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Metabolic adjustment enhances food web stability

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Abstract

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

Introduction

Identifying the mechanisms responsible for ecosystem stability is one of the main scientific tasks in ecology (de Ruiter, 2005; Montoya et al., 2006; Rooney and McCann, 2012; Loreau and de Mazancourt, 2013; Brose et al., 2017). A prevailing view in ecology is that large, complex ecosystems were particularly stable (in the sense of dynamic stability, defined by the equilibrium stability and the variability (Pimm, 1984; McCann, 2000)) thanks to many mechanisms resulting from the diversity of interacting species (MacArthur, 1955; Elton, 1958), but early mathematical models predicted the opposite results. However, mathematical models of ecosystems predicted opposite results. For instance, the theoretical study performed by May (1972) demonstrated that diversity, complexity (measured by the linkage probability between pairs of species) and the average interaction strength decreased the stability of random interaction networks (assessed by a linear stability analysis).

Subsequently, many mechanisms promoting food web stability were identified (McCann, 2000; Loeuille, 2010; Jacob et al., 2011; Rooney and McCann, 2012; Brose et al., 2017) and two of them inspired us to implement a new one in food web models. The first mechanism is the allometric scaling of biological rates (*e.g.* metabolic rate, feeding strength), describing them as power functions of individual body mass (Yodzis and Innes, 1992; Brown et al., 2004; Savage et al., 2004; Brose et al., 2008; Pawar et al., 2012; Kalinkat et al., 2013). These relationships provided a better prediction of species biomasses in empirical data than any other model parametrisation (Boit et al., 2012; Hudson and Reuman, 2013). In addition, allometric scaling coupled with size structured communities (*i.e.* consumers larger than their prey) lead to more stable food webs with fewer extinctions (Brose et al., 2006; Brose, 2008; Kartascheff et al., 2010). The second mechanism is adaptive foraging. Kondoh (2003) included adaptive foraging behaviour into food web models to enable the consumers to maximise their biomass income by preferentially hunting more abundant prey. The result is dramatic, with a reversion of the pattern predicted by May (1972): with adaptive foragers, increasing species richness and complexity enhances species persistence. Furthermore, food webs with randomly set interactions and adaptive foraging converge towards size-structured food webs with predators systematically larger than their prey (Heckmann et al., 2012). In such models, species biomasses are not the only dynamic variables, food web structures and interaction parameters are also dynamic (de Ruiter, 2005). However, one central parameter has always been considered constant in food web models: the metabolic rate. The closest examples to adjustable metabolic rates were given by Kuwamura et al. (2009), Nakazawa et al. (2011) and Wang and Jiang (2014) who considered simple models with a structured population of *Daphnia* including metabolically active adults and dormant eggs. In nature, however, many organisms exhibit phenotypic plasticity in the expression of metabolism (Brown et al., 2004; Glazier, 2005; Jeyasingh, 2007; Glazier, 2009a; Carey et al., 2013; Norin et al., 2015). In fact, Makarieva et al. (2005) pointed out that organisms with different body sizes can display similar metabolic rates depending on their activity. Moreover, animals from all major phyla are able to slow down their activity to face harsh conditions such as drought and starvation using body mass reduction (DeLong et al., 2014b), torpor, diapause (depression of 60-95%) or cryptobiosis (depression of 99-100%) (Guppy and Withers, 1999). Considering the metabolic activity of organisms as a constant parameter is a strong assumption despite its central role in food web models. In this study, we model the plastic response of metabolism similarly to adaptive foraging. As adaptive foraging maximises the growth rate of consumers by varying the foraging effort for the different prey, we pro-

pose that metabolic adjustment maximises the growth rate by varying the metabolic rate.

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

Material and Methods

We study the impact of metabolic adjustment on a simple tri-trophic food chain and complex food webs. Both are modified versions of the Allometric Trophic Network (ATN) (Brose et al., 2006) (Parameters listed in table 1). The complex food webs rely on the niche model for their structure Williams and Martinez (2000) and on the Yodzis and Innes (1992) predator-prey model for the dynamic equations and their parameters.

Food web structure

The construction of the complex food webs follows the niche model (Williams and Martinez, 2000; Brose et al., 2006; Heckmann et al., 2012; Binzer et al., 2016) as it successfully predicted the food web structures of natural communities. The trophic interactions across species are set according to the algorithm detailed by Williams and Martinez (2000) with an expected connectance equal to 0.15. The basal species described by Williams and Martinez (2000) are set as primary producers and the others as consumers. The niche values n_i (uniformly drawn in a $[0, 1]$ interval for each of the 40 initial species) used to parametrise the niche model are also used to calculate species body mass as follows (Heckmann et al., 2012).

$$M_i = 10^{N \cdot n_i} \tag{1}$$

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

Predator-prey population dynamics

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

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

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

These equations describe changes in relative, biomass densities of primary producers (2a) and consumer species (2b). In these equations B_i is the biomass of species i , r_i is the mass-specific maximum growth rate of primary producers, G_i is the logistic growth rate of primary producers (Equation (3)), x_i is i 's mass-specific metabolic rate, y_i is the maximum consumption rate of consumers relative to their metabolic rate, e_{ji} is j 's assimilation efficiency when consuming population i and F_{ij} describes the realised fraction of i 's maximum rate of consumption achieved when consuming j (equation (4)). Primary producers growth rate is modelled by a logistic growth with a shared carrying capacity K which ensures a comparable primary production among food webs, regardless the number of primary producers (equation 3).

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

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

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

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

Basically, mass specific biological rates (biomass production, metabolic rate and maximum consumption rate) follow the negative-quarter power-law relationship with species body masses as described by the metabolic theory of ecology (Brown et al., 2004; Savage et al., 2004). The time scale of the system is defined by normalising the biological rates to the mass-specific growth rate of the smallest primary producer as performed by Yodzis and Innes (1992); Brose et al. (2006); Williams et al. (2007) (Equations 5a and 5b). Then the maximum consumption rates are normalised by the metabolic rates (Equations 5c). Thus, the loss due to respiration and the gain due to consumption both directly depend

on the metabolic rate (Equation (2b)).

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

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

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

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

This model relies on strong assumptions such as the negative-quarter power-law relationship followed by all biological rates (not observed by Pawar et al. (2012), Rall et al. (2012) for the feeding rate and Hirt et al. (2017) for the maximal speed of animals), the independence of the maximum consumption rate to prey body mass or metabolic rate or values of parameters such as B_0 or c . The sensitivity of the results to these parameters or assumptions is assessed in the Supplementary material Appendix B, Fig.B1-B4 and Fig.B12-B14.

Metabolic adjustment model

We propose to model the metabolic adjustment by an optimisation of the mass-specific net growth rate g_i as in adaptive foraging models (Kondoh, 2003; Uchida et al., 2007) or in body mass plasticity models (DeLong et al., 2014b). Thus, the consumer adjusts its metabolic rate to maximise the balance between ingestion and respiration that both depend on metabolic rate. Metabolic adjustment does not apply to primary producers that are considered as basal resources species with constant resource supply (see equation (2a)).

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

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

$\partial g_i / \partial x_i$ (Equation 6a) is the variation of the net growth rate g_i when x_i increases (its sign drives the increase or decrease of the metabolic rate), x_i is the metabolic rate (the higher is the metabolic rate, the faster is the physiological response) and X is the metabolic adjustment coefficient representing the speed of the adjustment. The higher X is, the faster the response of species to modifications of their growth rate is. The metabolic rate is bounded by 1 and 0.001 to ensure a minimum metabolic rate and to prevent a destabilising high metabolic rate. The values predicted by the equation 5b fall in this interval that is consistent with Makarieva et al. (2005) (Supplementary material Appendix B, Fig.B5, B6,B7,B8). Such a large interval is meant to take into account the large variety of metabolic scopes across phyla: typically 10 for vertebrates and 10^5 for some tardigrades (Guppy and Withers, 1999).

Simulations

The model is coded in *C++* and the simulations performed with the *GSL* ODE solver. The simple tri-trophic food chain only contains a primary producer, a herbivore and a carnivore. Their body masses are respectively set to 1, 10^2 and 10^4 . A more simple predator-prey system is studied in the Supplementary material Appendix A, Fig.A2 and Fig.A3. For the complex food webs, each simulation is independent from the other and only differs in the body mass distribution and the architecture of the food web. The system starts with 40 species that all have an initial biomass density of 0.1 and the metabolic rates are initialised with the values predicted by the metabolic theory of ecology (Equation 5). The simulations are performed for 10,000 time steps and only the last 1000 steps are recorded. Species persistence is the proportion of the 40 initial species that survives until the end of the simulation (a species is considered as extinct if its biomass density falls below 10^{-30}). Each combination of parameters (carrying capacity K and metabolic adjustment coefficient X) is tested for 100 different food webs yielding a total of 555,100 simulated replicates. We use species persistence (fraction of surviving species at the end of the simulation) and biomass oscillation amplitude as measures of stability. Persistence represents the global stability of the food web as it shows the ability of species to coexist and the amplitude of biomass oscillations represents the time variability of species biomass. The amplitude of biomass oscillations is presented by bifurcation diagrams representing the local extrema of dynamics along a gradient in a parameter.

Table 1: Parameters and variables used in the model

Variable	Value	Description
B_i	$\text{kg}\cdot\text{m}^{-2}$	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	$0.5 \text{ kg}\cdot\text{m}^{-2}$	half saturation density for consumer functional response
c	$0.5 \text{ m}^2\cdot\text{kg}^{-1}$	predator interference
ω_{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	$\text{kg}\cdot\text{m}^{-2}$	carrying capacity of primary producers

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

Results

Effect of adaptive metabolic rate on tri-trophic chains

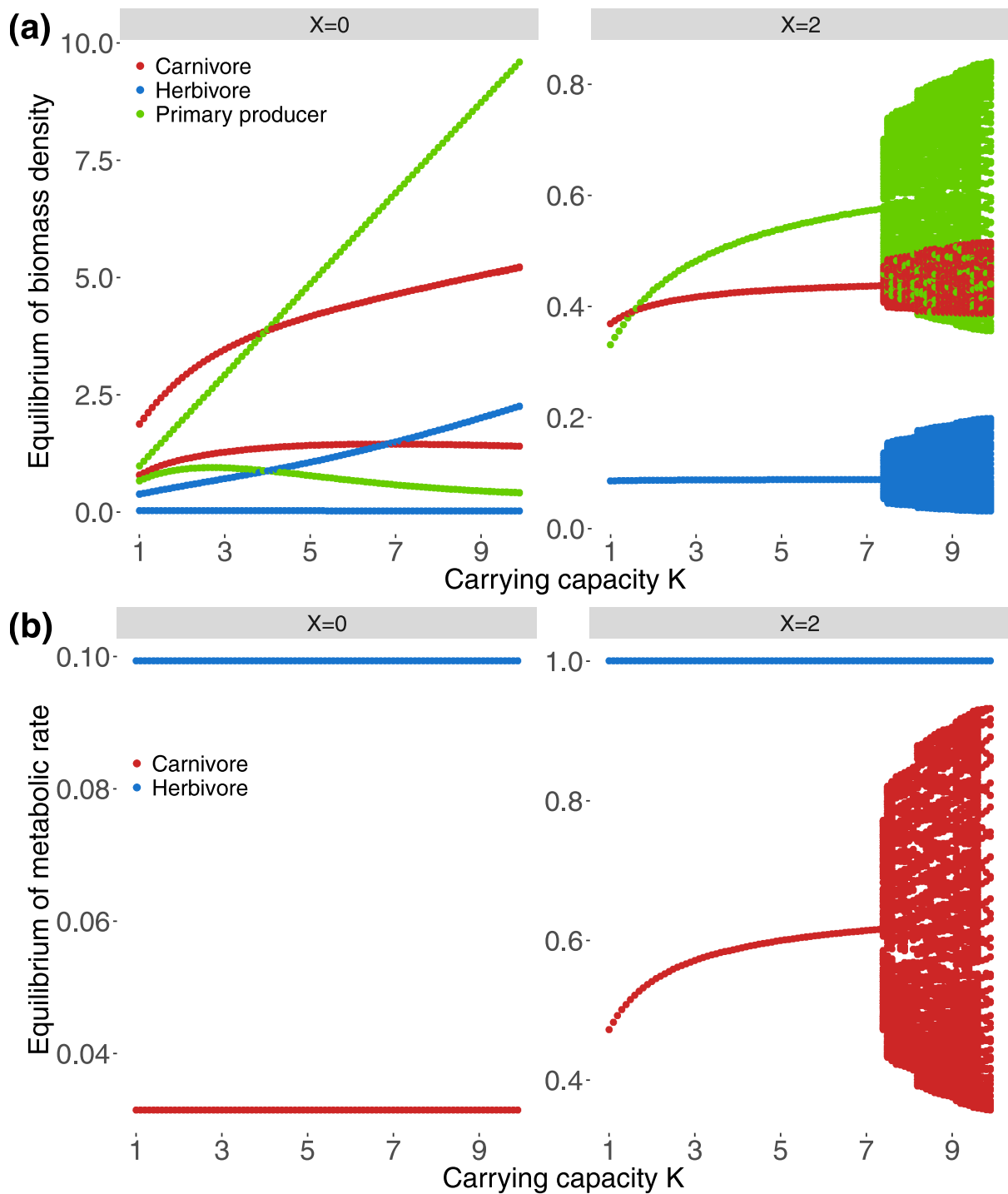


Figure 1: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the carrying capacity K for (a) biomass density and (b) metabolic rate for a metabolic adjustment coefficient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

