- ¹ Supplementary Material to:
- ² Does structural sensitivity alter complexity-stability

³ relationships?

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²⁰ 1 Niche model, primary producers and cannibal species

Food webs are composed by S species (sensu trophic species) and one resource. Species are linked by 21 L trophic interactions, so that food web connectance is $C = L/S^2$ (directed connectance, as defined by 22 Martinez, 1991). In order to statistically investigate the effect of trophic complexity, we need to produce 23 millions of different food webs. We use the niche model (Williams & Martinez, 2000) to randomly build 24 food webs with the desired number of species and an *a priori* fixed connectance. This stochastic model 25 generates quickly numerous food webs with patterns that are roughly empirically consistent (Allesina 26 et al., 2008; Cattin et al., 2004; Williams & Martinez, 2000). It is based on the principle of ecological 27 niche (Hutchinson, 1957). A species i is characterized by a niche value n_i , that indicate its position on the 28 segment [0, 1], the niche axis (figure 1). Each species is also characterized by a continuous feeding range, 29 a sub-interval of this axis. Species i feeds on all species whose niche value belongs to this range. It is 30 defined by its center c_i and its relative width r_i . So this feeding range is $[c_i \pm n_i r_i/2]$. The niche value n_i 31 is uniformly drawn in the interval [0, 1]. The relative width of the feeding range r_i is drawn from a beta 32 distribution $\mathcal{B}\left(1, \frac{1}{2C} - 1\right)$, where C is the desired food web connectance. If C is high (low), the expected 33 width of the feeding range is also high (low), and thus the expected number of prey species is high (low) 34 too. The center of the feeding range c_i is uniformly drawn in the interval $[n_i r_i/2, \min(n_i, 1 - n_i r_i/2)]$ 35 so that the feeding range is always a sub-interval of [0,1] (Williams & Martinez, 2004). Species whose 36 feeding range does not contain any other species niche value do not feed on any prev species and define 37 primary producers. Other species are called predators. Species whose niche value does not belong to any other species feeding range define top predators. Construction of the feeding range intervals allows the 39 possibility that the feeding range of a species contains its own niche value, so that it becomes its own 40 prey (this is cannibalism). A predator may even feed on prey of higher niche value than itself, what may 41 generate trophic loops in resulting food webs. In order to have at least one primary producer in the food 42 web, the species with the lowest n_i has always $r_i = 0$. 43

The construction method in the niche model is such that the average connectance among numerous generated food webs is equal to the desired *a priori* connectance (through the second parameter of the beta distribution). Nevertheless, due to the variability of random draws, all food webs do not have exactly this desired connectance. Beside that, some generated food webs present unrealistic patterns. So we added a rejection step after food webs construction. We only studied food webs with a connectance



Figure 1. Scheme of the principle of the niche model (left, redrawn from Williams & Martinez, 2000, 2004) and an example of a 20 species food web generated by this model (right). This model is used to build all food webs studied in the remaining of the paper. The left scheme represents a food web with S = 6 species. The set of all possible ecological niches is summarized by the segment [0, 1]. The ecological niche of each species *i* is summarized by a niche value $n_i \in [0, 1]$. Each species feeds on a continuous range of prey species defined by its center c_i and its relative width r_i . Species which do not have any prey species in their feeding range are defined as primary producers. See section 2.1 for details on how the parameters values are randomly drawn.

that deviated at most by 0.01 of the desired 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. The average number of primary producers and the average proportion of cannibal species in food webs generated by the niche model are shown in figure 2.

⁵³ 2 Algorithm to classify asymptotic dynamics

In order to characterize the asymptotic dynamics of the numerous food webs studied, we built the following automatized classification algorithm. The algorithm starts by a time T_{ini} of initial simulation in order to limit transient effects due to the arbitrary initial condition. After that, the asymptotic dynamics is considered as associated to extinction(s) if at least one species has a biomass that becomes lower than an arbitrary extinction threshold B_{min} . Else, if the system converges to a point in the phase space (criterion $\sum_{i \in S} |dB_i/B_i dt| < \varepsilon_{cv}$) where all eigenvalues of the jacobian matrix have negative real parts, the asymptotic dynamics is a positive equilibrium. As long as no criterion is reached, the simulation



