Discussion**

### 175 **3.1 Structural sensitivity vs. trophic complexity**

176 Both functional responses predict similar patterns of food web persistence as a function of trophic com-  
177 plexity (figure 2a,c). Within this range, Ivlev's FR predicts less extinctions than Holling's FR does (from  
178  $-11\%$  to  $+1\%$  food webs with at least one species extinction). With both functional responses, the  
179 proportion of non-persistent food webs increases with trophic complexity. This increase is higher with  
180 the number of species ( $\times 1.4$  with Holling's FR and  $\times 1.5$  with Ivlev's FR) than with connectance ( $\times 1.2$

181 and  $\times 1.3$ ). Functional responses are parameterized to predict quantitatively close predation fluxes, which  
 182 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

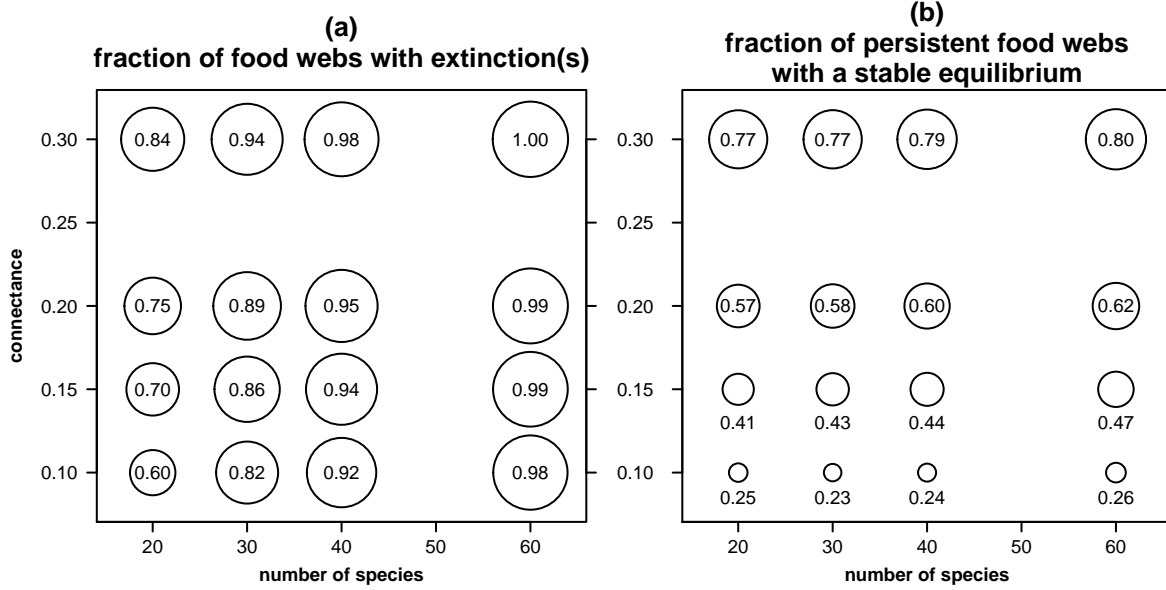
191 Model (1) applied to a one-predator/one-prey system owns an equilibrium which is stable with Ivlev’s FR  
 192 and unstable with Holling’s FR in 26 % to 49 % of the parameter space explored in Aldebert *et al.* (2016).  
 193 With Holling’s FR, dynamics converge on a stable limit cycle. Equilibrium 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:

