

# Metabolic adjustment enhances food web stability

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# 1 Abstract

2 Understanding ecosystem stability is one of the greatest challenges of ecology. Over several  
3 decades, it has been shown that allometric scaling of biological rates and feeding inter-  
4 actions provide stability to complex food web models. Moreover, introducing adaptive  
5 responses of organisms to environmental changes (*e.g.* like adaptive foraging that enables  
6 organisms to adapt their diets depending on resources abundance) improved species per-  
7 sistence in food webs. Here, we introduce the concept of metabolic adjustment, *i.e.* the  
8 ability of species to slow down their metabolic rates when facing starvation and to increase  
9 it in time of plenty. We study the reactions of such a model to nutrient enrichment and  
10 the adjustment speed of metabolic rates. We found that increasing nutrient enrichment  
11 leads to a paradox of enrichment (increase in biomasses and oscillation amplitudes and  
12 ultimately extinction of species) but metabolic adjustment stabilises the system by damp-  
13 ening the oscillations. Metabolic adjustment also increases the average biomass of the top  
14 predator in a tri-trophic food chain. In complex food webs, metabolic adjustment has a  
15 stabilising effect as it promotes species survival by creating a large diversity of metabolic  
16 rates. However, this stabilising effect is mitigated in enriched ecosystems. Phenotypic  
17 plasticity of organisms must be considered in food web models to better understand the  
18 response of organisms to their environment. As metabolic rate is central in describing  
19 biological rates, we must pay attention to its variations to fully understand the population  
20 dynamics of natural communities.

## 21 Introduction

22 Identifying the mechanisms responsible for ecosystem stability is one of the main sci-  
23 entific tasks in ecology (de Ruiter, 2005; Montoya et al., 2006; Rooney and McCann,  
24 2012; Loreau and de Mazancourt, 2013). Natural ecosystems are assumed to be stable  
25 (in the sense of dynamic stability, defined by the equilibrium stability and the variability  
26 (Pimm, 1984; McCann, 2000)) thanks to many mechanisms resulting from the diversity  
27 of interacting species (MacArthur, 1955; Elton, 1958). However, mathematical models of  
28 ecosystems predicted opposite results. For instance, the theoretical study performed by  
29 May (1972) demonstrated that diversity, complexity (measured by the linkage probability  
30 between pairs of species) and the average interaction strength decreased the stability of  
31 random interaction networks (assessed by a linear stability analysis). Subsequently, many  
32 mechanisms promoting food web stability were identified and two of them inspired us to  
33 implement a new one in food web models. The first mechanism is the allometric scaling  
34 of biological rates (*e.g.* metabolic rate, feeding strength), describing them as power func-  
35 tions of individual body mass (Yodzis and Innes, 1992; Brown et al., 2004; Savage et al.,  
36 2004; Brose et al., 2008; Pawar et al., 2012; Kalinkat et al., 2013). These relationships  
37 provided a better prediction of species biomasses in empirical data than any other model  
38 parametrisation (Boit et al., 2012; Hudson and Reuman, 2013). In addition, allometric  
39 scaling coupled with size structured communities (*i.e.* consumers larger than their prey)  
40 lead to more stable food webs with fewer extinctions (Brose et al., 2006; Brose, 2008;  
41 Kartascheff et al., 2010).

42

43 The second mechanism is adaptive foraging. Kondoh (2003) included adaptive forag-  
44 ing behaviour into food web models to enable the consumers to maximise their biomass  
45 income by preferentially hunting more abundant prey. The result is dramatic, with a

46 reversion of the pattern predicted by May: with adaptive foragers, increasing species  
47 richness and complexity enhances species persistence. Furthermore, food webs with ran-  
48 domly set interactions and adaptive foraging converge towards size-structured food webs  
49 with predators systematically larger than their prey (Heckmann et al., 2012). In such  
50 models, species biomasses are not the only dynamic variables, food web structures and  
51 interaction parameters are also dynamic (de Ruiter, 2005). However, one central param-  
52 eter has always been considered constant in food web models: the metabolic rate. The  
53 closest examples to adjustable metabolic rates were given by Kuwamura et al. (2009),  
54 Nakazawa et al. (2011) and Wang and Jiang (2014) who considered simple models with  
55 a structured population of *Daphnia* including metabolically active adults and dormant  
56 eggs. In nature, however, many organisms exhibit phenotypic plasticity in the expression  
57 of metabolism (Brown et al., 2004; Glazier, 2005; Jeyasingh, 2007; Glazier, 2009a; Carey  
58 et al., 2013; Norin et al., 2015). In fact, Makarieva et al. (2005) pointed out that or-  
59 ganisms with different body sizes can display similar metabolic rates depending on their  
60 activity. Moreover, animals from all major phyla are able to slow down their activity to  
61 face harsh conditions such as drought and starvation using body mass reduction (DeLong  
62 et al., 2014b), torpor, diapause (depression of 60-95%) or cryptobiosis (depression of 99-  
63 100%) (Guppy and Withers, 1999). Considering the metabolic activity of organisms as a  
64 constant parameter is a strong assumption despite its central role in food web models. In  
65 this study, we model the plastic response of metabolism similarly to adaptive foraging. As  
66 adaptive foraging maximises the growth rate of consumers by varying the foraging effort  
67 for the different prey, we propose that metabolic adjustment maximises the growth rate  
68 by varying the metabolic rate.

69

70 Based on prior studies on adaptive foraging, we can predict consequences of this ad-

71 justable metabolism for food web models. First, this adjustable behaviour should have a  
72 substantial impact on population dynamics. For instance, when the population density  
73 of the prey increases, consumers will raise their metabolic activity that is directly related  
74 to their consumption rate. The consequence is an increase in the predation pressure and  
75 top-down control imposed by consumers on their prey at high densities. On the contrary,  
76 in periods of starvation, consumers slow down their metabolic rate to minimise their loss  
77 in biomass caused by respiration, which keeps predator biomasses at a level high enough  
78 to avoid extinction (Chesson and Huntly, 1989; Polis et al., 1996; Chesson, 2000). In this  
79 study, we wonder whether the combination of these two effects stabilises the dynamics  
80 of the species (decreased amplitude and increased minima of population oscillations). In  
81 consequence our second prediction is that adaptive metabolic rates increase the persis-  
82 tence of complex food webs. As a measure of stability, we use the time variability of  
83 species biomasses (existence of fixed points and amplitude of biomass oscillation) and  
84 species persistence (proportion of surviving species in a food web).

## 85 **Material and Methods**

86 We study the impact of metabolic adjustment on a simple tri-trophic food chain and  
87 complex food webs. Both are modified versions of the Allometric Trophic Network (ATN)  
88 (Brose et al., 2006). The complex food webs rely on the Williams and Martinez (2000)  
89 niche model for their structure and on the Yodzis and Innes (1992) predator-prey model  
90 for the dynamic equations and their parameters.