Figure 2. Average number of primary producers and proportion of cannibal species in the food webs studied. These numbers vary with trophic complexity (number of species and connectance). Estimations are realized on 10 000 food webs generated using the niche model proposed by Williams & Martinez (2000, 2004) for each trophic complexity.

continues. The whole simulation is divided in subparts of length T_{sub} . After each subpart, jacobian's 61 eigenvalues at the temporal average of the dynamic during the current subpart are computed. If all 62 eigenvalues have a negative real part the simulation continues, and finally an equilibrium is reached in all 63 our simulations ending before T_{max} (see below). If at least one eigenvalue has a positive real part and if 64 fluctuations do not change significantly between subparts of the simulation $(\sum_{i \in S} |\bar{B_i}^m - \bar{B_i}^{m-1}| < \varepsilon_{mean})$ 65 with \bar{B}_i^m being the average of $B_i(t)$ for $t \in [T_{ini}, T_{ini} + mT_{sub}]$, the asymptotic dynamics will be 66 considered as a fluctuating dynamic without any extinction. This is done because the multiple estimations 67 of the jacobian matrix indicate that the flow is divergent at the average of the fluctuating dynamics. This 68 means that the presence of a stable equilibrium around this average is very unlikely. Sometimes, reaching 69 one of the criteria needs a long time of simulation. So we fixed a maximal time of simulation T_{max} . If 70 the algorithm fails to classify a food web dynamics in one of the three classes before the simulation end, 71 the dynamics is consider as unknown. 72

The algorithm used to solve ODEs is a Runge-Kutta-Fehlberg-4,5 numerical scheme, with absolute and relative error tolerances set to 10^{-6} . Preliminary tests showed that the choice of a specific numerical scheme among those tested does not affect the results. Tests were also done to choose the values of absolute

and relative error tolerance. The parameter values used for our algorithm were tuned after preliminary 76 tests to improve the algorithm efficiency. We set $T_{ini} = 500, T_{sub} = 5\ 000, T_{max} = 50T_{sub} + T_{ini}$ 77 $B_{min} = 10^{-6}$, $\varepsilon_{cv} = 10^{-6}$ and $\varepsilon_{mean} = 0.01$. Results are the same if a lower B_{min} value is used to define 78 extinctions. All simulations start with the arbitrary initial condition $B_i(0) = 1 \ \forall i$. We used only one 79 initial condition. Tests with 10 random initial conditions on 20-species food webs (connectance equals to 80 (0.15) indicate that a small fraction of these food webs (< 1%) can reach significantly different asymptotic 81 dynamics depending on the initial condition. For computational reasons, we choose to use only one initial 82 condition per food web. 83

The algorithm failed to classify food web dynamics before reaching T_{max} in 0.2 % of the food webs 84 with Holling's FR and 2 % with Ivley. However, a study of the calculus made by the algorithm along the 85 simulation allows to determine which asymptotic dynamics the system is likely to reach is the simulation 86 continues. The proportion of these food webs which will likely reach a positive equilibrium is close to 87 the proportion observed in food webs for which the algorithm determines the dynamics before T_{max} 88 is reached. For example, among the 2 % of unknown dynamics with Ivlev, 98.5 % are likely to reach 89 a positive equilibrium ($\varepsilon_{cv} < \sum_{i \in S} |dB_i/B_i dt| < 10^{-5}$) on average within the tested range of trophic 90 complexity. This proportion is roughly equal to that observed in food webs for which dynamics have 91 been determined (figure 2 in the article). So using a greater T_{max} will not significantly affect our results. 92 For some food webs which dynamics seems to converge on a positive equilibrium, the point reached 93 is unstable. We found for some of these food webs that in fact the dynamics converges on a limit cycle 94 which size is such that the algorithm considers it as an equilibrium. This happens when the food web is 95 closed to a Hopf bifurcation (i.e. a pair of complex conjugated eigenvalues have small positive real parts). 96 For some other food webs, we supposed that the dynamics fluctuates around one (or more) saddle(s) 97 connected by an homoclinic or an heteroclinic loop (one eigenvalue is real and slightly positive), but 98 stays bounded in a set of the phase space which size is again such that the algorithm considers it as an 99 equilibrium. This phenomenon is negligible with Holling's FR, with less than 10 cases observed among 100 the hundreds thousands positive equilibria studied. With Ivlev's functional response, it concerns up to 101 4.5 % of the food webs with a positive equilibrium. This proportion decreases with trophic complexity, 102 mainly with connectance. When functional response fit at low prey densities is improved (see section 3.3 103 in the article), it concerns up to 30 % of the food webs with a positive equilibrium. We consider these 104 food webs as food webs which reach a positive equilibrium, because the ecological meaning of such small 105

