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Identifying conversion efficiency as a key mechanism underlying food webs adaptive evolution: A step forward, or backward?

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Abstract

Body size or mass is one of the main factors underlying food webs structure. A large number of evolutionary models have shown that indeed, the adaptive evolution of body size (or mass) can give rise to hierarchically organised trophic levels with complex between and within trophic interactions. However, these models generally make strong arbitrary assumptions on how traits evolve, casting doubts on their robustness. In particular, biomass conversion efficiency is always considered independent of the predator and prey size, which contradicts with the literature. In this paper, we propose a general model encompassing most previous models which allows to show that relaxing arbitrary assumptions gives rise to unrealistic food webs. We then show that considering biomass conversion efficiency dependent on species size is certainly key for food webs adaptive evolution because realistic food webs can evolve, making obsolete the need of arbitrary constraints on traits' evolution. We finally conclude that, on the one hand, ecologists should pay attention to how biomass flows into food webs in models. On the other hand, we question more generally the robustness of evolutionary models for the study of food webs.

Keywords: food webs models, trophic interactions, networks, community ecology, ecosystem, adaptive dynamics, biomass conversion efficiency, energy conversion efficiency, reproduction efficiency

1 Introduction

Predicting the response of ecological systems to global change through the evolution of individuals' traits, such as size and feeding rates, is a challenge for modern theoretical ecology (Brown et al., 2004; Woodward et al., 2005). This is especially urgent in the contexts of fisheries management when harvesting increases (Laugen et al., 2014), or for anticipating how agrosystems' communities would evolve in response to agricultural practices change (Loeuille et al., 2013).

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Roughly, two categories of models are developed to address these issues and study the properties of food webs. A first category deals with the stability of a given food web for a given number of interacting species described by dynamical systems (*e.g.* Brose et al., 2006; Otto et al., 2007; Allesina and Tang, 2012; Miele et al., 2019). These models often aim at addressing how a particular interaction affects the stability of a community or the productivity of an ecosystem. However, in these models, the species' features are supposed known and fixed. In other words, these models only consider ecological time scales and neglect evolution and adaptation. In the present paper, we focus on a second category of models which addresses how and why food web structure and topology emerge on evolutionary time scales, especially the ones which are variations of the seminal work by Loeuille and Loreau (2005). These models are inspired by the adaptive dynamics framework (Metz et al., 1996; Geritz et al., 1998), *i.e.* mutations affecting one or several traits (especially body size or mass, or other parameters associated with predation such as predation preference) are recurrently introduced into the community. The evolution of traits can lead to evolutionary branching, *i.e.* a new species appears into the community, which affects the whole ecosystem since new ecological interactions emerge.

Despite the common foundations of these models (Loeuille and Loreau, 2005), their assumptions consistently vary (see Appendix D for an extended review and Table 1 for a compilation). First, regarding how individuals interact: Cannibalism can be allowed or not; Predation can be ordered such that bigger species only feed on smaller ones; In addition to competition for resources, interference competition can occur or not; And functional responses can follow different functional forms (Holling Types I or II, Beddington-DeAngelis, etc.). Second, regarding traits' evolution: body size (or mass) can evolve jointly or not with a trait affecting predation interactions (*e.g.* niche width or prey size difference); Body size (or mass) is considered on a linear or a logarithmic scale, strongly affecting the size difference between prey and predators (in particular, assuming a linear scale limits the minimal size of prey); Traits evolution is generally constrained by strict boundaries assuming artificial minimal and maximal possible values; Mutation kernels and size: mutation size can be large or small, and the distribution of the mutational effects can differ between models, centred on the parental value or not; Finally, allometries are generally considered but they can or cannot affect different processes: birth, death, and/or predation interactions.

In spite of the variability of their assumptions (Table 1), these models typically show that a food web can emerge with an increase in species number and a given topology for trophic interactions: a given species can preferentially consume a subset of the extant species and/or the resources. These models especially showed that 1) The adaptive evolution of body size or body mass could be a major mechanism explaining the structure of food webs, and especially the emergence of trophic levels (*e.g.* Loeuille and Loreau, 2005; Brännström et al., 2011); 2) Diversification in trophic networks is promoted by the number of evolving traits such as predation preference and niche width (Allhoff and Drossel, 2013; Allhoff et al., 2015; Allhoff and Drossel, 2016; Bolchoun et al., 2017) or abstract traits (Ritterskamp et al., 2016a); 3) There can exist a turnover of species in trophic networks, with species going extinct and replaced either by new species appeared by mutations, or because of the evolution of the niche of an extant species (Allhoff et al., 2015). On the

one hand, a shared typical outcome by the different models can be seen as the evidence that they indeed capture the fundamental mechanisms responsible for food webs evolution and diversification. However, on the other hand, because food webs do not emerge and diversify under similar parameter values, it casts doubts on their generality and the key mechanisms governing food webs evolution are yet to be identified. For instance, results are very sensitive to the size of mutations considered (Allhoff et al., 2015), and to the choice of trade-off functions (de Mazancourt and Dieckmann, 2004), questioning the plausibility and importance of evolutionary branching as an important process underlying the evolution of trophic networks. Furthermore, strong and arbitrary assumptions are shared among all models (*e.g.* only one trait evolves or body size is arbitrarily lower bounded, see Table 1). It is possible that the properties of these models are due to such arbitrary assumptions, which would make them much less satisfying and relevant for the study of the evolution of ecological networks.

Surprisingly, a single feature is common among all models: the *biomass conversion efficiency* (or conversion factor), *i.e.* the fraction of ingested biomass devoted to the production of biomass of newborns, is supposed constant. Most authors refer to Yodzis and Innes (1992) to justify their choice of a constant conversion efficiency, with a value often assumed to be 0.45 for herbivore and 0.85 for carnivores. Assuming that the conversion efficiency is independent of the mass / body size of predators and prey is undoubtedly important because it implies that the mass converted by individuals when consuming prey is increasingly large when feeding on larger prey, with no limit. This is in contradiction with empirical data from controlled experiments which show that there is a trade-off for predators between eating small and large prey (Baras et al., 2014; Norin and Clark, 2017), suggesting an optimal prey size for which the conversion efficiency is the highest. This also contradicts the results of functional and behavioural ecology models which predict that the net energy gain per unit of prey mass is not constant, bounded and can show an optimal values (Portalier et al., 2018; Pawar et al., 2019; Ho et al., 2019). This can be due to a trade-off between the low biomass given by small prey but lower costs to forage, handle and digest than for larger prey. Portalier et al. (2018) for instance showed that there are prey size limits within which the net energy gain for the predator is positive, which constrains the possible feeding interactions. It can also be due to the fact that predators can feed only on a part of a large prey: the biomass converted from a large prey attains a maximum. How the efficiency of biomass conversion affects the evolution of food webs has been ignored by extant models. One can for instance expect that if predator preference can evolve, it should correspond to the best compromise between eating small or large prey.

In this paper, our main goal is to explore the importance of the biomass conversion efficiency in the evolution of food webs. For that purpose, we propose a unifying framework which encompasses most of the previously published models. We show that some key properties of the biomass conversion efficiency govern the evolution food webs. We then show that relaxing strong assumptions made by previous models, especially artificial bounds on evolving traits, can give rise to unrealistic trophic networks. Finally, we discuss the robustness of these models and question the validity and generality of their predictions, especially if one aims at using these models for management or conservation

purposes.

2 Model description

2.1 A unifying model

Models of food web evolution derived from the seminal work of Loeuille and Loreau (2005) have similar structure. For the sake of comparison, we propose here a unifying model encompassing most of the models' features in Loeuille and Loreau (2005); Ingram et al. (2009); Brännström et al. (2011); Allhoff and Drossel (2013); Allhoff et al. (2015); Allhoff and Drossel (2016); Ritterskamp et al. (2016a,b); Bolchoun et al. (2017). All these models assume that new species are added to the food web at discrete mutation times and that between two mutations the densities of species of the food web follow deterministic dynamics. On a time interval between two mutations where the food web is composed of n species, species are assumed to be characterized by their average body mass r_i at maturity and we denote by N_i the population density of species i for all $i = 1 \dots n$. An autotrophic resource is present in the community, *i.e.* a species which does not consume any other species but can be consumed, which can organic or not. The density of the resource is indexed by $i = 0$. The basic dynamics for N_i takes the form

$$\frac{\dot{N}_i}{N_i} = \sum_{j=0}^{n} \lambda_{ij}\, \gamma_{ij}\, N_j - \sum_{j=1}^{n} \alpha_{ij}\, N_j - \sum_{j=1}^{n} \gamma_{ji}\, N_j - m_i\,, \qquad i = 1, \dots, n \tag{1}$$

where γ_{ij} is the consumption rate of prey j by predator i; m_i is the mortality rate of species i; α_{ij} is the interference competition rate between species i and j; finally, λ_{ij} is the reproduction efficiency due to the consumption of species j by species i, *i.e.* the per capita reproduction rate of species i per capita of ingested species j. This last quantity summarizes biomass conversion and reproduction. The reproduction efficiency λ_{ij} is related to the *biomass conversion efficiency* through predation of prey j by predator i, denoted ξ_{ij}, by $\lambda_{ij} = \xi_{ij} \frac{r_j}{r_i}$. The biomass conversion efficiency ξ_{ij} corresponds to the fraction of ingested biomass of species j converted through reproduction into biomass of species i. It is assumed in particular that $\xi_{ij} < 1$ to avoid biomass creation *ex nihilo*.

Species can feed on a common resource which can be interpreted as organic or inorganic nutrient. We denote the resource density by N_0 and by r_0 the resource (bio-)mass per unit density. The resource dynamics varies among references, apparently without significantly affecting the behaviour of the model. In this work, in line with Brännström et al. (2011), we consider the following logistic dynamics for the resource density:

$$\frac{\dot{N}_0}{N_0} = r_g - k_0\, N_0 - \sum_{i=1}^{n} \gamma_{i0}\, N_i \tag{2}$$

where r_g and k_0 are the reproductive rate and the intraspecific competition rate of the resource population, respectively.

The ecological parameters γ_{ij}, λ_{ij}, α_{ij} and m_i are functions of species phenotypes characterized by the average body mass r_i, the preferred predation distance (in terms

of body mass) d_i, and a predation range parameter s_i, often called "niche width". It is convenient to express the ecological parameters in terms of the log-body mass $z_i = \ln(r_i/r_0)$ instead of r_i in which case, the preferred distance of predation d_i is replaced by its logarithmic expression $\mu_i = \ln(r_i/(r_i - d_i))$, so that γ_{ij} is maximal when $z_j = z_i - \mu_i$, i.e. $r_j = e^{z_i - \mu_i} = e^{-\mu_i}\, r_i$. In other words, the favourite prey biomass of a species is expressed as a fraction of its own biomass. On the logarithmic scale, the corresponding niche width is denoted σ_i.

These phenotypes can evolve because of recurrent mutations and selection due to the competitive and predation interactions between individuals. In particular, r_i (or z_i) is considered as an evolving trait. Mutations are assumed to be rare, so that Eqs. (1) and (2) may reach a stationary state (if it exists) before the next mutation. The ancestral species producing the new (mutant) species is chosen with probability proportional to their density or biomass. The mutant trait is drawn according to a distribution which depends on the ancestral trait and introduced in the population at a given small density or biomass.

2.2 Parameterization: How ecological parameters depend on body mass or size

For comparison, Table 1 compiles assumptions made in models about how body size (or mass) affect ecological parameters such as predation, competition or reproduction rates. For reasons detailed in Section 2.3, in our model we consider the following parameterization. We consider two evolving traits for species i: the log-body mass z_i and the predation log-distance μ_i. We assume without loss of generality that $r_0 = 1$, so that $z_i = \log r_i$. The predation rate is given by

$$\gamma_{ij} = \gamma(z_i - z_j - \mu_i) := \frac{\gamma_0}{\sqrt{2\,\pi}\,\sigma_\gamma}\, \exp\left(-\frac{(z_i - z_j - \mu_i)^2}{2\,\sigma_\gamma^2}\right) . \tag{3}$$

In particular, all species can feed on any other species, but predation of species j by species i is significant only when z_j is close to $z_i - \mu_i$, within a range of the order of σ_γ (Fig. 2). The niche width σ_γ is assumed fixed.

The interference competition parameter α_{ij} follows a Gaussian function such as

$$\alpha_{ij} = \alpha(z_i - z_j) := \frac{\alpha_0}{\sqrt{2\,\pi}\,\sigma_\alpha}\, \exp\left(-\frac{(z_i - z_j)^2}{2\,\sigma_\alpha^2}\right) ,$$

where σ_α is the competition range on the logarithmic scale.

The mortality rate takes into account allometry, following well-known empirical observations of Peters (1983), as

$$m_i = m(z_i) := m_0\, e^{-0.25\, z_i} = m_0\, r_i^{-0.25} .$$

In all previously published models (Tab. 1), the biomass conversion efficiency ξ_{ij} is assumed to be constant, i.e. the biomass produced by reproduction is a fixed fraction of the ingested biomass. The reproduction efficiency λ_{ij} then increases with the prey mass / size without limits (see Figure 3, black thick lines). Experiments rather suggest that there

exist trade-offs between energy gains and loss linked to predation due to foraging, catch, ingestion and digestion (*e.g.* Baras et al., 2014; Norin and Clark, 2017). Generally, most ecological processes involved in predation interactions can depend on the size of the prey and the predator (see Fig. 1) as suggested by functional and behavioural ecology models (Portalier et al., 2018; Pawar et al., 2019; Ho et al., 2019). In particular, if individuals feed on larger prey, as suggested by functional and behavioural models, the hunting and handling costs per unit of biomass is likely to be larger than for smaller prey (Portalier et al., 2018). Moreover, large prey might not be totally ingested by predators. Conversely, if prey are small, a predator has to feed on a large number of prey and then the handling time (per unit of biomass) becomes critical. This suggests that ξ_{ij} should depend on the log-masses of the predator z_i and the prey z_j, and that for instance it can tend to zero when the relative size $z_i - z_j$ goes to $\pm\infty$ (as illustrated in Fig. 1). Hence, we assume the general reproduction efficiency

$$\lambda_{ij} = \lambda(z_i, z_j) = \frac{e^{z_j}\,\xi(z_i, z_j)}{e^{z_i}} = \xi(z_i, z_j)\,\frac{r_j}{r_i}\,. \tag{4}$$

The analysis of Section 3 is done on the general model described above. The numerical study of Section 4 assumes a specific form of the function $\xi(z_i, z_j)$, depending only on $z_i - z_j$.

2.3 Comparison with the parameterization of models derived from Loeuille and Loreau (2005)

In this section, we show how our model encompasses most of the models derived from Loeuille and Loreau (2005), focusing on the most important features except the biomass conversion efficiency which was thoroughly discussed previously (see Tab. 1 and App. D for a full review). Our aim is to minimize biological artificial constraints and arbitrary assumptions. Overall, our model is similar to the one by Brännström et al. (2011), except that we consider that both body size and preferred predation distance evolve, and that the biomass conversion efficiency depends on the prey and predators sizes.

All models, including ours, assume that the main trait driving evolution is body-mass, but there are many differences on other evolving traits. It is hard to know which are the most important traits for long term evolution of food webs. We chose to focus on log-body mass and predation log-distance because assuming fixed predation distances strongly constrains the dynamics and does not allow the evolution of cannibalism, although it is widespread in nature (Fox, 1975). For the sake of simplicity, we kept other ecological parameters constant, in particular the niche width σ_γ. Indeed, it has been shown by Ingram et al. (2009); Allhoff and Drossel (2013) that niche width generally evolves to very small values unless an *ad hoc* trade-off is introduced on niche width or parameters are tuned very finely.