### 91 **Food web construction**

92 The construction of the complex food webs follows the niche model (Williams and Mar-  
93 tinez, 2000; Brose et al., 2006; Heckmann et al., 2012; Binzer et al., 2016) as it successfully

94 predicted the food web structures of natural communities. The trophic interactions across  
95 species are set according to the algorithm detailed by Williams and Martinez (2000) with  
96 an expected connectance equal to 0.15. The basal species described by Williams and Mar-  
97 tinez (2000) are set as primary producers and the others as consumers. The niche values  $n_i$   
98 (uniformly drawn in a  $[0, 1]$  interval for each of the 40 initial species) used to parametrise  
99 the niche model are also used to calculate species body mass as follows (Heckmann et al.,  
100 2012).

$$M_i = 10^{N \cdot n_i} \quad (1)$$

101 Here  $N$  is equal to 6, that means the biggest species is one million times larger than the  
102 smallest ones.

### 103 **Predator-prey model**

104 The population dynamics of the food web follows the ATN model (Brose et al., 2006;  
105 Williams et al., 2007).

$$\frac{dB_i}{dt} = r_i G_i B_i - \sum_{j=\text{consumers}} x_j y_j B_j F_{ji} / e_{ji} \quad (2a)$$

$$\frac{dB_i}{dt} = -x_i B_i + \sum_{j=\text{prey}} x_i y_i B_i F_{ij} - \sum_{j=\text{consumers}} x_j y_j B_j F_{ji} / e_{ji} \quad (2b)$$

106 These equations describe changes in relative, biomass densities of primary producers (2a)  
107 and consumer species (2b). In these equations  $B_i$  is the biomass of species  $i$ ,  $r_i$  is the  
108 mass-specific maximum growth rate of primary producers,  $G_i$  is the logistic growth rate  
109 of primary producers (Equation (3)),  $x_i$  is  $i$ 's mass-specific metabolic rate,  $y_i$  is the maxi-

110 mum consumption rate of consumers relative to their metabolic rate,  $e_{ji}$  is  $j$ 's assimilation  
111 efficiency when consuming population  $i$  and  $F_{ij}$  describes the realised fraction of  $i$ 's maxi-  
112 mum rate of consumption achieved when consuming  $j$  (equation (4)). Primary producers  
113 growth rate is modelled by a logistic growth with a shared carrying capacity  $K$  which  
114 ensures a comparable primary production among food webs, regardless the number of  
115 primary producers (equation 3).

$$G_i = (K - \sum_{\substack{j=\text{primary} \\ \text{producers}}} B_j)/K \quad (3)$$

116 The consumption rate of prey depends on a Holling type II functional response with  
117 predator interference (Equation (4)). The preference of consumers for their prey  $\omega_{ij}$  are  
118 set to  $1/p_i$  with  $p_i$  the number of consumer  $i$ 's prey as we have no a priori information on  
119 preferences. Thus, all consumption rates are only driven by consumer body masses and  
120 prey biomass densities.  $\omega_{ij}$  are recalculated after each extinction to follow the changes of  
121 the number of prey  $p_i$ .

$$F_{ij} = \frac{\omega_{ij}B_j}{B_0 + cB_iB_0 + \sum_{k=\text{prey}} \omega_{ik}B_k} \quad (4)$$

122 Here  $B_0$  is the half-saturation density of  $i$  and  $c$  the predator interference.

123 Basically, mass specific biological rates (biomass production, metabolic rate and maximum  
124 consumption rate) follow the negative-quarter power-law relationship with species body  
125 masses as described by the metabolic theory of ecology (Brown et al., 2004; Savage et al.,  
126 2004). The time scale of the system is defined by normalising the biological rates to the  
127 mass-specific growth rate of the smallest primary producer as performed by Yodzis and

128 Innes (1992); Brose et al. (2006); Williams et al. (2007) (Equations 5a and 5b). Then  
129 the maximum consumption rates are normalised by the metabolic rates (Equations 5c).  
130 Thus, the loss due to respiration and the gain due to consumption both directly depend  
131 on the metabolic rate (Equation (2b)).

$$r_i = \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad (5a)$$

$$x_i = \frac{a_x}{a_r} \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad (5b)$$

$$y_i = \frac{a_y}{a_x} \quad (5c)$$

132

133 With  $M$  the body mass of species  $i$ ,  $M_{ref}$  the body mass of the smallest primary producer,  
134  $a_r$ ,  $a_x$  and  $a_y$  are allometric constants (see Brose et al. (2006) and Williams et al. (2007)  
135 for more details on the normalisation).

### 136 **Metabolic adjustment model**

137 We propose to model the metabolic adjustment by an optimisation of the mass-specific  
138 net growth rate  $g_i$  as in adaptive foraging models (Kondoh, 2003; Uchida et al., 2007)  
139 or in body mass plasticity models (DeLong et al., 2014b). Thus, the consumer adjusts  
140 its metabolic rate to maximise the balance between ingestion and respiration that both  
141 depend on metabolic rate. Metabolic adjustment does not apply to primary producers  
142 that are considered as basal resources species with constant resource supply (Equation



143 (2a)).

$$\frac{dx_i}{dt} = x_i X \frac{\partial g_i}{\partial x_i} = x_i X \left( -1 + \sum_{j=prey} e_{ij} y F_{ij} \right) \quad (6a)$$

$$g_i = -x_i + \sum_{j=prey} e_{ij} x_i y F_{ij} \quad (6b)$$

144 With  $X$  the metabolic adjustment coefficient representing the speed of the adjustment.  
145 The higher  $X$  is, the faster the response of species to modifications of their growth rate is.  
146 The metabolic rate is bounded by 1 and 0.001 to ensure a minimum metabolic rate and to  
147 prevent a destabilising high metabolic rate. The values predicted by the equation 5b fall  
148 in this interval that is consistent with Makarieva et al. (2005) (Supplementary material  
149 Appendix B, Fig.B5, B6,B7,B8).

## 150 Simulations

151 The model is coded in  $C++$  and the simulations performed with the  $GSL$  ODE solver.  
152 The simple tri-trophic food chain only contains a primary producer, a herbivore and a  
153 carnivore. Their body masses are respectively set to 1,  $10^2$  and  $10^4$ . For the complex food  
154 webs, each simulation is independent from the other and only differs in the body mass  
155 distribution and the architecture of the food web. The system starts with 40 species with  
156 initial biomass of 0.1 and the metabolic rates are initialised with the values predicted by  
157 the metabolic theory of ecology (Equation 5). The simulations are performed for 10,000  
158 time steps and only the last 1000 steps are recorded. Species persistence is the proportion  
159 of the 40 initial species that survives until the end of the simulation. Each combination  
160 of parameters is tested for 100 different food webs.