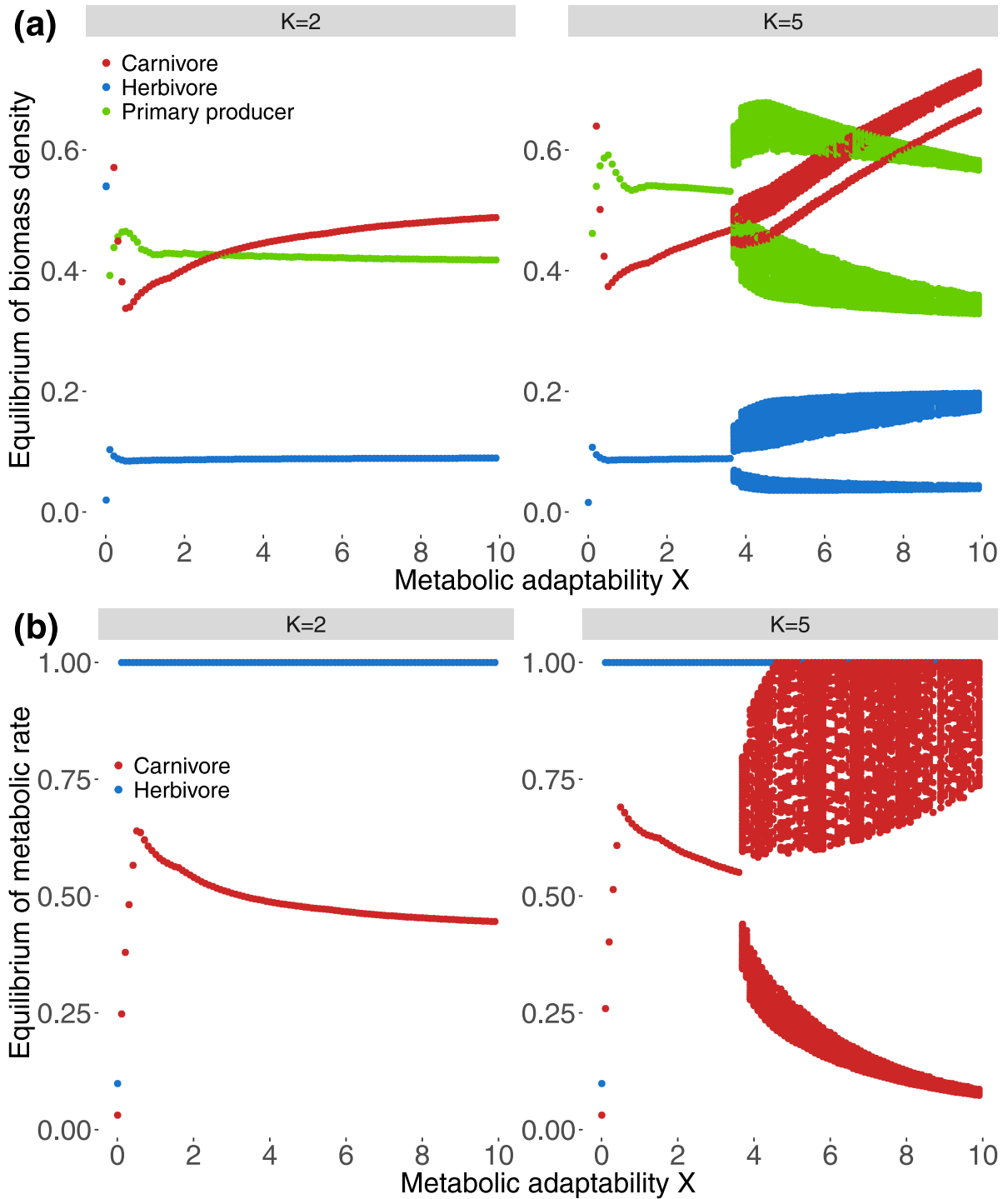


Figure 2: Bifurcation diagrams of the tri-trophic food-chain containing a primary producers (green), a herbivores (blue) and a carnivores (red). The bifurcation is performed along gradients in the metabolic adjustment coefficient X for (a) biomass density and (b) metabolic rate for a carrying capacity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

The first system we consider is a simple tri-trophic food chain containing a primary producer, a herbivore and a carnivore. The effects of the resource availability on species dynamics are represented by bifurcation diagrams (Fig.1). The food chain without metabolic adjustment ($X = 0$) displays large biomass oscillations whose amplitude increases with the carrying capacity K (Fig.1a) and the minima reaches extremely low values, especially for the herbivore (Supplementary material Appendix A, Fig.A1a). As there is no metabolic adjustment, the metabolic rates are constant (Fig.1b) and their values are those predicted

by the metabolic theory of ecology (Equations 5a,b,c). The food chain with metabolic adjustment ($X = 2$) has fixed points for $K \leq 7$ and oscillations for $K > 7$ (Fig.1a). Despite the multi-period oscillations, the system is not chaotic (Supplementary material Appendix A, Fig.A4a). The amplitude of oscillations increases with the carrying capacity for all species but remains lower than in the food chain without metabolic adjustment. The biomass minima increases with higher values of the metabolic adjustment coefficient (Supplementary material Appendix A, Fig.A1a). The herbivore metabolic rate remains constantly at the maximum value allowed by the model, whereas the carnivore metabolic rate increases with carrying capacity K until it oscillates for $K > 7$ (Fig.1b).

The tri-trophic food chain has fixed points along a gradient in metabolic adjustment coefficients for a carrying capacity $K = 2$ (Fig.2), except for $X = 0$ (origin of the x-axis corresponding to the situation described in Fig.1a). Increasing the metabolic adjustment coefficient increases the biomass of the herbivore and of the carnivore while it decreases the biomass of the primary producer. However, we observe an increase in the primary producer biomass and a decrease in the herbivore biomass for the low values of X . The metabolic rate of the herbivore is maximum for $X > 0$ and the metabolic rate of the carnivore first sharply increases with the increasing metabolic adjustment coefficient X and then it decreases (Fig.2b). The response is similar for $K = 5$ and $X < 4$ but for $X \geq 4$ the system oscillates (Fig.2a), yet it is not chaotic (Supplementary material Appendix A, Fig.A4b). Increasing the metabolic adjustment coefficient does not increase the amplitude of biomass oscillations, it even decreases them for the primary producer. The biomass of the carnivore increases with X , the amplitude of the oscillations of its metabolic rate increases (Fig.2b) while the amplitude of its biomass oscillations remains mostly unchanged. Increasing the metabolic adjustment coefficient also increases the biomass minima of each species (Supplementary material Appendix A, Fig.A1b).

Effect of adaptive metabolic rates on persistence

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

We can identify two groups of species in complex food webs: 'slow species' with a low biomass ($< 10^{-2}$) and a low metabolic rate ($< 10^{-2.5}$) and 'fast species' with a high biomass ($> 10^{-2}$) and a high metabolic rate ($> 10^{-2.5}$) (Fig.3b and 3c). Increasing the carrying capacity K does not seem to change the repartition of species in these two categories (Fig.3b) while more species are in an intermediate category (low biomass and high metabolic rate) at low values of metabolic adjustment coefficient X (Fig.3c). This difference is confirmed in Fig.3d where three groups of species can be identified for $X > 0.002$: (a) species with minimum or low metabolic rate, (b) species with intermediate metabolic rate and (c) species with maximum metabolic rate. (a) species correspond to

the slow species, (b) and (c) to the fast species. Such a non-differentiation of the metabolic profile of species for low metabolic adjustment coefficients may be the origin of the first decrease of species persistence with increasing X for $K > 3$ (Fig.3a).

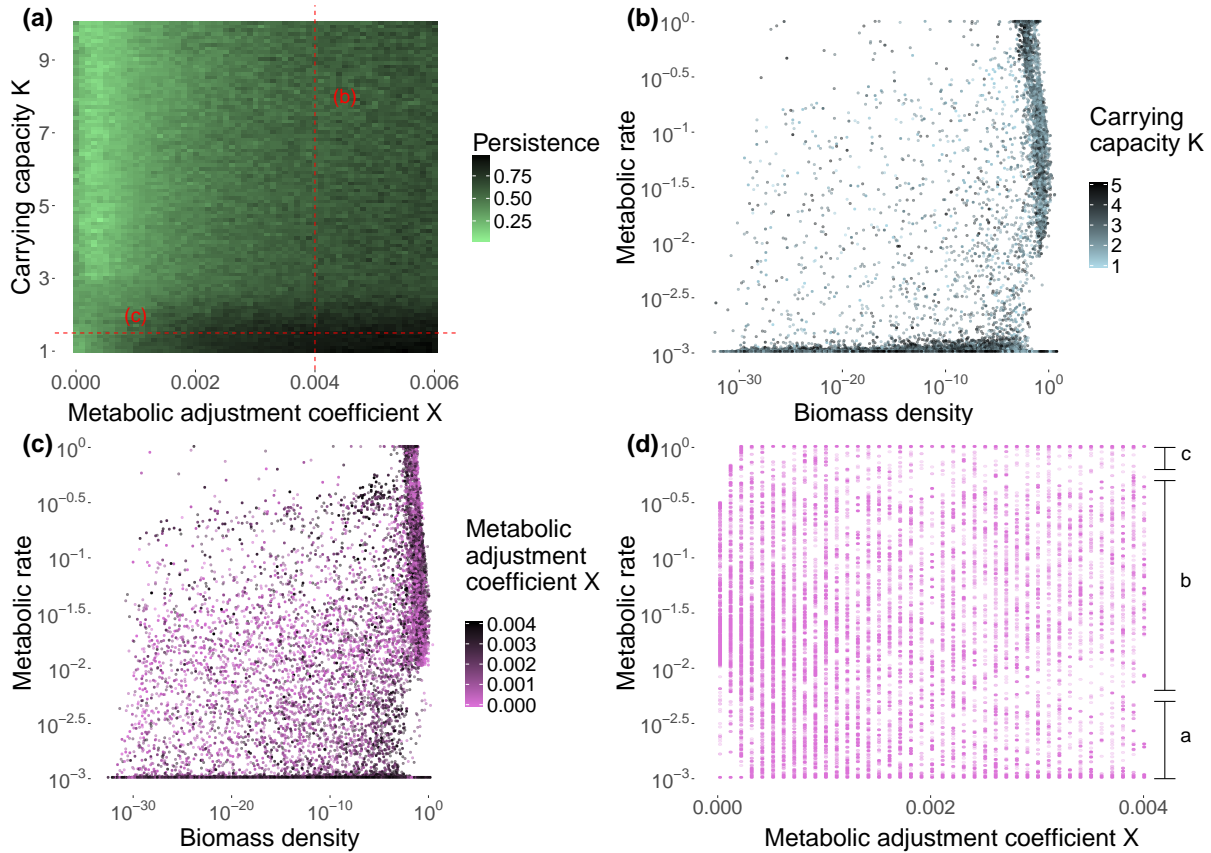


Figure 3: Effects of metabolic adjustment on complex food webs. **(a)** Persistence of species for different values of metabolic adjustment coefficient X and carrying capacity K . Each square represent the average persistence for 100 replicates. The dashed red lines represent the food webs whose species are represented in figures (b) and (c). **(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.

Discussion

We studied the consequences of an adaptive metabolic rate for different aspects of food web stability. We predicted that metabolic adjustment enables species to fit their metabolic rate to their energy budget and the resource availability. In times of bonanza, it allows species to increase their activity and then to exploit more resources. In harsh times, however, metabolic adjustment also lets organisms slow down their activity to save their energy until the next season of plenty (Polis et al., 1996). This behaviour is typically the case for microbial organisms that can get encysted or can produce spores (Dawes and Ribbons, 1962; Fenchel and Finlay, 1983; Glazier, 2009b) but also larger organisms that can shift between resting and activity metabolism (Glazier, 2008; Hudson et al., 2013) or

hibernating (Guppy and Withers, 1999). In the case of our models, adjustable metabolic rates reduce the magnitude of biomass oscillations and increase the average biomass of carnivores. Additionally, they greatly increase the stability of complex food webs by increasing species persistence at low resource densities.

Effect of adaptive metabolic rate on tri-trophic food chains

Our first aim was to provide a mechanistic insight in the consequences of metabolic adjustment for population dynamics. We followed prior studies employing tri-trophic food chains with allometric scaling of population parameters, which provides a fully deterministic and easily tractable system (Otto et al., 2007; Binzer et al., 2012). First, enrichment, through the increase of the carrying capacity K , has a destabilising effect on population dynamics (Rall et al., 2008; Schwarzmüller et al., 2015). Such a destabilisation, called paradox of enrichment, is due to the unbalance between the growth and the mortality of organisms (Rosenzweig, 1971; DeAngelis, 1992; Roy and Chattopadhyay, 2007; Rip and McCann, 2011). However, this destabilising effect is dampened by metabolic adjustment that promotes fixed points or reduces the amplitude of biomass oscillations and increases the biomass minima. Increasing the speed of adjustment (*i.e.* increasing the metabolic adjustment coefficient X) is destabilising because it promotes biomass oscillations, but it also increases the biomass of carnivores. We can compare our results to prior studies using adaptive foraging that inspired our modelling of metabolic adjustment (Kondoh, 2003, 2010; Křivan and Diehl, 2005; Mougi and Nishimura, 2008). The adaptability of predator attack rates or prey defences (Vos et al., 2004; Verschoor et al., 2004) also decreases in the amplitude of biomass oscillations, increases the average biomass of carnivores and keeps the minima away from the extinction threshold (Mougi and Nishimura, 2007). The outcome of these processes are similar because both rely on growth rate optimisation, which seems to highly improve the persistence of higher trophic levels that are generally most prone to extinction (Binzer et al., 2011). However, metabolic adjustment affects both the growth and the biomass loss rates of consumers while adaptive foraging only increases the growth rate and inducible defences decrease the mortality rate. In consequence, adaptive metabolic rates enables a better control of species dynamics, especially for top consumers whose loss rate only depends on the metabolic rate and not on predation. In our tri-trophic food chain, carnivores have a highly variable metabolic rate while the herbivore's metabolic rate always stays at the upper limit of metabolic rate range. This can be attributed to a trophic cascade: the carnivore controls the herbivore population and the primary producer thrives. Thus, the herbivore always has plenty of resources, and increasing the metabolic rate increases more the ingestion rate and the growth rate compared to the loss rate.