We do not impose any *a priori* constrains on which individuals feed on each other, contrarily to many models (see columns "Ordered predation", "Cannibalism" and "Predation rate" in Tab. 1): in our model cannibalism is allowed and predation is unordered meaning that species does not necessarily feed on smaller species. As a consequence, if

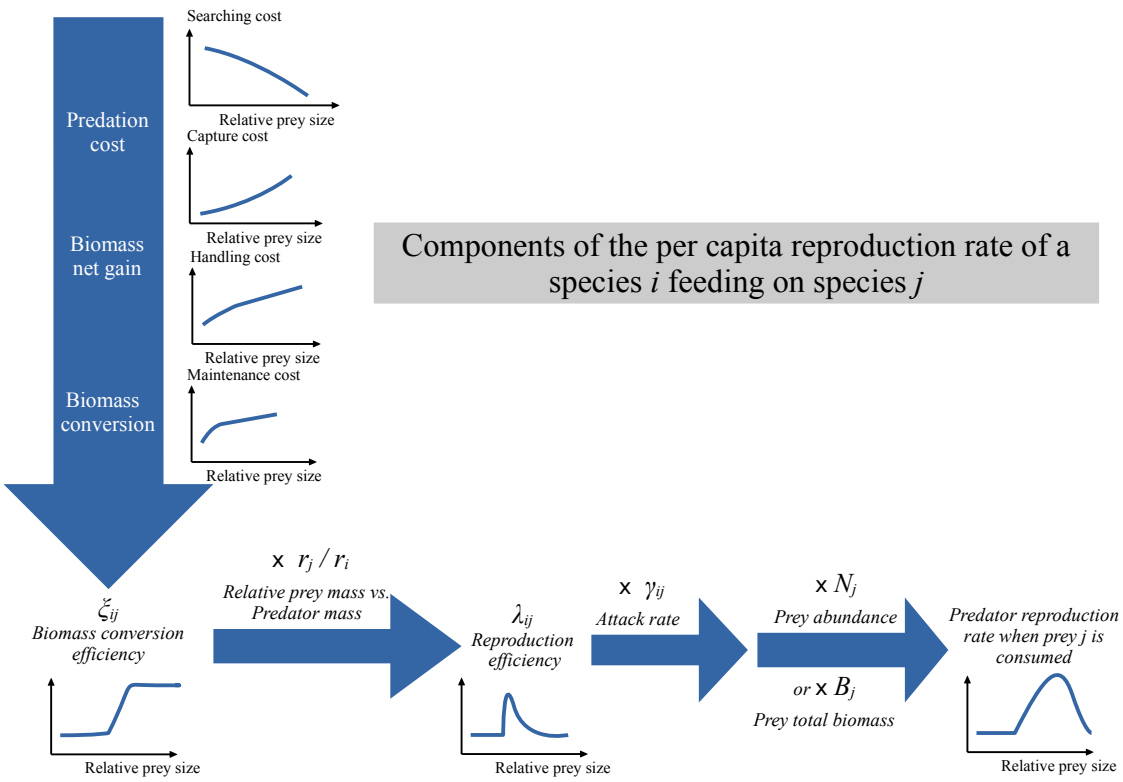
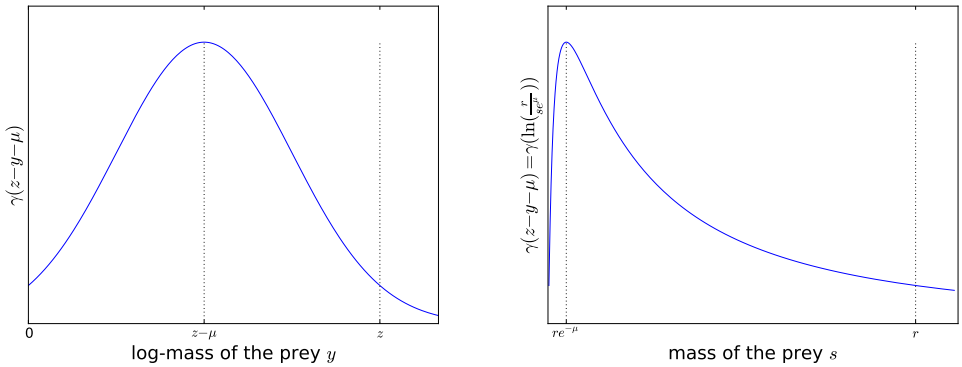


Figure 1: Why biomass conversion efficiency and reproduction efficiency depend on the size of the prey and the predators. The reproduction efficiency (per capita) is recursively decomposed into its different components, which illustrates how our model is built. Starting from the bottom right of the figure, it is first showed how predator reproduction rate depends on the reproduction efficiency λ_{ij}, the attack rate γ_{ij}, and the prey abundance N_j (or biomass B_j). Second, it is showed how reproduction efficiency is a function of the body mass of the prey r_j, of the body mas of the predator r_j, and of the biomass conversion efficiency ξ_{ij}. Third, the biomass conversion efficiency is decomposed into the ecological processes possibly involved in predation interactions. Since these ecological processes vary with prey size, consequently, the biomass conversion efficiency and the reproduction efficiency are not constant and should also depend on prey size.



(a) logarithm scale (b) linear scale

Figure 2: Predation rate from Eq. (3) represented on the logarithm (left) and linear (right) scales.

predation is ordered and if cannibalism is rare in the food web, these are *a posteriori* emerging properties derived from the ecological and evolutionary processes.

As shown in Eqs. (1) and (2), we modelize the dynamics of the density of the species N_i. In Loeuille and Loreau (2005); Allhoff and Drossel (2013); Ritterskamp et al. (2016b), populations dynamics are instead expressed in terms of species biomasses $B_i = N_i\, r_i$. In Table 1, the conversion of the dynamics on B_i to a dynamics on N_i is done using the assumption that $r_0 = 0$ and $B_0 = N_0$ and the fact that, if for all $i \geq 1$

$$\frac{\dot{B}_i}{B_i} = \sum_{j=0}^{n} \lambda_{ij}^B\, \gamma_{ij}^B\, B_j - \sum_{j=1}^{n} \alpha_{ij}^B\, B_j - \sum_{j=1}^{n} \gamma_{ji}^B\, B_j - m_i\,,$$

then

$$\lambda_{ij}^B = \begin{cases} \frac{r_i}{r_j}\,\lambda_{ij} & \text{if } j \geq 1 \\ r_i\,\lambda_{ij} & \text{if } j = 0 \end{cases}, \qquad \gamma_{ij}^B = \frac{\gamma_{ij}}{r_i}\,, \qquad \text{and} \qquad \alpha_{ij}^B = \frac{\alpha_{ij}}{r_j}\,. \tag{5}$$

Models considering the dynamics of the biomass instead of the density of species hence assume that the size of the autotrophic resource is null. This imposes that the species consuming the autotrophic resource can not be smaller than the resource since size cannot be negative. Here again, if species consuming the autotrophic resource in the food webs are always larger than the resource in the food webs emerged from our model, it is due to an emerging property.

Several models introduce additional arbitrary constraints on the possible values of evolving traits (see column "Boundaries" in Tab. 1). Assumptions made on mutation kernels can strongly constrain the evolution of phenotypes. For example, in Allhoff et al. (2015); Allhoff and Drossel (2016); Bolchoun et al. (2017), both predation distance and niche width can evolve, but mutations only produce trait values in a fixed interval. In particular, phenotypic traits can be limited to positive values (any mutations introducing a negative trait values in the population is arbitrarily discarded). It often appears that

these arbitrary boundaries are necessary otherwise degenerated trophic webs emerge. For instance, assuming that predation distance can not take negative values prevents the evolution of cannibalism or of species feeding on larger prey. In App. D we review in more detail why such arbitrary boundaries can bias the evolution of food webs in models.

Finally, in models by Loeuille and Loreau (2005); Ingram et al. (2009); Allhoff and Drossel (2013); Ritterskamp et al. (2016a), instead of resource dynamics described by Eq. 2, a chemostat equation is assumed for the dynamics of resources, with possible recycling of a fraction ν of biomass of dead individuals into resources:

$$\dot{N}_0 = I - eN_0 - \sum_{i=1}^{n} \gamma_{i0} N_i N_0 + \nu \sum_{i=0}^{n} r_i N_i \left(m_i + \sum_{j=1}^{n} \alpha_{ij} N_j + \sum_{j=1}^{i-1} (1 - \lambda_{ij}) \gamma_{ij} N_j \right), \quad (2')$$

where I and $e_0 N_0$ are the in- and out-flow of resources, respectively. The way the dynamics of the resources is considered does not seem to affect significantly the outcomes of models.

2.4 Criteria for deciding whether a food web is realistic or not

The assumptions made about which traits evolve, the boundaries of the phenotypic space, and the form of the biomass conversion efficiency strongly affect the evolutionary dynamics of food webs. This highlights the difficulty to define what one should consider as a realistic food web. Of course, a naive answer is that we expect food webs emerging from the models to look like "real food webs". However, how it translates into required qualitative and quantitative features are rarely precisely defined or justified. Generally, authors are satisfied when two conditions are fulfilled: diversification occurs and many species accumulate, and species feed on each other. What are the required topologies is however rarely thoroughly discussed. For instance, Loeuille and Loreau (2005) considered satisfying food webs showing a hierarchical linear structure with larger species feeding on smaller ones, even though there is no such simple food web in natural ecosystems. Allhoff et al. (2015) compare various topological features of simulated and empirical food webs, but it is hard to know which particular topological properties are needed to characterise realistic food webs.

Without a generally admitted definition of what is a realistic food web or not, we proceeded the other way around by clearly defining which food webs emerging from our model will be considered as unrealistic when 1) all species evolve to a size smaller than the autotrophic resources (hereafter called a *negative food web*), or 2) when species mostly feed on the autotrophic resource but little on the other species (hereafter called a *trivial food web*). In a trivial food web predation interactions can be totally absent, or the steady state community can be composed of a single species feeding on the resource. Hence, we consider that a food web is realistic when species remain larger than the resource and when at least one species mostly feed on other species. These simple rules allow us to limit *a priori* assumptions about the expected resulting food webs. In sections 3 and 4, we show that some properties of biomass conversion efficiency are key for the evolution of realistic food webs even without imposing arbitrary constraints.

	Evolving phenotypes	Boundaries	Model type	Ordered predation	Cannibalism	Allometries	Mutations size
LL05, RBB16b	mass r	$0 < r$	(1)-(2')	yes	no	birth & death	large
IHS09	mass r niche width s	$0 < r$ $0 < s$	$(1) - (2')$ with ST I-II	yes	no	birth & death	large
BLLD11	log-mass z	$z \in \mathbb{R}$	(1)-(2)	no	yes	death	small
AD13	mass r predation distance d niche width s	$0 < r$ $0 < d$ $0 < s$	(1)-(2')	yes	no	birth & death	large
ARRDG15, AD16 & BDA17	log-mass z predation log-distance μ niche width σ	$z \in \mathbb{R}$ $0.5 < \mu < 3$ $0.5 < \sigma < 1.5$	$(1) - (2)$ with BDA	no	yes	predation & death	large
RBB16a	log-mass z abstract trait x	$z \in \mathbb{R}$	$(1) - (2')$ with $\nu = 0$	no	no	predation & death	large
Our model	log- mass z predation log-distance μ	$z, \mu \in \mathbb{R}$	(1)-(2)	no	yes	death	small

	Predation rate γ_{ij}	Production efficiency λ_{ij}	Competition rate α_{ij}	Death rate m_i	Mutations
LL05, RBB16b	0 if $r_i \leq r_j$, otherwise: $r_i\, \gamma_0\, G_s(r_i - r_j - d)$	$\begin{cases} \lambda_0\, r_i^{-0.25}\, \frac{r_j}{r_i} & \text{if } j \neq 0 \\ \lambda_0\, r_i^{-1.25} & \text{if } j = 0 \end{cases}$	$\begin{cases} \alpha_0\, r_j & \text{if } \lvert r_i - r_j \rvert \leq \beta \\ 0 & \text{otherwise,} \end{cases}$	$m_0\, r_i^{-0.25}$	$r' \sim \mathcal{U}([0.8\, r; 1.2\, r])$
IHS09	0 if $r_i \leq r_j$, otherwise: $r_i\, \gamma_0(s_i)\, G_{s_i}(r_i - r_j - d)$	$\begin{cases} \lambda_0\, r_i^{-0.25}\, \frac{r_j}{r_i} & \text{if } j \neq 0 \\ \lambda_0\, r_i^{-1.25} & \text{if } j = 0 \end{cases}$	$\alpha_0\, r_j\, G_{\sigma_\alpha}(r_i - r_j)$	$m_0\, r_i^{-0.25}$	$r' \sim G_{\sigma_r}(r' - r)$ $s' \sim G_{\sigma_s}(s' - s)$
BLLD11	$\gamma_0\, G_{\sigma_\gamma}(z_i - z_j - \mu)$	$\lambda_0\, e^{z_j - z_i}$	$\alpha_0\, G_{\sigma_\alpha}(z_i - z_j)$	$m_0\, e^{-0.25\, z_i}$	$z' \sim G_{0.01}(z' - z)$
AD13	0 if $r_i \leq r_j$, otherwise: $r_i\, \gamma_0\, G_{s_i}(r_i - r_j - d_i)$	$\begin{cases} \lambda_0\, r_i^{-0.25}\, \frac{r_j}{r_i} & \text{if } j \neq 0 \\ \lambda_0\, r_i^{-1.25} & \text{if } j = 0 \end{cases}$	$\begin{cases} \alpha_0\, r_j & \text{if } \lvert r_i - r_j \rvert \leq \beta \max\{r_i, r_j\} \\ 0 & \text{otherwise,} \end{cases}$	$m_0\, r_i^{-0.25}$	$r' \sim \mathcal{U}([0.8\, r; 1.2\, r])$ $d' \sim \mathcal{U}([0.9\, d; 1.1\, d])$ $s' \sim \mathcal{U}([0.9\, s; 1.1\, s])$
ARRDG15, AD16, & BDA17	$\gamma_0\, e^{0.75\, z_i}\, G_{\sigma_i}(z_i - z_j - \mu_i)$	$\lambda_0\, e^{z_j - z_i}$	$\alpha_0 + \alpha_0'$ if $i = j$, otherwise: $\alpha_0\, \sigma_i\, G_{\sqrt{\sigma_i^2 + \sigma_j^2}}(z_i - \mu_i - z_j + \mu_j)$	$m_0\, e^{-0.25\, z_i}$	$z' \sim \mathcal{U}([z - 0.7; z + 0.7])$ $\mu' \sim \mathcal{U}([0.5; 3])$ $\sigma' \sim \mathcal{U}([0.5; 1.5])$
RBB16	0 if $i = j$, otherwise: $\gamma_0(x_i, x_j)\, e^{0.75\, z_i}\, G_\sigma(z_i - z_j - \mu)$	$\lambda_0\, e^{z_j - z_i}$	$\alpha_0(x_i, x_j)\, e^{z_j}\, G_{\sqrt{2}\,\sigma}(z_i - z_j)$	$m_0\, e^{-0.25\, z_i}$	$z' \sim \mathcal{U}([z - 0.7; z + 0.7])$
Our model	$\gamma_0\, G_{\sigma_\gamma}(z_i - z_j - \mu)$	$\xi(z_i - z_j)\, e^{z_j - z_i}$	$\alpha_0\, G_{\sigma_\alpha}(z_i - z_j)$	$m_0\, e^{-0.25\, z_i}$	$z' \sim G_{\sigma_z}(z' - z)$ $\mu' \sim G_{\sigma_\mu}(\mu' - \mu)$

Table 1: Food web models and predation, production efficiency (biomass conversion + reproduction), competition, death and mutation functions in models of Loeuille and Loreau (2005) (LL05), Ritterskamp et al. (2016b) (RBB16b), Ingram et al. (2009) (IHS09), Brännström et al. (2011) (BLLD11), Allhoff and Drossel (2013) (AD13), Allhoff et al. (2015) (ARRDG15), Allhoff and Drossel (2016) (AD16), Bolchoun et al. (2017) (BDA17), Ritterskamp et al. (2016a) (RBB16a) and our model. BDA means Beddington-DeAngelis functional response, ST I-II means Saturating Type I or II functional response, $G_\sigma(x) = \frac{1}{\sqrt{2\,\pi}\,\sigma} \exp\left(-\frac{x^2}{2\,\sigma^2}\right)$ is the centred Gaussian density with variance σ^2 and $\mathcal{U}([a, b])$ is a uniform distribution on the interval $[a, b]$. When models are expressed in terms of biomass, we convert the different parameters using (5).

3 Why biomass conversion efficiency is key for food web evolution

Our goal in this section is to identify general conditions on the biomass conversion efficiency $\xi_{ij} = \xi(z_i, z_j)$ and reproduction efficiency $\lambda_{ij} = \lambda(z_i, z_j)$ (Section 2.2) for the evolution of realistic food webs, or more precisely for preventing the emergence of negative or trivial food webs.

3.1 Negative food webs emerge for small variation of the biomass conversion efficiency with prey size

The invasion fitness of a mutant (y, η) in the food web $(z_i, \mu_i)_{1\leq i\leq n}$ is given by

$$\begin{aligned} f(y,\eta) = &\sum_{i=0}^{n} \lambda(y, z_i)\, \gamma(y - z_i - \eta)\, N_i^* \\ &- \sum_{i=1}^{n} \gamma(z_i - y - \mu_i)\, N_i^* - \sum_{i=1}^{n} \alpha(z_i - y)\, N_i^* - m(y) \end{aligned} \tag{6}$$

where N_0^* and $(N_i^*)_{1\leq i\leq n}$ are respectively the resource concentration and the population densities at the stationary state of the food web, *i.e.* which nullify Eq. (1) and (2). The sign of the invasion fitness determines whether a species (y, η) can invade the food web $(z_i, \mu_i)_{1\leq i\leq n}$ or not. In particular we have the classical relation $f(z_i, \mu_i) = 0$ for any $i \in \{1, \ldots, n\}$.

The analysis we develop here follows the adaptive dynamics framework (Metz et al., 1996; Geritz et al., 1998; Dieckmann and Law, 1996; Champagnat and Méléard, 2011; Champagnat et al., 2001). Under the assumption that mutations are small, the direction of evolution of a given species $(z, \mu) \in (z_i, \mu_i)_{1\leq i\leq n}$ is governed by the fitness gradient $\nabla f(y, \eta)|_{(y,\eta)=(z,\mu)}$, and the properties of evolutionary equilibria, such as evolutionary branching, are governed by the second order derivatives $\partial_y^2 f$ and $\partial_\eta^2 f$.