## 161 Results

### 162 Effect of adaptive metabolic rate on species dynamics

163 The first system we consider is a simple tri-trophic food chain containing a primary pro-  
164 ducer, a herbivore and a carnivore. The effects of the resource availability on species dy-  
165 namics are represented by bifurcation diagrams (Fig.1). The food chain without metabolic  
166 adjustment ( $X = 0$ ) displays large biomass oscillations whose amplitude increases with the  
167 carrying capacity  $K$  (Fig.1A) and the minima reaches extremely low values, especially for  
168 the herbivore (Supplementary material Appendix A, Fig.A1A). As there is no metabolic  
169 adjustment, the metabolic rates are constant (Fig.1B) and their values are those predicted  
170 by the metabolic theory of ecology (Equations 5a,b,c). The food chain with metabolic  
171 adjustment ( $X = 2$ ) has fixed points for  $K \leq 7$  and oscillations for  $K > 7$  (Fig. 1A).  
172 Despite the multi-period oscillations, the system is not chaotic (Supplementary material  
173 Appendix A, Fig.A4A). The amplitude of oscillations increases with the carrying capacity  
174 for all species but remains lower than in the food chain without metabolic adjustment.  
175 The biomass minima increases with higher values of the metabolic adjustment coefficient  
176 (Supplementary material Appendix A, Fig.A1A). The herbivore metabolic rate remains  
177 constantly at the maximum value allowed by the model, whereas the carnivore metabolic  
178 rate increases with carrying capacity  $K$  until it oscillates for  $K > 7$  (Fig.1B).

179

180 The tri-trophic food chain has fixed points along a gradient in metabolic adjustment co-  
181 efficients for a carrying capacity  $K = 2$  (Fig.2), except for  $X = 0$  (origin of the x-axis  
182 corresponding to the situation described in Fig.1A). Increasing the metabolic adjustment  
183 coefficient increases the biomass of the herbivore and of the carnivore while it decreases  
184 the biomass of the primary producer. However, we observe an increase in the primary  
185 producer biomass and a decrease in the herbivore biomass for the low values of  $X$ . The

186 metabolic rate of the herbivore is maximum for  $X > 0$  and the metabolic rate of the  
187 carnivore first sharply increases with the increasing metabolic adjustment coefficient  $X$   
188 and then it decreases (Fig.2B). The response is similar for  $K = 5$  and  $X < 4$  but for  
189  $X \geq 4$  the system oscillates (Fig.2A), yet it is not chaotic (Supplementary material Ap-  
190 pendix A, Fig.A4B). Increasing the metabolic adjustment coefficient does not increase  
191 the amplitude of biomass oscillations, it even decreases them for the primary producer.  
192 The biomass of the carnivore increases with  $X$ , the amplitude of the oscillations of its  
193 metabolic rate increases (Fig.2B) while the amplitude of its biomass oscillations remains  
194 mostly unchanged. Increasing the metabolic adjustment coefficient also increases the  
195 biomass minima of each species (Supplementary material Appendix A, Fig.A1B).

196

### 197 **Effect of adaptive metabolic rates on persistence**

198 The response of stability to metabolic adjustment and enrichment in complex food webs is  
199 assessed through the average species persistence (Fig.3A). In food webs without metabolic  
200 adjustment ( $X = 0$ ), increasing  $K$  does not significantly change species persistence that  
201 stays around 0.3. In food webs with metabolic adjustment ( $X > 0$ ), for a fixed carrying  
202 capacity  $K$ , increasing  $X$  promotes species persistence, especially at low values of  $K$  where  
203 all species can survive. If  $K > 3$ , species persistence first decreases and then increases as  
204  $X$  increases. For a fixed value of  $X$ , increasing  $K$  decreases species persistence and thus  
205 leads to an example of the paradox of enrichment. To sum up, enrichment through the  
206 increase of the carrying capacity has a destabilising effect on species persistence, whereas  
207 metabolic adjustment increases it substantially.

208

209 We can identify two groups of species in complex food webs: 'slow species' with a low

210 biomass ( $< 10^{-2}$ ) and a low metabolic rate ( $< 10^{-2.5}$ ) and 'fast species' with a high  
211 biomass ( $> 10^{-2}$ ) and a high metabolic rate ( $> 10^{-2.5}$ ) (Fig.3B and 3C). Increasing  
212 the carrying capacity  $K$  does not seem to change the repartition of species in these  
213 two categories (Fig.3B) while more species are in an intermediate category (low biomass  
214 and high metabolic rate) at low values of metabolic adjustment coefficient  $X$  (Fig.3C).  
215 This difference is confirmed in Fig.3D where three groups of species can be identified for  
216  $X > 0.002$ : (a) species with minimum or low metabolic rate, (b) species with intermediate  
217 metabolic rate and (c) species with maximum metabolic rate. (a) species correspond to  
218 the slow species, (b) and (c) to the fast species. Such a non-differentiation of the metabolic  
219 profile of species for low metabolic adjustment coefficients may be the origin of the first  
220 decrease of species persistence with increasing  $X$  for  $K > 3$  (Fig.3A).

## 221 Discussion

222 We studied the consequences of an adaptive metabolic rate for different aspects of food web  
223 stability. We predicted that metabolic adjustment enables species to fit their metabolic  
224 rate to their energy budget and the resource availability. In times of bonanza, it allows  
225 species to increase their activity and then to exploit more resources. In harsh times,  
226 however, metabolic adjustment also lets organisms slow down their activity to save their  
227 energy until the next season of plenty (Polis et al., 1996). This behaviour is typically  
228 the case for microbial organisms that can get encysted or can produce spores (Dawes and  
229 Ribbons, 1962; Fenchel and Finlay, 1983; Glazier, 2009b) but also larger organisms that  
230 can shift between resting and activity metabolism (Glazier, 2008; Hudson et al., 2013) or  
231 hibernating (Guppy and Withers, 1999). In the case of our models, adjustable metabolic  
232 rates reduce the magnitude of biomass oscillations and increase the average biomass of  
233 carnivores. Additionally, they greatly increase the stability of complex food webs by

234 increasing species persistence at low resource densities.

## 235 **Effect of adaptive metabolic rate on species dynamics**

236 Our first aim was to provide a mechanistic insight in the consequences of metabolic ad-  
237 justment for population dynamics. We followed prior studies employing tri-trophic food  
238 chains with allometric scaling of population parameters, which provides a fully determin-  
239 istic and easily tractable system (Otto et al., 2007; Binzer et al., 2012). First, enrichment,  
240 through the increase of the carrying capacity  $K$ , has a destabilising effect on population  
241 dynamics (Rall et al., 2008; Schwarzmüller et al., 2015). Such a destabilisation, called  
242 paradox of enrichment, is due to the unbalance between the growth and the mortality of  
243 organisms (Rosenzweig, 1971; DeAngelis, 1992; Roy and Chattopadhyay, 2007; Rip and  
244 McCann, 2011). However, this destabilising effect is dampened by metabolic adjustment  
245 that promotes fixed points or reduces the amplitude of biomass oscillations and increases  
246 the biomass minima. Increasing the speed of adjustment (*i.e.* increasing the metabolic  
247 adjustment coefficient  $X$ ) is destabilising because it promotes biomass oscillations, but  
248 it also increases the biomass of carnivores. We can compare our results to prior studies  
249 using adaptive foraging that inspired our modelling of metabolic adjustment (Kondoh,  
250 2003, 2010; Křivan and Diehl, 2005; Mougi and Nishimura, 2008). The adaptability of  
251 predator attack rates or prey defences (Vos et al., 2004; Verschoor et al., 2004) also  
252 decreases in the amplitude of biomass oscillations, increases the average biomass of carni-  
253 vores and keeps the minima away from the extinction threshold (Mougi and Nishimura,  
254 2007). The outcome of these processes are similar because both rely on growth rate opti-  
255 misation, which seems to highly improve the persistence of higher trophic levels that are  
256 generally most prone to extinction (Binzer et al., 2011). However, metabolic adjustment  
257 affects both the growth and the mortality rates of consumers while adaptive foraging only

