Collapse and rescue of evolutionary food webs under global warming

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Running headline

Food web evolutionary rescue

Abstract

1. Global warming is severely impacting ecosystems and threatening ecosystem services and human well-being. While some species face extinction risk, several studies have demonstrated the possibility that fast evolution may allow species adaptation and survival despite environmental change.
2. We aim to assess how such evolutionary rescue dynamics extend to multitrophic communities and whether evolution systematically preserve biodiversity under global warming.
3. Using a simplified consumer-resource model, we analyze mathematically how evolution of body mass and of foraging strategies affect coexistence. We then extend our analysis to diverse, multi-trophic networks of co-evolving morphs.
4. Our simulations predict that the long-term diversity loss triggered by warming is considerably higher in scenarios where evolution is slowed down or switched off completely, indicating that eco-evolutionary feedbacks indeed help to preserve biodiversity. Evolving webs however experience vast disruptions in their structure and functioning and reversing warming may not be sufficient to restore previous structures.
5. Our findings thus highlight how the interaction between evolutionary rescue and changes in trophic structures affects our understanding of ecosystem responses under warming with important implications for conservation and management policies.

Keywords

Adaptive Dynamics, Biodiversity conservation, Body mass evolution, Climate Change, Coevolution, Consumer-Resource model, Eco-evolutionary tipping point, Evolutionary rescue, Preadaptation, Trophic networks

Introduction

Ecosystems support human societies through ecosystem services, such as resource provisioning, pollination, and geochemical recycling, amongst others (Costanza & Daly, 1992). Recent global changes, planetary-scale human-driven changes rivaling some of the great forces of Nature and deeply impacting the Earth system functioning, however severely impact ecosystems. Current extinction rates suggest a sixth extinction crisis is under way (Barnosky et al., 2011) and major losses of biodiversity are expected (Thomas et al., 2004). Such extinctions, but also more largely impacts on species demography, ranges and phenologies (Parmesan & Yohe, 2003), changes in ecological interactions (Tylianakis et al., 2008) imply significant ecological networks reorganizations potentially threatening ecosystems functioning.

As food webs describe the distribution of energy and matter flows in ecosystems, they provide useful tools to discuss such functional changes. Current observations highlight how global warming may affect trophic interactions (Both et al., 2009). Under such stress, species evolution (or coevolution) within the network may constrain its maintenance and stability.

Existing models investigating ecosystem responses to global warming often ignore evolutionary processes and species interactions. This is particularly true for “niche” or “envelop” models (Colwell & Rangel, 2009) that link data of species occurrence with climatic variables to build a multivariate statistical representation of species niches. Future species distributions are then predicted according to different climate change scenarios (e.g. Pearson et al., 2002), implicitly assuming that the niches are fixed. Evolution may however affect species fundamental niches, especially given current strong selective pressures, while community turnover, also expected given current changes (Tylianakis et al., 2008), may modify realized niches. While envelop models are important first steps, they are thus limited in their ability to understand the effects of global warming, and to provide relevant conservation policies (Lavergne et al., 2010).

Ignoring evolution is based on the controversial assumption that ecological and evolutionary processes act on separate timescales, while recent studies show that evolution may act within decades or even years (Koch et al., 2014; Olsen et al., 2004). Anthropogenic disturbances create strong selective pressures that favor rapid evolution (Hendry et al., 2008) emphasizing the importance of considering evolution when addressing global warming issues. For instance, Bradshaw & Holzapfel (2001) showed that the genetically controlled photoperiodic response of the mosquito, *Wyeomyia smithii,* has shifted towards shorter, more southern day-lengths as growing seasons have become longer due to global warming. Their experimental design allows them to attribute this shift, which is detectable over a time interval as short as five years, to adaptive evolutionary change rather than phenotypic plasticity.

In some situations, evolution enables species to survive severe environmental change. Gomulkiewicz & Holt (1995) theorized this concept as "evolutionary rescue". Adaptive evolutionary change then restores positive growth to declining populations and prevents extinction. Using experimental evolution, Bell & Gonzalez (2009) exposed hundreds of populations of yeast to normally lethal conditions of salt and observed evolutionary rescue within a few generations. For a review on the different factors involved and a discussion on the empirical evidence for evolutionary rescue, see Carlson et al. (2014). Evolution may however also threaten species maintenance. Environmental change can for example bring an evolutionary attractor out of the viability area so that selection leads to a non-viable phenotype given the new ecological conditions ("evolutionary trapping", Ferriere & Legendre, 2012) or the evolution of one species can drive another interacting species to extinction ("evolutionary murder", e.g. Dieckmann, Marrow, & Law, 1995). Accounting for evolution is therefore critical to implement relevant conservation decisions (Stockwell, Hendry, & Kinnison, 2003).

Accounting for species interactions is equally crucial. Indeed, several examples highlight that complex unexpected behaviors can arise from the interplay between evolution

and species interactions. For instance, Norberg et al. (2012) analyzed a spatially explicit multi-species model and demonstrated that evolution under climate warming can create extinction debts, long after climate stabilization, but only when competitive interactions are accounted for. Osmond, Otto, & Klausmeier (2017) showed that the maximal environmental change rate an evolving prey population can support before going extinct may increase in the presence of a predator, which seems rather surprising at first. In fact, in some cases (e.g. selective predation of maladapted preys), the presence of a predator accelerates prey evolution, enabling the prey to follow the environmental optimum more closely. Therefore, within a network context, the conditions for and the mechanisms underlying evolutionary rescue can be much more complex. A focal species could be rescued by the evolution of another interacting species, a concept called "indirect evolutionary rescue" by Yamamichi & Miner (2015). On the contrary, if evolutionary rescue happens for various species within the network, a focal species could still go extinct if its enemies (resp. positive interactors) recovery is too fast (resp. too slow) compared to its own (Loeuille, 2019). If in addition this species is key to the network, vast disruptions are to be expected due to secondary extinctions.

A key question is therefore whether evolutionary rescue, derived from a monospecific approach, can extend to ecological networks. Models that consider evolutionary processes within multi-species communities, such as Norberg et al. (2012) are currently rare. Single or few species models are useful because they focus on essential mechanisms happening in more complex networks. Nevertheless, they provide a limited view of the complex indirect interactions occurring in diverse networks (Ellner & Becks, 2011). This is particularly true for the theory of evolutionary rescue. The goal of the present study is therefore to expand existing knowledge from simplified mono-specific systems to complex multi-species networks. More precisely, we ask whether evolutionary rescue effects can promote food web persistence under warming.

We propose to address this question following a two-level approach. First, we investigate the impact of temperature change on a simple consumer-resource model where the consumer body mass and foraging strategy undergo evolution. Within this framework, we analyze when evolution actually facilitates coexistence (trough evolutionary rescue) or threatens it (through trapping). We first study body mass evolution, then let foraging strategies evolve while fixing body mass. We finally give a brief glimpse on the two-trait coevolution scenario.

We then discuss how complex feedbacks occurring in more complicated settings affect our results, by allowing the food web module to evolve beyond the first diversification, resulting in complex multi-trophic networks. Trophic structures emerging from such evolutionary dynamics share many features with empirical food webs (Allhoff et al., 2015; Loeuille & Loreau, 2005). Such evolutionary food web models therefore provide a powerful tool to study community responses to changing environmental conditions. We investigate whether evolutionary rescue is likely in such diverse, multi-trophic communities and compare the results with the lower complexity approaches. Based on evolutionary rescue theory (Gomulkiewicz & Holt, 1995), we hypothesize that faster evolution and lesser warming will help the rescue process and facilitate community maintenance. We test this hypothesis using numerical simulations, keeping in mind that indirect effects may modify this prediction in many ways. We also expect upper trophic levels, more energy-limited and closer to the extinction threshold, to be more impacted (Binzer et al., 2012; Weinbach et al., in prep).