¹⁰⁶ fluctuating dynamics is the same as an equilibrium. Considering these food webs as food webs with ¹⁰⁷ fluctuating dynamics, or neglecting them, do not affect our qualitative results and conclusions.

¹⁰⁸ 3 Different parameter sets for Ivlev's functional response

Table 2 in the article presents the dynamics of 30 species food webs (with a connectance of 0.15) predicted by different parameter sets for Ivlev's FR. These parameter sets come from different ways to fit the functional responses. To test the robustness of our main conclusions to the method of fit, some of these parameter sets are used to predict complexity-stability relationships with Ivlev's FR. We used the parameter sets obtained with a fitting range $T_i \in [0, 3.5]$ with both weight functions (uniform $\omega_{\mathcal{U}}$ and $\omega_{\mathcal{P}}$ presented in figure 1b of the article), as well as the parameter set obtained using the empirical distribution of total prey biomass available predicted by Holling's FR (figure 3b in the article).

The three parameter sets predict the same qualitative complexity-stability relationships as the ones presented in figure 2 in the article (figures 3-5). The two parameter sets obtained with the more classical methods (see discussion in section 3.6 in the article) predict a higher frequency of equilibrium dynamics than Holling's FR (×2.1 for the uniform weight function, figure 3, and ×1.9 for the empirical distribution, figure 5). A higher frequency of equilibrium dynamics is also predicted by the parameter set derived using $\omega_{\mathcal{P}}$ over $T_i \in [0, 3.5]$, despite the difference is quantitatively lower (×1.2, figure 4).

¹²² 4 Changes in model assumptions

We tested the influence of three assumptions on food web dynamics: fixing the number of primary 123 producer species in food webs, deleting cannibalistic links, setting the body mass of primary producers 124 equals to 1. Some of these assumptions are made in some previous studies about complexity-stability 125 relationships in food webs, but the same combination is not always use. So we tested their influence in 126 order to get the widest picture as possible. These results are used in section 3.5 in the article to explain 127 the complexity-stability relationships predicted by the model. Here, we present the dynamics obtained 128 within the tested range of trophic complexity for different combinations of assumptions, as well as a short 129 description of their trends. 130

¹³¹ When food webs with a fixed number of five primary producer species are considered (figure 6),



Figure 3. Food web dynamics as a function of trophic complexity predicted by Ivlev's functional response, fitted using a uniform weight function over $T_i \in [0, 3.5]$. a: fraction of food webs with at least one species extinction. b: fraction of persistent food webs with a stable positive equilibrium. The number of food webs studied for each pair of parameters is enough to obtain 1 000 food webs with a stable positive equilibrium.

¹³² Ivlev's FR predicts on average less extinctions than Holling's FR (from -10 % to +3 %). Their frequency ¹³³ increases with the number of species (on average ×1.6 with Holling's FR and ×1.7 with Ivlev' FR) and ¹³⁴ decreases with connectance (×0.8 and ×0.9). On average, there are 2.6 times more equilibrium dynamics ¹³⁵ with Ivlev's FR (from 92 % to 99 %) than with Holling's FR (from 15 % to 78 %). The frequency of ¹³⁶ equilibrium dynamics increases with connectance (×4.3 with Holling's FR and +3 % with Ivlev's FR). ¹³⁷ We do not discuss any effect of the number of species as the number of food webs studied is lower for ¹³⁸ food webs with 40 and 60 species.