Effect of adaptive metabolic rate on species persistence

Our second aim was to address the impact of an adjustable metabolic rate on the species persistence of complex food webs. The null model is a classic allometric model (Brose et al., 2006) that displays an increase in persistence with increasing carrying capacity and increase in the energy flow in the system (Dunne et al., 2005; Rall et al., 2008). As expected, adding an adjustable metabolic rate increases the species persistence at low resources levels. Similarly to the results of studies on adaptive foraging (Kondoh, 2003; Heckmann et al., 2012), higher adjustment coefficients (the metabolic adjustment in our case) increase species persistence. These slow species could be species with few available resources that keep their metabolic rate low most of the time, and therefore they cannot

build up a high biomass densities. In contrast, fast species can exploit abundant resources and maintain a high metabolic rate to build up a high biomass density. In nature, such a pattern is represented by algal blooms and "seed banks" of micro-organisms (Lennon and Jones, 2011). However, no positive relationship between biomass density and metabolic rate has been reported across phyla in previous studies (DeLong et al., 2014a; Yashchenko et al., 2016). An opposite pattern can be seen in the tri-trophic food chain where the carnivore has a higher biomass than the herbivore and has a lower average metabolic rate. Alternatively, these slow species could just be slow in getting extinct because of their very low metabolic rate (which is the loss rate in our model). However, the substantial variation in metabolic rates of the fast species enables these species to better adapt to the specific situation concerning top-down control and resource availability in each food web, leading to an increased species persistence. The improvement in species persistence by the metabolic adjustment slips away as the carrying capacity increases. Our results obtained for the tri-trophic food chain demonstrate that metabolic adjustment dampens the paradox of enrichment but does not resolve it as in models with adaptive foraging (Mougi and Nishimura, 2007, 2008).

Conclusion and perspectives

Previous models studied mechanisms similar to the metabolic adjustment by using structured populations of consumers with active adults and dormant eggs (Kuwamura et al., 2009; Nakazawa et al., 2011; Wang and Jiang, 2014). In these models, the resting eggs act as a refuge for the consumer, enabling them to escape from starvation. This mechanism is very different from our representation of metabolic adjustment because metabolic adjustment is an energy budget optimisation process whereas the production of resting eggs forms a kind of seed bank maintaining a high biodiversity (Jones and Lennon, 2010). This difference is emphasised by our divergent results. In fact, Nakazawa et al. (2011) found that the production of resting eggs leads to more stable population dynamics as it responds more to seasonality than to non-seasonal variation in resource availability (in this case the effect of resting eggs is weak). Metabolic adjustment (*i.e.* response to resource availability) in food webs deeply changes the outcome of the model. In fact, adjustable metabolic rates greatly increase stability regarding many criteria: they increase the average biomass of top trophic levels, decrease the variability in population biomass density and increase the minima of population biomass density, keeping them away from the extinction threshold. Including metabolic adjustment in food web models improves the representation of a highly diverse group of organisms whose metabolic activity is not predicted by the metabolic theory 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; Marshall et al., 2011; Magozzi and Calosi, 2015) and must be disentangled from variability across the individuals of a population. 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 directly affected by the adjustable metabolic rate. Integrating metabolic adjustment in other food web models is also essential to test for the reproducibility of our results across different food web modelling frameworks. 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, adjustable metabolic rates holds great potential to represent the biology of many species in natural communities as the metabolic rate plays a central role in describing species biological functions. Hence, more experimental and field studies are necessary to better quantify metabolic rate dynamics while former studies generally focused on measuring resting or active metabolic rate. Integrated with our modelling approach, this will provide a deepened mechanistic understanding of how adjustable metabolic rates drive population and community dynamics and eventually food-web stability.

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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)).

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Metabolic adjustment enhances food web stability

Appendix oik-05422

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A Supplementary material: Complementary results

Effects of metabolic adjustment and carrying capacity on biomass extrema

Here are presented the minima from diagrams of bifurcation. Log transformations of minima presented in Fig.1 and 2 are used to show how the risk of extinction (i.e. having a biomass density close to zero) is affected by the carrying capacity K and the metabolic adjustment coefficient X .

Fig.A1a shows the minimal values of the diagrams of bifurcation presented in Fig.1 for different values of the metabolic adjustment coefficient X (represented by the color scale). In the null model ($X = 0$) coloured in light blue, the minimal values of biomass density of the primary producer and the carnivore tend to be much higher than for herbivore. Then adding an adjustable behaviour to the metabolic rates of the herbivore and the carnivore (darker curves in Fig.A1a) increases the minima of the herbivore while it decreases the minima of the primary producer and of the carnivore. Increasing the value of the metabolic adjustment coefficient X decreases the minima of the primary producer and of the herbivore while it increases the minima of the carnivore.

Fig.A1b shows the minimal values of the diagrams of bifurcation presented in Fig.2 for different values of carrying capacity K (represented by the colour scale). The null model ($X = 0$) is represented by the first points at the origin of the x-axis. For the herbivore and the carnivore, increasing metabolic adjustment coefficient X rises up minima, whatever the value taken by the carrying capacity K . But for the primary producer, the effect depends on the carrying capacity: at low carrying capacity, minima first sharply decrease, then increase and finally decrease with increasing carrying capacity.

This representation of minima gives us a more accurate insight of the stability of the system. In fact, a population with oscillating biomass densities is assumed to be more stable if the minima biomass densities stay far from zero. Here, metabolic adjustment only improves the stability of the herbivore and of the carnivore. We also notice that in food chains with metabolic adjustment, increasing resources availability rises up biomass

density minima and thus partially counters effects of "paradox of enrichment".

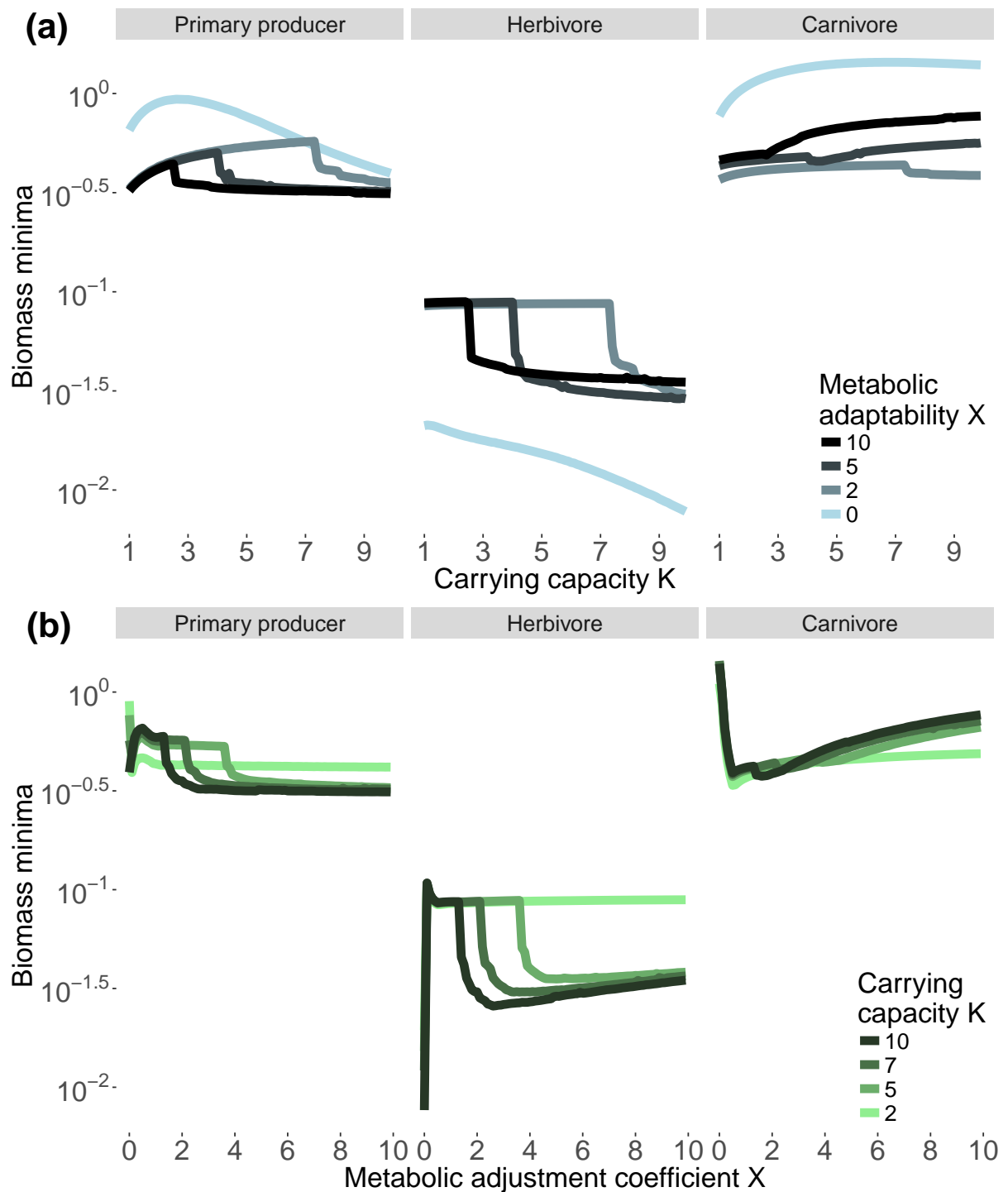


Figure A1: (a) Log transformation of minimum values taken by biomass densities in the tri-trophic food chain presented in Fig.1. The colour scale represents different values of metabolic adjustment coefficient X . (b) Log transformation of minimum values taken by biomass densities in the tri-trophic food chain presented in Fig.2. The colour scale represents different values of carrying capacity K .

Simple predator-prey system

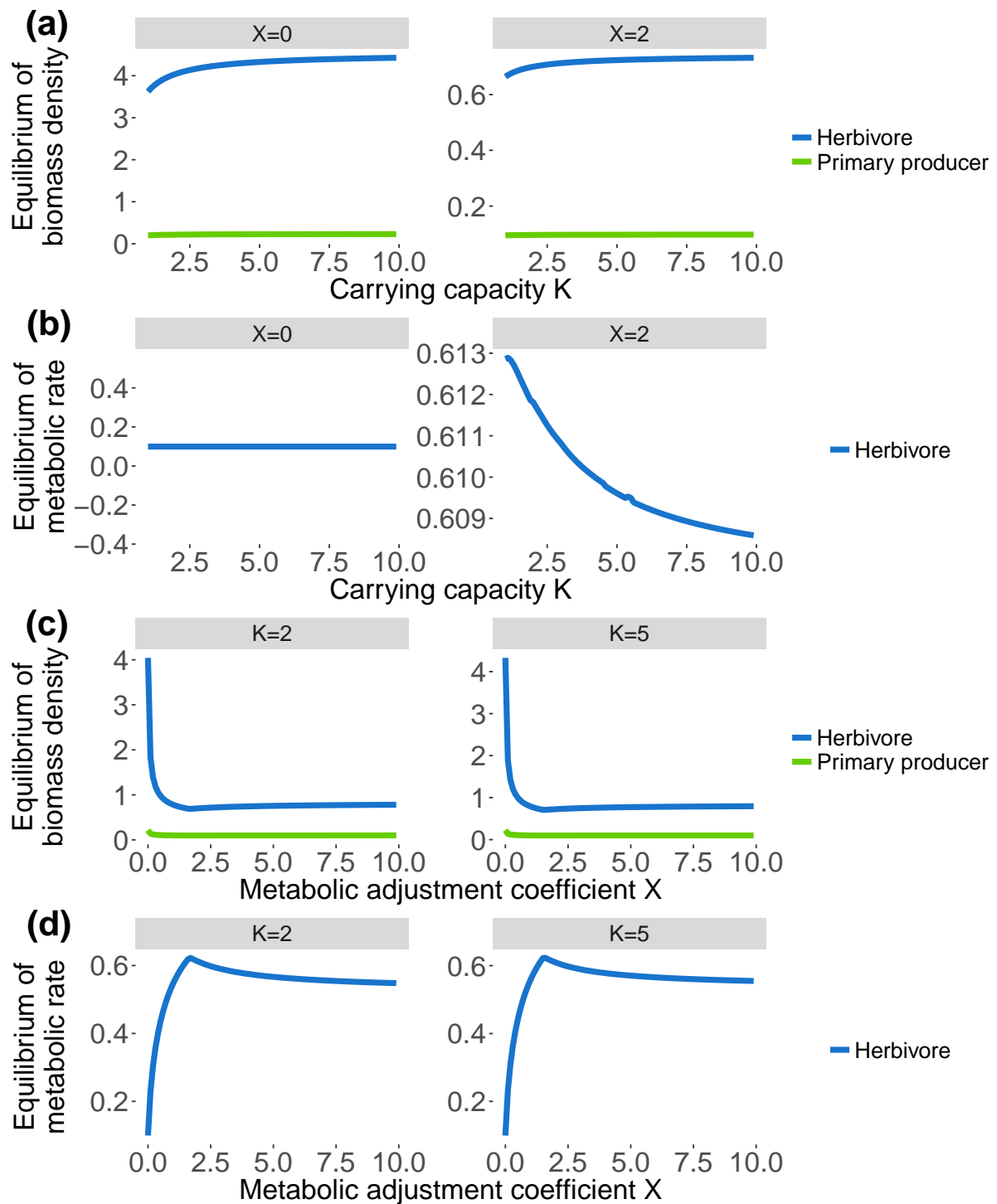


Figure A2: Predator-prey dynamics in a two species food chain. **(a)** Bifurcation diagrams of biomass and **(b)** metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 0$ and $X = 2$. **(c)** Bifurcation diagrams of biomass density and **(d)** metabolic rate along a metabolic adjustment gradient for a carrying capacity $K = 2$ and $K = 5$. The two species are a primary producer (green) and a herbivore (blue).