Model and Methods

Model presentation

Ecological dynamics

We model the trophic network using ordinary differential equations:

$$\frac{dB_0}{dt} = r\left(1 - \frac{B_0}{K}\right)B_0 - \sum_i a_{i0}B_0B_i \quad (1)$$

$$\frac{dB_i}{dt} = \sum_{j=ressource/prey} ea_{ij}B_jB_i - \sum_{j=predator} a_{ji}B_jB_i - \sum_{j=competitor} c_{ij}B_jB_i - d_iB_i \quad (2)$$

Where B_i is the biomass density of morph i; r and K are respectively the intrinsic growth rate and carrying capacity of the external resource; a_{ij} and c_{ij} are respectively the attack and competition rate of morph i on morph j; e is the conversion efficiency from prey to predator (set to 0.85 following Yodzis & Innes (1992)) and d_i is the death rate of morph i. Energy enters the system as an external resource of biomass density B_0 whose dynamics in the absence of interaction follows a logistic growth (1). Variations of consumer biomass density B_i (2) include four terms: a growth rate based on prey consumption, and loss terms due to predation, competition and natural death. See Table S1 (Supporting Information) for a complete list of variables and parameters.

Evolutionary processes and adaptive traits

Each consumer morph i has two adaptive traits: its body mass m_i and its feeding center f_i. Body mass largely constrain trophic interactions as observed empirically (Woodward et al., 2005) and within theoretical frameworks (Allhoff et al., 2015; Loeuille & Loreau, 2005). The feeding center of a consumer corresponds to the prey body mass allowing a maximal attack rate

and therefore describes its foraging strategy within our framework. The traits evolve following a mutation-selection process. The external resource is characterized by its body mass m_0 that is not allowed to evolve.

Eco-evolutionary framework

Many ecological parameters, such as mortality rates or attack rates, are known to scale with body mass (Brown et al., 2004; Peters, 1983). Also, we assume strong competition between two consumers with similar foraging strategies because of the resulting strong overlap in their ecological niches (Macarthur & Levins, 1967). We therefore assume:

$$d_i = {m_i}^{-0.25} d \tag{3}$$

$$a_{ij} = \frac{m_i^{-0.25}}{\sqrt{2\pi}s} e^{\frac{-(log(f_i)-log(m_j))^2}{2s^2}} \tag{4}$$

$$c_{ij} = \frac{c_0}{\sqrt{2\pi}s} e^{\frac{-(log(f_i)-log(f_j))^2}{4s^2}} \tag{5}$$

Where s is the feeding niche width (standard deviation of the gaussian feeding kernel (**Fig. 1**)), assumed constant and identical for all morphs, and c_0 is a scaling constant for the interference competition.

Temperature dependence

Biochemical reactions and thus metabolic rates are known to grow exponentially with temperature. Following Brown et al. (2004),we incorporate temperature dependency as an Arrhenius factor, into the resource growth rate r, and the mortality rate d_i of consumer i as follows:

$$r(T) = r_0 e^{\frac{-E(T_0-T)}{kTT_0}} \tag{6}$$

$$d_i(T) = d_0 m_i^{-0.25} e^{\frac{-E(T_0-T)}{kTT_0}} \quad (7)$$

Following Fussmann et al. (2014), we assume the carrying capacity decreases exponentially with temperature.

$$K(T) = K_0 e^{\frac{E(T_0-T)}{kTT_0}} \quad (8)$$

Here, k is the Boltzmann constant and E the activation energy (Table S1). These relationships hold over the temperature range of normal activity (0-40 °C for most organisms). Note that while (6) and (7) are widely accepted, (8) is likely to be context-dependent (see Uszko et al., 2017).

Framework to address evolutionary rescue

We first study the simple consumer-resource model (hereafter "Consumer-Resource" model). Then, we analyze the complex networks that may emerge from the evolutionary dynamics (hereafter Community Evolution Model, Loeuille & Loreau, 2010). **Fig. 1** shows a schematic view of the two models. Using this two-step approach, we aim at providing an encompassing view of the eco-evolutionary responses of food web to warming.

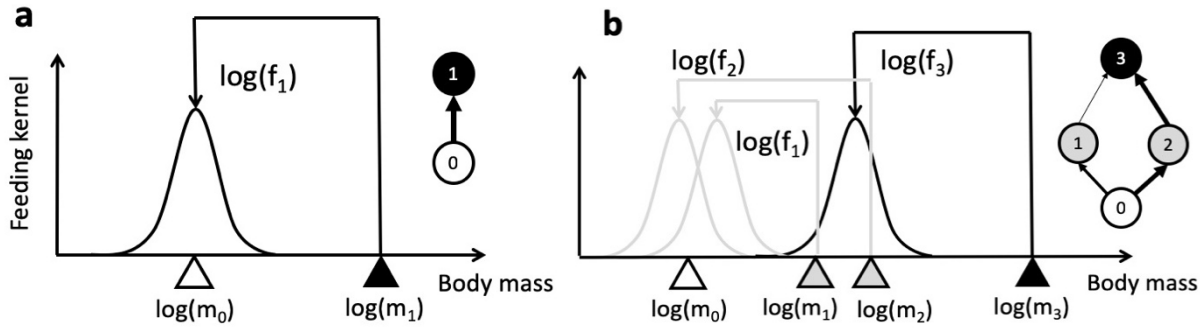

Figure 1: (Adapted from Allhoff et al., 2015). **a.** Schematic view of the Consumer-Resource model that allows for analytical investigations. The consumer (black triangle) is characterized by its body mass m_1 and its feeding center f_1 whose logarithm is the mean of the Gaussian function representing its attack rate kernel on the potential prey (black curve). Here the consumer feeds on an external resource (white triangle) with maximum attack rate. In the top right corner, the resulting two species trophic network is represented. **b.** Schematic view of the Community Evolution Model where large mutational steps are allowed facilitating diversification, emergence of higher trophic levels and leading to complex network structures. The snapshot here shows 3 morphs: morph 3 (black triangle) feeds on morph 1 and 2 (grey triangles) with respectively low and high attack rates, morph 2 and 1 feed on the external resource (white triangle) with respectively low and high attack rates. In the top right corner, the resulting trophic network is illustrated. Note that this is only a snapshot, the real network is dynamical and with typically contains many more morphs.

Consumer-Resource Model

The ecological dynamics of the Resource-Consumer model are derived from equation (1) and (2) in the case of only one consumer:

$$\frac{dB_0}{dt} = r\left(1 - \frac{B_0}{K}\right)B_0 - a_{10}B_1B_0 \tag{9}$$

$$\frac{dB_1}{dt} = ea_{10}B_0B_1 - (a_{11}(1-e) + c_{11})B_1^2 - d_1B_1 \tag{10}$$

We use adaptive dynamics (Dieckmann & Law, 1996; Metz, Nisbet, & Geritz, 1992) to investigate how warming affects the eco-evolutionary dynamics of the Consumer-Resource module. Two major assumptions are being made: first, evolution occurs at a much longer timescale than ecology and second, mutations are of small amplitude. The first assumption is in contradiction with the idea of evolutionary rescue that implies evolutionary and ecological

dynamics happen on overlapping timescales. We therefore relax this hypothesis when adaptive dynamics indicate the system is supposed to go extinct (Ferriere & Legendre, 2012). Thanks to the timescale separation hypothesis, the environment felt by the mutant can be clearly defined as the trait of the resident population associated with ecological equilibrium (B_0^*,B_1^*) whose expression can be found in the supporting information (Appendix S1 A.1).

In the case of body mass (m_1) evolution, the relative fitness $w(m_1^{mut}, m_1^{res})$ of a rare mutant corresponds to its growth rate in the resident population:

$$w(m_1^{mut}, m_1^{res}) = \left[\frac{1}{B_1^{mut}} \frac{dB_1^{mut}}{dt}\right]_{B_0^*, B_1^*, B_1^{mut} \ll B_1^*} \tag{11}$$

Positive values of *w* indicate that the mutant frequency increases within the resident population, eventually replacing it. The sequence of trait substitutions describes the evolutionary dynamics of the system. Such a sequence can be approximated by the canonical equation (Dieckmann & Law, 1996):

$$\frac{dm_1}{dt} = CN_1^* \mu \sigma^2 \left[\frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}}\right]_{m_1^{mut} = m_1^{res} = m_1} \tag{12}$$

where $C, N_1{}^*, \mu, \sigma$ are respectively a homogenizing constant, the resident density at ecological equilibrium, the mutation rate and the amplitude of mutations. The zeros of equation (12) are called evolutionary singularities, m_1^*, and verify:

$$\left[\frac{\partial w(m_1^{mut}, m_1^{res})}{\partial m_1^{mut}}\right]_{m_1^{mut} = m_1^{res} = m_1} = 0 \tag{13}$$

A singularity is convergent when evolutionary dynamics starting close to it select traits that are even closer and it is invasible when, being at the singularity, nearby mutants can invade (Geritz et al., 1998). The conditions for invasibility and convergence can be determined based on the sign of the second derivatives of the invasion fitness function (11) (see Appendix S1 B.2.d). A

non-invasible and convergent evolutionary singularity is a Continuously Stable Strategy (CSS, Eshel, 1983), which corresponds to an evolutionary endpoint (i.e., evolution stops at the selected singularity). An invasible and convergent singularity is called a Branching Point and may lead to a stable dimorphism in the population (i.e., emergence and coexistence of two consumer populations that differ in their body mass, due to disruptive selection, (Geritz et al., 1997)). An invasible and divergent singularity is called a Repellor.