In cases where the predation preference trait μ evolves sufficiently fast, the evolution of the food web is mostly governed by the partial derivative of the conversion efficiency

$$\partial_y \lambda(y, z) = \left[\frac{\partial_y \xi(y, z)}{\xi(y, z)} - 1\right] \lambda(y, z)\,.$$

In this case, the fitness gradient can be approximated by (see Appendix A for details)

$$\partial_1 f(z, \mu) = \partial_y f(y, \eta)|_{(y,\eta)=(z,\mu)} \approx \partial_1 \lambda(z, \widetilde{z})\, \gamma(0)\, \widetilde{N}^* - m'(z), \tag{7}$$

where $\widetilde{z}$ and $\widetilde{N}^*$ respectively are the size of the major prey of species (z, μ), and the total density of the major prey of species (z, μ) (possibly including the autotrophic resource). If $\widetilde{N}^*$ is large enough, the last quantity has the same sign as $\partial_1 \lambda(z, \widetilde{z})$.

All models compiled in Tab. 1 assume ξ is constant so that $\partial_1 \lambda(z, \widetilde{z}) = -\lambda(z, \widetilde{z})$, which implies that decreasing predator's body mass while the prey size remains constant necessarily yields a higher reproductive output and a gain in fitness. Simultaneously,

predator's feeding preference will evolve to larger prey's body mass. This is a consequence of the absence of trade-off on the biomass conversion efficiency, which leads to a strong benefit on the reproductive efficiency λ when feeding on large species (see Figure 3).

For a negative food web to emerge, a species (z, μ) close to the point $(0, 0)$ (hereafter called a *resource-like* species) needs to cross the point $(0, 0)$. When this occurs, the autotrophic resource and the resource-like species can be considered as a single species for which the competition from the other species is negligible if other species have log-size sufficiently far from 0. Under these assumptions, the fitness gradient experienced by the resource-like species is approached by

$$\partial_1 f(0,0) \approx \partial_1 \lambda(0,0)\, \gamma(0)\, (N_0^* + N_1^*) - m'(0)$$

where N_1^* is the density of the resource-like species. Hence, provided that $m'(0)$ is small enough, the sign of $\partial_1 f(0, 0)$ is mainly given by the sign of $\partial_1 \lambda(0, 0)$. Therefore, the resource-like species will cross $(0, 0)$, hence initiating the emergence of a negative food web, when $\partial_1 \lambda(0, 0) \lessapprox 0$. Expressed in terms of biomass conversion efficiency, this corresponds to the condition

$$\frac{\partial_1 \xi(0,0)}{\xi(0,0)} \lessapprox 1.$$

In other words, if the biomass conversion efficiency increases too rapidly with the increase of the prey size, our model predicts that species smaller than the autotrophic species should evolve, because consuming a larger prey is always favored for a smaller predator. This finally results in the emergence of a negative food web.

This result is illustrated in Section 4.1 (see also Appendix E), where species evolve toward very small body mass and the stationary state of food webs shows negative structures. As shown in Table 1, in all models where the predation (log-)distance can evolve, this unrealistic behaviour is not observed because of artificial constraints on the trait values or mutation kernels.

3.2 Trivial food webs emerge when biomass conversion efficiency is large

We now investigate conditions on the biomass conversion efficiency which favour the emergence of trivial food webs, composed of a single species. This means that, when only two coexisting species remained in the food web, one of them was competitively excluded by the other. Hence we consider two species (z, μ) and (y, η) and apply the competitive exclusion principle: species (z, μ) is excluded by species (y, η) if the invasion fitness $f(z, \mu)$ of species (z, μ) in the food web containing only species (y, η) is negative, where

$$\begin{aligned} f(z,\mu) = {} & \lambda(z,0)\gamma(z-\mu)N_0^* + \lambda(z,y)\gamma(z-y-\mu)N_1^* \\ & - \alpha(y-z)N_1^* - \gamma(y-z-\eta)N_1^* - m(z), \end{aligned} \tag{8}$$

and N_0^* and N_1^* are the equilibrium densities of resource and species (y, η) respectively, when species (z, μ) is extinct. For $\lambda(y, 0)$ not too small (so that $N_1^* > 0$),

$$N_1^* = \frac{\lambda(y,0)\gamma(y-\eta)\frac{r_g}{k_0} - m(y)}{\frac{\lambda(y,0)\gamma(y-\eta)^2}{k_0} + (1-\lambda(y,y))\gamma(-\eta) + \alpha(0)} \quad \text{and} \quad N_0^* = \frac{r_g - \gamma(y-\eta)N_1^*}{k_0}.$$

The sign of (8) is hard to evaluate without further information on the values of (z, μ) and (y, η). We observe in Section 4.3 that the typical situation where the food web evolves to a trivial one corresponds to the case where species (y, η) is a resource-like species, that is $(y, \eta) \approx (0, 0)$. In this case, the sign of $f(z, \mu)$ is approximately given by a criterion on the ratio $\lambda(y, 0)/\lambda(z, 0) \approx \lambda(0, 0)/\lambda(z, 0)$ (see Appendix B for computation details). More precisely, the fitness is negative, which means that species (z, μ) is excluded by the resource-like species if

$$\frac{\lambda(0,0)}{\lambda(z,0)} \geq \frac{(\gamma(0)+\alpha(0))N_1^* + m_0}{(\alpha(-z)+\gamma(-z))\,N_1^* + m(z)} \frac{\gamma(z-\mu)}{\gamma(0)}\,, \tag{9}$$

where N_0^* and N_1^* are the equilibrium densities of the autotrophic resource and the resource-like species respectively, when species (z, μ) is extinct. The criterion (9) can be expressed in terms of biomass conversion efficiency as follows:

$$\frac{\xi(0,0)}{\xi(z,0)} \geq \frac{(\gamma(0)+\alpha(0))N_1^* + m_0}{(\alpha(-z)+\gamma(-z))\,N_1^* + m(z)} \frac{\gamma(z-\mu)}{\gamma(0)}\, e^{-z}. \tag{10}$$

The right-hand-side of (9) still depends on z and μ. However, we will observe in the simulations of Section 4.3 that this quantity stays within a limited range when varying $\lambda(0, 0)$. This shows that a threshold exists on the quantity $\frac{\lambda(0,0)}{\lambda(z,0)}$: if it is too large, competitive exclusion of species (z, μ) occurs, leading to a trivial food web where only remains a single species feeding on the autotrophic resource.

4 Numerical study

In this section we will illustrate with numerical studies the general results obtained in the previous section about the properties of the biomass conversion for which realistic food webs can evolve. We consider the following family of functions ξ, parameterised by $a, b > 0$ and $\xi_{\max} \in (0, 1)$:

$$\xi(z,y) = \xi(z-y) = \begin{cases} 0 & \text{if } z-y \leq -1/a, \\ a\,b\,(z-y)+b & \text{if } -1/a \leq z-y \leq \frac{\xi_{\max}-b}{a\,b}, \\ \xi_{\max} & \text{if } z-y \geq \frac{\xi_{\max}-b}{a\,b}. \end{cases} \tag{11}$$

ξ is a linear function with slope $a\,b$, such that $\xi(0) = b$ and truncated below 0 and above $\xi_{\max}$, with $b < \xi_{\max}$. This last condition means that predation becomes harder in terms of conversion efficiency when feeding on larger prey in an interval of prey sizes containing the predator size. Examples of such functions are given in Figure 3. To avoid problems of irregularity of fitness functions, simulations of Figures 5-7 are realised with a regularised version of the previous curves (see Appendix C.2).

We assume that mutations occur at regular time units; the species (z, μ) producing a mutant is drawn proportionally to its individual density (number of individuals); the mutant (z', μ') is drawn such that z' and μ' are independent and Gaussian with means z and μ and variances σ_z^2 and σ_μ^2 respectively. The resulting food webs are represented with

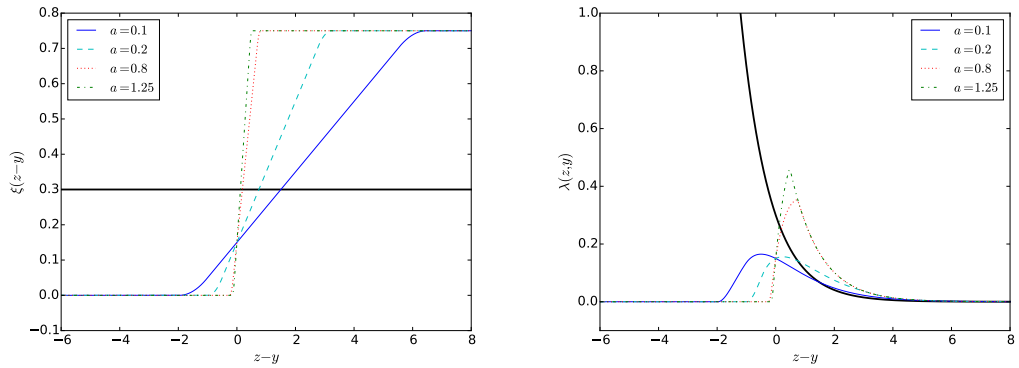


Figure 3: Possible shapes of the trade-off in the biomass conversion efficiency ξ (left) and the reproduction efficiency λ (right) defined by Eq. (11) and (4) respectively, with $\xi_{\max} = 0.75$ and $b = 0.15$ and for the model of Brännström et al. (2011), that is $a = 0$ and $b = 0.3$ (black thick line).

an edge drawn between predator i and prey j (or a loop if $j = i$) if predation of j by i (or cannibalism if $j = i$) is responsible for more than 10% (5% for dashed edges) of the reproduction of species i. On Figures 4 to 7, a green edge means that the bigger species feeds on the smaller one and conversely for magenta edges. More details about simulations methods are given in App. C.1.

Our numerical study will focus on the influence on the evolutionary dynamics of food webs of the parameters a, b, $\xi_{\max}$, σ_z and σ_μ which determine the functional form of the biomass conversion efficiency. All other parameters are the same as in Brännström et al. (2011), except for the range of competition σ_α which is a bit smaller in order to favour diversification events in the food web evolution (see Appendix C.4). These parameters are given in Table 2.

Parameters	Values
σ_γ	1.5
γ_0	10
σ_α	0.5
α_0	1
λ_0	0.3
m_0	0.1
r_g	10
k_0	0.01

Table 2: Simulation parameters.

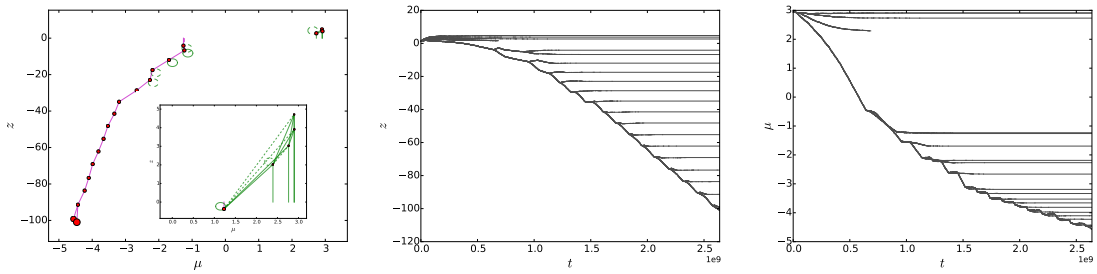


Figure 4: Food web evolution with constant biomass conversion efficiency. From left to right: food web at final time of the simulation ($T = 2.6\,10^9$, overlay at intermediate time $t = 4.\,10^8$); evolution of the log-mass z; evolution of the predation preference μ, letting z and μ evolving in the model of Brännström et al. (2011) (i.e. model of Section 2.2 with a constant biomass conversion efficiency ξ), with $\xi \equiv 0.3$, mutation variances $\sigma_z = 0.01$, $\sigma_\mu = 0.001$ and parameters of Table 2.

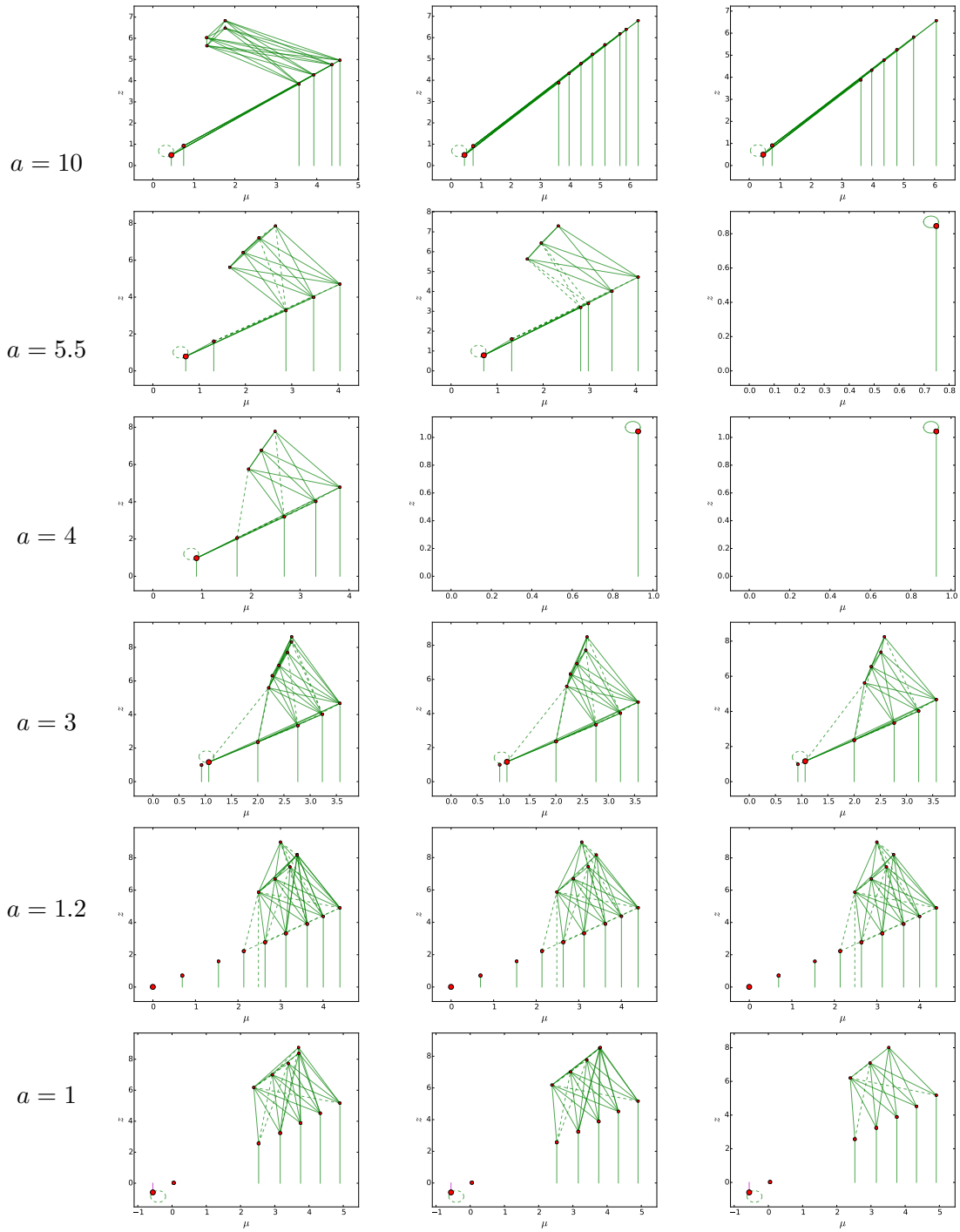
4.1 Constant conversion efficiency: emergence of negative food webs

We illustrate the emergence of unrealistic food webs when the conversion efficiency ξ is constant. In this case, our model corresponds to the model of Brännström et al. (2011) but where both z and μ can evolve. Figure 4 shows simulations with much smaller mutations on μ than z. The food web initially evolves as observed by Brännström et al. (2011) without mutations on μ: several evolutionary branchings occur and the food web gets structured. However, the smallest species progressively evolves to smaller body size and predation log-distance until they both become negative. This means that this species feeds on a larger prey: the resource. After this, the richness of the positive part of the food web, composed of the species with positive body masses and positive predation log-distance, becomes smaller and the negative part of the food web progressively diversifies, producing a negative food web with more and more species. The stationary state of the food web is not reached at the end of the simulation, as the food web seems to evolve similarly endlessly. As discussed below, the evolution to a negative food web is due to the fact that the parameter a is 0 in this case. As mentioned in Section 2.3, this problem did not occur in other models allowing evolution of both traits z and μ because of artificial constraints on the range of phenotypes accessible by mutations (see also Appendix E).