¹³⁹ When body mass is set to 1 for primary producers (figures 7a,b and 8a,b), Ivlev's FR predicts on ¹⁴⁰ average less extinctions than Holling's FR (from -5% to +2%). Their frequency increases more with the ¹⁴¹ number of species (×1.6 with Holling's FR and ×1.7 with Ivlev's FR) than with connectance (×1.2 with ¹⁴² Holling's FR and ×1.3 with Ivlev's FR). Within the tested range of trophic complexity, the proportion ¹⁴³ of persistent food webs reaching an equilibrium is always 100 % with Ivlev's FR and ranges from 38 % ¹⁴⁴ to 86 % with Holling's FR. With the latter, this proportion increases with connectance (×2.2) and does ¹⁴⁵ not show a clear trend with the number of species (from -3% to +4% depending on connectance).

¹⁴⁶ When cannibalistic link are deleted and body mass is set to 1 for primary producers (figures 7c,d



Figure 4. Food web dynamics as a function of trophic complexity predicted by Ivlev's functional response, fitted using the weight function $\omega_{\mathcal{P}}$ over $T_i \in [0, 3.5]$. a: fraction of food webs with at least one species extinction. b: fraction of persistent food webs with a stable positive equilibrium. NA means that the precise data has not been acquired for computational reasons (fraction of food webs with extinction(s) close to 1). The number of food webs studied for each pair of parameters is enough to obtain 1 000 food webs with a stable positive equilibrium.

and 8c,d), Ivlev's FR predicts less extinction(s) than Holling's FR (from -9 % to no difference). Their frequency increases more with the number of species (×1.4 with Holling's FR and ×1.5 with Ivlev's FR) than with connectance (×1.2 and ×1.3). Within the tested range of trophic complexity, the proportion of persistent food webs reaching an equilibrium is always 100 % with Ivlev's FR and ranges from 35 % to 81 % with Holling's FR. With the latter, this proportion increases more with connectance (×2.2) than with the number of species (from -2 % to +7 % depending on connectance).

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 $\mathbf{5}$

Different metrics to quantify food web persistence and variability

We tested different metrics to quantify food web persistence and variability. Their estimation is based on the analysis of species biomass after a simulation of 100 000 time steps. Mean and variation coefficient were computed for each species over the last 10 000 time steps of the simulation.

Relationships between these metrics and those used in the article are presented in figures 9 and 10



Figure 5. Food web dynamics as a function of trophic complexity predicted by Ivlev's functional response, fitted using the empirical distribution of prey biomass observed with Holling's disc equation (figure 3b in the article). a: fraction of food webs with at least one species extinction. b: fraction of persistent food webs with a stable positive equilibrium. The number of food webs studied for each pair of parameters is enough to obtain 1 000 food webs with a stable positive equilibrium.

for Holling's FR and Ivlev's FR respectively. Both functional responses again predict similar food web 159 persistence if it is quantified using the average proportion of extincted species in networks (mean species 160 biomass below 10^{-6} , panel a in both figures). Using this metrics, food web persistence also decreases 161 more with the number of species than with connectance. Food web variability is again significantly 162 lower with Ivlev's FR (non-overlapping ranges of values between formulations) when different metrics 163 are used. Metrics based on the variation coefficient predict different complexity-stability relationships 164 between formulations (panels c and d). However, we will not discuss relationships obtained with Ivlev as 165 the estimated values are close to 0 and within a small range of variations. Opposite complexity-stability 166 relationships are also obtained if we focus on the fraction of food webs with fluctuating dynamics, whatever 167 the number of species extinctions that occured (panel b). However, the predicted food web variability 168 is still lower with Ivlev. Furthermore, considering food webs with extinctions, as for all these metrics, 169 introduces a biais as the number of species and connectance are changed during simulation. 170



Holling's disc equation

0.10 1.00 0.10 0.98 0.97 0.96 0.72 0.96 1.00 0.92 20 20 30 40 50 60 30 40 50 60 number of species number of species Figure 6. Food web dynamics as a function of trophic complexity predicted by Holling's (a, b) and Ivlev's functional responses (c, d) for food webs with a fixed number of five primary producer species. a, c: fraction of food webs with at least one species extinction. b, d: fraction of persistent food webs with a stable positive equilibrium. NA means that the precise data has not been acquired for computational reasons (fraction of food webs with extinction(s) close to 1). The number of food webs studied for each pair of parameters is enough to obtain N food webs with a stable positive