258 increases the growth rate and inducible defences decrease the mortality rate. In conse-  
259 quence, adaptive metabolic rates enables a better control of species dynamics, especially  
260 for top consumers whose loss rate only depends on metabolic rate and not on predation.  
261 In our tri-trophic food chain, carnivores have a highly variable metabolic rate while the  
262 herbivore's metabolic rate always stays at the upper limit of metabolic rate range. This  
263 can be attributed to a trophic cascade: the carnivore controls the herbivore population  
264 and the primary producer thrives. Thus, the herbivore always has plenty of resources,  
265 and increasing the metabolic rate increases more the ingestion rate and the growth rate  
266 compared to the loss rate.

### 267 **Effect of adaptive metabolic rate on species persistence**

268 Our second aim was to address the impact of an adjustable metabolic rate on the species  
269 persistence of complex food webs. The null model is a classic allometric model (Brose  
270 et al., 2006) that displays an increase in persistence with increasing carrying capacity  
271 and increase in the energy flow in the system (Dunne et al., 2005; Rall et al., 2008).  
272 As expected, adding an adjustable metabolic rate increases the species persistence at  
273 low resources levels. Similarly to the results of studies on adaptive foraging (Kondoh,  
274 2003; Heckmann et al., 2012), higher adjustment coefficients (the metabolic adjustment  
275 in our case) increase species persistence. Such an increase in persistence can be partially  
276 attributed to the slow species with a low biomass and a low metabolic rate described in  
277 our study. However, no positive relationship between density and metabolic rate has been  
278 reported in previous studies (DeLong et al., 2014a; Yashchenko et al., 2016). Alternatively,  
279 these slow species could just be slow in getting extinct because of their very low metabolic  
280 rate (which is the loss rate in our model). However, the large diversity of metabolic rates  
281 in the fast species enables these species to better adapt to the specific situation concerning

282 top-down control and resource availability of each food web, leading to an increased species  
283 persistence. The improvement in species persistence by the metabolic adjustment slips  
284 away as the carrying capacity increases. Our results obtained for the tri-trophic food chain  
285 demonstrate that metabolic adjustment dampens the paradox of enrichment but does not  
286 resolve it as in models with adaptive foraging (Mougi and Nishimura, 2007, 2008).

## 287 **Conclusion and perspectives**

288 Previous models studied mechanisms similar to the metabolic adjustment by using struc-  
289 tured populations of consumers with active adults and dormant eggs (Kuwamura et al.,  
290 2009; Nakazawa et al., 2011; Wang and Jiang, 2014). In these models, the resting eggs act  
291 as a refuge for the consumer, enabling them to escape from starvation. This mechanisms  
292 is very different of our representation of metabolic adjustment because metabolic adjust-  
293 ment is an energy budget optimisation process while the production of resting eggs forms  
294 a seed bank maintaining a high biodiversity (Jones and Lennon, 2010). This difference  
295 is emphasised by our divergent results. In fact, Nakazawa et al. (2011) found that the  
296 production of resting eggs leads to more stable population dynamics as it responds more  
297 to seasonality than to non-seasonal variation in resource availability (in this case the effect  
298 of resting eggs is weak). Metabolic adjustment (*i.e.* response to resource availability) in  
299 food webs deeply changes the outcome of the model. In fact, adjustable metabolic rates  
300 greatly increase stability regarding many criteria: they increase the average biomass of  
301 top trophic levels, decrease the variability in population biomass density and increase the  
302 minima of population biomass density, keeping them away from the extinction threshold.  
303 Including metabolic adjustment in food web models improves the representation of the  
304 diversity of organisms whose metabolic activity is not predicted by the metabolic theory  
305 of ecology (Guppy and Withers, 1999; Glazier, 2005; Makarieva et al., 2008; DeLong et al.,

2014b). More broadly, considering phenotypic plasticity (as it was extensively done for  
adaptive foraging or inducible defences for instance) is crucial to better understand the  
fast response of organisms to environmental changes (Marshall and McQuaid, 2011; Mar-  
shall et al., 2011; Magozzi and Calosi, 2015). Interesting future directions in this research  
agenda would be to extend metabolic adjustment to primary producers depending on the  
supply of non-biotic resources affected by seasonality (*e.g.* nutrients, sun light, water...)  
or to include more parameters such as the attack rate in the list of biological rates di-  
rectly affected by the adjustable metabolic rate. Finally, it would also be interesting to  
set the metabolic adjustment coefficient  $X$  as an allometric parameter because single cell  
organisms are expected to respond faster than large animals for instance. Overall, ad-  
justable metabolic rates holds great potential to represent the biology of many species in  
natural communities as metabolic rate plays a central role in describing species biological  
functions.

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### Data accessibility

All data are included in the manuscript and its supporting information. The codes are  
available on Zenodo and GitHub (doi:[10.5281/zenodo.1170138](https://doi.org/10.5281/zenodo.1170138)).



## 329 **Supplementary materials**

330 Supplementary material (available online as Appendix XXXXX (insert manuscript num-  
331 ber) at LÄNK). Appendix 1–2

## 332 **References**

333 Benettin, G., Galgani, L., Giorgilli, A. and Strelcyn, J.-M. 1980. Lyapunov Characteristic  
334 Exponents for smooth dynamical systems and for hamiltonian systems; a method for  
335 computing all of them. Part 1: Theory. – *Meccanica* 15(1): 9–20.

336 Binzer, A., Brose, U., Curtsdotter, A., Eklöf, A., Rall, B. C., Riede, J. O. and de Castro,  
337 F. 2011. The susceptibility of species to extinctions in model communities. – *Basic and*  
338 *Applied Ecology* 12(7): 590–599.

339 Binzer, A., Guill, C., Brose, U. and Rall, B. C. 2012. The dynamics of food chains under  
340 climate change and nutrient enrichment. – *Philosophical Transactions of the Royal*  
341 *Society B: Biological Sciences* 367(1605): 2935–2944.