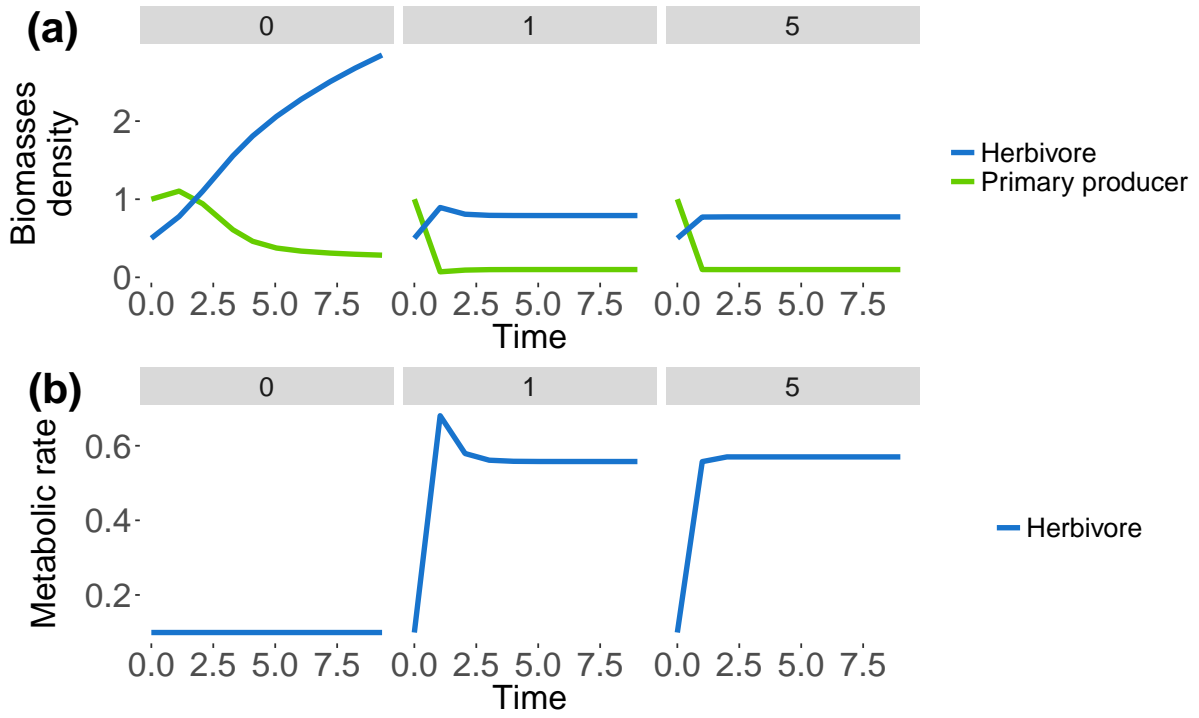


Figure A3: Predator-prey dynamics in a two species food chain. (a) Biomass densities and (b) metabolic rate dynamics for a metabolic adjustment coefficient $X = 0$ and $X = 2$ (carrying capacity $K = 5$). The two species are a primary producer (green) and a herbivore (blue).

No oscillations are observed in the predator-prey system containing a primary producer and a herbivore. The herbivore biomass is higher without metabolic adjustment (Fig.A2a) because the metabolic rate is higher with metabolic adjustment (Fig.A2b). This leads to higher loss of biomass and thus a reduced biomass stock at equilibrium. Increasing the carrying capacity weakly affects the biomass stock and the metabolic rate of the herbivore. Increasing the metabolic adjustment coefficient X strongly decreases the biomass of the herbivore whatever the value of the carrying capacity (Fig.A2c). This decrease is due to the increase of the metabolic rate with the carrying capacity (Fig.A2d). The decrease of the biomass of the herbivore at equilibrium in systems with metabolic adjustment is due to the increase of the metabolic rate (Fig.A3a and b). Metabolic adjustment maximises the growth rate and the system quickly reach its equilibrium: primary producer biomass decreases quickly and the herbivore cannot accumulate biomass (Fig.A3a). At last, the two species food chain only has fixed points while the tri-trophic food chain is oscillating at steady state in the same parameter space.

Lyapunov exponents of the food chain

The calculation of the Lyapunov spectrum is performed according to the method described by Wolf et al. (1985) and Ramasubramanian and Sriram (2000) (originally developed by Shimada and Nagashima (1979) and Benettin et al. (1980) independently). The ODE system comprises the non linear equations of the three-trophic food chain (equations 7a-e describing the dynamics of species biomasses B_i and their metabolic rates x_i) and the linearised equations defined by the matrix product $J.X$, where J is the Jacobian matrix (the elements j_{ij} defined in the equations 8a-y) and X the tangent vectors. The maximum Lyapunov exponent corresponding to the three-trophic food chain, whose diagram of bifurcations are drawn in Fig.1 and 2, is given in Fig.A4. The value of the maximum

Lyapunov exponent is very close to zero ($\sim 10^{-4}$) and the system can be considered as non chaotic.

$$\frac{dB_1}{dt} = r\left(\frac{K - B_1}{K}\right)B_1 - \frac{x_2yB_1B_2}{e_2(B_0 + cB_2B_0 + B_1)} \quad (7a)$$

$$\frac{dB_2}{dt} = -x_2B_2 + \frac{x_2yB_1B_2}{B_0 + cB_2B_0 + B_1} - \frac{x_3yB_2B_3}{e_3(B_0 + cB_3B_0 + B_2)} \quad (7b)$$

$$\frac{dB_3}{dt} = -x_3B_3 + \frac{x_3yB_2B_3}{B_0 + cB_3B_0 + B_2} \quad (7c)$$

$$\frac{dx_2}{dt} = x_2X\left(-1 + \frac{yB_1}{B_0 + cB_2B_0 + B_1}\right) \quad (7d)$$

$$\frac{dx_3}{dt} = x_3X\left(-1 + \frac{yB_2}{B_0 + cB_3B_0 + B_2}\right) \quad (7e)$$

$$j_{11} = \frac{\partial^2 B_1}{\partial t \partial B_1} = r\left(\frac{K - 2B_1}{K}\right) - \frac{x_2yB_2B_0(1 + cB_2)}{e_2(B_0 + cB_2B_0 + B_1)^2} \quad (8a)$$

$$j_{12} = \frac{\partial^2 B_1}{\partial t \partial B_2} = -\frac{x_2yB_1(B_0 + B_1)}{e_2(B_0 + cB_2B_0 + B_1)^2} \quad (8b)$$

$$j_{13} = \frac{\partial^2 B_1}{\partial t \partial B_3} = 0 \quad (8c)$$

$$j_{14} = \frac{\partial^2 B_1}{\partial t \partial x_2} = -\frac{yB_1B_2}{e_2(B_0 + cB_2B_0 + B_1)} \quad (8d)$$

$$j_{15} = \frac{\partial^2 B_1}{\partial t \partial x_3} = 0 \quad (8e)$$

$$j_{21} = \frac{\partial^2 B_2}{\partial t \partial B_1} = \frac{x_2yB_2B_0(1 + cB_2)}{(B_0 + cB_2B_0 + B_1)^2} \quad (8f)$$

$$j_{22} = \frac{\partial^2 B_2}{\partial t \partial B_2} = -x_2 + \frac{x_2yB_1(B_0 + B_1)}{(B_0 + cB_2B_0 + B_1)^2} - \frac{x_3yB_3B_0(1 + cB_3)}{e_3(B_0 + cB_3B_0 + B_2)^2} \quad (8g)$$

$$j_{23} = \frac{\partial^2 B_2}{\partial t \partial B_3} = -\frac{x_3yB_2(B_0 + B_2)}{e_3(B_0 + cB_3B_0 + B_2)^2} \quad (8h)$$

$$j_{24} = \frac{\partial^2 B_2}{\partial t \partial x_2} = -B_2 + \frac{yB_1B_2}{B_0 + cB_2B_0 + B_1} \quad (8i)$$

$$j_{25} = \frac{\partial^2 B_2}{\partial t \partial x_3} = -\frac{yB_2B_3}{e_3(B_0 + cB_3B_0 + B_2)} \quad (8j)$$

$$j_{31} = \frac{\partial^2 B_3}{\partial t \partial B_1} = 0 \quad (8k)$$

$$j_{32} = \frac{\partial^2 B_3}{\partial t \partial B_2} = \frac{x_3yB_3B_0(1 + cB_3)}{(B_0 + cB_3B_0 + B_2)^2} \quad (8l)$$

$$j_{33} = \frac{\partial^2 B_3}{\partial t \partial B_3} = -x_3 + \frac{x_3yB_2(B_0 + B_2)}{(B_0 + cB_3B_0 + B_2)^2} \quad (8m)$$

$$j_{34} = \frac{\partial^2 B_3}{\partial t \partial x_2} = 0 \quad (8n)$$

$$j_{35} = \frac{\partial^2 B_3}{\partial t \partial x_3} = -B_3 + \frac{yB_2B_3}{B_0 + cB_3B_0 + B_2} \quad (8o)$$

$$j_{41} = \frac{\partial^2 x_2}{\partial t \partial B_1} = \frac{x_2 X y B_0 (1 + c B_2)}{(B_0 + c B_2 B_0 + B_1)^2} \quad (8p)$$

$$j_{42} = \frac{\partial^2 x_2}{\partial t \partial B_2} = -\frac{x_2 X y B_1 c B_0}{(B_0 + c B_2 B_0 + B_1)^2} \quad (8q)$$

$$j_{43} = \frac{\partial^2 x_2}{\partial t \partial B_3} = 0 \quad (8r)$$

$$j_{44} = \frac{\partial^2 x_2}{\partial t \partial x_2} = X \left(-1 + \frac{y B_1}{B_0 + c B_2 B_0 + B_1} \right) \quad (8s)$$

$$j_{45} = \frac{\partial^2 x_2}{\partial t \partial x_3} = 0 \quad (8t)$$

$$j_{51} = \frac{\partial^2 x_2}{\partial t \partial B_1} = 0 \quad (8u)$$

$$j_{52} = \frac{\partial^2 x_2}{\partial t \partial B_2} = \frac{x_3 X y B_0 (1 + c B_3)}{(B_0 + c B_3 B_0 + B_2)^2} \quad (8v)$$

$$j_{53} = \frac{\partial^2 x_2}{\partial t \partial B_3} = -\frac{x_3 X y B_2 c B_0}{(B_0 + c B_3 B_0 + B_2)^2} \quad (8w)$$

$$j_{54} = \frac{\partial^2 x_2}{\partial t \partial x_2} = 0 \quad (8x)$$

$$j_{55} = \frac{\partial^2 x_2}{\partial t \partial x_3} = X \left(-1 + \frac{y B_2}{B_0 + c B_3 B_0 + B_2} \right) \quad (8y)$$

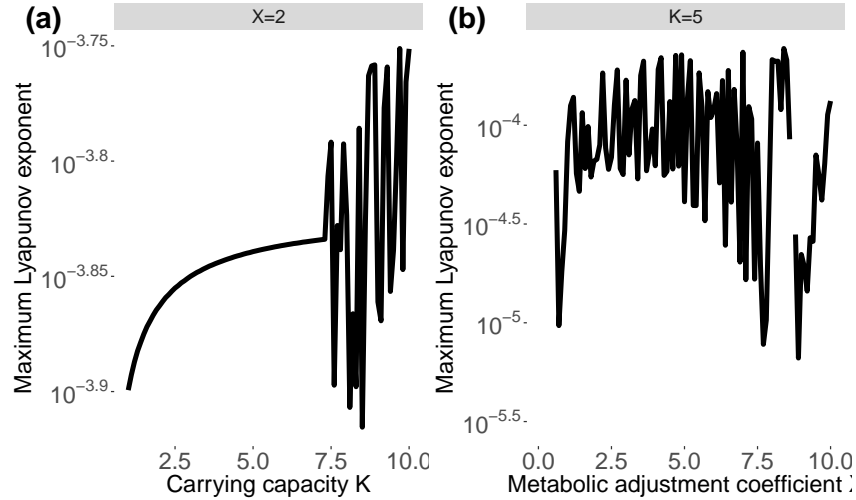


Figure A4: Maximum Lyapunov exponent of the tri-trophic food chain **(a)** along a carrying capacity gradient for $X = 2$ and **(b)** along a metabolic adjustment coefficient gradient for $K = 5$.

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B Supplementary material: Sensitivity analysis

Predator-prey interactions

Complex food webs

Increasing the half saturation density B_0 increases species persistence at low carrying capacity K and low metabolic adjustment X in particular (Fig.B1a). A very low value of B_0 leads to a low species persistence for all combinations of K and X , and species persistence becomes insensitive to enrichment (*i.e.* increase of K). At low half saturation density B_0 , consumers can strongly exploit their prey even if their density is low, leading to an increased risk of overexploitation and extinction. At higher B_0 , the consumption rate of prey is lower when their density is higher. Thus, increasing B_0 and X decreases the risk of overexploitation and promotes species persistence. Whatever the value of B_0 , we always observe an increase of species persistence when metabolic adjustment X increases, thus the stabilising effect of metabolic adjustment on food web is robust to variations of B_0 .

Predator interference c has only slight effect (Fig.B1b). There is only an increased species persistence in food webs without metabolic adjustment as seen in Rall et al. (2008). Our results are then not sensitive to predator interference at all.

Type III functional response leads to extremely stable food webs and increasing carrying capacity K weakly increases persistence only at low metabolic adjustment X (Fig.B1c). As in Rall et al. (2008), species persistence reaches a plateau when K increases, the paradox of enrichment is not visible. Increasing metabolic adjustment X strongly increases species persistence whatever the value of the carrying capacity K . Thus, the stabilising effect of metabolic adjustment exists whatever the functional response type but it is less robust at higher carrying capacity K due to the paradox of enrichment.