We first fix the consumer feeding center and let only its body mass evolve, then, we fix the consumer body mass and let the feeding center evolve. Finally, we give a glimpse on what can happen when both traits coevolve. By analyzing how the pattern of evolutionary singularities changes with temperature, we discuss the maintenance of the trophic module confronted with warming.

Community Evolution Model

We let the Consumer-Resource module evolve (both body mass and feeding center) beyond the first diversification, which leads to the emergence of a multi-trophic network (Allhoff et al., 2015; Loeuille & Loreau, 2005). Simulations start with a single ancestor morph with body mass $m_1 = 100$ and feeding center $f_1 = 1$ feeding on the external resource with body mass $m_0 = 1$. We define a mutational frequency μ so that a mutation event takes place every $1/\mu$ time steps. At each mutation event, a parent morph i is chosen randomly and proportionally to its population density. The mutant j's traits are set as follows: $log10(m_j)$ (resp. $log10(f_j)$) is randomly selected from a normal distribution of mean $log10(m_i)$ (resp. $log10(f_i)$) and variance σ^2. The value of σ is chosen (0.25) so that occasional big mutational steps are allowed: 5% of the mutations result in $m_j < \frac{m_i}{3}$ or $m_j > 3m_i$. The mutant's initial biomass density B_j is set to ε taken from the parent's biomass density B_i. ε is also the extinction threshold below which a morph population is removed from to system (Table S1).

We define evolutionary rescue at the network scale starting from the most general definition proposed by Ferriere & Legendre (2012): "evolutionary rescue occurs when a population subject to environmental change 'performs better' under the operation of evolutionary processes than without these processes". We adapt the definition by assessing not the performance of a given population but rather the performance of the whole network, given different rules of coevolution and different warming intensities.

Performance is measured based on the maintenance of diversity. The most straightforward diversity measure in our model is the trait diversity, i.e. the cardinality of the set of all (m_i, f_i) at a given time. While this is certainly a valuable measure from a functional and structural point of view, a large focus exists in conservation biology on the preservation of species diversity. Because our model ignores genetic details and focuses on phenotypes, the definition of species is notoriously tricky. For lack of better criteria, we define species as clusters in the phenotypic space (using the silhouette method (Rousseeuw, 1987) on the k-means algorithm, Appendix S2).

Diversity is measured before and after warming. Due to the constant mutation/extinction events, diversity measures are subject to stochastic variations. Therefore, we need a criterion to assess whether the system has reached a 'stable state' before and after disturbance. We consider the system to be stable when the ratio between the trait diversity standard deviation and mean (coefficient of variation) over a time window of 2.10^6 mutation events is below 0.045. Such a criterion allows for at least 95% of the observed trait diversity over this time window to be within the range of $\pm 10\%$ of the observed trait diversity mean over the same period. We are thus not focusing on the transient state following perturbation but rather build our community-scale evolutionary rescue definition on the long-term response of the network to warming.

We consider different scenarios with evolution ("scenario E") and without evolution ("scenario NE"). In a "scenario NE μ", the network is built up with a mutation frequency μ.

The first time stability is reached, evolution stops ($\mu = 0$). When a new equilibrium is reached (pre-disturbance state), warming occurs and we reach a third equilibrium situation (post-disturbance state). This separation in two steps allows to distinguish the effect of warming from the effect of competitive exclusion between mutant and resident morphs that would happen regardless of changes in temperature. Effects of warming are here based on the comparison of diversity between post and pre-disturbance states. In a "scenario E μ", the network is built up with a mutation frequency μ. The first time stability is reached, warming occurs. The second time, the simulation ends.

All in all, we launched 420 simulations, with initial temperature 275 K, with 10 replicas per condition. Conditions are with versus without evolution (scenario NE or E), mutation frequency (10^{-1},10^{-2},10^{-3}) and warming intensity (0,2,4,6,8,10 or 20 K). We assess trait and species diversity maintenance comparing their means before (d_{bef}) and after the warming (d_{aft}) through their quotient d_{aft}/d_{bef} (hereafter "persistence"). We use statistical models implemented in R-software to explain this persistence by the different conditions.

Results

Resource-Consumer model

For convenience, the following notations are introduced:

$$M_{\underset{0}{1}} \stackrel{\text{def}}{=} log_{10}(m_{\underset{0}{1}}) \qquad F_1 \stackrel{\text{def}}{=} log_{10}(f_1) \tag{14}$$

Considering the evolution of m_1 (resp.f_1) is thus equivalent to considering the evolution of M_1(resp. F_1).

How does the selected body mass depend on temperature?

The evolving trait is the consumer body mass M_1 while the feeding center F_1 is fixed and matches the resource body mass $\log_{10}(m0) = 0$.

Two important results arise. First, conditions for $B_1^* > 0$ show that above a critical temperature T_{lim}, the consumer population goes extinct no matter its body mass so that no evolutionary rescue is possible (Appendix S1 A.2). Second, using adaptive dynamics, we derive equation (15) (Appendix S1 B.1.b) and conclude that the body mass at the evolutionary singularity does not depend on temperature since temperature does not influence any parameter of this equation.

$$c_0 + a_{11}(M_1^*) * \left(1 - \frac{4(M_1^* - F_1)}{s^2\, ln(10)}\right) = 0 \tag{15}$$

Fig. 2 is an E^3-diagram showing the dependence of evolutionary singularities on temperature. The temperature T is represented by the x-axis while the evolving trait is represented by the y-axes. The curves correspond to the evolutionary singularities and the trait types and colors indicate their nature. Numerical calculations show there are two singularities, a repellor and a CSS, whose values do not depend on the temperature in agreement with

equation (15). Above temperature T_{lim} (see Appendix S1 A.2 for an analytical expression), the net energy flow from resource to consumer is not sufficient to compensate for consumer mortality losses.

At T_{lim}, the CSS collide with the non-viability area. This is a case of "evolutionary trapping" (Ferriere & Legendre, 2012). No evolutionary rescue is possible since the CSS is within the non-viability area no matter the temperature above T_{lim}. Hence, consumer survival depends on the intensity of warming: a warming from T_1 to T_2 will not threaten the consumer population while a warming from T_1 to T_3 will make the consumer population go extinct.

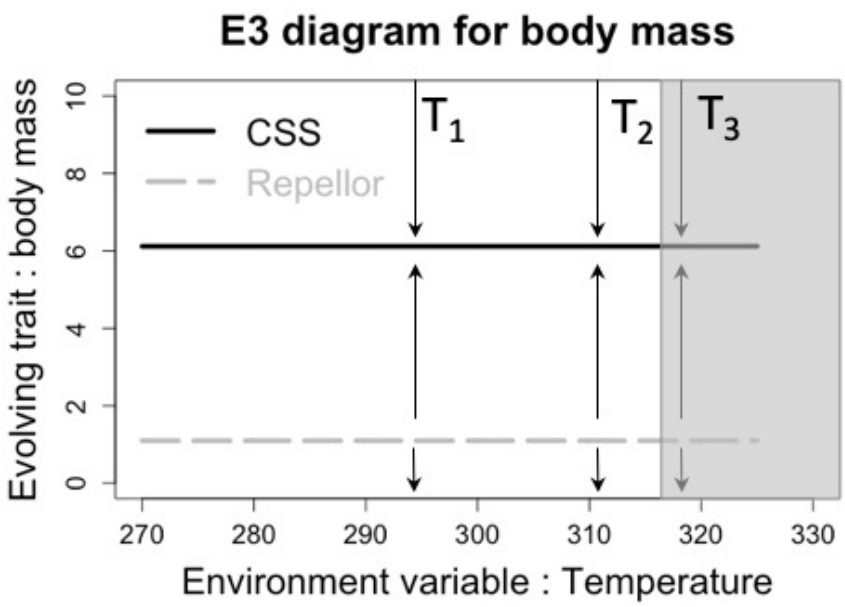

Figure 2: E^3-diagram Body Mass-Temperature. Nature of singularities is given by line type and color. Grey area is the non-viability area (i.e. representing consumer extinction). The arrows indicate the direction of evolutionary trajectories. The temperatures $\boldsymbol{T_1}, \boldsymbol{T_2}, \boldsymbol{T_3}$ are used to discuss the impact of warming. Parameters values used are the ones in table S1.