342 Binzer, A., Guill, C., Rall, B. C. and Brose, U. 2016. Interactive effects of warming,  
343 eutrophication and size structure: impacts on biodiversity and food-web structure. –  
344 *Global Change Biology* 22(1): 220–227.

345 Boit, A., Martinez, N. D., Williams, R. J. and Gaedke, U. 2012. Mechanistic theory and  
346 modelling of complex food-web dynamics in Lake Constance. – *Ecology Letters* 15(6):  
347 594–602.

348 Brose, U. 2008. Complex food webs prevent competitive exclusion among producer  
349 species. – *Proceedings of the Royal Society of London B: Biological Sciences* 275(1650):  
350 2507–2514.

- 351 Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L. and Scheu, S. 2008.  
352 Foraging theory predicts predator-prey energy fluxes. – *Journal of Animal Ecology*  
353 77(5): 1072–1078.
- 354 Brose, U., Williams, R. J. and Martinez, N. D. 2006. Allometric scaling enhances stability  
355 in complex food webs. – *Ecology Letters* 9(11): 1228–1236.
- 356 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. 2004. Toward  
357 a metabolic theory of ecology. – *Ecology* 85(7): 1771–1789.
- 358 Carey, N., Sigwart, J. D. and Richards, J. G. 2013. Economies of scaling: More evidence  
359 that allometry of metabolism is linked to activity, metabolic rate and habitat. – *Journal*  
360 *of Experimental Marine Biology and Ecology* 439: 7–14.
- 361 Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annual Review of*  
362 *Ecology and Systematics* 31(1): 343–366.
- 363 Chesson, P. and Huntly, N. 1989. Short-term instabilities and long-term community  
364 dynamics. – *Trends in Ecology & Evolution* 4(10): 293–298.
- 365 Dawes, E. A. and Ribbons, D. W. 1962. The endogenous metabolism of microorganisms. –  
366 *Annual Review of Microbiology* 16(1): 241–264.
- 367 DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. – No. 9 in *Population*  
368 *and community biology series*. Chapman & Hall, 1st ed.
- 369 DeLong, J. P., Hanley, T. C. and Vasseur, D. A. 2014a. Competition and the density  
370 dependence of metabolic rates. – *Journal of Animal Ecology* 83(1): 51–58.
- 371 — 2014b. Predator–prey dynamics and the plasticity of predator body size. – *Functional*  
372 *Ecology* 28(2): 487–493.

- 373 Dunne, J. A., Brose, U., Williams, R. J. and Martinez, N. D. 2005. Modeling food  
374 web dynamics: complexity-stability implications. – In: Aquatic Food Webs. Oxford  
375 University Press, pp. 117–129.
- 376 Elton, C. S. 1958. The ecology of invasions by animals and plants. – Chapman & Hall.
- 377 Fenchel, T. and Finlay, B. J. 1983. Respiration rates in heterotrophic, free-living proto-  
378 zoa. – *Microbial Ecology* 9(2): 99–122.
- 379 Glazier, D. S. 2005. Beyond the : variation in the intra- and interspecific scaling of  
380 metabolic rate in animals. – *Biological Reviews* 80(04): 611.
- 381 — 2008. Effects of metabolic level on the body size scaling of metabolic rate in birds  
382 and mammals. – *Proceedings of the Royal Society B: Biological Sciences* 275(1641):  
383 1405–1410.
- 384 — 2009a. Activity affects intraspecific body-size scaling of metabolic rate in ectothermic  
385 animals. – *Journal of Comparative Physiology B* 179(7): 821–828.
- 386 — 2009b. Metabolic level and size scaling of rates of respiration and growth in unicellular  
387 organisms. – *Functional Ecology* 23(5): 963–968.
- 388 Guppy, M. and Withers, P. 1999. Metabolic depression in animals: physiological perspec-  
389 tives and biochemical generalizations. – *Biological Reviews of the Cambridge Philo-  
390 sophical Society* 74(1): 1–40.
- 391 Heckmann, L., Drossel, B., Brose, U. and Guill, C. 2012. Interactive effects of body-  
392 size structure and adaptive foraging on food-web stability: Body size, adaptivity and  
393 food-web stability. – *Ecology Letters* 15(3): 243–250.
- 394 Hudson, L. N., Isaac, N. J. B. and Reuman, D. C. 2013. The relationship between

- 395 body mass and field metabolic rate among individual birds and mammals. – *Journal of*  
396 *Animal Ecology* 82(5): 1009–1020.
- 397 Hudson, L. N. and Reuman, D. C. 2013. A cure for the plague of parameters: constraining  
398 models of complex population dynamics with allometries. – *Proc. R. Soc. B* 280(1770):  
399 20131901.
- 400 Jeyasingh, P. D. 2007. Plasticity in metabolic allometry: the role of dietary stoichiome-  
401 try. – *Ecology Letters* 10(4): 282–289.
- 402 Jones, S. E. and Lennon, J. T. 2010. Dormancy contributes to the maintenance of micro-  
403 bial diversity. – *Proceedings of the National Academy of Sciences* 107(13): 5881–5886.
- 404 Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C. and Brose, U. 2013.  
405 Body masses, functional responses and predator-prey stability. – *Ecology Letters* 16(9):  
406 1126–1134.
- 407 Kartascheff, B., Heckmann, L., Drossel, B. and Guill, C. 2010. Why allometric scaling  
408 enhances stability in food web models. – *Theoretical Ecology* 3(3): 195–208.
- 409 Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity  
410 and stability. – *Science* 299(5611): 1388–1391.
- 411 — 2010. Linking learning adaptation to trophic interactions: a brain size-based ap-  
412 proach. – *Functional Ecology* 24(1): 35–43.
- 413 Křivan, V. and Diehl, S. 2005. Adaptive omnivory and species coexistence in tri-trophic  
414 food webs. – *Theoretical Population Biology* 67(2): 85–99.
- 415 Kuwamura, M., Nakazawa, T. and Ogawa, T. 2009. A minimum model of prey-predator  
416 system with dormancy of predators and the paradox of enrichment. – *Journal of Math-*  
417 *ematical Biology* 58(3): 459–479.