0.15

0.98

0.97

0.97

0.98

1.00

0.67

0.15

0.94

0.99

if S = 60, $N = 1\ 000$ if S = 40 and $N = 10\ 000$ otherwise.

equilibrium. For computational reasons, the value of N depends on the number of species (S), N = 100



 $M_i = 1$ for primary producers

 $M_i = 1$ for primary producers and absence of cannibalism



Figure 7. Food web dynamics as a function of trophic complexity predicted by Holling's disc equation, if the body mass M_i of all primary producer species is set to 1, for food webs in which cannibalistic links are kept (a, b) or removed (c, d). a, c: fraction of food webs with at least one species extinction. b, d: fraction 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.



 $M_i = 1$ for primary producers





Figure 8. Food web dynamics as a function of trophic complexity predicted by Ivlev's functional response, if the body mass M_i of all primary producer species is set to 1, for food webs in which cannibalistic links are kept (a, b) or removed (c, d). a, c: fraction of food webs with at least one species extinction. b, d: fraction 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 9. Relationships between different measures of the persistence (a) and the variability (b-d) of the food webs modeled using Holling's disc equation. The x-axis corresponds to the measure used in our study whereas the y-axis corresponds to another one. Each point indicates the values obtained for 10 000 food webs with the same number of species and connectance. Sixteen pairs of values are studied: four number of species (20: circle, 30: square, 40: diamond, 60: triangle) times four connectance levels (0.10: blue, 0.15: green, 0.20: red, 0.30: black). Simulations of 100 000 time units were performed to estimate the measures which are not used in the remaining of our study. The average and the standard deviation of species biomass were calculated across the 10 000 last time units. Extincted species are those with an average biomass below 10^{-6} .



Figure 10. Relationships between different measures of the persistence (a) and the variability (b-d) of the food webs modeled using Ivlev's functional response. The x-axis corresponds to the measure used in our study whereas the y-axis corresponds to another one. Each point indicates the values obtained for 10 000 food webs with the same number of species and connectance. Sixteen pairs of values are studied: four number of species (20: circle, 30: square, 40: diamond, 60: triangle) times four connectance levels (0.10: blue, 0.15: green, 0.20: red, 0.30: black). Simulations of 100 000 time units were performed to estimate the measures which are not used in the remaining of our study. The average and the standard deviation of species biomass were calculated across the 10 000 last time units. Extincted species are those with an average biomass below 10^{-6} .

¹⁷¹ 6 Identification of stabilizing factors through Generalized Mod ¹⁷² elling

We want to identify the stabilizing factors in the food web model for any type-II functional response and use them to explain our results from dynamical simulations. Here, we start by explaining how we derived the generalized model use to identify these factors expressed in terms of generalized parameters. Then we summarize the key results about the role of generalized parameters in equilibria stability. Finally, these generalized parameters are calculated in food webs at equilibrium in our dynamical simulations to explain why more equilibrium dynamics are predicted by Ivlev's FR.

To build the generalized model, we first consider the differential system made of S equations corresponding to S species (1) (see section 2.2 of the article for details):

1 00

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

without specifying the functional response $G_{i,j}^{\phi}$ and the parameter values. We only claim that the functional response assumes no prey switching with constant fractional foraging effort, fulfills properties):