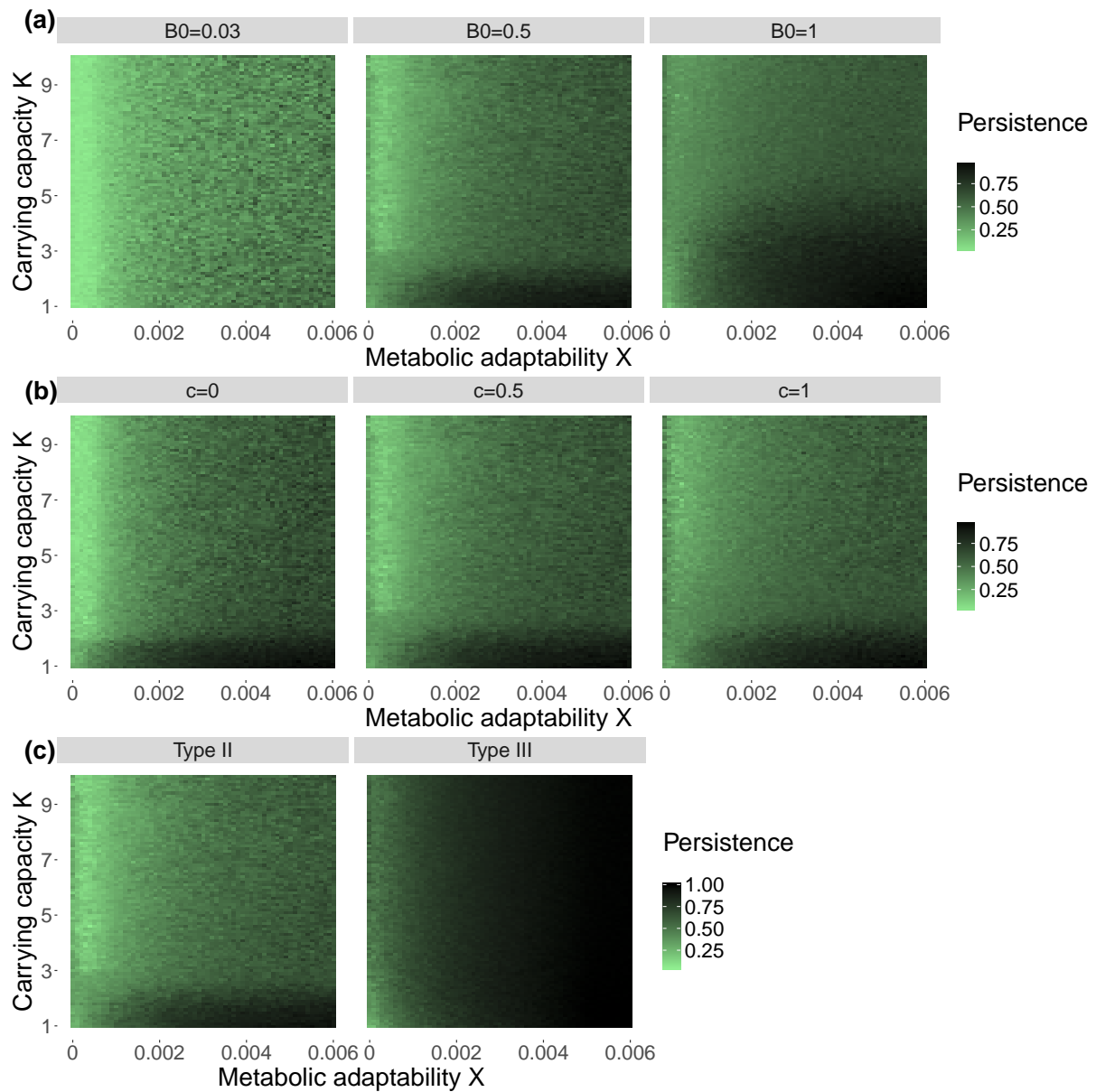


Figure B1: Effects of the predator-prey interaction parameters on species persistence in complex food webs for different values of metabolic adjustment coefficient X and carrying capacity K . Effect of (a) half saturation density B_0 , (b) predator interference c and (c) functional response type. Each square represents the average persistence in 100 simulated food webs.

Tri-trophic food chains

The dynamics in the tri-trophic food chain are highly sensitive to the half saturation density B_0 (Fig.B2). In a tri-trophic food chain with metabolic adjustment ($X=2$), $B_0 = 0.03$ drives consumers to extinction, $B_0 = 0.5$ (value used in the main study) enables the coexistence of the three species with oscillation of species biomasses at higher carrying capacity K while $B_0 = 1$ leads to fixed points for the three species (Fig.B2a). Increasing the metabolic adjustment coefficient X leads to the survival of all species for the three values of B_0 (Fig.B2c). Increasing B_0 decreases the amplitude of species biomass oscillations and even leads to fixed points. The metabolic rate of the carnivore responses similarly and the metabolic rate of herbivore is always equal to its maximum possible value (Fig.B2b and B2D). The results are sensitive to B_0 but increasing the metabolic adjustment always stabilises the biomass dynamics by promoting survival and by reducing the amplitude of biomass oscillations.

Predator interference c has similar effects on dynamics. Increasing c stabilises species biomass dynamics along the enrichment gradient (Fig.B3a) and metabolic adjustment coefficient gradient (Fig.B3c) by reducing the amplitude of biomass oscillations and promoting fixed points. The same response is observed for the metabolic rates (Fig.B3b and B3D) and the herbivore has always its metabolic rate equal to its maximum possible value. Such a stabilising effect of predator interference confirms previous results (Skalski and Gilliam, 2001; Lang et al., 2012)

The type III functional response always leads to fixed points for biomasses and metabolic rates (Fig.B4). The herbivore has also its metabolic rate equal to its maximum possible value.

The half saturation density B_0 , the predator interference c and the functional response change the response of the tri-trophic food chain dynamics to metabolic adjustment. The dynamics observed in the main study are thus sensitive to these parameters. However, the stabilising effect of metabolic adjustment is always observed, thus the stabilising effect of metabolic adjustment is robust to these parameters.

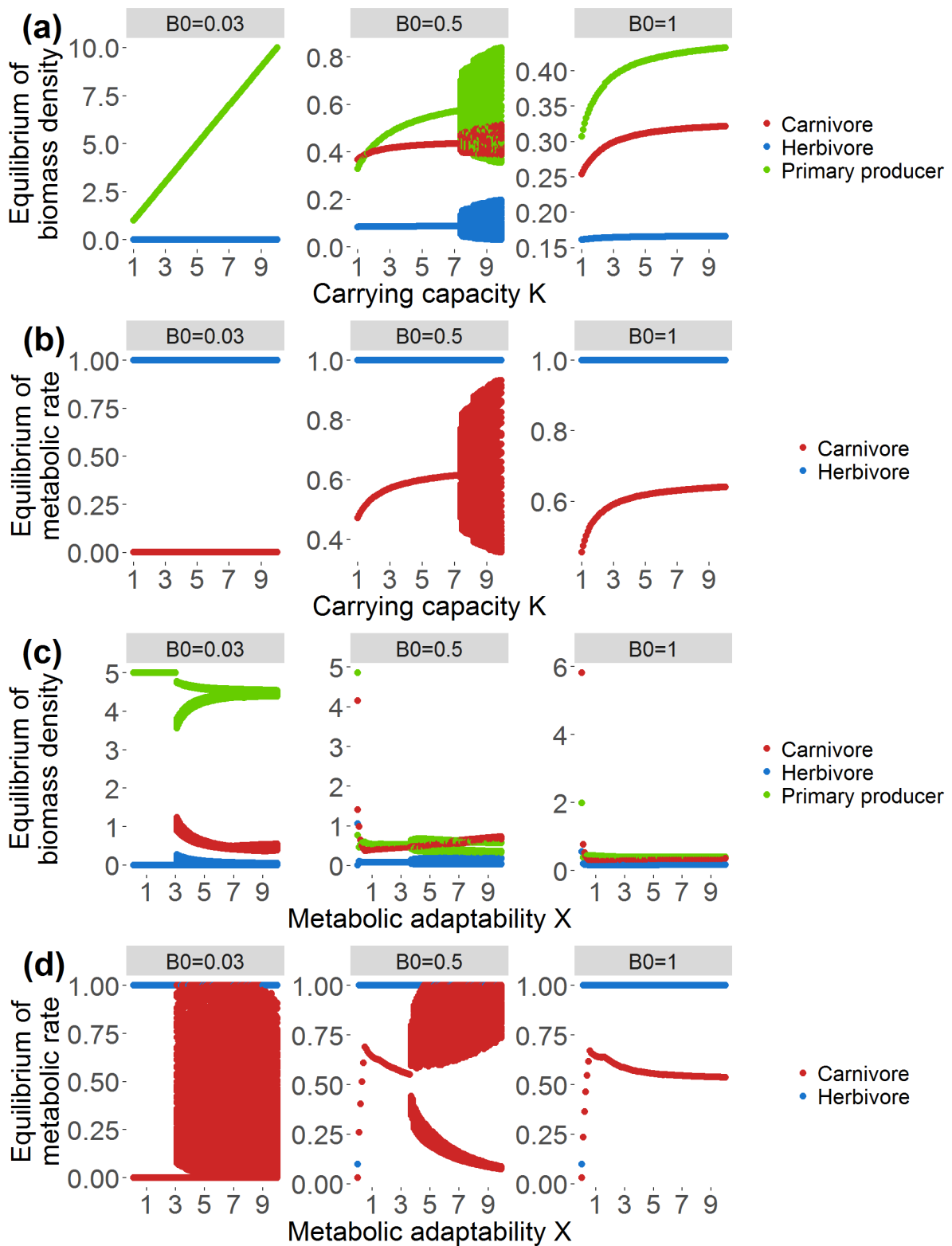


Figure B2: Effect of half saturation density B_0 on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

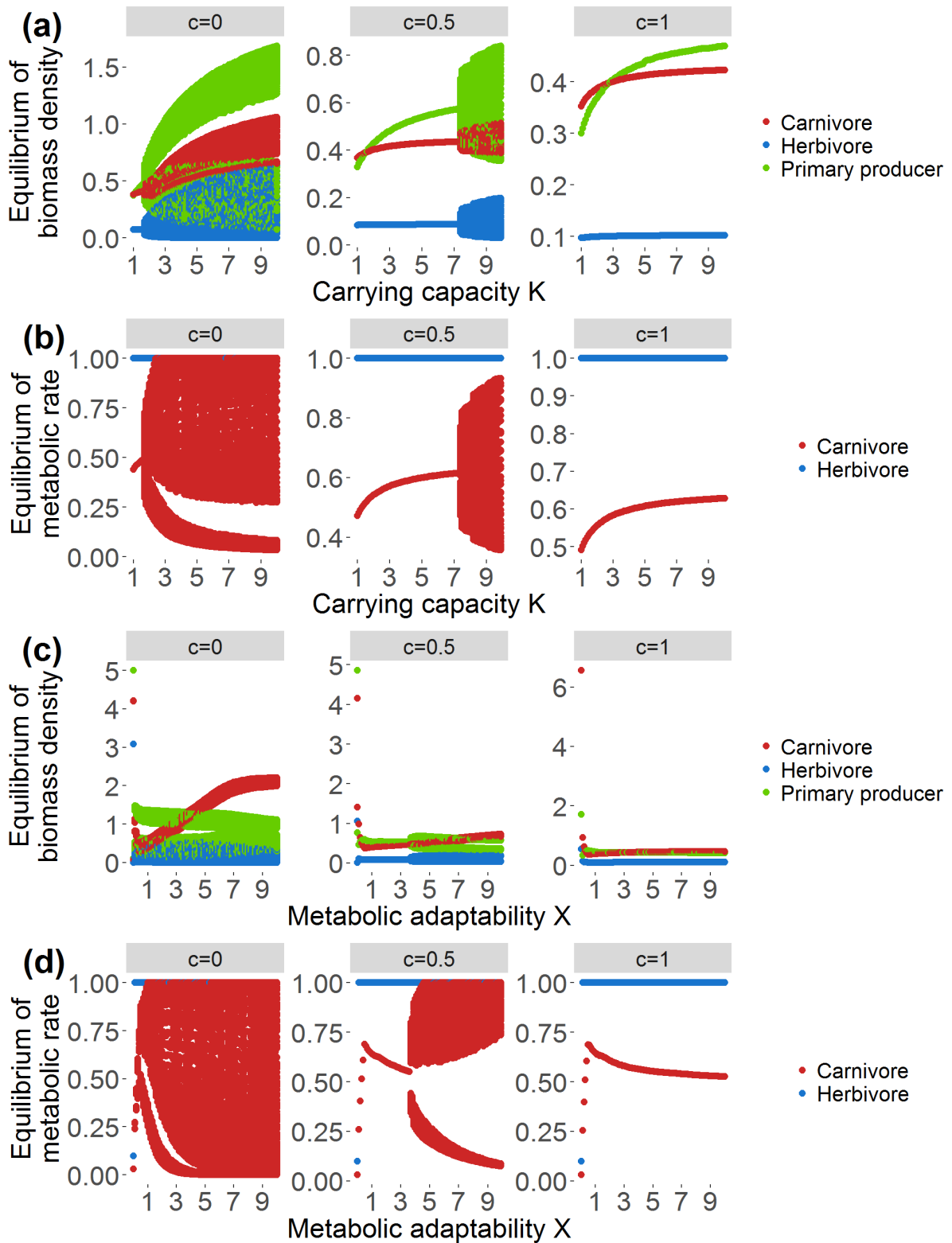


Figure B3: Effect of predator interference c on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