- 418 Lang, B., Rall, B. C. and Brose, U. 2012. Warming effects on consumption and intraspe-  
419 cific interference competition depend on predator metabolism. – *Journal of Animal*  
420 *Ecology* 81(3): 516–523.
- 421 Loreau, M. and de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis  
422 of underlying mechanisms. – *Ecology Letters* 16: 106–115.
- 423 MacArthur, R. 1955. Fluctuations of animal populations and a measure of community  
424 stability. – *Ecology* 36(3): 533.
- 425 Magozzi, S. and Calosi, P. 2015. Integrating metabolic performance, thermal tolerance,  
426 and plasticity enables for more accurate predictions on species vulnerability to acute  
427 and chronic effects of global warming. – *Global Change Biology* 21(1): 181–194.
- 428 Makarieva, A. M., Gorshkov, V. G. and Li, B.-L. 2005. Energetics of the smallest: do  
429 bacteria breathe at the same rate as whales?. – *Proceedings of the Royal Society B:*  
430 *Biological Sciences* 272(1577): 2219–2224.
- 431 Makarieva, A. M., Gorshkov, V. G., Li, B.-L., Chown, S. L., Reich, P. B. and Gavrillov,  
432 V. M. 2008. Mean mass-specific metabolic rates are strikingly similar across life's  
433 major domains: Evidence for life's metabolic optimum. – *Proceedings of the National*  
434 *Academy of Sciences* 105(44): 16994–16999.
- 435 Marshall, D. J., Dong, Y.-w., McQuaid, C. D. and Williams, G. A. 2011. Thermal  
436 adaptation in the intertidal snail *Echinolittorina malaccana* contradicts current theory  
437 by revealing the crucial roles of resting metabolism. – *Journal of Experimental Biology*  
438 214(21): 3649–3657.
- 439 Marshall, D. J. and McQuaid, C. D. 2011. Warming reduces metabolic rate in marine

- 440 snails: adaptation to fluctuating high temperatures challenges the metabolic theory of  
441 ecology. – *Proceedings of the Royal Society B: Biological Sciences* 278(1703): 281–288.
- 442 May, R. M. 1972. Will a large complex system be stable?. – *Nature* 238(5364): 413–414.
- 443 McCann, K. S. 2000. The diversity–stability debate. – *Nature* 405(6783): 228–233.
- 444 Montoya, J. M., Pimm, S. L. and Solé, R. V. 2006. Ecological networks and their fragility. –  
445 *Nature* 442(7100): 259–264.
- 446 Mougi, A. and Nishimura, K. 2007. A resolution of the paradox of enrichment. – *Journal*  
447 *of Theoretical Biology* 248(1): 194–201.
- 448 — 2008. The paradox of enrichment in an adaptive world. – *Proceedings of the Royal*  
449 *Society B: Biological Sciences* 275(1651): 2563–2568.
- 450 Nakazawa, T., Kuwamura, M. and Yamamura, N. 2011. Implications of resting eggs of  
451 zooplankton for the paradox of enrichment. – *Population Ecology* 53(2): 341–350.
- 452 Norin, T., Malte, H. and Clark, T. D. 2015. Differential plasticity of metabolic rate  
453 phenotypes in a tropical fish facing environmental change. – *Functional Ecology* pp.  
454 n/a–n/a.
- 455 Otto, S. B., Rall, B. C. and Brose, U. 2007. Allometric degree distributions facilitate  
456 food-web stability. – *Nature* 450(7173): 1226–1229.
- 457 Pawar, S., Dell, A. I. and Savage, V. M. 2012. Dimensionality of consumer search space  
458 drives trophic interaction strengths. – *Nature* .
- 459 Pimm, S. L. 1984. The complexity and stability of ecosystems. – *Nature* 307(5949):  
460 321–326.

- 461 Polis, G. A., Holt, R. D., Menge, B. A. and Winemiller, K. O. 1996. Time, space, and  
462 life history: influences on food webs. – In: Polis, G. A. and Winemiller, K. O. (eds.),  
463 Food Webs. Springer US, pp. 435–460.
- 464 Rall, B., Guill, C. and Brose, U. 2008. Food-web connectance and predator interference  
465 dampen the paradox of enrichment. – *Oikos* 117(2): 202–213.
- 466 Ramasubramanian, K. and Sriram, M. S. 2000. A comparative study of computation of  
467 Lyapunov spectra with different algorithms. – *Physica D: Nonlinear Phenomena* 139(1-  
468 2): 72–86. ArXiv: [chao-dyn/9909029](https://arxiv.org/abs/chao-dyn/9909029).
- 469 Rip, J. M. K. and McCann, K. S. 2011. Cross-ecosystem differences in stability and the  
470 principle of energy flux. – *Ecology Letters* 14(8): 733–740.
- 471 Rooney, N. and McCann, K. S. 2012. Integrating food web diversity, structure and  
472 stability. – *Trends in Ecology & Evolution* 27(1): 40–46.
- 473 Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems  
474 in ecological time. – *Science (New York, N.Y.)* 171(3969): 385–387.
- 475 Roy, S. and Chattopadhyay, J. 2007. The stability of ecosystems: A brief overview of the  
476 paradox of enrichment. – *Journal of Biosciences* 32(2): 421–428.
- 477 de Ruiter, P. C. 2005. Food web ecology: playing Jenga and beyond. – *Science* 309(5731):  
478 68–71.
- 479 Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist,  
480 B. J. and Brown, J. H. 2004. The predominance of quarter-power scaling in biology. –  
481 *Functional Ecology* 18(2): 257–282.
- 482 Schwarzmüller, F., Eisenhauer, N. and Brose, U. 2015. ‘Trophic whales’ as biotic buffers:

- 483 weak interactions stabilize ecosystems against nutrient enrichment. – *Journal of Animal*  
484 *Ecology* 84(3): 680–691.
- 485 Shimada, I. and Nagashima, T. 1979. A numerical approach to ergodic problem of dissi-  
486 pative dynamical systems. – *Progress of Theoretical Physics* 61(6): 1605–1616.
- 487 Skalski, G. T. and Gilliam, J. F. 2001. Functional responses with predator interference:  
488 viable alternatives to the Holling type II model. – *Ecology* 82(11): 3083–3092.
- 489 Uchida, S., Drossel, B. and Brose, U. 2007. The structure of food webs with adaptive  
490 behaviour. – *Ecological Modelling* 206(3-4): 263–276.
- 491 Verschoor, A. M., Vos, M. and Van Der Stap, I. 2004. Inducible defences prevent strong  
492 population fluctuations in bi- and tritrophic food chains. – *Ecology Letters* 7(12): 1143–  
493 1148.
- 494 Vos, M., Kooi, B. W., DeAngelis, D. L. and Mooij, W. M. 2004. Inducible defences and  
495 the paradox of enrichment. – *Oikos* 105(3): 471–480.
- 496 Wang, J. and Jiang, W. 2014. Impulsive perturbations in a predator–prey model with  
497 dormancy of predators. – *Applied Mathematical Modelling* 38(9-10): 2533–2542.
- 498 Williams, R. J., Brose, U. and Martinez, N. D. 2007. Homage to Yodzis and Innes 1992:  
499 Scaling up feeding-based population dynamics to complex ecological networks. – In:  
500 *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*.  
501 Springer, Dordrecht, pp. 37–51. DOI: 10.1007/978-1-4020-5337-5\_2.
- 502 Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – *Nature*  
503 404(6774): 180–183.
- 504 Wolf, A., Swift, J. B., Swinney, H. L. and Vastano, J. A. 1985. Determining Lyapunov  
505 exponents from a time series. – *Physica D: Nonlinear Phenomena* 16(3): 285–317.