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

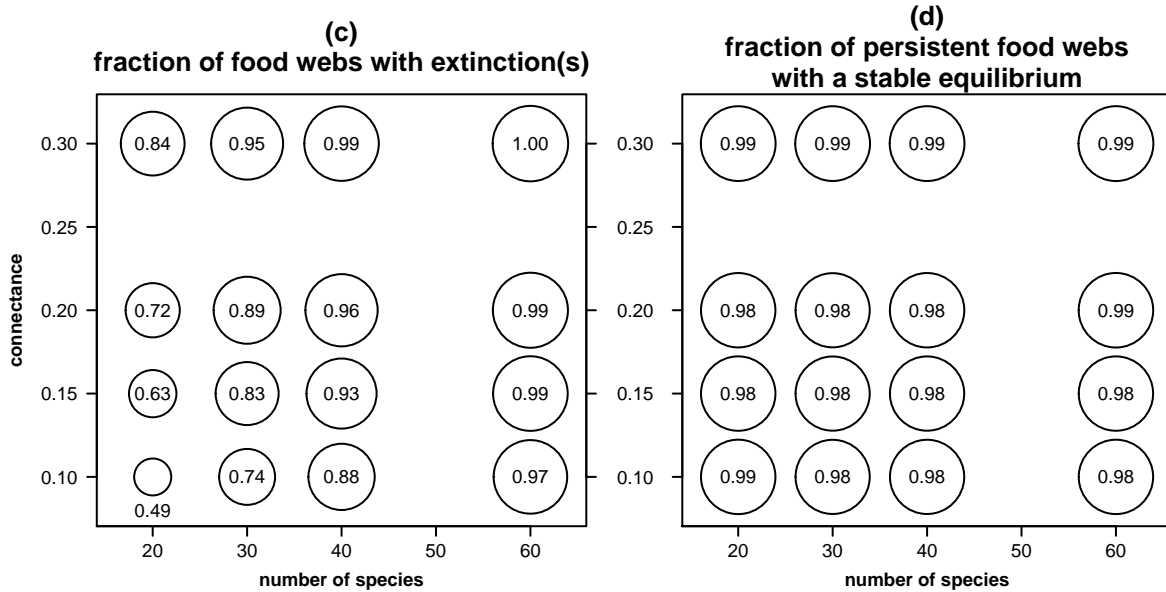
196 where the normalized functional response equals 1 at equilibrium ( $g_i^{\phi}(1) = 1$ ). A high elasticity  $\gamma_i$   
 197 stabilizes equilibria in predator-prey (Aldebert *et al.*, 2016; Yeakel *et al.*, 2011) and food web models  
 198 (section 6 of SOM).

199 The elasticity depends on prey biomass at equilibrium, which has a similar distribution between  
 200 functional responses (figure 3). However, Ivlev’s FR has a higher elasticity than Holling’s FR for low  
 201 prey biomass values (figure 4b). As a consequence, the realized  $\gamma_i$  distribution in food web simulations  
 202 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  
 203 latter, one can expect that stable equilibria are closer to a bifurcation threshold (with respect to  $\gamma_i$ ).  
 204 Thus, more food webs are likely to be on the unstable side of this bifurcation with Holling’s FR. This  
 205 can explain why this function leads more frequently to fluctuating dynamics. This reasoning extends the  
 206 previous mechanism found in predator-prey models (Fussmann & Blasius, 2005) to the scale of complex