4.2 Threshold on a for negative food webs

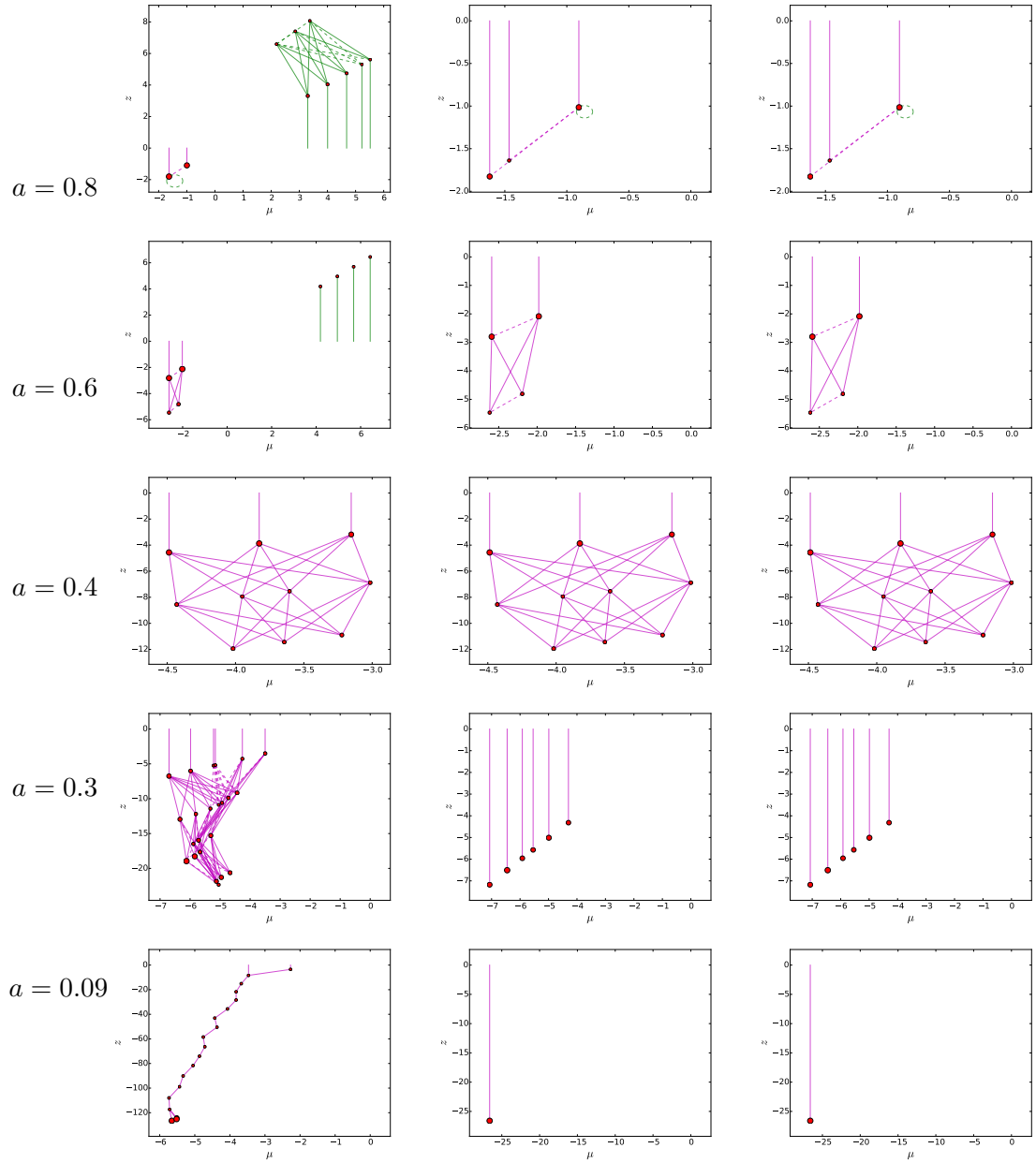
The arguments of Section 3.1 suggest that species with negative phenotypes could emerge in the food web only if $\xi'(0)/\xi(0) = a \lessapprox 1$. This is confirmed by the numerical study shown in Figures 5 and 6.

These figures show typical food web structures at the stationary state (except for four particular simulations, see legend and Appendix C.3) for several values of a (in rows) and several relative speeds of evolution σ_z and σ_μ of the two traits (in columns). Figures 5 and 6 show that the variation of reproduction efficiency, governed by parameter $a = \xi'(0)/\xi(0)$,



(a) $\sigma_z > \sigma_\mu$ (b) $\sigma_z = \sigma_\mu$ (c) $\sigma_z < \sigma_\mu$

Figure 5: Food web at the stationary state (except for $a = 5.5$ and $\sigma_z \geq \sigma_\mu$ and for $a = 10$ and $\sigma_z > \sigma_\mu$ which produce oscillations, see Figure 8) for different values of $a \geq 1$ and for mutation variances $\sigma_z = 0.001 < \sigma_\mu = 0.01$ (a), $\sigma_z = \sigma_\mu = 0.01$ (b) and $\sigma_z = 0.01 > \sigma_\mu = 0.001$ (c). $b = 0.15$ and $\xi_{\max} = 0.75$. Other parameters are given in Table 2.



(a) $\sigma_z > \sigma_\mu$ (b) $\sigma_z = \sigma_\mu$ (c) $\sigma_z < \sigma_\mu$

Figure 6: Food web at the stationary state (except for $\sigma_z > \sigma_\mu$, $a = 0.09$) for different values of $a < 1$ and for mutation variances $\sigma_z = 0.001 < \sigma_\mu = 0.01$ (a), $\sigma_z = \sigma_\mu = 0.01$ (b) and $\sigma_z = 0.01 > \sigma_\mu = 0.001$ (c). $b = 0.15$ and $\xi_{\max} = 0.75$. Other parameters are given in Table 2.

strongly affects the structure of the food webs (compare rows), while the relative speed of evolution generally has little effect, except for particular values of a (compare columns).

When the body size evolves faster than the predation log-distance (*i.e.* $\sigma_z > \sigma_\mu$), realistic food webs (*i.e.* non-negative and non-trivial) emerge when the slope of ξ is large ($a \geq 1.2$): starting with a single heterotrophic species, the community diversifies and the trophic network evolves until a steady state is reached, where all species have positive traits and some species feed mainly on other species and not on the autotrophic resource (Figures 5a and 6a). When $1.2 \leq a < 3$ the food web contains a resource-like species which evolves to a size and a preferred predation distance closer to zero as a decreases. The resource-like species thus suffers strong cannibalism. When $a < 1.2$, the resource-like species evolves to a negative log-mass and starts feeding on prey (the resource) larger than itself. Meanwhile, the richness of the food web decreases progressively until $a \approx 0.6$. Finally, when $a \to 0$, the conversion efficiency ξ converges to the constant function b. We observe that the positive part of the food web goes extinct and the food web diversifies with only species smaller than the autotrophic resource (as in Figure 4). As predicted in Section 3.1, the threshold at which the food web becomes partly negative is $a \approx 1$. With the parameters in Table 2, approximation (7) becomes $\partial_1 f(0,0) \approx 2.66[a-1]b(N_0^* + N_1^*) + 0.025$. In all simulations shown in Figures 5 and 6, 0.025 is negligible with respect to $2.66b(N_0^* + N_1^*)$ (for example, for $a = 1.2$, the latter is larger than 10). This confirms that the sign of $\partial_1 f(0,0)$ is most often the same as $a - 1$, so that a resource-like species can evolve to a negative log-mass if $a \lessapprox 1$. In our numerical study, the fact that this threshold seems to be closer to 1.2 than to 1 can be explained by the approximations we made to derive (7) (see Appendix A).

When the body size evolves at the same rate or more slowly than the preferred predation distance (*i.e.* $\sigma_z \leq \sigma_\mu$), the evolution of food webs generally show similar patterns than previously described when $\sigma_z > \sigma_\mu$ except for some intermediate values of a where there is no diversification, leading to a trivial food web (Figures 5b and 5c with $a = 4$ and $a = 5.5$). A detailed study of the fitness landscape shows that, when $a = 4$ and $a = 5.5$, the first diversification event in the food web is due to evolutionary branching along slow directional evolution (*sensu* Ito and Dieckmann (2014)). When mutations are too fast on trait μ, evolution becomes too fast to allow evolutionary branching, and the system reaches an evolutionary stable strategy corresponding to a trivial food web (see Appendix F for details).

4.3 Threshold on $b/\xi_{\mathbf{max}}$ for trivial food webs

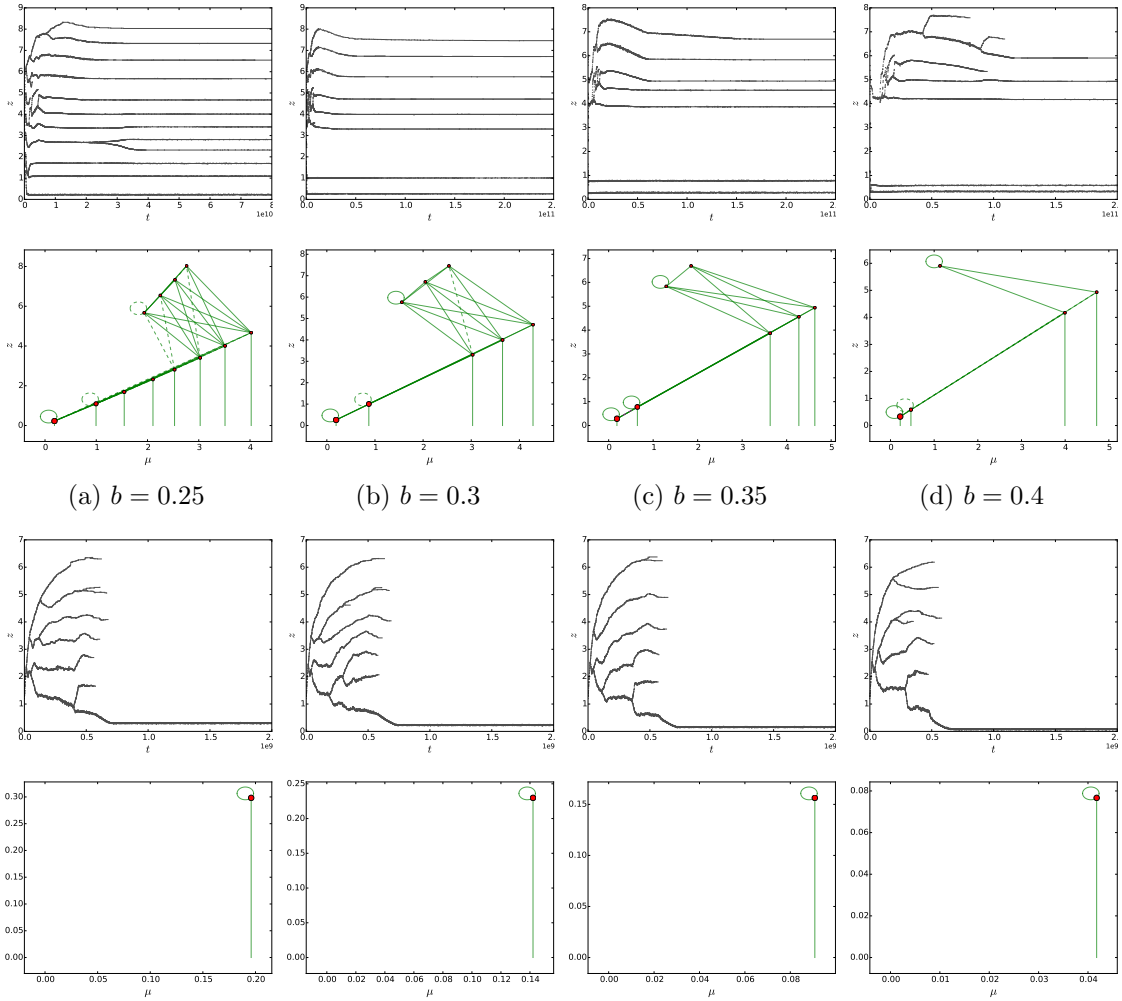
Figure 7 shows that the food webs structure strongly depends on the parameter $b = \xi(0)$, corresponding to the biomass conversion efficiency when a predator feeds on a prey with an identical log-body mass. For all values of b, the initial food web dynamics shows progressive diversification as in Figure 5a, but when the smallest species becomes too close to 0, different behaviours are observed. When b is small, the food web stabilises in a relevant pattern. When b increases, the richness of the food web progressively decreases: species with intermediate body masses go extinct, until $b = 0.4$ where only three species with large body masses remain. For $b \geq 0.45$, only the resource-like species survives and no further diversification occurs. This can be understood from the argument of

Section 3.2: in the situation where few species are present in the food web, among which a resource-like species, the resource-like species competitively excludes the others when the criterion (10) is satisfied. With the chosen parameterization of ξ, $\xi(0,0)/\xi(z,0) \approx b/\xi_{\max}$ for all sufficiently large log-body masses z of non resource-like species. Using parameters in Table 2 and the observed trait values for the last surviving non resource-like species in Figure 7, we obtain an approximate threshold $b/\xi_{\max} \gtrapprox 0.41$ for the emergence of trivial food webs, which is consistent with our simulations (see Appendix B for computation details).

5 Discussion

In this paper, we analyse a unifying model of food webs adaptive evolution that embraces most of the peculiarities of the eco-evolutionary models which followed the seminal work by Loeuille and Loreau (2005). We introduce in particular a non-constant biomass conversion efficiency as suggested by data and physical and behavioural models. We show that relaxing the arbitrary constraints that are often assumed in the literature can generally yield unrealistic food webs structures (*e.g.* relaxing the assumption of fixed preferred predation distance in Brännström et al. (2011), or the constraints on parameters range values in Allhoff et al. (2015); Allhoff and Drossel (2016)). We show that assuming that the biomass conversion efficiency depends on prey and predator log-sizes restores the possibility of realistic food webs topologies without the need of arbitrary constraints: body sizes of the species remain larger than the basic resources size, and trophic levels emerge. We also show that trophic networks evolution strongly depends on the assumed form of the biomass conversion efficiency.

There are two manners to interpret our results. On the positive side, we can conclude that our results bring a lot in identifying the key mechanisms underlying the evolution of food webs. Indeed, we showed that simply considering a non-constant biomass conversion efficiency can solve most problems encountered with previous models. In addition, empirical data suggest that there is indeed an optimal size of prey size where predation is the most efficient (Baras et al., 2014; Norin and Clark, 2017; Ho et al., 2019; Pawar et al., 2019; Portalier et al., 2018). Our model is, in a sense, closer to data and observations and one might argue that such adaptive dynamics models really tell us how food webs emerge from eco-evolutionary processes. We can then go further into the analysis of our results and discuss the importance of the biomass conversion efficiency and its form. We numerically explored a single family of functions for the biomass conversion efficiency ξ (linear w.r.t. the size difference between prey and predator and truncated above and below fixed thresholds), but the fitness analysis shows that we can extend the observed results to more general functions. We exhibited the effect of two parameters on the expected trophic networks (Fig. 5, 6 and 7): the slope of biomass conversion efficiency at 0 (*i.e.* $\partial_1\xi(0,0)/\xi(0,0)$) and the relative conversion efficiency $\xi(0,0)/\xi_{\max}$, (Eq. (11), Fig. 3). Both parameters have threshold values at which networks evolve such as either all species have a size smaller than the resource, or the network is not stable and only one species remains. Assuming that the biomass conversion efficiency ξ is constant (*i.e.*



(a) $b = 0.25$ (b) $b = 0.3$ (c) $b = 0.35$ (d) $b = 0.4$

(e) $b = 0.45$ (f) $b = 0.5$ (g) $b = 0.55$ (h) $b = 0.6$

Figure 7: Evolution of the log-mass z (top) and food web at the stationary state (bottom) for b varying from 0.25 to 0.6 with mutation variances $\sigma_z = 0.01 > \sigma_\mu = 0.001$, $a = 1.2$ and $\xi_{\max} = 0.75$. Other parameters are given in Table 2.

$\partial_1\xi(0,0)/\xi(0,0) = 0$) leads to resource-like species converting more energy into reproduction as they feed on larger prey. Mutants decreasing size are thus necessarily favored and invade. Assuming a non-constant biomass conversion efficiency ξ, depending on the log-sizes of prey and predator species, our results show that: 1) $\xi(0,0)/\xi_{\max}$ must be low enough to avoid the evolution to a network with a single resource-like species, and 2) $\partial_1\xi(0,0)/\xi(0,0)$ must be large enough to avoid too large benefits for resource-like species to feed on larger prey and to avoid the evolution to a network with species smaller than the resource. In line with physical and behavioural models (Ho et al., 2019; Pawar et al., 2019; Portalier et al., 2018), our results suggest that mechanisms underlying how energy is transferred from prey to predators, and how it is converted into predators biomass, are key for the evolution and stability of food webs.