- 506 Yashchenko, V., Fossen, E. I., Kielland, Ø. N. and Einum, S. 2016. Negative relationships  
507 between population density and metabolic rates are not general. – *Journal of Animal*  
508 *Ecology* 85(4): 1070–1077.
- 509 Yodzis, P. and Innes, S. 1992. Body size and consumer-resource dynamics. – *The American*  
510 *Naturalist* 139(6): 1151.

Table 1: Parameters and variables used in the model

Variable	Value	Description
$B_i$	$\text{kg.m}^{-2}$	biomass density of species $i$
$r_i$	dimensionless	scaled mass specific maximum growth rate of species $i$
$x_i$	dimensionless	scaled mass specific metabolic rate of species $i$
$y_i$	8	scaled mass specific maximum consumption rate
$e_{ji}$	0.45	assimilation efficiency of species $i$ by species $j$ (herbivores)
	0.85	assimilation efficiency of species $i$ by species $j$ (carnivores)
$G_i$	dimensionless	density dependent growth rate of species $i$
$F_{ij}$	dimensionless	functional response of species $i$ feeding on species $j$
$B_0$	$0.5 \text{ kg.m}^{-2}$	half saturation density for consumer functional response
$c$	$0.5 \text{ m}^2.\text{kg}^{-1}$	predator interference
$\omega_{ij}$	1/nbr prey	predator $i$ preference for species $j$
$a_x/a_r$	0.138	metabolic rate allometric constant (primary producers)
	0.314	metabolic rate allometric constant (invertebrates consumers)
$X$	dimensionless	metabolic adjustment coefficient
$K$	$\text{kg.m}^{-2}$	carrying capacity of primary producers

Note: All these parameters come from Brose et al. (2006).

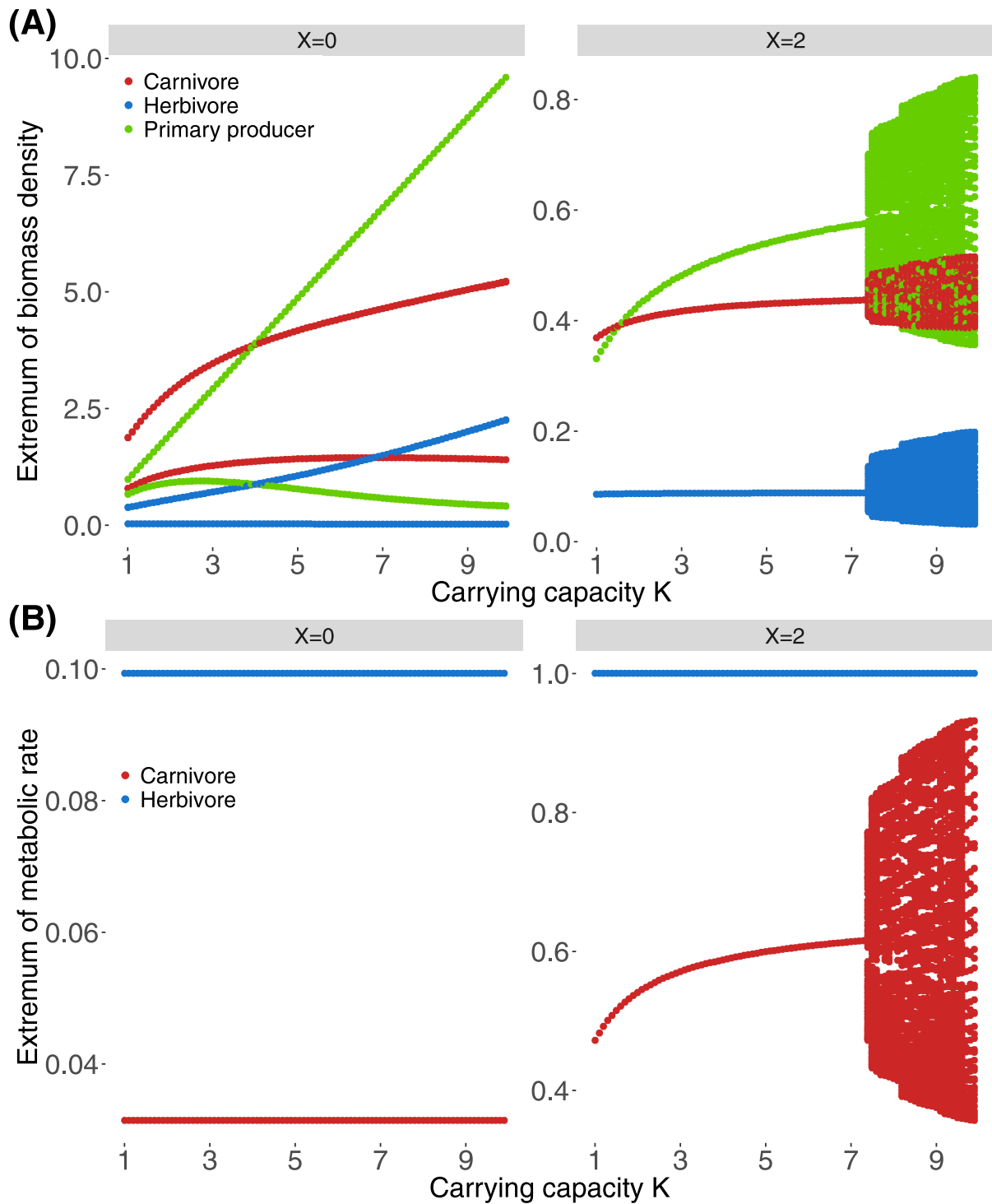


Figure 1: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the carrying capacity  $K$  for **A)** biomass density and **B)** metabolic rate for a metabolic adjustment coefficient  $X = 0$  or  $X = 2$ .