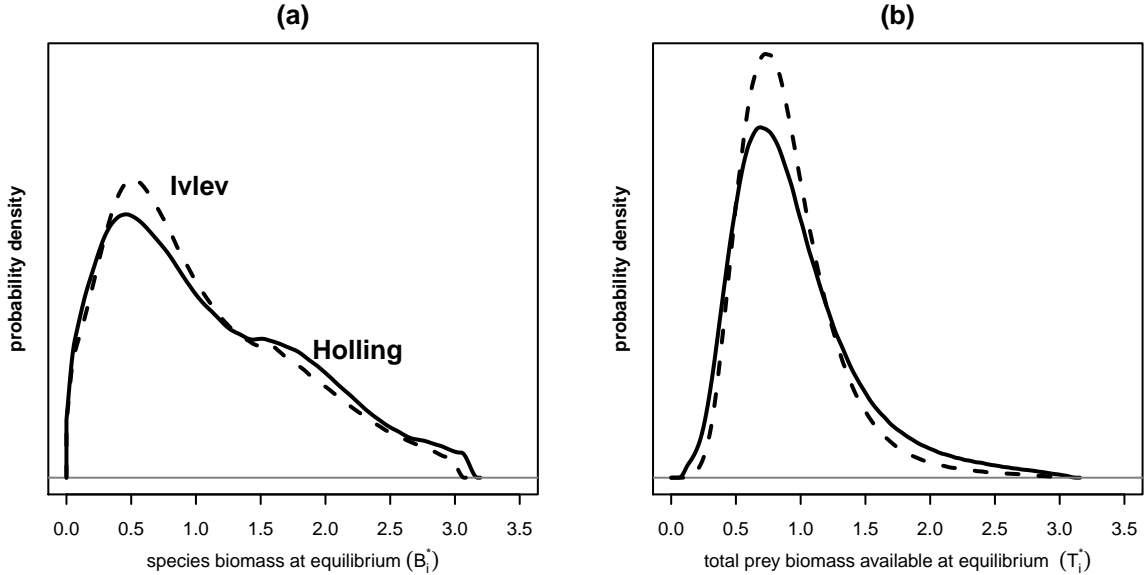
*Holling's disc equation*



*Ivlev's functional response*



**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.

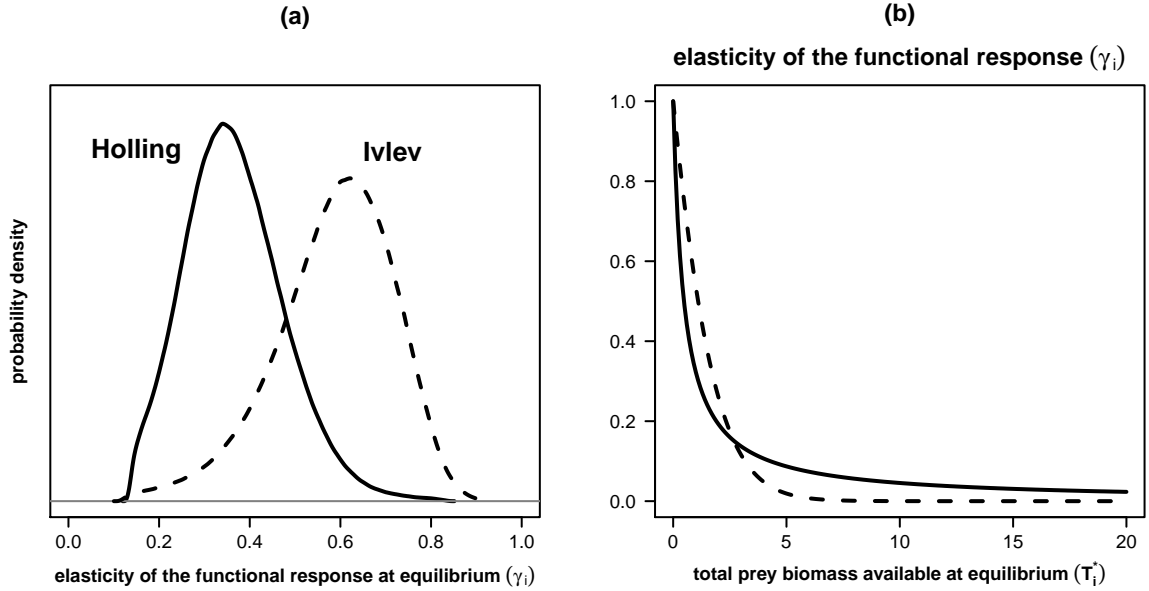


**Figure 3.** Estimated densities of species biomass (a) and total prey biomass available for predator species (b) in food webs reaching a positive equilibrium with Holling’s (plain) or Ivlev’s (dashed) functional response. Computed from 160 000 food webs of varying complexity (4 levels of connectance 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

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

216 Parameter sets that give a better fit to Holling’s FR at low prey biomass (closer  $a^\phi$  value) predict a  
 217 closer value of food web variability between functional responses (table 2 and figure 5). However, they also  
 218 predict more distant primary productivity ( $\approx 1/h^\phi$  value) and predicted value of food web persistence.  
 219 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 ( $a^{\phi}$ ), 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