However, one can interpret our results on a more negative side. Our results can also suggest that such models are not robust enough to gain informative insights about food webs evolution. First because we show that relaxing arbitrary hypotheses can lead to the emergence of qualitatively different and unrealistic networks topologies. Such models are thus very sensitive to assumptions and lack robustness. We showed that assuming a non-constant biomass conversion efficiency can solve problems but one can argue that such biomass efficiency (as well as many other parameters of the model) can also evolve at the same time than body size and predation distance, which could yield to different food webs evolution. Second, because one would expect that such models would be self-sufficient regarding certain general properties of trophic networks. In particular, if size effectively structures trophic networks with large species feeding on smaller ones, and if cannibalism is rare, this should emerge from the trait evolution and should not be due to arbitrary constraints. The model analysed by Brännström et al. (2011) does not assume arbitrary constraints on the parameters range values, yet its results are not robust to the hypothesis of fixed preferred predation distance. Other models which avoid cannibalism by *a priori* excluding it (Loeuille and Loreau, 2005; Ritterskamp et al., 2016a) obtain hierarchically structured trophic networks by assuming that species can not feed on larger prey (Loeuille and Loreau, 2005), assume large mutations to observe network emergence (Allhoff and Drossel, 2013) or arbitrarily constrain parameters range values in order to obtain non-degenerated networks (Tab. 1). A general robustness analysis of such models appears necessary before generalising their results, such as the one performed by Brännström et al. (2011). Finally, we show that, even after introducing appropriate forms of the conversion efficiency and in agreement with other authors, emerged food webs are very sensitive to mutation sizes and the speed of evolution, the number of evolving traits and the strength of interference competition, *i.e.* competition which is not due to resources and prey consumption. In particular, interference competition seems unreasonably necessary for the evolution of food webs: it is not clear whether there are good reasons why a non-trophic ecological process would be so important in food webs evolution, especially in models mostly based on competition for resources. Hence, our results altogether with results by previous authors can cast doubts on the explanatory and predictive power of such models.

One of the most important problem with the interpretation of such models is that it is difficult to avoid circular reasoning. In most previous papers, the authors claim that they are satisfied with the model's results *because* they give realistic or relevant food webs structures. Some authors even justify arbitrary assumptions, such as a limited range for possible parameters values (*e.g.* Allhoff and Drossel, 2013), because otherwise results are not satisfying. We use ourselves such a circular reasoning to justify that assuming a non-constant biomass conversion efficiency ξ actually solves many problems encountered by the models, which is not a satisfying argument. It is necessary to find ways to evaluate these models in a non-circular manner. A possibility would be to identify quantitative independent predictions that could be compared with food webs features. For instance, some macroscopic properties are shared among observed networks such as the distribution of the body log-mass ratio between prey and predators. Considering non-constant biomass conversion efficiency yields distribution which are close to the ones observed in empirical networks (see Fig. 10 in App. C.5) which suggests that biomass conversion is indeed a key parameter underlying food webs evolution. Another direction for testing the validity of models would be to consider the limitation of the current models which *a priori* assume allometric relationships between size and parameters, generally as a power of 1/4 (Peters, 1983). However, one should observe that allometries measured in natural populations are *evolved* values and not fixed parameters. In models, including ours, allometric relationships are input parameters while they should be output parameters. We suggest that a possible way to evaluate such models would be to compare output allometric relationships to observed data as already done by Loeuille and Loreau (2006).

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A Detailed computation for the emergence of negative food webs

Since we consider small mutations, the direction of evolution of a given species (z, μ) is governed by the fitness gradient $\nabla_{(y,\eta)} f(y,\eta)|_{(y,\eta)=(z,\mu)}$ (Metz et al., 1996; Geritz et al., 1998; Dieckmann and Law, 1996; Champagnat and Méléard, 2011; Champagnat et al., 2001), where

$$\begin{aligned}\partial_y f(y,\eta) = &\sum_{i=0}^{n} \left[\partial_y \lambda(y,z_i) - \frac{y - z_i - \eta}{\sigma_\gamma^2}\,\lambda(y,z_i)\right] \gamma(y - z_i - \eta)\, N_i^* \\ &- \sum_{i=1}^{n} \frac{z_i - y - \mu_i}{\sigma_\gamma^2}\,\gamma(z_i - y - \mu_i)\, N_i^* + \sum_{i=1}^{n} \alpha'(z_i - y)\, N_i^* - m'(y) \qquad (12)\end{aligned}$$

and

$$\partial_\eta f(y,\eta) = \sum_{i=0}^{n} \frac{y - z_i - \eta}{\sigma_\gamma^2}\, \lambda(y, z_i)\, \gamma(y - z_i - \eta)\, N_i^* \,. \tag{13}$$

If ξ is constant then $\partial_y \lambda(y, z_i) = -\lambda(y, z_i)$, it follows from these expressions that a specialist species (*i.e.* a species whose growth is mainly due to a single prey size) has a tendency to evolve toward smaller traits. Indeed, for such a species $(z, \mu) \in (z_i, \mu_i)_{1 \le i \le n}$, assuming that its major prey all have log-mass $\widetilde{z}$ with total density $\widetilde{N}^*$ (which is the sum of the resource density and the density of the resource-like species when $\widetilde{z} = 0$)

$$\partial_\eta f(y,\eta)|_{(y,\eta)=(z,\mu)} \approx \frac{z - \widetilde{z} - \mu}{\sigma_\gamma^2} \lambda(z, \widetilde{z}) \gamma(z - \widetilde{z} - \mu) \widetilde{N}^*,$$

which makes the trait μ evolve to $z - \widetilde{z}$. Provided μ evolves fast enough, we can assume that $\mu \approx z - \widetilde{z}$, and then

$$\begin{aligned}\partial_1 f(z,\mu) = \partial_y f(y,\eta)|_{(y,\eta)=(z,\mu)} \approx & \partial_1 \lambda(z, \widetilde{z})\, \gamma(0)\, \widetilde{N}^* - \sum_{i=1}^{n} \frac{z_i - z - \mu_i}{\sigma_\gamma^2}\, \gamma(z_i - z - \mu_i)\, N_i^* \\ & + \sum_{i=1}^{n} \alpha'(z_i - z)\, N_i^* - m'(z).\end{aligned}$$

If we assume in addition that all species (z_i, μ_i) predating (z, μ) (*i.e.* such that $\gamma(z_i - z - \mu_i)$ is not negligible) are also such that $\mu_i \approx z_i - z$, and that other species than (z, μ) have different enough sizes so that the main part of competition acting on (z, μ) is exerted by species (z, μ) itself, we obtain (using that $\alpha'(0) = 0$)

$$\partial_1 f(z,\mu) \approx \partial_1 \lambda(z, \widetilde{z})\, \gamma(0)\, \widetilde{N}^* - m'(z).$$

If $\widetilde{N}^*$ is large enough, the last quantity has the same sign as $\partial_1 \lambda(z, \widetilde{z})$, which is negative if ξ is constant. If ξ is not constant and such as $\partial_1 \lambda(z, \widetilde{z})$ is positive, this trend is reversed.

This argument applies in particular to cases with a resource-like species, *i.e.* a species with trait $(z, \mu) \approx (0, 0)$. In the simulations of Figures 5, 6 and 8, the loss of richness of the food web and the appearance of unrealistic (negative) patterns seem closely related to the situations where a resource-like species evolves to negative sizes. In these simulations, at the time where the resource-like species crosses $(0, 0)$, the resource and resource-like species can be considered as a single species, which is relatively far from the rest of the food web, so that competition from other species is negligible and predation is exerted on this species only from specialist species. Therefore, letting 1 be the index of the resource-like species

$$\partial_1 f(0,0) \approx \partial_1 \lambda(0,0)\, \gamma(0)\, (N_0^* + N_1^*) - m'(0).$$

B Detailed computation for the emergence of trivial food webs

We assume that the food web is composed of the resource, a resource-like species for which we shall assume for simplicity that trait is $(y, \eta) = (0, 0)$ (*i.e.* resource consumption is optimal for this species), and a second species with traits z and μ.

In this case, we shall use the competitive exclusion principle to decide whether the species (z, μ) is excluded by the resource like-species $(0, 0)$. This will occur if the fitness $f(z, \mu)$ of the species (z, μ) is negative, where

$$f(z,\mu) = \lambda(z,0)\gamma(z-\mu)(N_0^* + N_1^*) - \alpha(-z)N_1^* - \gamma(-z)N_1^* - m(z), \tag{14}$$

and N_0^* and N_1^* are the equilibrium densities of resource and resource-like species respectively, when the species (z, μ) is extinct. Hence for $\lambda(0, 0)$ not too small (so that $N_1^* > 0$)

$$N_1^* = \frac{\lambda(0,0)\gamma(0)\frac{r_g}{k_0} - m(0)}{\frac{\lambda(0,0)\gamma(0)^2}{k_0} + (1-\lambda(0,0))\gamma(0) + \alpha(0)} \quad \text{and} \quad N_1^* + N_0^* = \frac{m(0) + (\gamma(0)+\alpha(0))N_1^*}{\lambda(0,0)\gamma(0)}.$$

We then obtain

$$f(z,\mu) = \frac{\lambda(z,0)\,\gamma(z-\mu)}{\lambda(0,0)\,\gamma(0)}\left[(\gamma(0)+\alpha(0))N_1^* + m_0\right] - (\alpha(-z)+\gamma(-z))\,N_1^* - m(z).$$

Then the species (z, μ) cannot survive if

$$\frac{\lambda(0,0)}{\lambda(z,0)} = \frac{\xi(0,0)}{\xi(z,0)\,e^{-z}} \geq \frac{(\gamma(0)+\alpha(0))N_1^* + m_0}{(\alpha(-z)+\gamma(-z))\,N_1^* + m(z)}\frac{\gamma(z-\mu)}{\gamma(0)}.$$

This criteria explains the collapse of the food web observed in Figure 7, with ξ defined by (11), for large values of b when the trait of the smallest species approaches $(0, 0)$. Observing that $\xi(0, 0) = b$ and assuming that a and z are large enough so that $\xi(z, 0) = \xi_{\max}$ (and indeed the observed values of z are between 4 and 5 in simulations of Figure 7), we obtain, with the values of the parameters of Table 2,

$$N_1^* = \frac{b\,2.66\frac{10}{0.01} - 0.1}{\frac{b\,2.66^2}{0.01} + (1-b)\,2.66 + 0.8} \approx \frac{b\,2.66\frac{10}{0.01}}{\frac{b\,2.66^2}{0.01}} \approx 3.76,$$

so that the species cannot survive if

$$\frac{b}{\xi_{\max}} \gtrapprox \frac{4.93\,\gamma(z-\mu)e^{-z}}{3.76\,(\alpha(-z)+\gamma(-z)) + 0.1\,e^{-z/4}}$$

Therefore, we obtain a threshold effect for large values of $b/\xi_{\max}$, and we indeed observe in the simulations of Figure 7 trait values of the last surviving non resource-like species close to $z = 4$ and $\mu = 2.8$, which gives an approximate threshold of 0.41 for b, above which we predict that the food web should collapse when the smallest species gets too close to trait $(0, 0)$. This is consistent with the simulations of Figure 7. Biologically, when b increases, the resource-like species is more adapted for the resources consumption and for cannibalism. Then, for large b, the resource-like species is too competitive for other species to survive.

C Numerical methods and additional simulations

C.1 Food web simulation method

The details of the computational methods slightly vary among references. Here we applied the following scheme[1].

Between mutation events, we compute the solution of Eq. (1)-(2) using the `odeint` python solver. Mutations are assumed to occur each $t_m = 5.10^4$ time units. This gives similar, yet faster, results to alternative schemes where mutations occur with a small probability at each time steps. The species (z, μ) producing a mutant is drawn proportionally to its individual density. The mutant (z', μ') is drawn such that z' and μ' are independent and Gaussian with means z and μ and variances σ_z^2 and σ_μ^2 respectively. The mutant initial density is a small value ε and species are assumed to go extinct if their densities go below the same threshold ε. All simulations were performed with $\varepsilon = 0.0001$. The density of the initial species and the initial resource concentration are the equilibrium of the system (1)-(2) with $n = 1$ given by

$$N_1^* = \frac{\lambda_{10}\,\gamma_{10}\,r_g - k_0\,m_1}{\lambda_{10}\gamma_{10}^2 + k_0\,((1-\lambda_{11})\,\gamma_{11} + \alpha_{11})}\,, \qquad N_0^* = \frac{r_g - \gamma_{10}\,N_1^*}{k_0} \tag{15}$$

assuming that the fitness of species 1 satisfies $\lambda_{10}\,\gamma_{10}\,r_g - k_0\,m_1 > 0$, where m_1, λ_{10}, λ_{11}, γ_{10} and γ_{11} are the death rate, production efficiencies and predation rates (here reduced to resource consumption and cannibalism) associated to the initial species.

The resulting food webs are represented with an edge drawn between predator i and prey j (or a loop if $j = i$) if predation of j by i (or cannibalism if $j = i$) is responsible for more than 10% (5% for dashed edges) of the reproduction of species i, *i.e.*

$$\frac{\lambda_{ij}\,\gamma_{ij}\,N_j}{\sum_{k=0}^{n}\lambda_{ik}\,\gamma_{ik}\,N_k} > 0.1\,. \tag{16}$$

Note that links between species are drawn based on reproduction rates $\lambda_{ij}\gamma_{ij}\,N_j$ rather than on predation rates only $\gamma_{ij}\,N_j$ because, due to the dependency of λ_{ij} on the prey and the predator sizes, even if a prey is little consumed compared to other prey, it may contribute to a large part of reproduction of its predator. This is particularly true for large prey, for example with cannibalism.

C.2 Regularisation of ξ

To avoid problems of irregularity of fitness functions, we use in simulations a regularisation of the function ξ defined by (11). The function ξ can be obtained as an affine transformation of the function ξ_0 defined by

$$\xi_0(x) = \begin{cases} 0 & \text{if } x \leq -1 \\ 1 + x & \text{if } -1 \leq x \leq 1 \\ 2 & \text{if } x \geq 1. \end{cases}$$

[1] Simulations are run on the *babycluster* of the *Institut Élie Cartan de Lorraine* : `http://babycluster.iecl.univ-lorraine.fr/`

The regularisation of ξ is obtained with the same affine transformation applied to the following regularisation of ξ_0

$$\widetilde{\xi}_0(x) = \begin{cases} 0 & \text{if } x \leq -1-\varepsilon \\ \frac{(x+1+\varepsilon)^3}{6\,\varepsilon^2} & \text{if } -1-\varepsilon \leq x \leq -1 \\ -\frac{(x+1-\varepsilon)^3}{6\,\varepsilon^2} + x + 1 & \text{if } -1 \leq x \leq -1+\varepsilon \\ (x+1) & \text{if } -1+\varepsilon \leq x \leq 1-\varepsilon \\ -\frac{(x-1+\varepsilon)^3}{6\,\varepsilon^2} + x + 1 & \text{if } 1-\varepsilon \leq x \leq 1 \\ \frac{(x-1-\varepsilon)^3}{6\,\varepsilon^2} + 2 & \text{if } 1 \leq x \leq 1+\varepsilon \\ 2 & \text{if } x \geq 1+\varepsilon \end{cases} \tag{17}$$

with $\varepsilon = 0.7$.

C.3 Food web dynamics

The dynamics of some simulations of Figures 5 and 6 are shown in Figure 8. They confirm that the food webs shown in Figures 5 and 6 are stationary, except for $a = 5.5$ and $\sigma_z > \sigma_\mu$, where periodic dynamics occur in the evolution of both traits z and μ (similar behaviour is observed for $a = 10$ and $\sigma_z > \sigma_\mu$ and for $a = 5.5$ and $\sigma_z = \sigma_\mu$). The emergence of evolutionary cycles as observed for $a = 5.5$ and $\sigma_z > \sigma_\mu$ was studied in Ritterskamp et al. (2016b). In the simulation with $a = 0.09$ and $\sigma_z > \sigma_\mu$, the food web does not reach a stationary state either and seems to evolve endlessly to smaller negative log-masses as in Figure 4. We also see that, for values of a much smaller than 1, the food web first evolves to a realistic shape, similar to those observed for larger values of a, until the smallest body mass becomes too negative. After this, the positive part of the food web collapses and only the negative part remains.

C.4 Effect of the variance of the interference competition kernel

As observed previously (*e.g.* Brännström et al., 2011) the variance σ_α of the competition kernel has a strong influence on the richness of the food web. Indeed, Figure 9 shows that the smaller σ_α, the richer the stationary food webs.

C.5 Predicted distribution of prey *vs.* predator body size

Figure 10 describes the distribution of the predator and prey sizes in the stationary food web presented in Figure 5 with $a = 1.2$ and $\sigma_z > \sigma_\mu$. Even though the number of species in the food web emerging from our model is lower than in observed food webs, the distribution are very similar (compare for instance Figure 5 in Ho et al. (2019)).