How does the selected foraging strategy depend on temperature?

The feeding center F_1 now evolves while the body mass M_1 is fixed (0 for small masses and 2 for big masses). As detailed in Appendix S1 (B.2.b), evolutionary singularities F_1^* verify:

$$(M_1 - F_1^*)a_{11}B_1^* - (F_1^* - M_0)a_{10}B_0^* = 0 \qquad (16)$$

Given equation (16), we prove analytically that at least one evolutionary singularity exists and that all singularities verify $M_0 < F_1^* < M_1$ (Appendix S1 B.2.b).

For convenience, we define:

$$\alpha \epsilon \mathbb{R} \text{ such as: } F_1 \stackrel{\text{def}}{=} \alpha M_0 + (1-\alpha)M_1 \qquad L \stackrel{\text{def}}{=} \frac{M_1 - M_0}{s} \qquad (17)\ (18)$$

α characterizes the consumer foraging strategy. Such strategies vary between two extreme scenarios: $\alpha = 1$ (the consumer specializes on the resource) and $\alpha = 0$ (the consumer specializes on cannibalism). Equation (17) being a bijection, considering the evolution of F_1 is equivalent to considering the evolution of α.

Since $B_0^*(T)$ and $B_1^*(T)$ depend on the temperature, equation (16) indicates the latter has an impact on the value of the evolutionary singularities α^* and hence the evolutionary dynamics. Equation (16) is rewritten separating the temperature T and the singularity α^*which allows for further insights regarding the effects of warming. The mathematical analysis (Appendix S1 B.2.c) shows there are four possible scenarios corresponding to four different qualitative outcomes of warming. Scenarios are presented in table 1, with their biological meaning. The scenarios differ in the consumer to resource body mass ratio (parameter L) and/or consumer body mass M_1. For a given value of M_1, we note $L^c(M_1)$ the critical value of L at which the change of outcome occurs.

When the ratio between consumer and resource body masses is small (scenario A), warming leads to a CSS that increases with temperature (**Fig. 3a**). Selected foraging strategies therefore increasingly rely on resource consumption under warming.

For intermediate values of consumer to resource body mass ratio (scenario B), in addition to increasing the selected α, warming also changes the nature of the singularity from branching point to CSS (**Fig. 3c**). To further investigate the consequences of branching events happening at low and intermediate temperatures, we simulated the corresponding eco-evolutionary dynamics. Diversification leads to the emergence of a new upper trophic level as presented in **Fig. 4**. The new module is a three-level food chain consisting of a consumer specialized in its resource ($\alpha \simeq 1$ corresponding to the first trophic level and another consumer with the same body mass specialized in the former consumer and himself ($\alpha \simeq 0$). Warming from T_1 to T_2 on **Fig. 3a** therefore reduces diversity by impeding the branching (3-level food chain) and replacing it by a CSS (2-level food chain).

Finally, consider scenarios with big consumer to resource body mass ratios. At small consumer masses (scenario C), three singularities exist for low temperatures: a branching point, a repellor and a CSS. Branching point and CSS values increase with temperature while the value of the repellor decreases with temperature. The branching point and the repellor eventually collide, letting the system with only a CSS close to one: a consumer specialized on its resource (**Fig. 3f)**. Again, we investigated the branching outcome: the emerging food chain is qualitatively similar to the one obtained after branching in the case of intermediate CR body masses ratio (**Fig. 4b**). At large masses (Scenario D, **Fig. 3h**), the system is characterized by an increasing CSS with warming.

414 In all scenarios, a limit temperature T_{lim} exists (see Appendix S1 A.2 for an analytical
415 expression) above which the consumer population cannot survive whatever the value of the
416 foraging trait α. No evolutionary rescue can happen for temperatures above T_{lim} .

417 If the final temperature is below T_{lim}, evolutionary rescue is always possible. In all four
418 scenarios, consumers might adapt fast enough to the new conditions and avoid extinction.

419 For instance, at small CR body mass ratios (**scenario A, Fig. 3a**), a warming from T_1 to
420 T_3 leads the system to enter the non-viability area (black circle). The food chain can however
421 persist if evolutionary rescue occurs (white arrow) as larger values of α are selected and
422 eventually allow consumer survival. Such an outcome is simulated on **Fig. 3b**: warming (sun
423 symbol) provokes the collapse of the consumer population (black curve) but if α increases fast
424 enough (grey curve), population recovery occurs. Note that given the very small population size
425 after disturbance, in nature, the consumer population may still go extinct due to demographic
426 stochasticity or genetic drift (not accounted for here).

427 It should nevertheless be noted that if warming is progressive from T_1 to T_2 first and
428 then from T_2 to T_3 (**Fig. 3a**), the consumer population is never endangered as the trait remains
429 close to the CSS curve, with a small lag: progressive warming decreases extinction risk, in
430 accordance with both theoretical (Gomulkiewicz & Holt, 1995) and empirical works (Bell &
431 Gonzalez, 2009). This is true for all 4 scenarios.

432

433 Rescue is not the only evolutionary process constraining diversity and persistence.
434 Consider intermediate body mass ratios (scenario B, **Fig. 3c**), and a warming from T_1 to T_2
435 occurring just before (**Fig. 3d**) or long after branching (**Fig. 3e**). Because branching changes
436 the food chain structure (**Fig. 4b**), the time of warming matters. Warming before branching
437 leads to potential evolutionary rescue as described above (**Fig. 3d**). Warming occurring after
438 branching is however less threatening as the consumer population now occupies two ecological

niches unlikely to be simultaneously destroyed by warming (**Fig. 4b**). Note that the higher branch (**Fig. 4a**) has a trait value close to the strategy selected under warmed conditions. **In Fig. 3e,** such a scenario is simulated: population of the top trophic level (low branch) decreases while the population of the intermediate consumer (high branch) increases under warming; total consumer biomass increases. Branching therefore allows a preadaptation in scenario C.

Under scenario C, warming can be responsible for crossing eco-evolutionary tipping points (here around 300 K). A warming from T_1 to T_2 (**Fig. 3f**) utterly modifies the number of convergent singularities. At T_1, the system is characterized by the existence of three singularities (CSS, repellor and branching point) while at T_2 only the CSS still exists. Consequently, if initially the system is in the branching attraction area, such a warming would be responsible for a reduction of diversity, as the system moves from a polymorphic situation (branching) to a monomorphic situation (CSS). While similar to scenario B, a major difference exists. Given the convergent properties of the CSS, decreasing temperature will not recover the initial diversity, as phenotypes remain at the CSS. This is a case of evolutionary hysteresis. We simulated such a scenario in **Fig. 3g**: starting near branching, the system is warmed from T_1 to T_2 (sun symbol), note that the branching is lost. When the system is cooled back to T_1 (snowflake symbol), it remains monomorphic.

Warming impacts the CR evolutionary dynamics: the 4 possible scenarios

Scenario	CR body mass ratio	Consumer body mass	Mathematical significance	Qualitative outcomes
A	Small	Any	$L \ll L^c(M_1)$	• One singularity: a CSS that increases with temperature
B	Intermediate	Any	$L < L^c(M_1)$ $L \approx L^c(M_1)$	• One singularity whose value increases with warming • Warming switches the selection regime from disruptive (BP) to stabilizing (CSS)
C	Big	Small	$L > L^c(M_1)$	• Three singularities (CSS, Repellor and BP) for low temperatures and only one (CSS) for high temperatures • Evolutionary hysteresis
D		Big		• One singularity: a CSS that increases with warming

Table 1: The four scenarios with their biological and mathematical significances. $\boldsymbol{L^c(M_1)}$ is the value of L, determined numerically and $\boldsymbol{M_1}$-dependant, around which the behavioral change occurs**.** CR stands for Consumer-resource and BP for branching point.