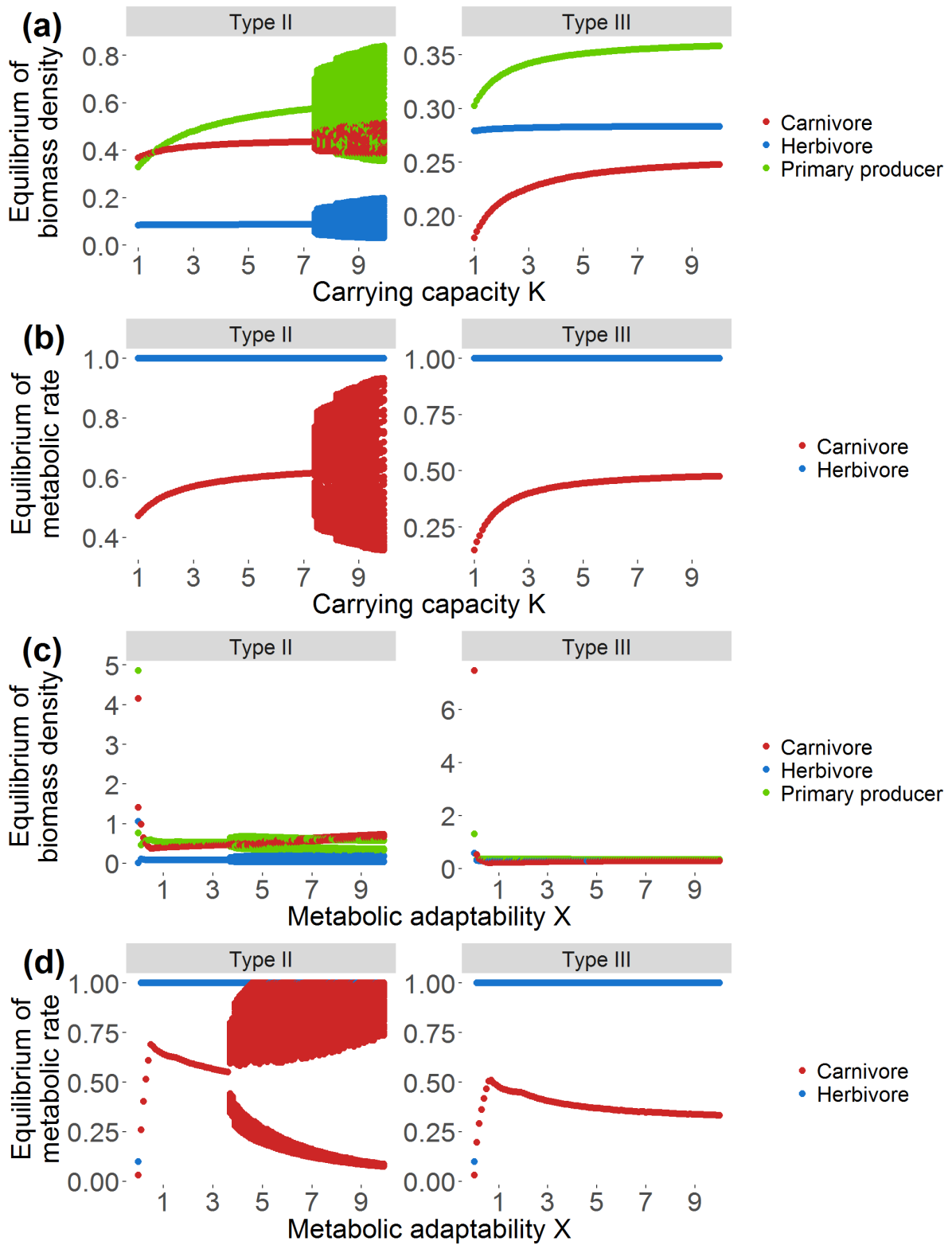


Figure B4: Effect of the functional response type on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

Metabolic rate boundaries

Minimum and maximum of metabolic rate

The boundaries of the metabolic rate were chosen to include the values predicted by the MTE (Fig.B5). We tested metabolic intervals ranging over four orders of magnitude to be consistent with Makarieva et al. (2005). Changing the lower limits of metabolic rates does not affect species persistence in complex food webs (Fig.B6) and species biomass or metabolic rate dynamics in tri-trophic food chains (Fig.B7). Changing the upper limit does not affect species persistence in complex food webs (Fig.B6) but it can lead to the extinction of the carnivore in tri-trophic food chains (Fig.B8). Thus, to ensure species survival, we set the lower limit at $x_{min} = 0.001$ and the upper limit at $x_{max} = 1$ for simulations.

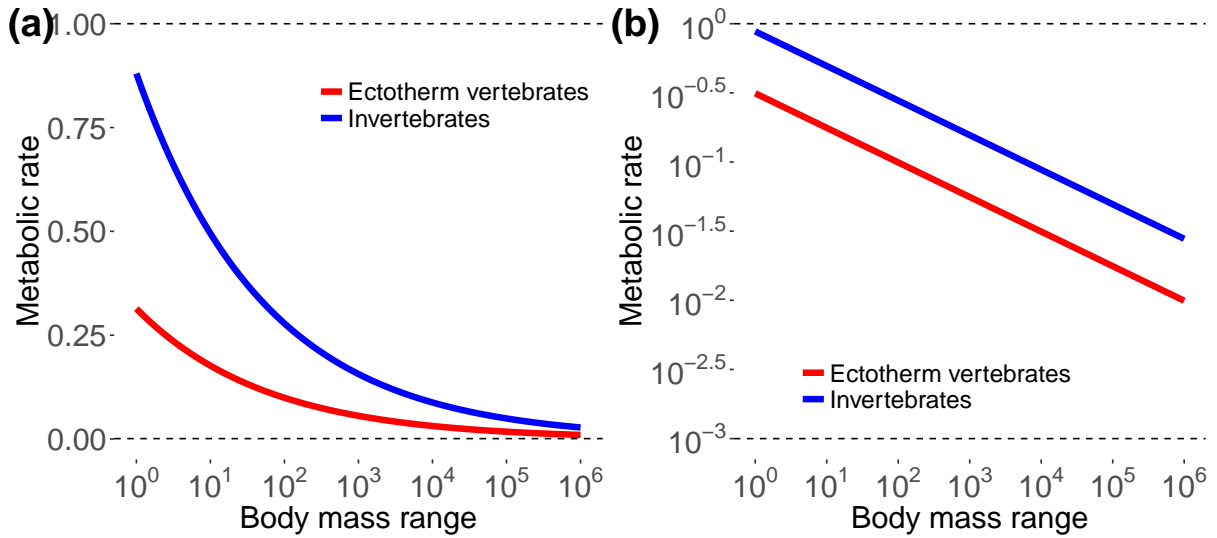


Figure B5: Normalised values of metabolic rates predicted by the MTE. Metabolic rates are calculated for invertebrates (blue) and ectotherm vertebrates (red) whose body mass ranges over six orders of magnitude. The values are represented in linear (a) and log scales (b).

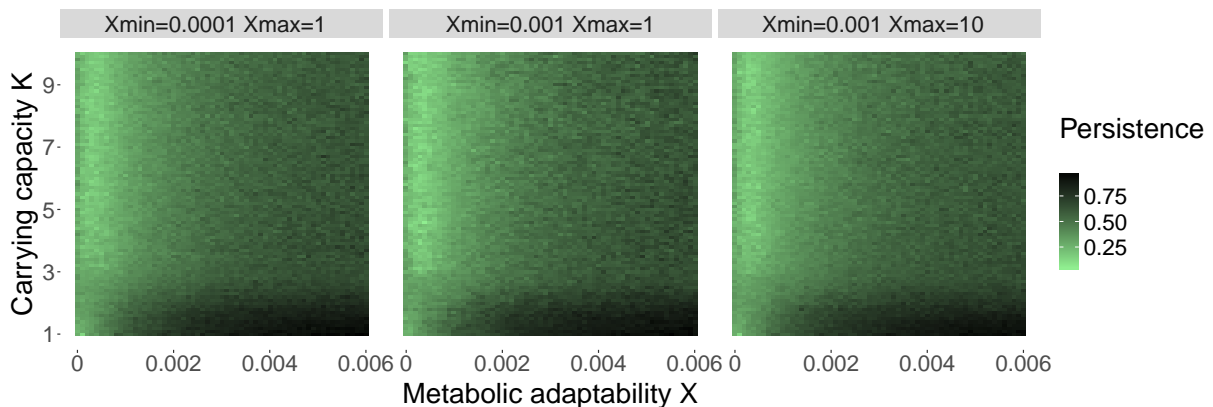


Figure B6: Effect of metabolic rate boundaries on species persistence for different values of metabolic adjustment coefficient X and carrying capacity K . Each square represents the average species persistence in 100 simulated food webs.

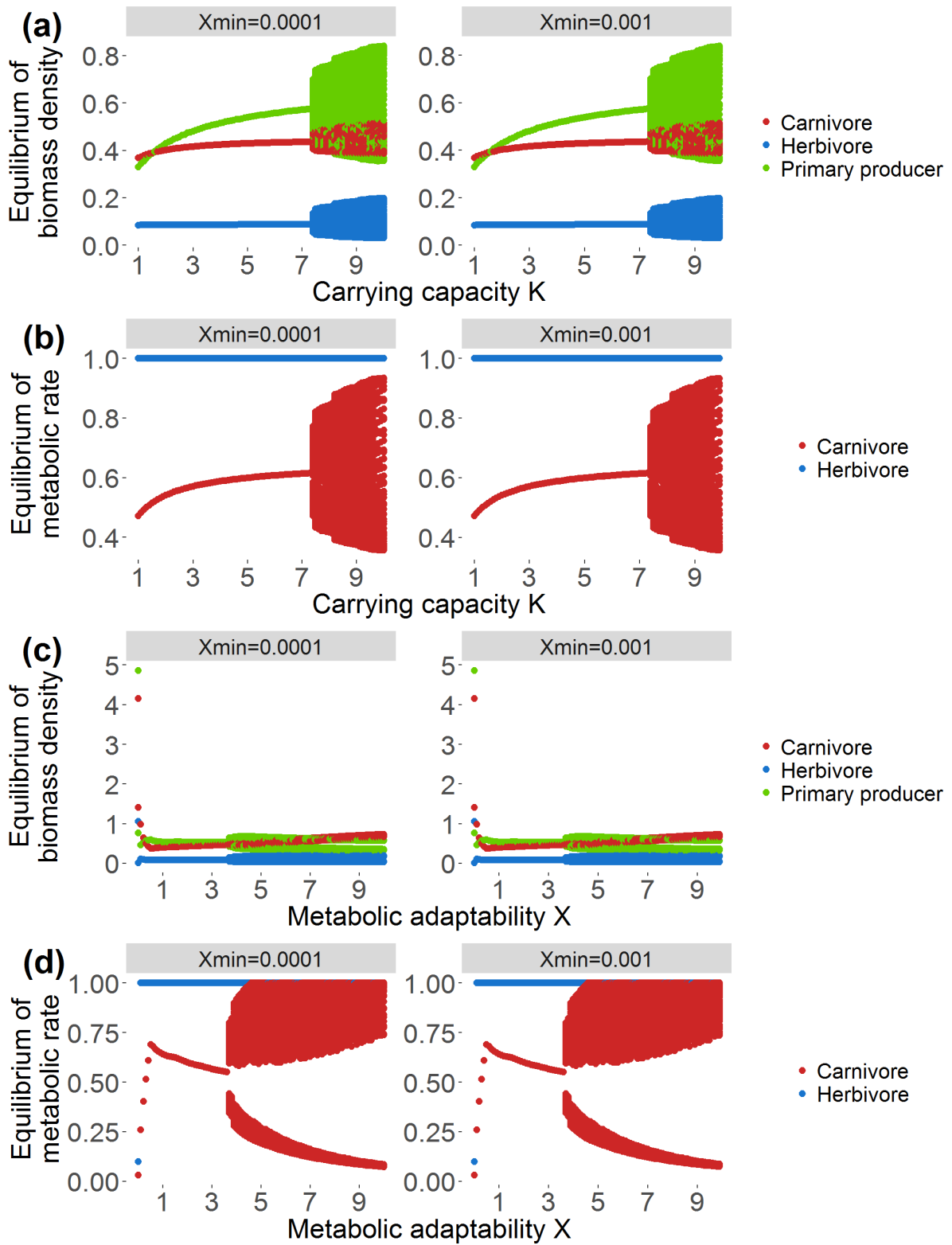


Figure B7: Effect of the lower limit of the metabolic rate in tri-trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