D A review of food web evolution models following Loeuille and Loreau (2005)

Eco-evolutionary models of food web evolution derived from Loeuille and Loreau (2005) are inspired by the adaptive dynamics framework. Clonal species are supposed to evolve

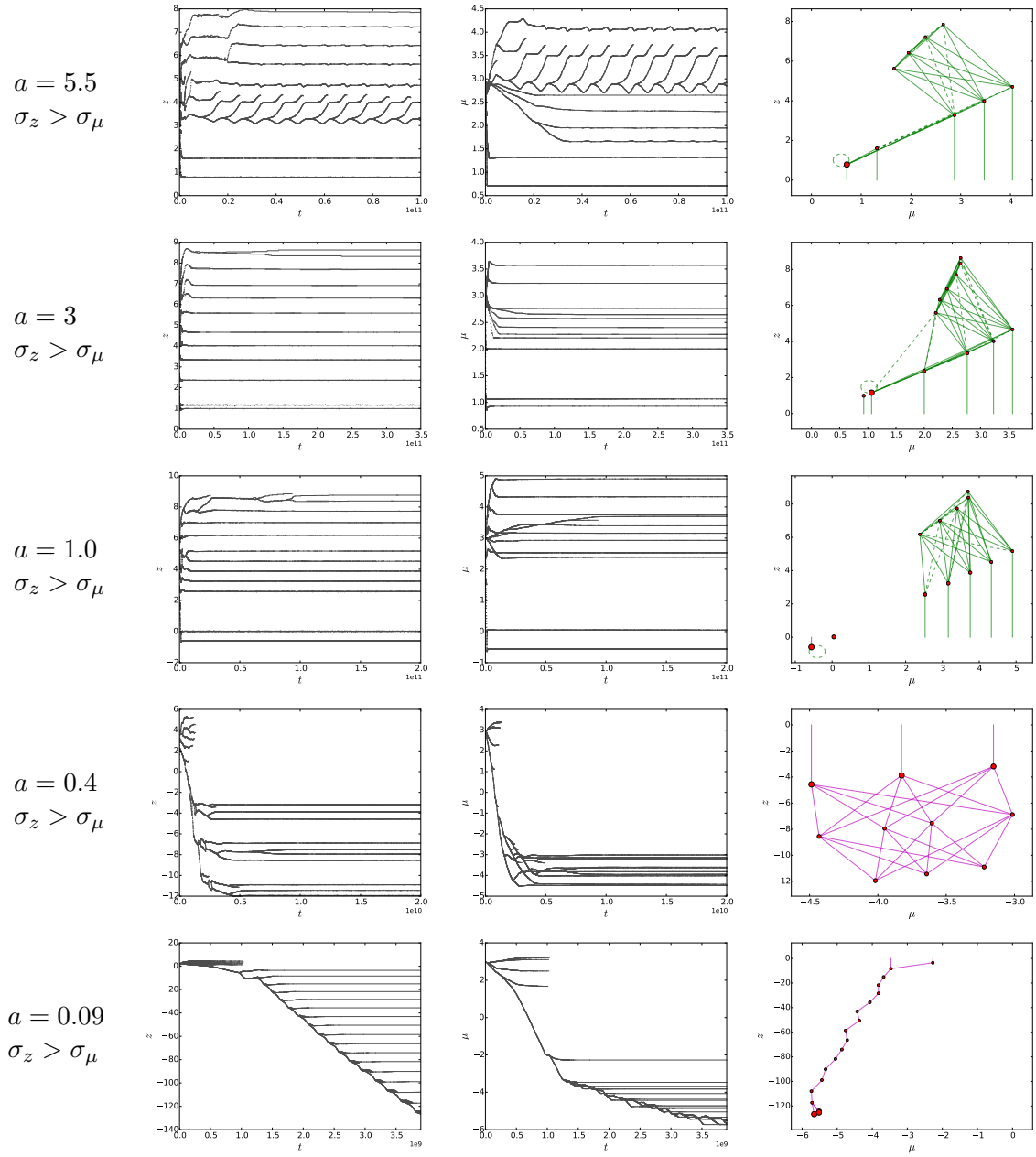
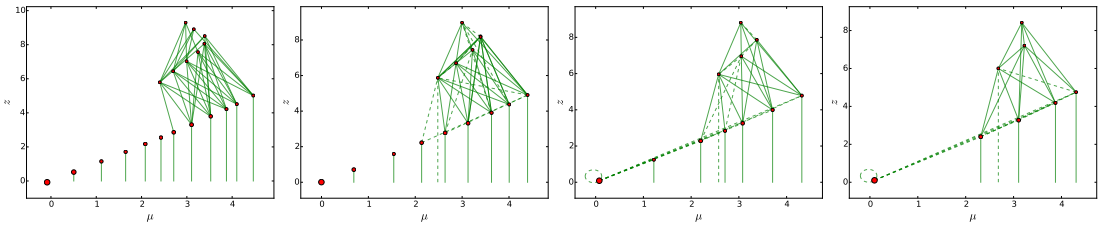


Figure 8: Evolution of the log-mass z (left), evolution of the predation preference μ (middle) and the final food web (right), for ξ defined by (11) with $\xi_{\max} = 0.75$, $b = 0.15$, $\sigma_z = 0.01 > \sigma_\mu = 0.001$ and a varying between 0.09 and 5.5.



(a) $\sigma_\alpha = 0.4$ (b) $\sigma_\alpha = 0.5$ (c) $\sigma_\alpha = 0.6$ (d) $\sigma_\alpha = 0.7$

Figure 9: Food web at the stationary state for different values of the competition kernel width (a) $\sigma_\alpha = 0.4$, (b) $\sigma_\alpha = 0.5$, (c) $\sigma_\alpha = 0.6$, (d) $\sigma_\alpha = 0.7$ with mutation variances $\sigma_z = 0.01 > \sigma_\mu = 0.001$, $a = 1.2$, $b = 0.15$ and $\xi_{\max} = 0.75$. Other parameters are given in Table 2.

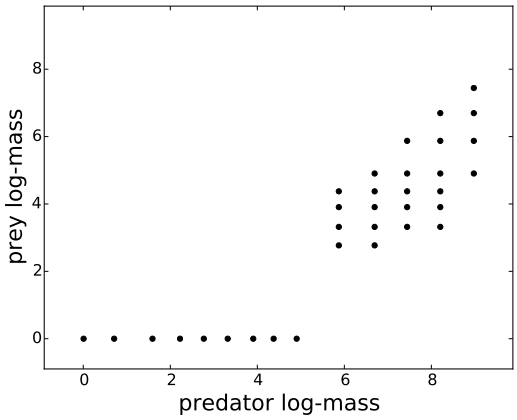


Figure 10: Distribution of the predator *vs.* prey size in a stationary food web. A dot depicts a predation interaction between two species where the biomass flux between the prey and predator is significant. This distribution corresponds to the food web presented in Fig.5 where $a = 1.2$ and $\sigma_z > \sigma_\mu$.

because of successive invasions of mutations introduced into a population at ecological equilibrium. Ecological dynamics are given by a set of deterministic Lotka-Volterra equations, including resource consumption, predation, competition, birth and death. A resource is also considered, with its own dynamics on while species may feeds and with input independant of the rest of the system. The main idea behind these models is that food web structure is driven by traits of the species, especially individuals' size or mass. Other traits are also considered, such as the preferred relative size of prey and niche width of predators. In general, a higher dimensional trait space is known to promote branching (Ispolatov et al., 2015; Doebeli and Ispolatov, 2017). In all models, allometric scaling relationships are considered between one or several parameters, for instance individual death or reproduction rates, and the size or the body mass of individuals, following well-known empirical observations (Peters, 1983).

In all models, at least size (or body mass) is affected by mutations corresponding to the introduction of new species (or morphs) in the food web and evolves, assuming separation of timescales between ecological and evolutionary processes: new (mutant) species are introduced one after another on a long timescale, allowing ecological equilibrium to be reached between mutations. These models' assumptions and objectives are thus different than the ones studying communities and ecosystems stability at short ecological timescale (*e.g.* Brose et al., 2006; Otto et al., 2007; Allesina and Tang, 2012; Miele et al., 2019). Mutant traits are drawn from a random distribution. A mutant species can be favored or not depending on the species already present in the environment. If it is favored, the mutant species invades and either replaces resident species or coexist with at least one other species. The analysis of the model is generally conducted using numerical simulations following a Piecewise-Deterministic Markov Process: population dynamics are deterministic and random mutations are introduced at random or fixed times.

All models assume that a single species is initially present in the environment, with the resources. Two phenomena can produce species diversification and the emergence of a food web. When only small mutations are considered, the food web gets enriched by a new species through evolutionary branching (*sensu* Adaptive Dynamics). When large mutations are possible, a new species may by chance appear in trait regions allowing invasion and coexistence with extant species, even though the parent species is locally stable (seeming rather like an immigration phenomenon). In all cases, models show that for a given set of parameters, the number of species can increase. Trophic interactions between species evolve since species i) can feed on other species, ii) have a preferred size of prey, iii) are more or less specialised on a prey size, iv) at least individuals' size evolves. The results are hence generally presented as an interaction network, with the species as nodes, and trophic interactions between species as edges. Finally, all models claim that for a set of reasonable parameter values, food webs can emerge and evolve, and their structure can be close to trophic networks encountered in nature.

In the following, we review adaptive evolution models of food webs derived from the seminal work by Loeuille and Loreau (2005). Despite that these models share common foundations, some of their assumptions can substantially vary. Table 1 compiles the models we review here and gives details about how they differ and why it matters.

Which traits evolve? The number of evolving traits can differ, giving rise to a large

variability of results. When only size evolves (Loeuille and Loreau, 2005; Brännström et al., 2011), food webs are structured mostly linearly, like a linear food chain, and trophic levels are clearly defined. Similar results are obtained if size evolves with other traits such that relative prey size preference or niche width (Ingram et al., 2009; Allhoff and Drossel, 2013; Allhoff et al., 2015; Allhoff and Drossel, 2016; Bolchoun et al., 2017). However, in some cases food webs can show unrealistic structures, *e.g.* with many species in a single trophic level, all feeding on the resource (Allhoff and Drossel, 2013). In the work of Ritterskamp et al. (2016a), in addition to size, an abstract trait also evolves, which facilitates the emergence of food webs with different trophic levels and many different species. This shows that food web evolution largely depends on *a priori* assumptions about the evolving traits.

Mass/size or log mass/log size? Models either assume that food webs are structured with individuals size/mass or log size/log mass. The choice is important since, on the one hand, if the food web is structured linearly with absolute size or mass, it implies that trophic interactions and predation rates depend on the absolute size difference between predators and prey (Loeuille and Loreau, 2005; Allhoff and Drossel, 2013). If the predation distance (*i.e.* the optimal predator-prey body mass difference) is not subject to mutation and is then the same for all species, relatively to their masses, small species feed on relatively much smaller species whereas large species feed on very similar species. Furthermore, for a given and fixed prey size preference, a small species cannot feed on any other species because no species could be small enough, hence giving artificial constraints to the minimal possible size of species. In addition, models considering a structure with the absolute size/mass also assume that the resource has a size/mass equal to 0, which prevents species to be smaller than the resource, a constraint that can be considered artificial. On the other hand, assuming log size/log mass (as in Brännström et al., 2011; Allhoff et al., 2015; Ritterskamp et al., 2016a; Allhoff and Drossel, 2016) allows to describe trophic interactions and predation rates that depend on the relative size between prey and predators through a predation log-distance (*i.e.* the optimal predator-prey body mass ratio) rather than a predation distance. Models on the log-scale seem to be more realistic for food webs with fixed predation (log-)distance containing a large extent of (log) masses/(log) sizes. Moreover, models on the log-scale assume that the resource has a log size/log mass equals to 0 which allows species to become smaller than the resource if log masses/log sizes are allowed to reach negative values. Overall, it appears that food web models would rather be structured following log size/log mass in order to introduce the least artificial constraints.

Boundaries. Models make different implicit assumptions regarding the boundaries of possible values of evolving traits. As said previously, assuming absolute rather than relative body size/mass inherently generates artificial boundaries. When other traits evolve with body size/mass, *e.g.* with prey size preference or predation niche width, boundaries are also assumed. For example, the predation log-distance and the niche width are constrained to a fixed interval in Allhoff et al. (2015); Allhoff and Drossel (2016); Bolchoun et al. (2017) (see Table 1). The reason why such boundaries are assumed is not clear. It appears in some cases that if no boundary constraints are assumed, the models generally give aberrant or trivial resulting trophic networks (*e.g.* Allhoff and Drossel, 2013 where

final food webs contain only one hyper-specialised species or a single trophic level; see also Allhoff and Drossel, 2016). This problem has been solved by Ingram et al. (2009) assuming that evolution of niche width is constrained by a trade-off on the predation rate. However, the chosen form of trade-off is hard to justify and the existence of a direct trade-off on niche width is not supported by biological observations, contrary to the trade-off on biomass conversion efficiency that we use. If giving constrained boundaries to evolving traits is necessary to avoid unrealistic results, the validity of such a theoretical framework can be questioned. On the other hand, one can expect that if such models capture the fundamental mechanisms underlying the evolution of food webs, then traits should evolve to realistic values on their own, without being artificially constrained.

Cannibalism, or not? Cannibalism is excluded in some models, either because species are assumed to feed only on strictly smaller species (Loeuille and Loreau, 2005; Allhoff and Drossel, 2013), or because an abstract trait is supposed as structuring the food web and species with identical body masses / sizes can feed on species which do not share the same abstract trait (Ritterskamp et al., 2016a). *A priori* excluding cannibalism has several caveats. First, cannibalism is widespread in nature (Fox, 1975), and one can expect that models of food web evolution reflect all features of observed trophic networks, including cannibalism. Second, excluding cannibalism artificially constraints the fate of mutants. For example, in the works of Loeuille and Loreau (2005) and Allhoff and Drossel (2013), individuals with a very small size difference can feed on and/or be eaten by each other while individuals with exactly the same trait can not. In Loeuille and Loreau (2005) this distinction has negligible effects since predation distance is fixed to a large value while in Allhoff and Drossel (2013) this distance may evolve to small, positive values. Why biomass flows are possible between very similar (but different) species and not for identical species is not clear. Furthermore, this introduces an additional selective pressure on neighbouring mutants: mutations close to their parent, which should be beneficial in cases with cannibalism (for instance by reducing direct competition), will usually be deleterious without cannibalism. Third, giving a justification for models excluding cannibalism based on individual-based models in the way of Costa et al. (2016) (see also Champagnat and Méléard, 2011; Takahashi et al., 2013; Champagnat et al., 2014; Campillo and Fritsch, 2015) would require discontinuous predation kernels (with a different value when predating preys with exactly the same traits). This would introduce artificial singularities in fitness landscapes.

Ordered predation. Some models (Loeuille and Loreau, 2005; Allhoff and Drossel, 2013) *a priori* assume an order for predation: species can only feed on smaller species. It necessarily excludes cannibalism. Ordered predation also arbitrarily implies that in the case of species with very similar size, only the larger can feed on the smaller. Consequently, in the case of small mutations, it prevents trophic interaction changes: a prey can not become a predator. On the other hand, in the case of large mutations, a prey mutant can instantly become a predator if its size is larger than the size of the predator. This also introduces an asymmetry in the fate of mutants: larger mutants are predators of their parent species whereas smaller mutants are prey of their parent species, even though both species may be very similar. Overall, assuming an ordered predation kernel imposes a structure to the food web and strongly constrains the evolution of trophic interactions.

Mutation kernels. Mutation kernels are assumed either Uniform or Gaussian, generally centred around the parents value, but not necessarily. Mutations can have effect proportional to the parental value (Loeuille and Loreau, 2005; Allhoff and Drossel, 2013) or independent of parental value, sometimes mixing both assumptions if several traits evolve (Allhoff et al., 2015; Allhoff and Drossel, 2016). Since models can make very different assumptions regarding their mutation kernels, it is difficult to compare them. For instance, assuming mutations not centred on the parental value (Allhoff et al., 2015) mimics migration from a regional pool of species rather than mutations.

Mutation size. All models, except the one of Brännström et al. (2011), assume that mutation effects are large. Some authors even show that if mutations are too small then diversification cannot occur (Allhoff et al., 2015). If mutations should have large effects, then evolutionary branching is certainly not an important phenomenon in the evolution of trophic networks, since it requires small mutations in the adaptive dynamics framework. However, the model by Brännström et al. (2011) showed that small mutations can be sufficient to make a relevant trophic network emerge. Overall, it is neither clear why small mutations are sufficient under some conditions and not under others, nor whether the assumptions about the mutation kernel can strongly affect the evolution of food webs.

Interference competition. In all models we reviewed a direct competition between species is added. Direct competition does not depend on trophic interactions but is supposed to be due to other mechanisms such as competitive interference, for instance for space. Inter and intraspecific interference competitions are generally identified as important driving forces behind food web evolution because of two main reasons (see *e.g.* Allhoff et al., 2015). First, strong intraspecific interference competition forces populations to stay small, allowing more species to co-exist on the same amount of resource. This leads to higher diversity and larger networks. Second, strong interspecific interference competition induces similar species to evolve to different trait values hence allowing the emergence of different feeding strategies. Strong competition also affects the stability of food webs, as observed by Ritterskamp et al. (2016b): it prevents the emergence of complex evolutionary dynamics, such as oscillating or even chaotic dynamics. However, the parameterization of this important mechanism is tricky. Usually, competition follows either a Gaussian function of the difference of traits, or an indicator function of an interval (*i.e.* a constant function truncated out of this interval), most of the time without real justification. It may also be included in various ways in the functional response (additive factor, Beddington-DeAngelis, etc.). However, it is well-known that the shape of a competition kernel strongly influences the evolutionary patterns one may observe, specifically regarding the structuring of the population into well-separated sub-populations, interpreted here as distinct species (cf. *e.g.* Leimar et al., 2008; Genieys et al., 2009). Therefore, the choice of a competition model is of great importance to shape food webs. Some attempts were done in Allhoff et al. (2015); Ritterskamp et al. (2016a) to justify the chosen form of interference competition kernels, but this issue remains largely open.