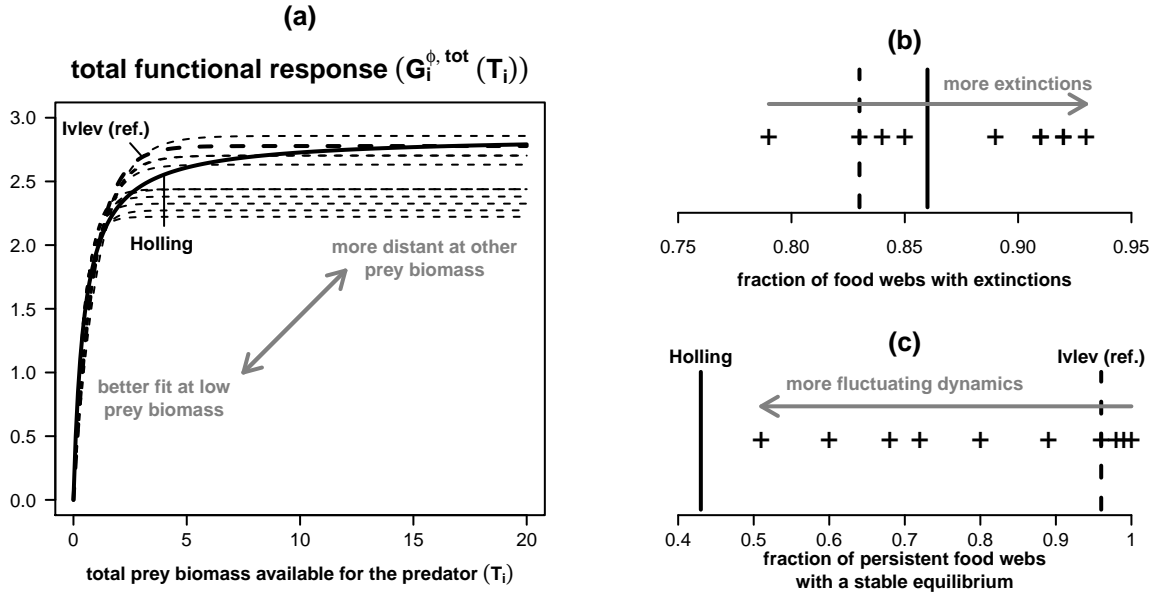
230 Even with the simplifying assumption that parameter values scale allometrically, a full parameter sensi-  
 231 tivity analysis requires a high computational effort. Indeed, to be reasonably exhaustive it is necessary  
 232 to study thousands of food webs with different numbers of species and connectance 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 ( $a^\phi$  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	$T_i \in A$	$a^\phi$	$h^\phi$	$S_{\omega_U, [0, 3.5]}$	$S_{\omega_U, [3.5, 500]}$	extinction(s)	equilibrium
$\omega_U$	$[0, 500]$	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
	$[0, 15]$	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
$\omega_P$	<b><math>[0, 500]</math></b>	<b>3.17</b>	<b>0.36</b>	<b>0.036</b>	<b>0.005</b>	<b>0.83</b>	<b>0.98</b>
	$[0, 20]$	4.67	0.41	0.007	0.165	0.91	0.72
	$[0, 15]$	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

parameter 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

251 Different combinations of model assumptions are made by recent studies on food webs, often for sim-  
 252 plifying reasons (Brose *et al.*, 2006; Gross *et al.*, 2009; Heckmann *et al.*, 2012; Kartascheff *et al.*, 2010;  
 253 Plitzko *et al.*, 2012; Stouffer & Bascompte, 2010, 2011; Williams, 2008). The impact of these assumptions  
 254 is detailed in section 4 of SOM and summarized in table 4. In all cases, equilibrium dynamics are more  
 255 frequent with Ivlev’s FR than with Holling’s FR. In addition, both functional responses show the same  
 256 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  $a^\phi$  times 5 values of  $h^\phi$ ), 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	$a^\phi$	$h^\phi$	functional response
extinction(s)	<b>0.76</b>	0.37	0.12	0.07	-0.17
equilibrium	NS	0.36	-0.22	0.07	<b>0.82</b>

**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)			equilibrium		
		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 + no cannibalism	Holling	[0.60, 1.00]	$\times 1.4$	$\times 1.2$	[0.35, 0.81]	$\times 1.05$	$\times 2.2$
	Ivlev	[0.51, 1.00]	$\times 1.5$	$\times 1.3$	1.00	=	=

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

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

### 276 **3.6 Structural sensitivity and modelling biological systems**

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

283 Here, we used the first method in different ways. The most classical ones, namely a fit with a uniform  
284 weight over the range of biomass observed or a fit using the empirical biomass distribution, lead to  
285 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.

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

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

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452 **Appendix S1: the jacobian matrix**

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