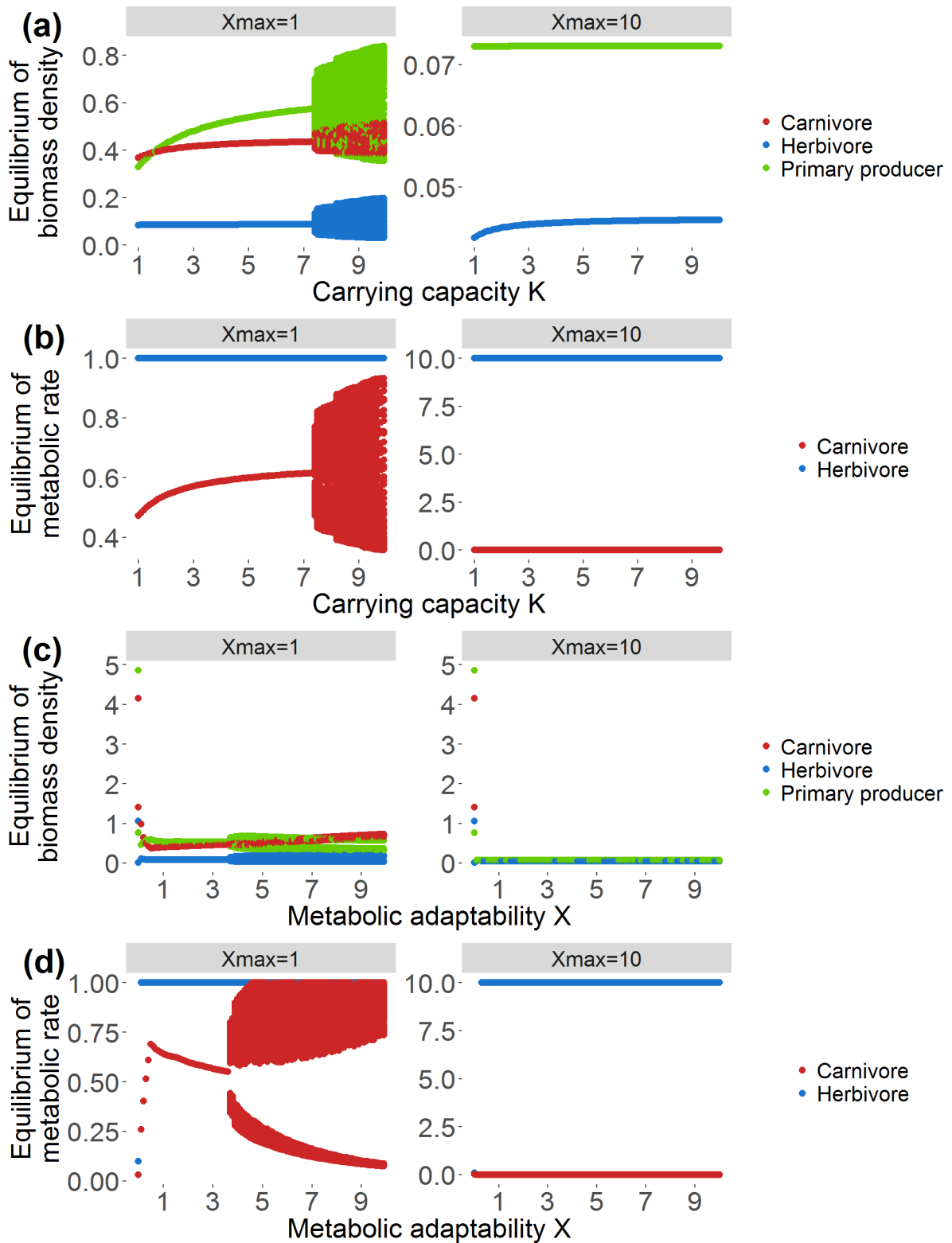


Figure B8: Effect of the upper limit of the metabolic rate in tri-trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

Amplitude of metabolic rate variations

We also varied the maximal amplitude of the variations of metabolic rates. As the values predicted by the MTE range over two orders of magnitude (Fig.B5), the intervals of one and two orders of magnitudes were log centred on the values predicted by the MTE (the interval is also bounded by the absolute limits). Thus, the metabolic rates vary in intervals consistent with the values predicted by the MTE (see Fig.B9).

We observe a poor persistence over all the values of metabolic adjustment coefficient X and carrying capacity K in food webs where metabolic rates vary in one or two order of magnitude (even if the interval is centred or not)(Fig.B10a,b and d) compared to the three order of magnitude interval used in the main study (Fig.B10c). This could be due to the impossibility of species to lower their metabolic rate low enough to balance their energy budget in periods of starvation. However, we see a better persistence in food webs with no centring of the interval of metabolic rate variations (Fig.B10d), probably because small species can decrease their metabolic rate at lower values. We also see that the improvement of species persistence only occur at high values of metabolic adaptability coefficient X , then a higher speed of adjustment may be necessary to compensate the narrower interval of possible variations.

In the tri-trophic food chain (Fig.B11), we do not see strong oscillations when the interval of metabolic rate variations is centred. The food chain with a two orders of magnitude wide interval, that is not centred on the values predicted by the MTE, displays similar variations than in the food chain with a three orders of magnitude interval (Fig.2 and Fig.1). This is explained by the convergence of metabolic rates to constant values (Fig.B11b and d). However, we still see an increase of primary producer and carnivore biomasses with the carrying capacity (Fig.B11a and c).

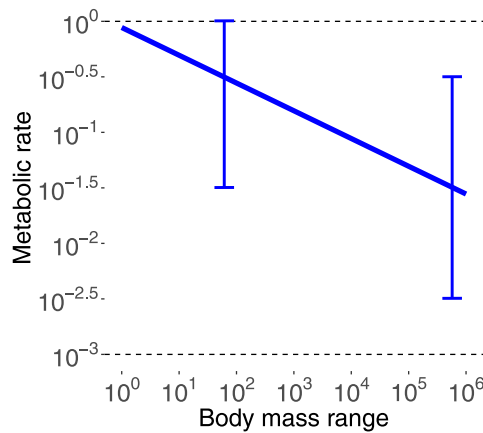


Figure B9: Example of the interval of variation of metabolic rates (blue vertical segments) centred on the values predicted by the MTE (blue line). Here metabolic rates vary in a two orders of magnitude wide interval but it is still bounded by absolute limits that are represented by the dotted lines.

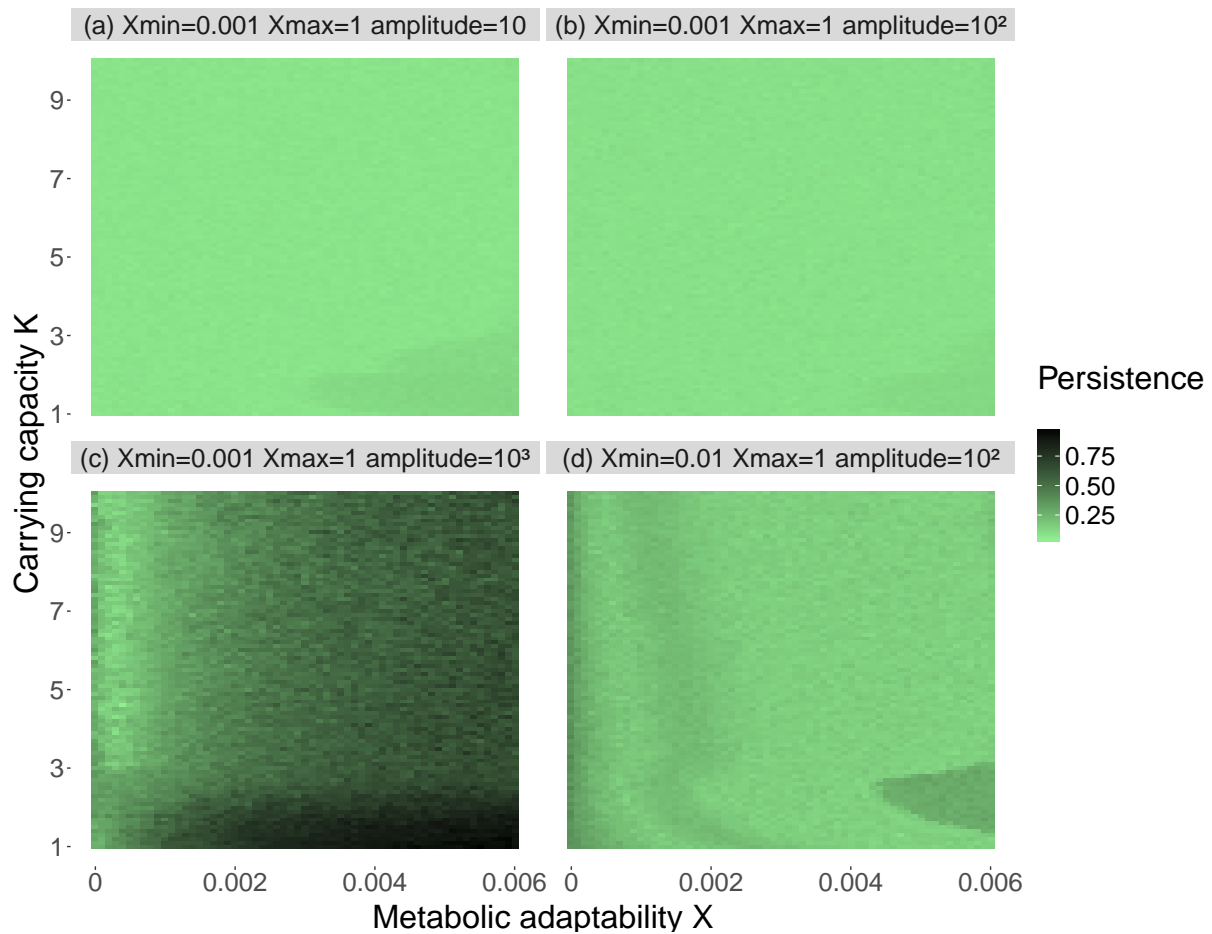


Figure B10: Effect of the amplitude of metabolic rates on species persistence for different values of metabolic adjustment coefficient X and carrying capacity K . **(a)** One order of magnitude interval of metabolic rate centred on the values predicted by the MTE. **(b)** Two orders of magnitude interval of metabolic rate centred on values predicted by the MTE. **(c)** Absolute interval used in the main study. **(d)** Two order of magnitude interval with absolute boundaries for all species (no centring of the interval). Each square represents the average species persistence of 100 simulated food webs.

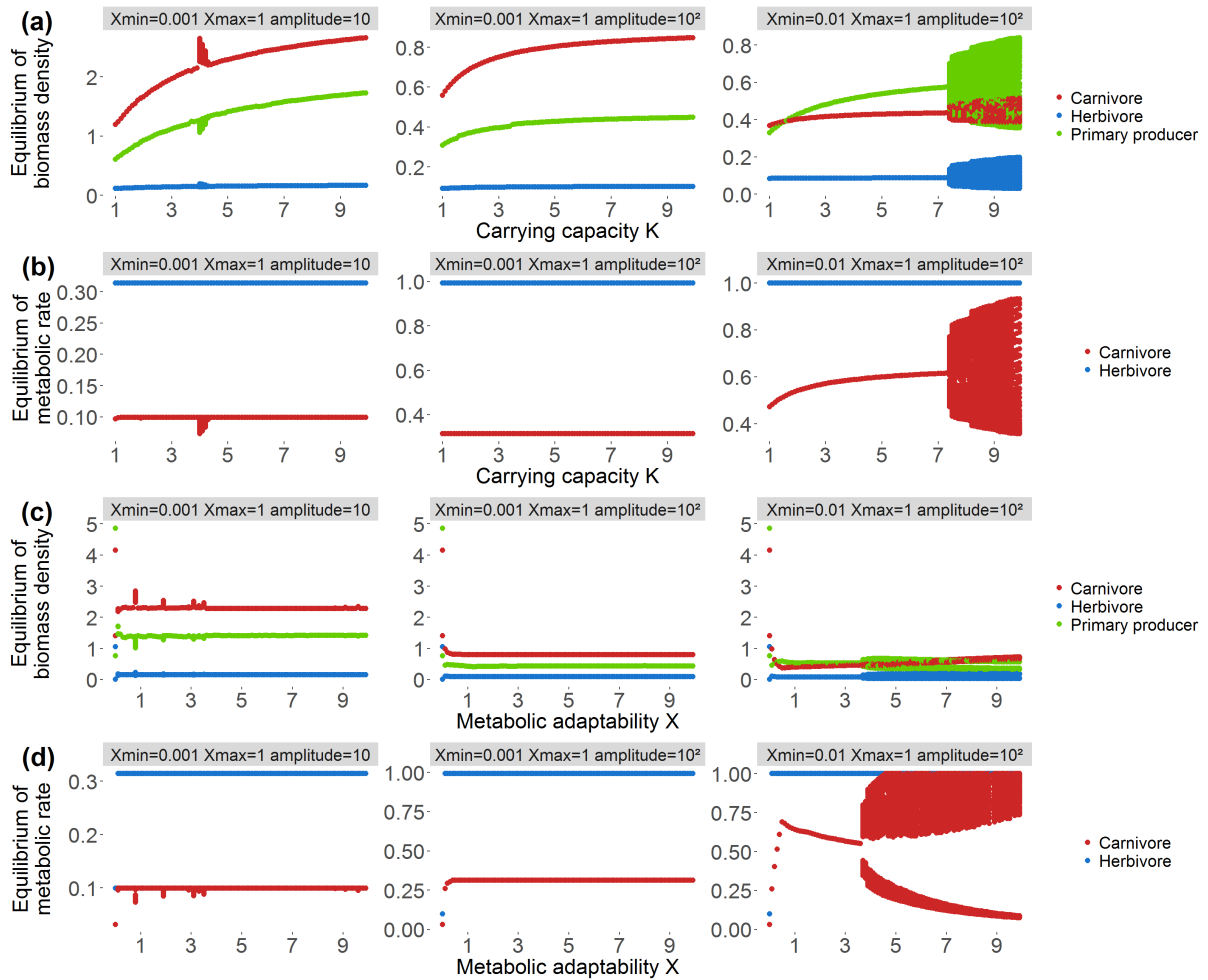


Figure B11: Effect of the amplitude of metabolic rates on tri-trophic food-chain dynamics. **(a)** Bifurcation diagrams of biomass and **(b)** metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. **(c)** Bifurcation diagrams of biomass density and **(d)** metabolic rate along gradient in metabolic adjustment for a carrying capacity $K = 5$. Each time, food chains with metabolic rates varying in intervals of respectively one and two orders of magnitude (centred on the value predicted by the MTE) and on two orders of magnitude not centred, are represented. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

Allometric scaling of biological rates

Metabolic type

Consumer organisms can be considered as ectotherm vertebrates ($a_x = 0.88$ and $y_i = 4$) or as invertebrates ($a_x = 0.314$ and $y_i = 8$) (Brose et al., 2006), thus changing the values of metabolic rates and ingestion rates. In our main study, we use values for invertebrates but we see a similar response of species persistence to the metabolic adjustment coefficient X and the carrying capacity K with ectotherm vertebrates parameters (Fig.B12a). The increase of species persistence is less sharp with the increase of the metabolic adjustment coefficient X (see Fig.B12b to see the response for higher values of X). Food webs are also less sensitive to enrichment and persistence stays high for higher values of the carrying capacities K . In spite of these differences, the overall response of species persistence remains unchanged.