Variations of other features. Models can also differ for other features, more or less importantly. Loeuille and Loreau (2006) studied the emerging allometries between species densities and body masses in the model by Loeuille and Loreau (2005). They concluded that the exponent of allometry is strongly influenced by predation parameters.

Ritterskamp et al. (2016c) considered two resources; Guill and Drossel (2008) assumed a variation of the form of the Beddington-DeAngelis functional response; Allhoff et al. (2015) and Ingram et al. (2009) extended Loeuille and Loreau (2005)'s model to evolving feeding niche width and include a Beddington-DeAngelis functional response. We also did not review models assuming that the food web is structured on another trait than size or body mass: Drossel et al. (2001, 2004); Rossberg et al. (2008); Takahashi et al. (2013) assumed an abstract discrete binary trait governing morphology, behaviour or predation interactions *via* foraging and vulnerability. We invite the reader to read the above-cited references for further details. Even though these variations in assumptions seem minor at first glance, it is not clear whether or not they can significantly affect food webs evolution. However, for simplicity, we did not include these minor variations into our analysis.

Biomass conversion efficiency. Surprisingly, a single feature is common among all models: the *biomass conversion efficiency* (or conversion factor), *i.e.* the fraction of ingested biomass devoted to the production of biomass of newborns, is supposed constant. Assuming that the conversion efficiency is independent of the mass / body size of predators and prey is undoubtedly important because it implies that the mass converted by individuals when consuming prey is increasingly large when feeding on larger prey, with no limit. In other words, there is no cost for predation: feeding on larger prey is not more costly than on smaller prey. This is in contradiction with empirical data which show that there is a trade-off for predators between eating small and large prey (Baras et al., 2014; Norin and Clark, 2017): there is an optimal prey size for which the conversion efficiency is the highest. This can be due to a trade-off between the low biomass given by small prey but lower costs to forage, handle and digest than for larger prey. It can also be due to the fact that predators can feed only on a part of a large prey: the biomass converted from a large prey attains a maximum. This is also in contradiction with another common assumption of these models: if there exists a preferred size for prey, and if this preference can evolve, it should correspond to the best compromise between eating small or large prey. How the efficiency of biomass conversion affects the evolution of food webs has been ignored by extant models. We show in the following that it is certainly a major mechanism underlying the evolution of trophic networks.

Overall, synthesising the common and different assumptions of the models of food webs evolution derived from Loeuille and Loreau (2005) shows that the important mechanisms underlying the diversification and evolution of trophic networks are not clear. It is not clear whether there is a single major mechanism that could give rise to relevant structured networks, or whether combinations of different assumptions can give rise to similar results. This statement can cast doubt on the significance of such models for the study of food web evolution because model construction, analysis and exploration can be biased by *a priori* expectations of network structure and general features. This is not necessarily because some combinations of assumptions give rise to relevant network structure that the underlying mechanisms are correct. At best, such models can give directions to what should be empirically verified: for instance, is it true that biomass conversion efficiency is constant? At worst, relaxing some of the assumptions made by the extant models, especially artificial constraints such as excluding cannibalism or imposing boundaries to evolving traits, could totally change the models' results and give aberrant, trivial or unrealistic network

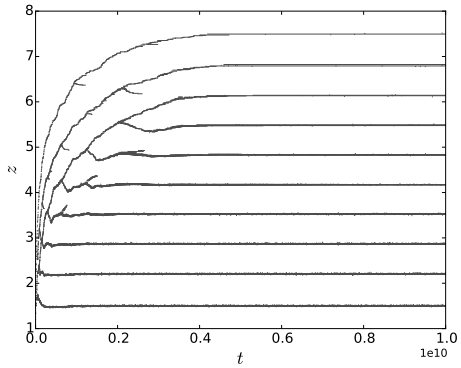


Figure 11: Evolution of the log-mass in the model by Brännström et al. (2011) with a single initial species with log-body mass $z = 1.2$, variance of the mutation distribution $\sigma_z = 0.01$, predation preference $\mu = 3$ (other parameters are given in Table 2).

structure. This is what we will explore in the following. We first propose a general model, unifying a large range of extant models. Second, we use our model to explore the results given by extant models when relaxing some of their assumptions. Finally, we use our model to explore the importance of the conversion efficiency.

E Emergence of unrealistic food webs under relaxed constraints

In line with Brännström et al. (2011), with log-mass as the unique evolving trait, we obtain diversification by branching (see Figure 11) for identical parameters (given in Table 2), except for the range of competition σ_α which is a bit smaller in order to favour branching events (see Figure 9).

Figure 12 shows three simulations where z and μ can both evolve, with much smaller mutations on μ than z. In Figure 12a, the food web initially evolves as expected: several branching occur and the food web gets structured. However, the smallest species progressively evolves to smaller body size and predation preference until they both become negative. This means that this species feeds on a larger prey: the resource. After this, the richness of the positive part of the food web (*i.e.* the network composed of species with positive body masses and positive predation preferences) decreases and the negative part of the food web progressively diversifies, producing a linear food web with more and more negative traits. The stationary state of the food web is not reached at the end of the simulation, as the food web seems to evolve similarly endlessly.

We ran simulations imposing positivity constraints on z and μ (by truncating mutation distributions below 0) and obtained Figure 12b. The behaviour of the food web is similar to the one of Figure 12a until the species with the smallest body mass reaches zero. After this time, this body mass remains close to zero and the predation preference goes to zero. This produces a progressive loss of species ending finally with a single resource-like

species (*i.e.* a species whose the size is close to the size of the resource species), with body mass and predation preference close to zero. Again the behaviour is unrealistic and occurs for a wide range of parameters values. An interpretation for this behaviour is that the smallest species progressively adapts to the optimal consumption of resource. Since, in addition, the resource-like species is subject to strong cannibalism, its density and the density of resource become too low for other species to survive. In Figure 12a, a small part of the positive food web remains because the body mass of the smallest species becomes negative before being optimally adapted to the consumption of resources ($z \approx \mu$), hence the remaining resources are sufficient to feed the positive part of the food web.

Replacing the artificial constraints on z and μ at 0 by a constraint at 1, we obtain Figure 12c. Contrary to what Figure 12b shows, the food web has a non-trivial structure where several species progressively evolve to the constraint: three species have trait $\mu = 1$ and one of them has also a log-mass $z = 1$. We emphasise that the artificial constraints that we put in the model in Figures 12b-12c play a key role in the food web evolution since some species reach the boundary of this constraint. Moreover, the sign of the invasion fitness (bottom of Figure 12) in the neighbourhood of these species shows that crossing these boundaries should be the natural evolution of the model.

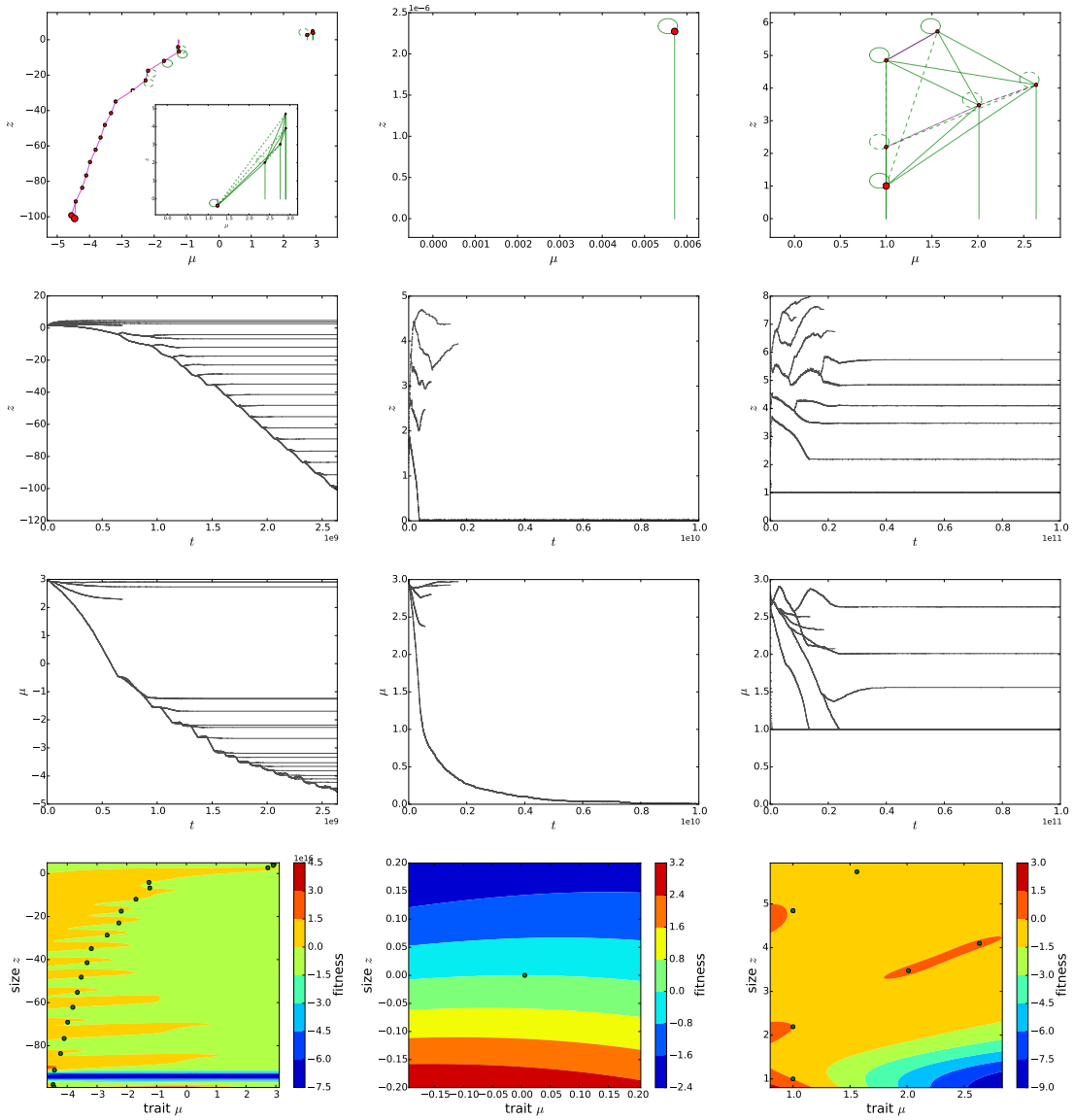
Figure 12 thus suggests that Loeuille and Loreau (2005) and Allhoff and Drossel (2013) obtained non-trivial food webs only because of artificial and hidden constraints due to the fact that $r_0 = 0$ and r_i is positive for all $i \geq 1$. In Allhoff et al. (2015) and Allhoff and Drossel (2016) the constraints on μ (and σ_γ) are due to the mutation kernels which restrict them to an interval far from zero (see Table 1). They actually justify this choice because otherwise μ (and σ_γ) can evolve to arbitrarily small values (see also Allhoff and Drossel, 2013).

Note that other unrealistic patterns were also observed in Allhoff and Drossel (2013) in the case where only z and μ evolve: the food web becomes composed mainly of a very large number of species on the first trophic level (with $z \approx \mu$) with a very wide range of body sizes, and a few species on the second trophic level. We do not observe this kind of phenomenon, neither in the extension of the model of Brännström et al. (2011) proposed in this section nor in the one studied in the next section.

Overall, our results suggest that relevant and non-trivial food webs emerge from models derived from Loeuille and Loreau (2005) only because of either artificial constraints imposed on the range values of the evolving traits, or because only one trait (size/body mass) evolves (Table 1). In the next section, we propose that relevant food webs could evolve without artificial constraints when considering that biomass conversion is not constant but depends on the relative size of the two interacting species.

F First evolutionary branching and the effect of the relative speed of evolution of the two traits

We analyse, in this section, the condition under which the first evolutionary branching occurs, *i.e.* when a single species coexist with the resource. We shall use the standard theory of adaptive dynamics to study the first branching event in the food web. We



(a) without positivity constraints

(b) with positivity constraints

(c) with constraints larger than 1

Figure 12: Food web evolution relaxing the constraint of fixed predation distance μ. From top to bottom: food web at final time of the simulation ($T = 2.6\,10^9$, overlay at intermediate time $t = 4.\,10^8$ (a); $T = 1.\,10^{10}$ (b); $T = 1.\,10^{11}$ (c)); evolution of the log-mass z; evolution of the predation preference μ; fitness landscape at time $T = 2.6\,10^9$ (a); $T = 1.\,10^{10}$ (b) and $T = 1.\,10^{11}$ (c) letting z and μ evolving in the model of Brännström et al. (2011) (see Table 1 and Section 2.2) without (a), with (b) positivity constraints and with constraints larger than 1 (c) on evolving traits z and μ with parameters of Table 2, variances of the mutation distributions $\sigma_z = 0.01$ and $\sigma_\mu = 0.001$.

consider a single species (z, μ) and study the fitness of mutant traits (y, η). The possibility of evolutionary branching is linked to the existence of directions of local convexity of $f(y, \eta)$ in the neighbourhood of (z, μ) (Leimar, 2001). In this case, (6) becomes

$$\begin{aligned} f(y,\eta) = \lambda(y,0)\,\gamma(y-\eta)\,N_0^* + \lambda(y,z)\,\gamma(y-z-\eta)\,N_1^* \\ - \gamma(z-y-\mu)\,N_1^* - \alpha(y-z)\,N_1^* - m(y), \end{aligned}$$

where we deduce from (15) that

$$N_1^* = \frac{\lambda(z,0)\gamma(z-\mu)\frac{r_g}{k_0} - m(z)}{\frac{\lambda(z,0)\gamma(z-\mu)^2}{k_0} + (1-\lambda(z,z))\gamma(-\mu) + \alpha(0)} \quad \text{and} \quad N_0^* = \frac{r_g - \gamma(z-\mu)N_1^*}{k_0}.$$

Figure 13 show the dynamics of the initial single species for different evolution speeds of both traits (in rows) and two values of the slope of ξ (in columns) with ξ defined by (11). In Figure 13 we follow the evolution of both traits of the species. A possible evolutionary pathway is represented by the successive black dots (and greys dots in case of branching[2]) starting from the red dot. The coloured regions give the direction of evolution for both traits (see legend on the right), with respect to the sign of both components of the fitness gradient at the point (z, μ) given by

$$\begin{aligned} \partial_y f(y,\eta)|_{(y,\eta)=(z,\mu)} = & \left[\frac{\partial_1\lambda(z,0)}{\lambda(z,0)} - \frac{z-\mu}{\sigma_\gamma^2}\right]\lambda(z,0)\,\gamma(z-\mu)\,N_0^* \\ & + \left[\frac{\partial_1\lambda(z,z)}{\lambda(z,z)} + \frac{\mu}{\sigma_\gamma^2}\right]\lambda(z,z)\,\gamma(-\mu)\,N_1^* \\ & + \frac{\mu}{\sigma_\gamma^2}\,\gamma(-\mu)\,N_1^* + \frac{m(z)}{4} \end{aligned} \tag{18}$$