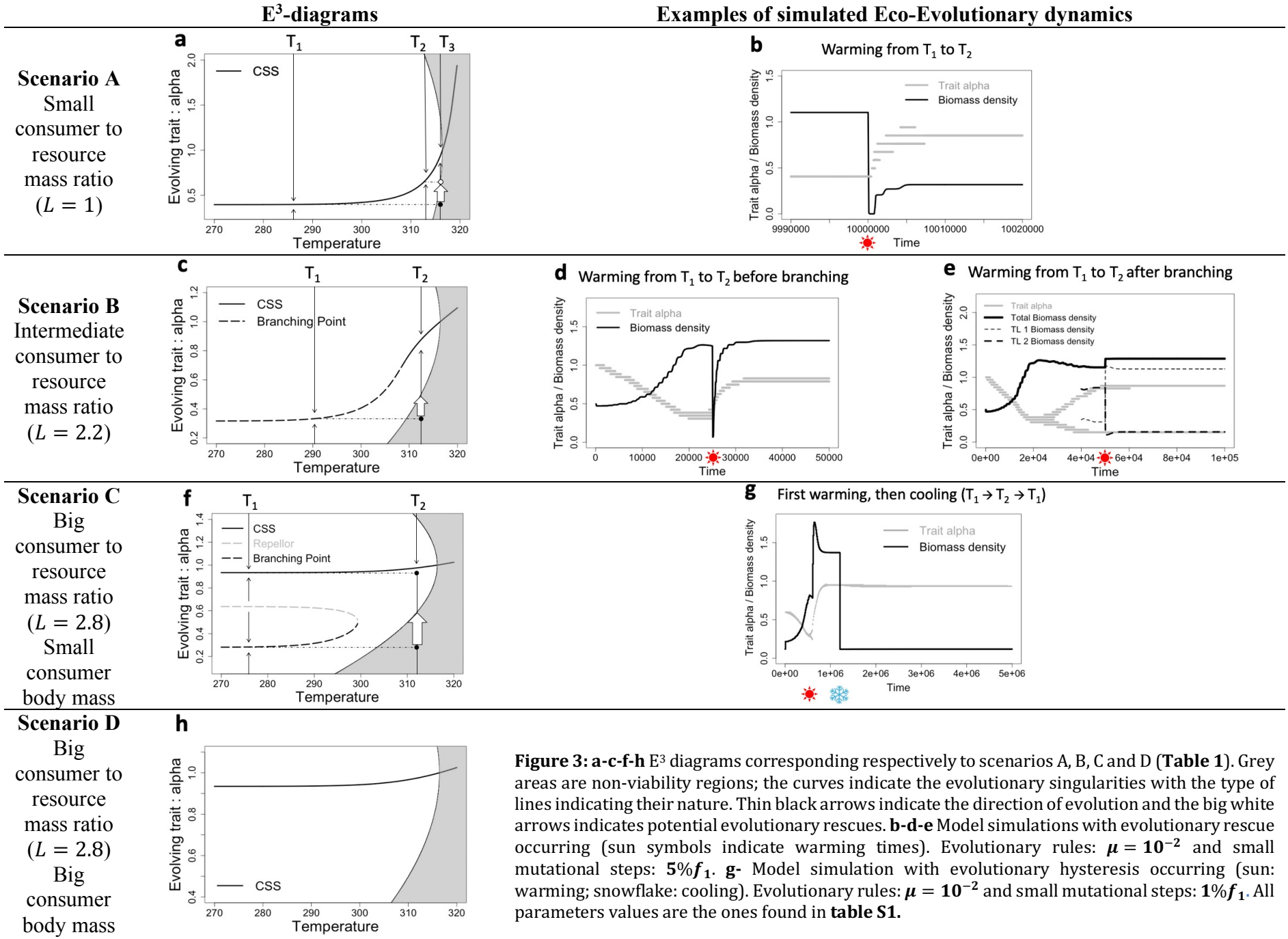

Figure 3: a-c-f-h E³ diagrams corresponding respectively to scenarios A, B, C and D (**Table 1**). Grey areas are non-viability regions; the curves indicate the evolutionary singularities with the type of lines indicating their nature. Thin black arrows indicate the direction of evolution and the big white arrows indicates potential evolutionary rescues. **b-d-e** Model simulations with evolutionary rescue occurring (sun symbols indicate warming times). Evolutionary rules: $\boldsymbol{\mu = 10^{-2}}$ and small mutational steps: $\mathbf{5\%}\boldsymbol{f_1}$. **g-** Model simulation with evolutionary hysteresis occurring (sun: warming; snowflake: cooling). Evolutionary rules: $\boldsymbol{\mu = 10^{-2}}$ and small mutational steps: $\mathbf{1\%}\boldsymbol{f_1}$. All parameters values are the ones found in **table S1.**

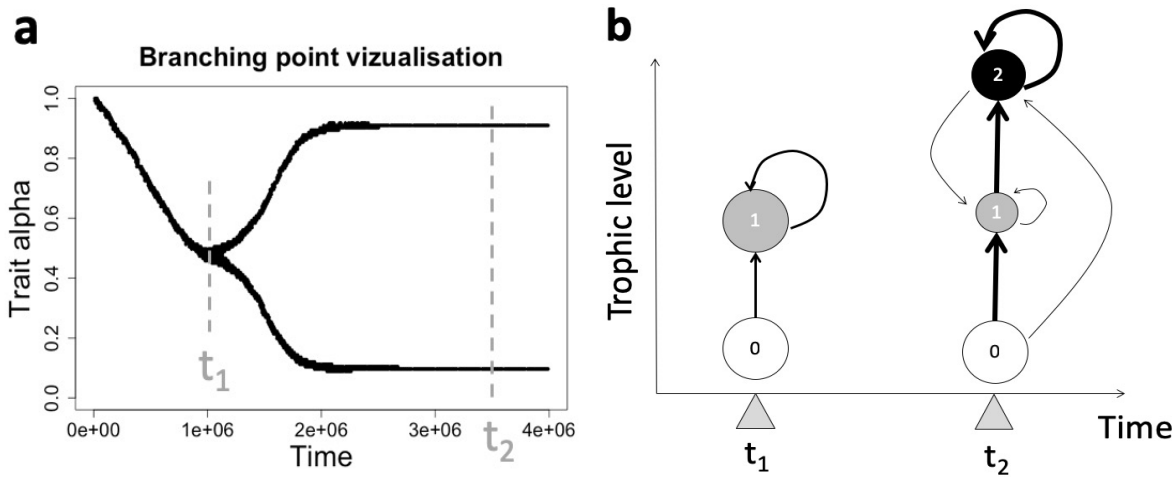

Figure 4: Branching point issued from numerical simulation of the Consumer-Resource model with consumer body mass $\boldsymbol{m_1 = 100}$, intermediate CR body masses ratio $\boldsymbol{L = 2.2}$ and temperature $\boldsymbol{T = 275K}$. Mutation rate of 10^{-2} and mutational steps of $\boldsymbol{\pm 1\%}$. **a. Trait alpha through time**: branching point occurring for $\boldsymbol{\alpha \simeq 0.5}$ and time $\boldsymbol{t_1 \simeq 10^6}$. **b. Schematic view of the trophic network before and long after branching.** The arrows thickness indicates the intensity of trophic interactions. The size of each circle is proportional to the biomass density of the morph it represents. The branching leads to the emergence of a new upper trophic network and intensifies trophic interactions within the network. Values for other parameters are in **table S1.**

Co-evolution of body mass and foraging strategy under warming

While the results presented so far provide a first understanding of evolutionary responses to warming, they have to be considered with caution in the context of complex coevolving networks. Especially, the separation between body mass and feeding center evolution is utterly artificial: in nature, both coevolve and exert selective pressures one on another. We simulated two coevolutionary scenarios that differ in the mutational frequencies (10^{-2} for both traits in scenario 1 and 10^{-2} (resp. 10^{-3}) for body mass (resp. feeding center) in scenario 2 and a warming from 280 to 316.4 K (slightly below T_{lim})). A graphical visualization of the evolutionary trajectories is available in the supporting information (Fig. S1). Evolutionary rescue occurs and enables food chain persistence. Note two important results. First, the two scenarios yield different evolutionary trajectories. The relative speed of evolution between the two evolving traits therefore affect evolutionary dynamics, possibly constraining evolutionary rescue.