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

¹⁸³ So we consider in fact a family of models. Generalized modelling supposes that some models in this ¹⁸⁴ family have positive equilibria. The qualitative stability of a positive equilibrium is then studied using ¹⁸⁵ the Jacobian matrix:

$$\begin{pmatrix}
J_{i,i}^{\phi} = \lambda \left[q_{i}^{\phi} + G_{i}^{\phi,tot*} + B_{i}^{*} \left. \frac{\partial G_{i}^{\phi,tot}}{\partial B_{i}} \right|_{\mathbf{B}^{*}} \right] - G_{i,i}^{\phi*} - \sum_{k \in C_{i}} B_{k}^{*} \left. \frac{\partial G_{k,i}^{\phi}}{\partial B_{i}} \right|_{\mathbf{B}^{*}} - \alpha_{i} - 2\beta_{i}B_{i}^{*} \quad i = 1, ..., S$$

$$J_{i,j}^{\phi} = \lambda B_{i}^{*} \left. \frac{\partial G_{i}^{\phi,tot}}{\partial B_{j}} \right|_{\mathbf{B}^{*}} - G_{j,i}^{\phi*} + \sum_{k \in C_{i}} \left. \frac{\partial G_{k,i}^{\phi}}{\partial B_{j}} \right|_{\mathbf{B}^{*}} \quad i, j = 1, ..., S, \ j \neq i$$

$$(3)$$

evaluated at a positive equilibrium $\mathbf{B}^* = (..., B_i^*, ...)$. Then we re-write this matrix using generalized

¹⁸⁷ parameters that describe the system close to this equilibrium (table 1):

$$\begin{cases}
J_{i,i} = \tau_i \left[1 - (1 - \delta_i)\mu_i - \delta_i \left(\rho_{i,i}(1 - \lambda\gamma_i) + \sum_{k \in C_i} \rho_{k,i}[(\gamma_k - 1)\chi_{k,i} + 1] \right) \right] & \forall i, j \in \{1, ..., S\} \\
J_{i,j} = \tau_i \nu_{i,j} \left[\theta_i \gamma_i \chi_{i,j} - \delta_i \left(\rho_{j,i} + \sum_{k \in C_i} \rho_{k,i}(\gamma_k - 1)\chi_{k,j} \right) \right] & j \neq i \end{cases}$$
(4)

Details on the derivation procedure to define generalized parameters are presented in Gross & Feudel (2006) and Yeakel *et al.* (2011). Then, equilibrium stability is studied as a function of the generalized parameter values without specific assumptions on the functions and original parameter (such as a^{ϕ} or h^{ϕ}) values behind them.

This generalized model is an extension of a model proposed by Plitzko *et al.* (2012). First, we correct a mistake in Plitzko *et al.* (2012)'s calculus by adding the parameter $\nu_{i,j}$ (a biomass ratio) to non-diagonal terms. We checked that this mistake does not affect results presented by Plitzko *et al.* (2012) under the assumptions they made for their numerical study. Second, we also complete the diagonal terms to take cannibalism into account. Finally, we provide a generalized parameter formulation independent of a specific functional response.

For food webs made with S species, there are 5S(S+1)/2 degrees of freedom in the parameter set 198 of the generalized model (4) if no special assumption is made. It is not possible to realize a bifurcation 199 analysis like for a predator-prey model (Aldebert et al., 2016). Furthermore, results depend on the trophic 200 complexity and food web structure. So, numerous food webs have to be studied to obtain statistical 201 results. To avoid unreasonable computing costs, we need to make some assumptions to decrease the 202 number of degrees of freedom and study only some parameters of interest. As in all this study, we first 203 assume that a species is either a primary producer ($\theta_i = 0$) or a predator ($\theta_i = 1$), the selection being 204 done during food web construction by the niche model (see section 2.1 in the article for details). Since 205 Gross et al. (2009) reported that the time scale τ_i does not significantly affect equilibria stability, it is 206 arbitrarily set to 1 for all species. Then, as the mean biomass ratio is $\bar{\nu} = 1$ by definition, we assume 207 $\nu_{i,j} = 1 \ \forall i, j.$ It implies that $B_i^* = B_j^* \ \forall i, j$ and so that $\chi_{i,j} = 1/|R_i|$ if $j \in R_i$ (0 otherwise). Note that 208 $1/|R_i|$ is also by definition the mean fraction of total prey biomass represented by each prey of species *i*. 209 Similarly, $1/|C_i|$ is by definition the mean fraction of total predative losses represented by each predator 210 of species i. We assume $\rho_{j,i} = 1/|C_i|$ if $j \in C_i$ (0 otherwise). Values of other parameters are assumed 211