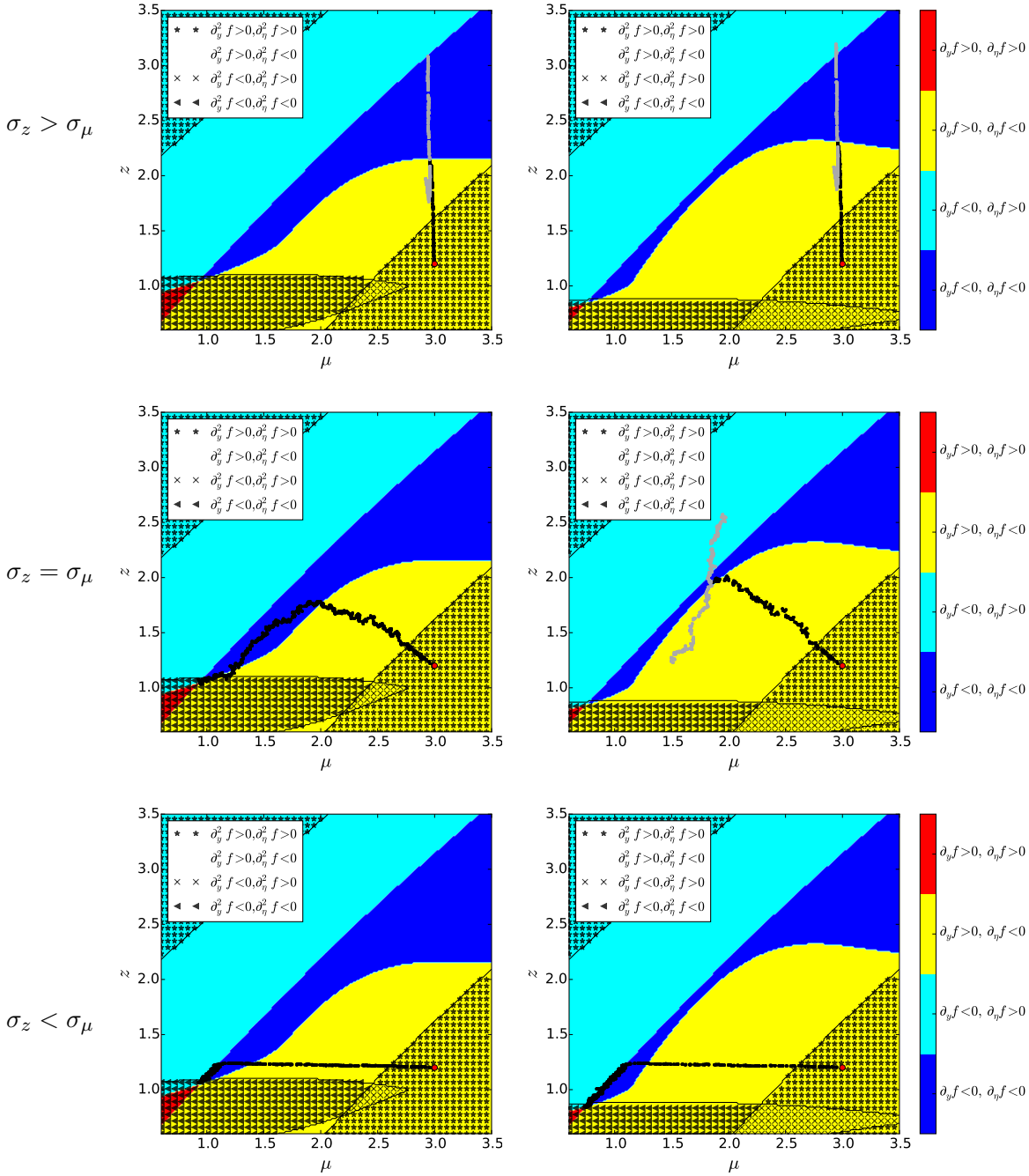
and

$$\partial_\eta f(y,\eta)|_{(y,\eta)=(z,\mu)} = \frac{z-\mu}{\sigma_\gamma^2}\,\lambda(z,0)\,\gamma(z-\mu)\,N_0^* - \frac{\mu}{\sigma_\gamma^2}\,\lambda(z,z)\,\gamma(-\mu)\,N_1^*\,. \tag{19}$$

For instance, in the yellow region the evolution follows the fitness gradient $\partial_y f > 0$ and $\partial_\eta f < 0$ meaning that the log-body size y increases and the preferred predation distance η decreases. At least in the beginning of the simulations, the initial species has a tendency to approach the curves $\partial_y f = 0$ and $\partial_\eta f = 0$ (respectively the frontiers between the yellow and the dark blue region, and between the light blue and dark blue region), consistently with the classical theory of adaptive dynamics. Note that if $\sigma_z = 10\sigma_\mu$ (resp. $\sigma_z = 0.1\sigma_\mu$), evolution is much faster in the z direction (resp. μ direction) and the population first reaches the line $\partial_y f = 0$ (resp. $\partial_\eta f = 0$).

The coloured regions are also filled with symbols giving the sign of the second order

[2]Note that after the branching times (for grey dots), the fitness landscapes are different from the ones of Figure 13 which are represented for one single species.



(a) $a = 4$ (b) $a = 5.5$

Figure 13: Sign of the first derivatives (18) and (19) and the second derivatives (20) and (21) of the invasion fitnesses for ξ defined by (11) with $a = 4$ (a) and $a = 5.5$ (b) and for mutation variances $0.01 = \sigma_z > \sigma_\mu = 0.001$, $\sigma_z = \sigma_\mu = 0.01$ and $0.001 = \sigma_z < \sigma_\mu = 0.01$ (from top to bottom). $b = 0.15$ and $\xi_{\max} = 0.75$. The red dot corresponds to the starting point of the simulation and the black path to the initial evolution of the single species, possibly leading to branching (grey paths correspond to the evolution of both branches).

derivative of fitness, given by

$$\partial_y^2 f(y,\eta)\big|_{(y,\eta)=(z,\mu)} = \left(\left[\frac{\partial_1\lambda(z,0)}{\lambda(z,0)} - \frac{z-\mu}{\sigma_\gamma^2}\right]^2 + \frac{\partial_1^2\lambda(z,0)}{\lambda(z,0)} - \left(\frac{\partial_1\lambda(z,0)}{\lambda(z,0)}\right)^2 - \frac{1}{\sigma_\gamma^2}\right)\lambda(z,0)\,\gamma(z-\mu)\,N_0^*$$
$$+\left(\left[\frac{\partial_1\lambda(z,z)}{\lambda(z,z)} + \frac{\mu}{\sigma_\gamma^2}\right]^2 + \frac{\partial_1^2\lambda(z,z)}{\lambda(z,z)} - \left(\frac{\partial_1\lambda(z,z)}{\lambda(z,z)}\right)^2 - \frac{1}{\sigma_\gamma^2}\right)\lambda(z,z)\,\gamma(-\mu)\,N_1^*$$
$$-\left[\left(\frac{\mu}{\sigma_\gamma^2}\right)^2 - \frac{1}{\sigma_\gamma^2}\right]\gamma(-\mu)\,N_1^* + \frac{1}{\sigma_\alpha^2}\alpha(0)\,N_1^* - \frac{m(z)}{16}, \tag{20}$$

$$\partial_{y,\eta}^2 f(y,\eta)\big|_{(y,\eta)=(z,\mu)} = \left(\frac{\partial_1\lambda(z,0)}{\lambda(z,0)}\,\frac{z-\mu}{\sigma_\gamma^2} - \frac{(z-\mu)^2}{\sigma_\gamma^4} + \frac{1}{\sigma_\gamma^2}\right)\lambda(z,0)\,\gamma(z-\mu)\,N_0^*$$
$$+\left(-\frac{\partial_1\lambda(z,z)}{\lambda(z,z)}\,\frac{\mu}{\sigma_\gamma^2} - \frac{\mu^2}{\sigma_\gamma^4} + \frac{1}{\sigma_\gamma^2}\right)\lambda(z,z)\,\gamma(-\mu)\,N_1^*$$

and

$$\partial_\eta^2 f(y,\eta)\big|_{(y,\eta)=(z,\mu)} = \left(\left[\frac{z-\mu}{\sigma_\gamma^2}\right]^2 - \frac{1}{\sigma_\gamma^2}\right)\lambda(z,0)\,\gamma(z-\mu)\,N_0^*$$
$$+\left(\left[\frac{\mu}{\sigma_\gamma^2}\right]^2 - \frac{1}{\sigma_\gamma^2}\right)\lambda(z,z)\,\gamma(-\mu)\,N_1^*. \tag{21}$$

Evolutionary branching is only possible when the second order derivative is positive at the isofitness line. As observed in Figure 13, we deduce from these expressions that the curves $\partial_\eta f = 0$, $\partial_\eta^2 f = 0$ are close to the line $z = \mu$ and the pair of lines $z = \mu \pm \sigma_\gamma$, respectively. This is due to the fact that, in the range of parameters we consider, the terms involving N_1^* are negligible with respect to those involving N_0^*. This implies that $\partial_\eta^2 f < 0$ whenever $\partial_\eta f = 0$, so that evolutionary branching can only occur in the direction z of the trait space.

Both for $a = 4$ and $a = 5.5$, the only evolutionary singularity in the region of traits we consider is located at the bottom left of the pictures (the border point of the red, yellow, light blue and dark blue regions), where both $\partial_y^2 f$ and $\partial_\eta^2 f$ are negative. Hence, this border point is a (local) evolutionary stable strategy where evolutionary branching cannot occur (note that for others values of a, the two regions can overlap such that evolutionary branching can occur in log-body size). However, for $a = 4$ and $\sigma_z > \sigma_\mu$, and $a = 5.5$ and $\sigma_z \geq \sigma_\mu$, we observe an evolutionary branching in Figure 13 which does not take place at the evolutionary singularity. It takes place along the line $\partial_y f = 0$ at points away from the curve $\partial_\eta f = 0$. This is explained by evolutionary branching along slow directional evolution, as described and analysed by Ito and Dieckmann (2014). They claim that such evolutionary branching can occur along one direction of the trait space when the evolution in the orthogonal directions of the trait space is slow. The canonical equation of adaptive dynamics (Dieckmann and Law, 1996; Champagnat et al., 2001) predicts that the speed of evolution in the μ direction of the trait space is proportional to the fitness gradient $\partial_\eta f$

and the mutation variance σ_μ^2. In cases where $\sigma_\mu = 0.1\sigma_z$, evolution in the μ direction is slow. When $\sigma_z = \sigma_\mu$ and $a = 5.5$, it is slow enough only because in this case the branching takes place at a point close to the line $\partial_\eta f = 0$, hence such that $\partial_\eta f$ is close to zero.

Overall, the first diversification occurs because of evolutionary branching of the log-body size. Once two morphs with different body size have emerged, both morphs can also evolve diverging preferred predation distance. Moreover the direction of evolution and its diversification strongly depends on the relative speed of the two traits.

References

Allesina, S., and Tang, S. (2012) Stability criteria for complex ecosystems. *Nature*, 483:205-208.

Allhoff, K. T. and Drossel, B. (2013). When do evolutionary food web models generate complex networks? *Journal of Theoretical Biology*, 334(Supplement C):122 – 129.

Allhoff, K. T. and Drossel, B. (2016). Biodiversity and ecosystem functioning in evolving food webs. *Philosophical Transactions of the Royal Society of London B*, 371.

Allhoff, K. T., Ritterskamp, D., Rall, B., Drossel, B., and Guill, C. (2015). Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. *Scientific Reports*, 5:10955.

Baras, E., Dugué, R., and Legendre, M. (2014). Do cannibalistic fish forage optimally? an experimental study of prey size preference, bioenergetics of cannibalism and their ontogenetic variations in the african catfish heterobranchus longifilis. *Aquatic Living Resources*, 27(2):51–62.

Bolchoun, L., Drossel, B., and Allhoff, K. T. (2017). Spatial topologies affect local food web structure and diversity in evolutionary metacommunities. *Scientific Reports*, 7:1818.

Brännström, Å., Loeuille, N., Loreau, M., and Dieckmann, U. (2011). Emergence and maintenance of biodiversity in an evolutionary food-web model. *Theoretical Ecology*, 4(4):467–478.

Brose, U., Williams, R. J., and Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letter*, 9:1228–1236.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789.

Campillo, F. and Fritsch, C. (2015). Weak convergence of a mass-structured individual-based model. *Applied Mathematics & Optimization*, 72(1):37–73.

Champagnat, N., Ferrière, R., and Ben Arous, G. (2001). The canonical equation of adaptive dynamics: a mathematical view. *Selection*, 2(1-2):73–83.

Champagnat, N., Jabin, P.-E., and Méléard, S. (2014). Adaptation in a stochastic multi-resources chemostat model. *Journal de Mathématiques Pures et Appliquées*, 101(6):755–788.

Champagnat, N. and Méléard, S. (2011). Polymorphic evolution sequence and evolutionary branching. *Probab. Theory Related Fields*, 151(1-2):45–94.

Costa, M., Hauzy, C., Loeuille, N., and Méléard, S. (2016). Stochastic eco-evolutionary model of a prey-predator community. *Journal of Mathematical Biology*, 72(3):573–622.

de Mazancourt, C. and Dieckmann, U. (2004). Trade-off geometries and frequency-dependent selection. *The American Naturalist*, 164(6):765–778. PMID: 29641922.

Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34(5):579–612.

Doebeli, M. and Ispolatov, I. (2017). Diversity and coevolutionary dynamics in high-dimensional phenotype spaces. *The American Naturalist*, 189(2):105–120.

Drossel, B. and Higgs, P.G., and McKane, A. J. (2001). The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology"*, 208(1):91–107.

Drossel, B., McKane, A. J., and Quince, C. (2004). The impact of nonlinear functional responses on the long-term evolution of food web structure. *Journal of Theoretical Biology"*, 229(4):539–548.

Fox, L. R. (1975). Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, 6(1):87–106.

Genieys, S., Bessonov, N., and Volpert, V (2009). Mathematical model of evolutionary branching. *Math. Comput. Modelling,*, 49(11-12):2109-2115.

Geritz, S. A. H., Ksidi, E., Meszéna, G., and Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12:35–57.

Guill, C., and Drossel, B. (2008). Emergence of complexity in evolving niche-model food webs. *Journal of theoretical biology*, 251(1):108–120.

Ho, H.-C., Tylianakis, J.M., Zheng, J.X., and Pawar, S. (2019). Predation risk influences food-web structure by constraining species diet choice *Ecology Letters*, 22:1734–1745.

Ingram, T., Harmon, L. J., and Shurin, J. B. (2009). Niche evolution, trophic structure, and species turnover in model food webs. *The American Naturalist*, 174(1):56–67.

Ispolatov, I., Madhok, V., Allende, S., and Doebeli, M. (2015). Chaos in high-dimensional dissipative dynamical systems. *Scientific reports*, 5:12506.

Ito, H. C. and Dieckmann, U. (2014). Evolutionary branching under slow directional evolution. *Journal of Theoretical Biology*, 360:290 – 314.

Laugen, A.T., Engelhard, G.H., Whitlock, R., Arlinghaus, R., Dankel, D.J., Dunlop, E.S., Eikeset, A.M., Enberg, K., Jørgensen, C., Matsumura, S., Nusslé, S., Urbach, D., Baulier, L., Boukal, D.S., Ernande, B., Johnston, F.D., Mollet, F., Pardoe, H., Therkildsen, N.O., Uusi-Heikkilä, S., Vainikka, A., Heino, M., Rijnsdorp, A.D., and Dieckmann, U. (2014). Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management *Fish and Fisheries*, 15:65–96.

Leimar, O. (2001). Multidimensional continuous stability and the canonical equation of adaptive dynamics. In Metz, J. A. J. and Dieckmann, U., editors, *Elements of Adaptive Dynamics*. Cambridge University Press.

Leimar O., Doebeli M., Dieckmann U. (2008). Evolution of phenotypic clusters through competition and local adaptation along an environmental gradient. *Evolution*, 62(4):807 – 822.

Loeuille, N. and Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102(6):5761–5766.

Loeuille, N. and Loreau, M. (2006). Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecology Letters*, 9(2):171–178.

Loeuille, N., Barot, S., Georgelin, E., Kylafis, G., and Lavigne, C. (2013). Eco-evolutionary dynamics of agricultural networks: Implications for sustainable management *Advances in Ecological Research*, 49:339–435.

Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A., and van Heerwaarden, J. S. (1996). Adaptive dynamics: A geometric study of the consequences of nearly faithful reproduction. In van Strien, S. J. and Verduyn-Lunel, S. M., editors, *Stochastic and spatial structures of dynamical systems (Amsterdam, 1995)*, pages 183–231. North-Holland.

Miele, V., Guill, C., Ramos-Jiliberto, R., and Kefi, S. (2019) Non-trophic interactions strengthen the diversity-functioning relationship in an ecological bioenergetic network model. *PLoS Computational Biology*, 15:e1007269.

Norin, T. and Clark, T. D. (2017). Fish face a trade-off between 'eating big' for growth efficiency and 'eating small' to retain aerobic capacity. *Biology Letters*, 13(9).

Otto, S. B., Rall, B. C., and Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, 450:1226–1229.

Pawar, S., Dell, A.I., Lin, T., Wieczynski, D.J., and Savage, V.M. (2019). Interaction dimensionality scales up to generate bimodal consumer-resource size-ratio distributions in ecological communities *Frontiers in Ecology and Evolution*, 7:1–11.

Peters, R. H. (1983). *The ecological implications of body size.* Press Syndicate of the University of Cambridge.

Portalier, S.M.J., Fussmann, G.F., Loreau, M., and Cherif, M. (2018). The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios *Functional Ecology*, 33:323–334.

Ritterskamp, D., Bearup, D., and Blasius, B. (2016a). A new dimension: Evolutionary food web dynamics in two dimensional trait space. *Journal of Theoretical Biology*, 405:66 – 81. Advances in Modelling Biological Evolution: Linking Mathematical Theories with Empirical Realities.

Ritterskamp, D., Bearup, D., and Blasius, B. (2016b). Emergence of evolutionary cycles in size-structured food webs. *Journal of Theoretical Biology*, 408:187 – 197.

Ritterskamp, D., Feenders, C., Bearup, D., and Blasius, B. (2016c). Evolutionary food web models: effects of an additional resource. *Theoretical Ecology*, 9(5):501 – 512.

Rossberg, A.G., Ishii, R., Amemiya, T., and Itoh, K. (2008). The top-down mechanism for body-mass-abundance scaling. *Ecology*, 89:567 – 580.

Takahashi, D., Brännström, Å., Mazzucco, R., Yamauchi, A., and Dieckmann, U. (2013). Abrupt community transitions and cyclic evolutionary dynamics in complex food webs. *Journal of Theoretical Biology*, 337:181 – 189.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., and Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, 20(7):402 – 409.

Yodzis, P. and Innes, S. (1992). Body size and consumer-resource dynamics. *American Society of Naturalists*, 139(6):1151 – 1175.