Second, while we would have expected no evolution of body mass under warming from the previous analysis, such an evolution occurs when we allow coevolution. Both body mass and feeding center are affected by warming (squares and triangles trajectories in **Fig. S1a**). Evolutionary rescue trajectories (**Fig. S1b**) then involve the effective evolution of both traits.

Evolutionary rescue at the community scale

We now compare the diversity response within multi-trophic networks with and without evolution (**Fig 5**). We assume a 20K warming. While this value is beyond current predictions of temperature change, we choose it for illustrative purposes. Results remain qualitatively similar, though less impressive, for smaller warmings. In both cases, warming is responsible for a loss of trait and species diversity (**Figs 5a&d).** The drop is of comparable sizes but in evolutionary scenarios, we observe a recovery so that the final state is as diverse as before the perturbation. Upper trophic levels suffer most (**Figs 5b&e**). The whole fourth trophic level goes extinct, but recovers if evolution is allowed. Large body masses and/or large feeding centers, mainly corresponding to upper trophic levels, are primarily affected (**Figs 5c&f**). Some of them go extinct; others evolve. Small body masses and/or small feeding centers are less affected (**figures 5c&f**). Evolution seems to eventually rescue the network.

We now analyze how warming intensity and evolutionary potential affect the rescue process. Boxplots are shown in **figures 5g&h**: as expected, the bigger the temperature difference, the higher the diversity loss. This is particularly obvious in the absence of evolution. Persistence is higher when evolution is allowed, especially at high levels of warming.

For each mutational frequency, we fitted two ANCOVAs to link trait or species diversity persistence with evolutionary scenarios (evolution vs no evolution) and warming intensity. All details are presented in Appendix S2 and **table S2** summarizes the whole statistical analysis

results. For brevity, we present here the main conclusions on trait diversity persistence when mutational frequency is $\mathbf{10^{-2}}$. Results for other evolution rates and diversity measures are qualitatively similar.

The model explains more than half of the observed variance. Evolution has a positive effect on diversity persistence. This effect is both direct ($Evolution_{Effect} = 0.06$, $p_{value} = 0.0204$, $Var_{explained} = 28.4\%$) and indirect, increasing in importance with warming ($Interaction_{Effect} = 0.017$, $p_{value} < 10^{-8}$, $Var_{explained} = 9.5\%$). The intensity of warming has a negative effect on diversity persistence when no evolution occurs ($Warming_{Effect} = -0.024$,$p_{value} < 2.10^{-16}$, $Var_{explained} = 30.3\%$). With evolution, warming effects are still significantly negative but much less pronounced ($Warming_{Effect} + Interaction_{Effect} = -0.07$,$p_{value} < 10^{-3}$). Note that for other evolution rates, this effect is no longer significantly different from 0 indicating evolution totally mitigates diversity losses in these cases. Evolutionary rescue therefore clearly acts at the community scale.

An additional ANCOVA was fitted to assess whether the evolution rate (i.e. the mutational frequency) has an effect on diversity persistence (Appendix S2). Here, the explanatory variables are the evolution rate (3 levels: $10^{-1}, 10^{-2}, 10^{-3}$) and the warming intensity. No significant effect of the evolution rate has been detected for both diversity measures ($Evolution\ Rate_{\ Effect}$: $p_{value} > 0.12$; $Interaction_{Effect}$: $p_{value} > 0.08$). Using the Mann–Whitney U test for each warming scenario, we confirmed this result by a pairwise comparison between the different evolution rates.

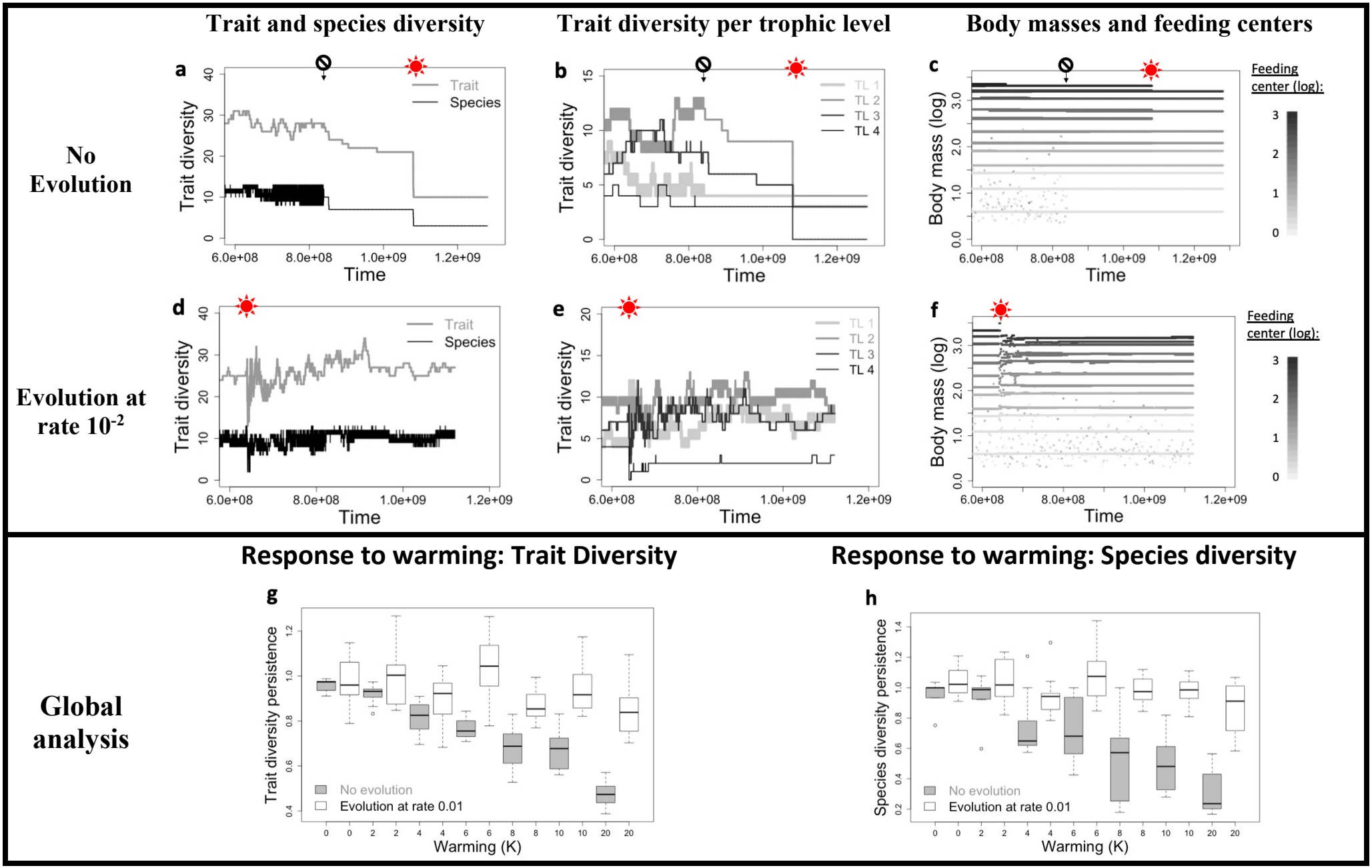

Figure 5: Diversity response to warming. a-b-c: Diversity and evolutionary dynamics of a simulation where evolution has been stopped (prohibition symbol indicates stopping time) before warming from 275 K to 295 K (sun symbol); **d-e-f:** Same outputs with ongoing evolution ($\mu = 10^{-2}$) at warming. **g-h:** Boxplots of trait and species diversity persistence according to different warming intensities for scenarios with or without evolution. Each box corresponds to 10 independent replicas. See Table S1 for parameters values.