However, species biomasses and metabolic rates are more stable with the ectotherm ver-

tebrates parameters (only fixed points and no oscillations) but the three species persist whatever the metabolic types (Fig.B13a and B13b). Increasing the metabolic adjustment coefficient X also increases the average biomass of the carnivore (Fig.B13c) and the metabolic rate of herbivore still has its maximum possible value (Fig.B13b and B13d). Whatever the metabolic type we always observe a stabilising effect of metabolic adjustment on food webs by increasing species persistence and by reducing the amplitude of species biomass oscillations compared to food chains without metabolic adjustment.

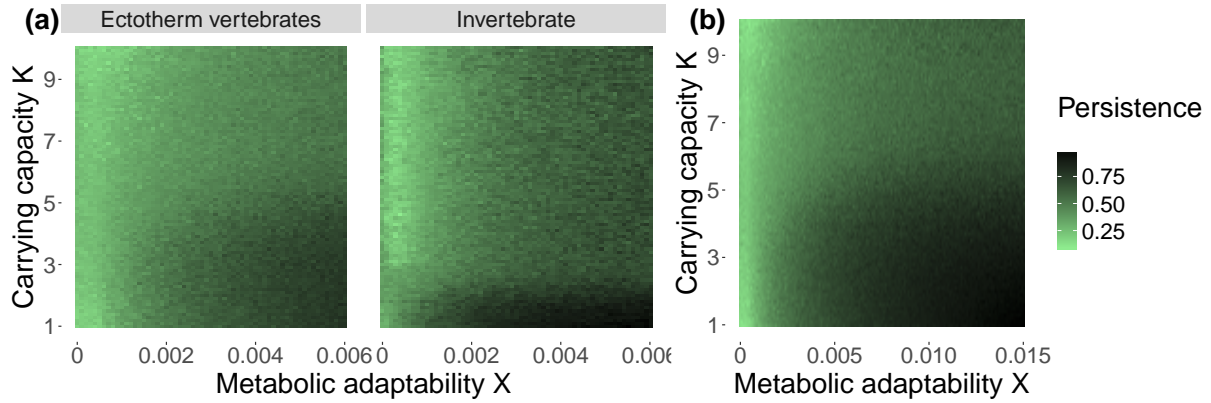


Figure B12: Effect of the metabolic type of consumers ($y_i = 4$ for ectotherm vertebrates and $y_i = 8$ for invertebrates) on (a) species persistence for different values of metabolic adjustment coefficient X and carrying capacity K and (b) for an extended range of values of metabolic adjustment X . Each square represents the average persistence of 100 simulated food webs.

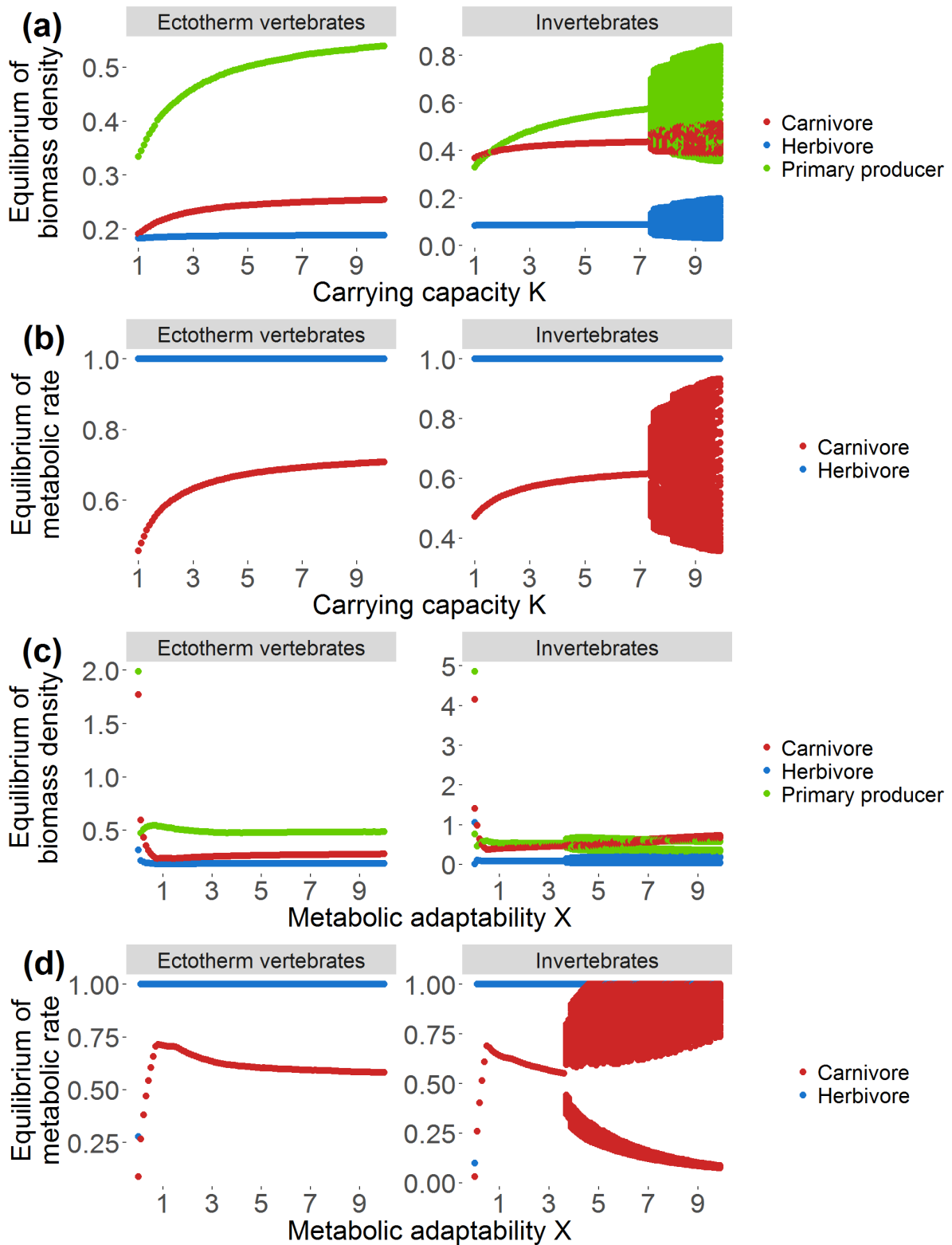


Figure B13: Effect of the metabolic type of consumers ($y_i = 4$ for ectotherm vertebrates and $y_i = 8$ for invertebrates) on three trophic food-chain dynamics. (a) Bifurcation diagrams of biomass and (b) metabolic rate along an enrichment gradient for a metabolic adjustment coefficient $X = 2$. (c) Bifurcation diagrams of biomass density and (d) metabolic rate along a gradient in metabolic adjustment for a carrying capacity $K = 5$. The three species are a primary producer (green), a herbivore (blue) and a carnivore (red).

Deviation from the quarter power law

The Allometric Trophic Network (ATN) model (Brose et al., 2006) was chosen to conduct this study because of the direct relationship between the maximum ingestion rate and the metabolic rate. y_i is constant because the metabolic rate and the maximum ingestion rate follow quarter power law of the body mass of consumers. However, Pawar et al. (2012) showed that the consumption rate allometric exponent depends on the dimensionality of consumers search space. Thus, we have a new expression of the standardised ingestion rate:

$$\frac{Y_C}{X_C} = \frac{a_y M_C^{s_y}}{a_x M_C^{s_x}} = \frac{a_y}{a_x} M_C^{s_y - s_x} = y_i M_C^{s_y - s_x} \quad (9)$$

With Y_C the ingestion rate of consumers, X_C the metabolic rate of consumers, a_y and a_x their allometric coefficients, s_y and s_x their allometric scaling exponents, and M_C the body mass of the consumer. $M_C^{s_y - s_x}$ corresponds to the deviation of the ingestion rate from the quarter power law and is estimated in Fig.B14b for 2D and 3D search spaces. $s_x = -0.25$, $s_y = -0.15$ in 2D and $s_y = 0.06$ in 3D search spaces.

Species persistence increases in 2D environment at low carrying capacity for ectotherm invertebrates but it decreases for invertebrates (Fig.B14a). In 3D environments species persistence is lower and the area of maximum persistence for low carrying capacity K is nearly absent. However, increasing the metabolic adjustment coefficient X increases species persistence for each metabolic type and each dimensionality. The stabilising effect of metabolic adjustment is preserved even if the ingestion rate is not a linear function of metabolic rate. The difference of species persistence can be due to the deviation from the quarter power law that strongly increases the ingestion rate for large consumers that have a 3D search space. Such a high consumption rate might promote prey overexploitation and thus leads to extinctions.

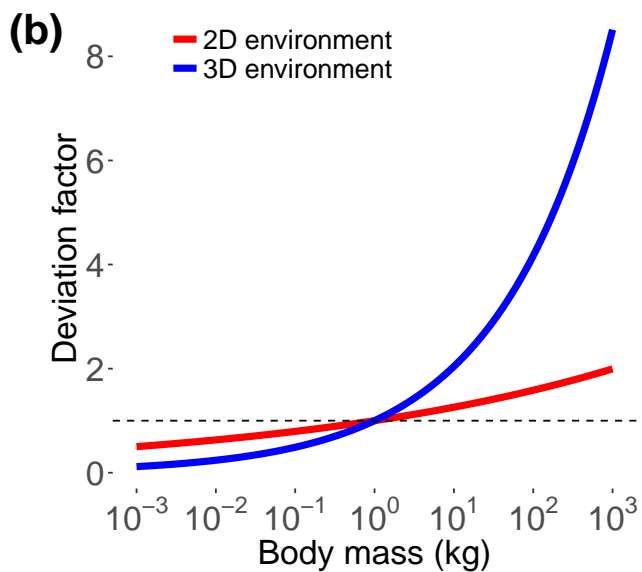
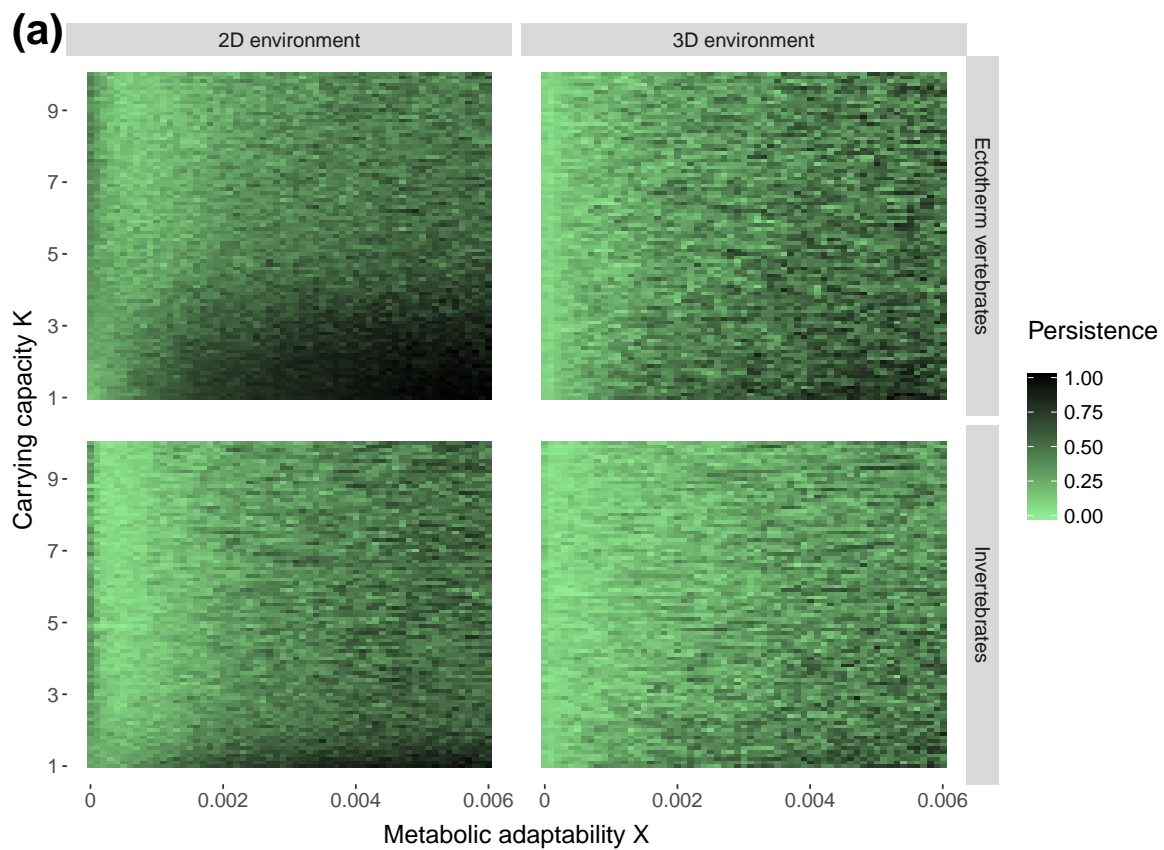


Figure B14: Sensitivity to deviations of allometric scaling of the maximal consumption rate from the quarter-power law. **(a)** Effect of metabolic type and space dimensionality on species persistence for different values of metabolic adjustment coefficient X and carrying capacity K . Each square represent the average persistence in 20 simulated food webs. **(b)** Deviation factor of the ingestion rate from the quarter power law along a gradient in species body mass in 2D (red) and 3D (blue) environments. The dashed line ($y_i = 1$) represents the non-deviation from the quarter-power law.

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