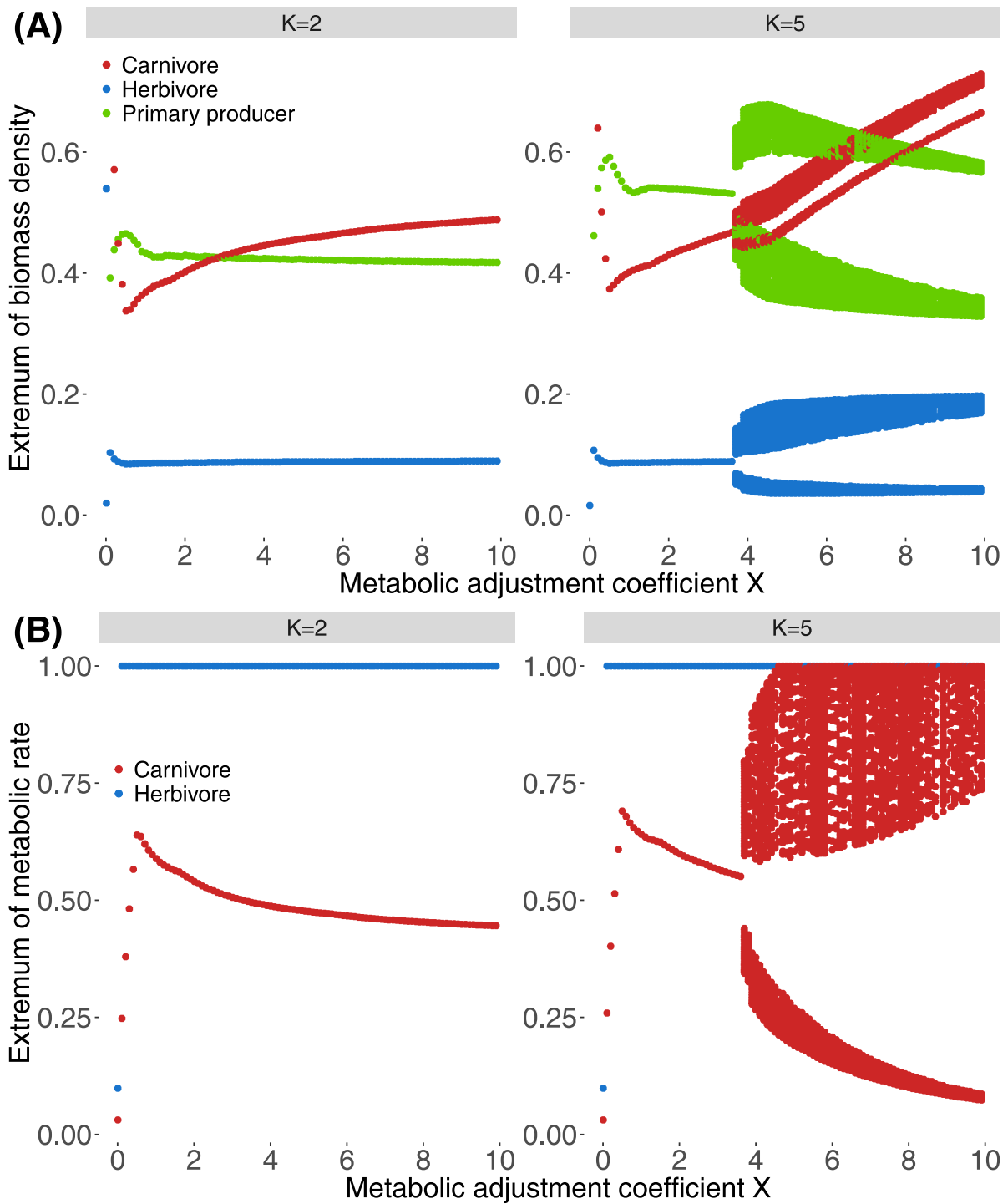


Figure 2: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the metabolic adjustment coefficient  $X$  for **A)** biomass density and **B)** metabolic rate for a carrying capacity  $K = 1$  or  $K = 2$ .

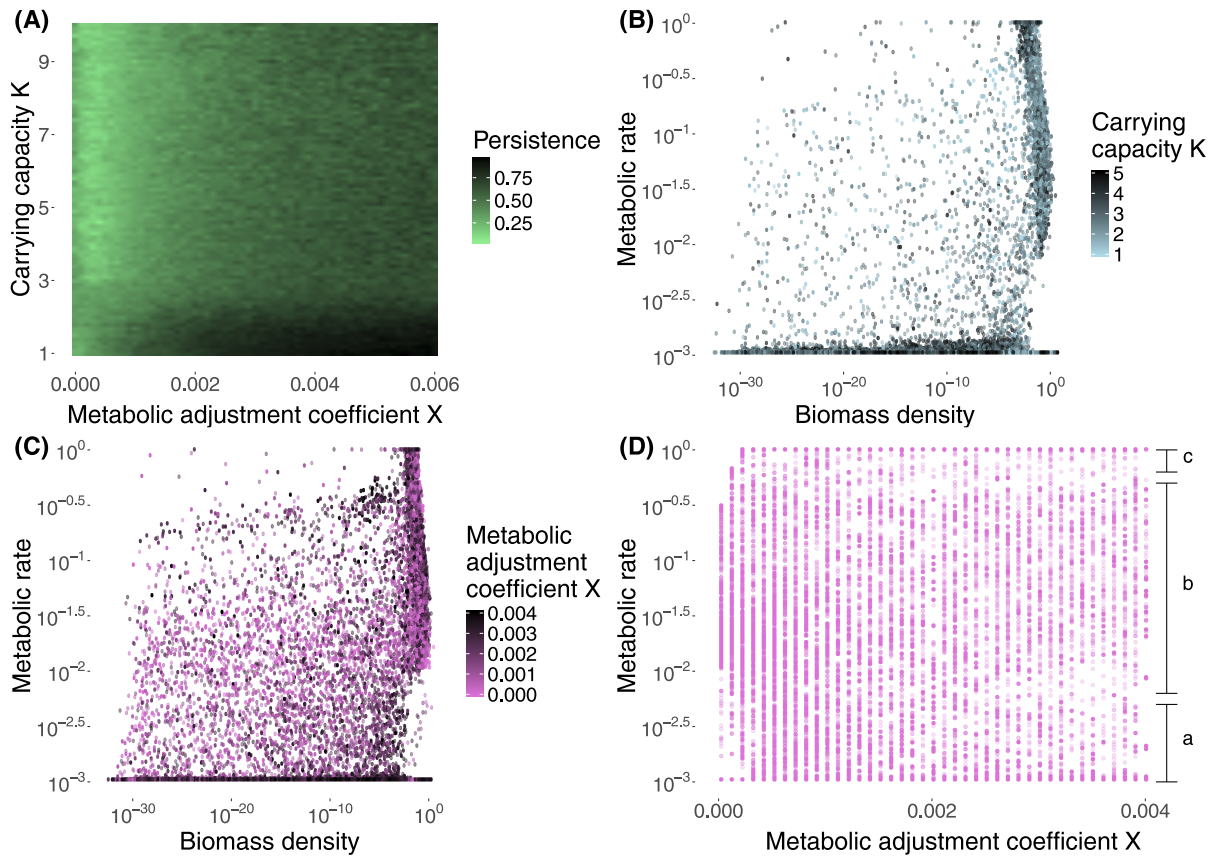


Figure 3: Effects of metabolic adjustment on complex food webs. **A)** Persistence of species for different values of metabolic adjustment coefficient  $X$  and carrying capacity  $K$ . Each square represent the average persistence for 100 replicates. **B)** Metabolic rate versus biomass density along gradient in carrying capacity  $K$  ( $X = 0.004$ ). **C)** Metabolic rate versus biomass density along a metabolic adjustment coefficient gradient ( $K = 1.5$ ). Each point represents one species and 100 food webs are tested for each combination of  $K$  and  $X$ . **D)** Distribution of the average metabolic rate of each species along a metabolic adjustment coefficient gradient ( $K = 1.5$ ). The domains a, b and c represent respectively species with minimum or low metabolic rate, species with intermediate metabolic rate and species with maximum metabolic rate.