Discussion

In this study, we investigated the effect of global warming on food webs, incorporating evolution explicitly into our framework. Our results suggest that evolution can mitigate warming effects through two main mechanisms: evolutionary rescue and preadaptation. Nevertheless, warming is still expected to negatively impact trophic networks, as evolutionary trapping is always observed above a critical temperature. Consistent with previous works, we also find that higher trophic levels are more prone to extinction (Binzer et al., 2012; Weinbach et al., in prep). Warming can even reduce the potential for diversification with long-lasting consequences for the recovery of the trophic community. Our results have important implications for the conservation and the management of networks in the context of global change.

Evolution can help consumers to persist as shown within our consumer-resource framework. For instance, the evolution of foraging strategies leads to higher resource consumption and lower cannibalism under warming conditions. Provided such an adaptation occurs fast enough, it may allow the consumer maintenance (see white arrows in **Fig. 3**). In such instances, evolution allows higher energy acquisition, balancing the increase in metabolic requirements due to warming. Changes in foraging strategies in response to climate change have also been documented in nature. For instance, in the United Kingdom, Pateman et al. (2012) showed that the butterfly *Aricia agestis*, originally a specialist of *Helianthemum nummularium* as a larval host plant, now also largely use *Geranium molle,* the latter being more abundant in warmer climates. This evolutionary adaptation (Buckley, Butlin, & Bridle, (2012) showed a genetic basis) from specialism to generalism not only permitted *A.agestis* to survive but to extend its geographical range.

Next to evolutionary rescue, our work reveals another evolutionary process favoring persistence: preadaptation. Preadaptation happens when evolutionary dynamics allow the

567 system to reach a pre-warming state that, once warming happens, will be resistant to the
568 temperature change. Branching and dimorphism (or polymorphism) here favor preadaptation,
569 by allowing the emergence of contrasted strategies. Pre-warming evolutionary dynamics then
570 lead to a system in which a variety of niches are occupied, with a higher likelihood that some
571 of these selected strategies are resistant to temperature changes, a mechanism akin to the
572 insurance hypothesis (Yachi & Loreau, 1999).

573 Despite these positive effects (rescue and preadaptation), evolution does not
574 systematically save the consumer population. Above a critical warming, evolutionary trapping
575 is inevitable. Evolution, no matter how fast, then cannot prevent the consumer extinction when
576 disturbances are large enough. In some cases, evolutionary dynamics even constrain persistence
577 or recovery. Indeed, warming can change the selection regime from disruptive to stabilizing,
578 reducing polymorphism and diversification potentials (as shown in **fig. 3c**). If we are to
579 conserve biodiversity, fostering conditions under which eco-evolutionary processes maintain
580 genetic diversity and facilitate speciation should also be preserved. Losing such processes
581 potentially has major consequences as biodiversity loss may deteriorate ecosystem functioning
582 and stability (see Hooper et al. (2005) for a review). In particular, less diverse ecosystems are
583 expected to be more vulnerable to other disturbances such as pests (Wasilewska, 1995) or
584 invasive species (Tilman, 1997). Amplifying interactions between different drivers of global
585 change have already been observed and research needs to further investigate such scenarios
586 (Brook, Sodhi, & Bradshaw, 2008). As conservation ecology moves to focus less on diversity
587 patterns and more on preserving processes (Smith, Bruford, & Wayne, 1993), our results point
588 out how interactions between warming and evolution (or coevolution (Northfield & Ives,
589 2013)) should be carefully assessed.

590 Our results have important implications for conservation and restoration policies.
591 Consequences of warming can be long lasting, difficult to predict and to reverse. Our results

592 for instance suggest the possibility of evolutionary hysteresis **(Figs 3f&g)**. In our case, warming
593 led to a switch from a dimorphic (branching) to a monomorphic (CSS) situation. Convergent
594 properties then prevent branching recovery even after cooling the system. While such tipping
595 points are often described based on the ecological state of the system (Suding & Hobbs, 2009),
596 evolutionary dynamics may hasten or delay ecological tipping points (Dakos et al., 2019). In
597 our case, tipping points in fact emerge from the presence of alternative convergent strategies.
598 In a context of global change where selective pressures are likely strong, our work suggests that
599 related eco-evolutionary dynamics can lead to tipping points.
600
601 In our multi-trophic networks, warming impact is trophic-level dependent, upper trophic
602 levels being more likely to go extinct. Because the ratio of ingestion to metabolism decreases
603 with warming (Binzer et al., 2012), energy flows across food chains do not compensate
604 increased respiration rate under warming. Nevertheless, evolution in such networks can help to
605 restore biodiversity in the long-term. Statistical analysis shows this positive effect is both direct
606 and indirect, increasing with warming (**figure 5g&h, table S2**) with important consequences
607 for our prediction of future diversity. For instance, this suggests that predictions based on
608 models that ignore evolutionary dynamics may be increasingly inaccurate when warming is
609 expected to be intense (IPCC, 2014). This emphasizes the limits of the widely used climatic
610 niche models and the need for a better integration of evolution and species interactions into the
611 predictive frameworks on which decision makers rely.
612
613 It is rather surprising that evolutionary rescue applies, within our framework, both at the
614 consumer-resource and at the community scale. We would have expected, given the many
615 indirect effects within complex networks, evolutionary rescue may not apply so well (Loeuille
616 2019). Our hypothesis is that, by allowing big mutational steps, we may have facilitated rescue

processes. Future work is needed to investigate how the mutational regime impacts the role of evolution in maintaining diversity at the community scale.

That being said, we emphasize that such network-level rescues need to be considered with caution, as does the optimistic view that evolution eventually restores trophic networks. First, before the network recovery, the transient state, characterized by a very fragile community, is likely unable to support proper ecosystem functioning and associated services. While we assume populations go extinct when very low, we do not explicitly model ecological effects happening at such low levels (Allee effect, demographic stochasticity…). Therefore, we might be overestimating the transient state diversity and ignoring cases of total collapse, in which evolution would have no effect on diversity persistence since there is no diversity left for evolutionary processes to act on. Large density variations and large extinction rates such as the ones we observe in the transient state may also impact the evolution of other interactions we do not model here. For instance, it has been argued that evolutionary deterioration of mutualistic interactions may happen under global change (Toby Kiers et al., 2010), further impacting ecological networks. Finally, our approach of species diversity is clearly oversimplified as we do not model speciation explicitly, but rather phenotypic differentiation. As speciation also requires time for genetic isolation among incipient species to happen, we are likely underestimating the time needed for species diversity to recover in real systems. Apart from that, we only analyzed diversity but we did not investigate whether warming leaves a fingerprint on community structure and composition (see Tylianakis et al., 2008).

Our results may be difficult to test empirically, as separating warming from other effects of global changes in empirical datasets is not straightforward. Microcosm or mesocosm experiments are more appropriate. Trophic network consisting of rotifer-alga (Yoshida et al., 2003) or phytoplankton-zooplankton-fish (Hulot et al., 2000) are already being used for

experimental evolution. The main challenge is to be able to modulate evolutionary speed. This necessitate cooperation between geneticists and evolutionary biologists (Kokko et al., 2017). Manipulating the number of clones can allow experimental manipulation of evolutionary potential (e.g. Yoshida et al., 2003). Several of our results could then be tested: the positive effect of evolution on the long-term diversity persistence, the differential impact of warming on trophic levels or the selection toward less cannibalism and more resource consumption due to warming as many zooplankton species are cannibalistic.

All in all, our work reveals a potential for evolutionary rescue and preadaptation in food webs confronted with global warming. This optimistic message is however to be modulated by the fact that above a certain temperature, evolution does not act efficiently and because transient collapse is still expected. The variety of possible responses to warming that we observed in our study furthermore suggests that the consequences of warming for a specific ecosystem might be more than challenging to forecast, since too many factors play a role in shaping these eco-evolutionary dynamics. In general, we can only predict that these consequences can be dramatic and long lasting, potentially threatening ecosystem stability and functioning with large consequences for human populations. Conservation and biodiversity management policies should integrate such evolutionary components to better address the issues raised by global changes.