Table 1. Formulation and ecological meaning of the generalized parameters used to build the generalized model. Generalized parameters are used in the generalized model to describe the local dynamics of the system close to an equilibrium. Their value are independent of the specific formulation of the functional response because they only describe a local dynamics. So the stability of an equilibrium depends only of their value at these equilibrium. The scale parameters describe the time scale of species dynamics (for τ_i) and the relative contribution of the different processes to this dynamics. Elasticities (called exponent parameters by some authors) measure the non-linearity of processes.

generalized parameter formulation	ecological meaning		
scale parameters			
$\tau_{i} = \lambda \left(q_{i}^{\phi} + G_{i}^{\phi, tot*} \right) \\ = \sum_{j \in C_{i}} G_{j,i}^{\phi*} \frac{B_{j}^{*}}{B_{i}^{*}} + \left(\alpha + \beta B_{i}^{*} \right) M_{i}^{-0.25}$	time scale of species i 's dynamics		
$ heta_i = rac{1}{ au_i^{\phi}} \lambda G_i^{\phi, tot*}$	fraction of gains of species i obtained by predation		
$1 - heta_i = rac{1}{ au_i^\phi} \lambda q_i^\phi$	fraction of gains of species i obtained by primary production		
$\delta_i = \frac{1}{\tau_i^{\phi}} \sum_{j \in C_i} G_{j,i}^{\phi*} \frac{B_j^*}{B_i^*}$	fraction of losses of species i due to predation		
$1 - \delta_i = \frac{1}{\tau_i^{\phi}} \left(\alpha + \beta B_i^* \right) M_i^{-0.25}$	fraction of losses of species i due to intrinsic dynamics		
$\chi_{i,j} = \begin{cases} \frac{B_j^*}{T_i^*} & \text{if } j \in R_i \\ 0 & \text{otherwise} \end{cases}$	fraction of gains by predation of species i from species j		
$\rho_{i,j} = \begin{cases} \frac{1}{\tau_i^{\phi} \delta_i^{\phi}} G_{j,i}^{\phi*} \frac{B_j^*}{B_i^*} & \text{if } i \in R_j \\ 0 & \text{otherwise} \end{cases}$	fraction of losses by predation of species i due to species j		
$\nu_{i,j} = \tilde{B}_i^* / B_j^*$	biomass ratio between species i and j		
elasticities (also called exponent parameters) $\mu_{i} = 1 + \frac{\beta B_{i}^{*}}{\alpha + \beta B_{i}^{*}} \in [1, 2]$ $\gamma_{i} = -e^{\phi'}(1) \in [0, 1]$	non-linearity of intrinsic mortality for species i		

$$\begin{aligned} \gamma_i &= g_i^{-}(1) \in [0, 1] \\ \text{with } t_i &= \frac{T_i}{T_i^*} \text{ and } g_i^{\phi}(t_i) \coloneqq \frac{G_i^{\phi, tot}(t_i T_i^*)}{G_i^{\phi, tot}(T_i^*)} \end{aligned} \text{ slope of the normalized functional response of species } i \end{aligned}$$

to be constant across a food web. Numerical simulations were realized with $\mu_i = \mu \in \{4/3, 3/2, 5/3\}$, $\delta_i = \delta \in \{1/3, 1/2, 2/3\}$ if species *i* has predators and $\delta_i = 0$ if species *i* is a top-predator, $\gamma_i = \gamma \in [0, 1]$ (discretized by step of 0.01) and $\lambda \in \{0, 1/4, 1/2, 3/4, 1\}$. We studied food webs of varying number of species $S \in \{20, 30, 40, 60\}$ and connectance $C \in \{0.10, 0.15, 0.20, 0.30\}$ as in the rest of this study.

According to the jacobian matrix of the generalized model (4), the proportion of food webs with a stable positive equilibrium is higher if density-dependent mortality is high (high value of μ) and/or if there is a small fraction of losses due to predation (low value of δ , figure 11). This corresponds to a high value of $(1 - \delta)\mu$, which plays a negative role in the diagonal elements of the jacobian matrix. Negative terms in diagonal elements of the jacobian matrix are known to increase local stability of equilibria in some food web models (Takeuchi, 1996). If $(1 - \delta)\mu$ is high, more food webs have a stable equilibrium for intermediate values of γ , whatever the trophic complexity. Otherwise, the proportion of all the food webs with a stable equilibrium increases on average with γ values.

For each set of generalized parameter valued, we use a statistical linear model to quantify the effect of 224 the number of species and connectance on the proportion of food webs with a stable positive equilibrium 225 (arrows in figure 11). For low values of γ (high prey biomass), there is a positive complexity-stability 226 relationship. It is mainly due to connectance, which affect more the fraction of food webs with a stable 227 equilibrium than the number of species. For intermediate values of γ , the fraction of food webs with a 228 stable equilibrium is increased by connectance and decreased by the number of species. For high values 229 of γ (low prey biomass), there is a negative complexity-stability relationship, with a similar impact of the 230 number of species and connectance. The assimilation efficiency λ slightly affects the quantitative results. 231 but not the qualitative trends (figures 12 and 13). The highest proportions of food webs with a stable 232 equilibrium are obtained in the limit case of $\lambda = 0$, and the lowest in the opposite limit case $\lambda = 1$. On 233 average, deleting cannibalistic links decreases the proportion of food webs with a stable equilibrium but 234 do not affect the qualitative results on complexity-stability relationships (figure 14). Considering only 235 food webs with a fixed number of primary producers has only a little quantitative impact on the results 236 (figures 15 and 16) as the positive equilibrium is assumed to exist. 237

To summarize, the stabilizing factors of positive equilibria found in a predator-prey model (Aldebert et al., 2016) are also observed at the food web scale. Nevertheless they are less straightforward, because of the interplay with trophic complexity. For example, highest stability is found for a high or intermediate slope of the functional response γ , depending on other parameter values and trophic complexity.

We calculated generalized parameters for food webs at positive equilibrium simulated in figure 3 of 242 the article. Generalized parameters can be viewed as indicators of the food web functioning close to this 243 equilibrium. Because the statistical distributions of species biomass at equilibrium are similar between 24 functional responses (figure 17a), similar distributions for the parameters (such as δ_i) and for the non-245 linearity of species mortality μ_i are also observed (figure 17c,d). At the opposite, different distributions are 246 observed for the normalized slope of the functional response γ_i (figure 17b). The average value obtained 247 with Ivlev's FR ($\bar{\gamma} = 0.60$) is 1.6 times higher than the average obtained with Holling's functional response 248 $(\bar{\gamma} = 0.37).$ 249



Figure 11. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance). Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs are studied. Assimilation efficiency λ is set to 0.75 (the value has a little impact on the results).



Figure 12. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance) when assimilation efficiency λ is set to 0. Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs are studied.



Figure 13. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance) when assimilation efficiency λ is set to 1. Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs are studied.



Figure 14. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance) in absence of cannibalism. Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs in which cannibalistic links have been removed are studied.



Figure 15. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance) for food webs with a fixed number of primary producer species. Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs with five primary producers are studied. Assimilation efficiency λ is set to 0.75 (the value has a little impact on the results).



Figure 16. Fraction of food webs with a stable positive equilibrium for the generalized model, as a function of generalized parameters values and trophic complexity (number of species and connectance) for food webs with a fixed number of primary producer species and in absence of cannibalism. Food web topology is generated using niche model (Williams & Martinez, 2000, 2004). For each set of parameters, 10000 food webs with five primary producers and in which cannibalistic links have been removed are studied.



Figure 17. Estimated probability densities of the species biomass and 3 generalized parameters for food webs which reach a positive equilibrium at the end of the dynamical simulations for Holling's disc equation (plain) and Ivlev's functional response (dashed). Generalized parameters are here used as indicators to describe system dynamics close to equilibrium. Results are obtained from 160 000 food webs with 16 pairs of number of species and connectance values (10 000 food webs by pair of values). The null values (γ_i for primary producers and δ_i for top-predators) are not taken into account. Density estimates are realized using non-parametric kernel methods (Simonoff, 1996) with the same weight for all simulated food webs.

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