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Author's contributions statement:

NL, KTA and YY conceived the ideas and designed methodology. The analysis was conducted by AW (body mass evolution) and YY (feeding center evolution and coevolution of body mass and feeding center). Concerning the community evolution model, KTA developed the code used and adapted by YY to do the simulations. Results analysis was done by NL, KTA and YY. YY wrote the first draft of the manuscript that has been subsequently reviewed and edited by NL and KTA. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Table S1: List of all the parameters and variables in the model with biological significance, values and units.

Appendix S1: Eco-evolutionary dynamics of the Consumer-Resource model

Appendix S2: Community Evolution Model: species diversity and statistical analysis

Fig. S1: Consumer Resource model: the two-trait coevolution scenario

Table S2: Diversity persistence in the community evolution model according to evolutionary scenarios: statistical analysis summary

Table S1: List of all the parameters and variables in the model with biological significance, values and units.

Variables and parameters		Biological meaning	Value	Unit
Variables	B_i	Biomass density of morph *i*		$Kg.m^{-2}$
	m_i	Body mass of morph *i*		Kg
	f_i	Feeding center of morph *i*		Kg
Temperature parameters	T	Temperature	[275,320]	K
	T_0	Reference temperature of empirical parameters	293	K
	E	Energy of activation	0.65	eV
	k	Boltzmann Constant	$8.617\ 10^{-5}$	$eV.K^{-1}$
Ecological parameters	r_0	Growth rate at temperature T_0	1	s^{-1}
	r(T)	Growth rate of external resource		s^{-1}
	K_0	Carrying capacity at temperature T_0	10	$Kg.m^{-2}$
	K(T)	Carrying capacity of external resource		$Kg.m^{-2}$
	d_0	Mortality rate scaling term at temperature T_0	0.3	$Kg^{0.25}.s^{-1}$
	$d_i(T)$	Mortality rate of morph *i*		s^{-1}
	e	Conversion efficiency	0.85	1
	c_0	Intra-morph competition	0.15	$m^2.s^{-1}$
	c_{ij}	Competition between morph *i* and morph *j*		$Kg^{-1}.m^2.s^{-1}$
	a_{ij}	Attack rate of morph *i* on morph *j*		$Kg^{-1}.m^2.s^{-1}$
	s	Feeding range or width of consumption niche	0.25	Kg
	ε	Extinction threshold	$2\ 10^{-6}$	$Kg.m^{-2}$
Evolutionary parameters	μ	Mutational frequency	$(10^{-1}, 10^{-2}, 10^{-3})$	s^{-1}
	σ	Mutational amplitude	0.25	Kg

Table S1: Parameter dependence on temperature is explicitly indicated. The values are the ones used in the numerical simulations except explicit mention.

Appendix S1: Eco-evolutionary dynamics of the Consumer-Resource model

This document is dedicated to the analysis of the consumer-resource eco-evolutionary dynamics. Throughout this analysis, the equations presented in the main document are proved. In order to avoid confusion, these equations are indexed using the same number used in the main document while new equations are indexed using a letter. The same applies for figures or tables. Important equations are framed.

A. Ecological dynamics:

Population dynamics are given by the following equations:

$$\frac{dB_0}{dt} = r\left(1 - \frac{B_0}{K}\right)B_0 - a_{10}B_1B_0 \tag{9}$$

$$\frac{dB_1}{dt} = ea_{10}B_0B_1 - (a_{11}(1-e) + c_{11})B_1^2 - d_1B_1 \tag{10}$$

1. Ecological equilibriums:

Ecological equilibria are given by resolving $\frac{dB_0}{dt} = 0$ and $\frac{dB_1}{dt} = 0$ which leads to 4 possible solutions:

$$\{B_0^* = 0\,;B_1^* = 0\}$$

$$\{B_0^* = K\,;B_1^* = 0\}$$

$$\left\{B_0^* = 0\,;B_1^* = \frac{-d_1}{(a_{11}(1-e) + c_{11})}\right\}$$

$$\left\{B_0^* = K\left(1 - \frac{a_{10}\left(ea_{10} - \frac{d_1}{K}\right)}{\frac{R}{K}(a_{11}(1-e) + c_0) + ea_{10}^2}\right)\,;B_1^* = \frac{R(ea_{10} - \frac{d_1}{K})}{\frac{R}{K}(a_{11}(1-e) + c_0) + ea_{10}^2}\right\}$$

The third equilibrium is not reachable because $B_1^* < 0$. The fourth equilibrium is called the coexistence equilibrium.

2. Condition for coexistence and expression of T_{lim}:

The coexistence equilibrium is possible when $B_0^* \geq 0$ and $B_1^* \geq 0$.

Fist, we demonstrate: $\forall T \geq 0, B_0^* \geq 0$ at the coexistence equilibrium.

$$B_0^* > 0 \Leftrightarrow \frac{R}{K}(a_{11}(1-e)+c_{11}) + ea_{10}^2 - a_{10}\left(ea_{10} - \frac{d_1}{K}\right) > 0$$

$$\Leftrightarrow \frac{R}{K}(a_{11}(1-e)+c_{11}) + a_{10}\frac{d_1}{K} > 0$$

The last relation is always true which ends the proof. For B_1^* we have:

$$B_1^* \geq 0 \Leftrightarrow ea_{10} \geq \frac{d_1}{K} \Leftrightarrow \frac{e}{\sqrt{2\pi}s}\exp\left(-\frac{(F_1-M_0)^2}{2s^2}\right) \geq \frac{d_0}{K_0}\exp\left(\frac{-2E(T_0-T)}{kTT_0}\right)$$

$$\Leftrightarrow \frac{(F_1-M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0-T)}{kTT_0}$$

$$\Leftrightarrow T \leq \frac{2E}{\frac{2E}{T_0} + k\left[\frac{(F_1-M_0)^2}{2s^2} + \ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right)\right]}$$

In the case of body mass evolution, $F_1 = M_0$ so that the condition for coexistence can be rewritten:

$$\boxed{T \leq \frac{2E}{\frac{2E}{T_0} + k\left(\ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right)\right)} \stackrel{\text{def}}{=} T_{lim} \qquad \text{(B)}}$$

With the standard parameter values presented in table S1, $T_{lim} \approx 316.4$ K.

In the case of feeding center evolution, F_1 can evolve. The condition for coexistence can be rewritten:

$$\frac{(F_1 - M_0)^2}{2s^2} \leq \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}$$

$$\Leftrightarrow \left(\begin{array}{c} \ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0} \geq 0 \\ -\sqrt{2s^2\left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}\right]} \leq F_1 - M_0 \leq \sqrt{2s^2\left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}\right]} \end{array} \right)$$

$$\boxed{\left(\begin{array}{c} T \leq \frac{2E}{\frac{2E}{T_0} + k\left(\ln\left(\frac{\sqrt{2\pi}sd_0}{eK_0}\right)\right)} \stackrel{\text{def}}{=} T_{lim} \\ -\sqrt{2s^2\left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}\right]} \leq F_1 - M_0 \leq \sqrt{2s^2\left[\ln\left(\frac{eK_0}{\sqrt{2\pi}sd_0}\right) + \frac{2E(T_0 - T)}{kTT_0}\right]} \end{array} \right) \quad \text{(C)}}$$

B. Evolutionary dynamics:

Reminder: we define M_0 , M_1 , F_1 by $M_{\substack{1\\0}} \stackrel{\text{def}}{=} log_{10}(m_{\substack{1\\0}})$ $F_1 \stackrel{\text{def}}{=} log_{10}(f_1)$

1. How does the selected body mass depend on temperature?

a. Fitness of invasion

Here, we expose the whole approach to determine the invasion fitness function in the adaptive dynamics' framework:

We consider a rare mutant 1' appearing in the resident population 1, given the population dynamics equations, we have:

$$\frac{1}{B_{1'}}\frac{dB_{1'}}{dt} = \underbrace{ea_{1'0}B_0}_{ressource} - \overbrace{(c_{1'1'}B_{1'} + c_{1'1}B_1)}^{competition} + \underbrace{(ea_{1'1}B_1 - a_{11'}B_1 - (1-e)a_{1'1'}B_{1'})}_{comsumption\ interaction\ between\ 1\ and\ 1'} - d_{1'}$$

Given 1 and 1' have the same feeding center, we have $c_{1'1'} = c_{1'1} = c_0$ and $a_{11'} = a_{1'1'}$. Also, $B_{1'} \ll B_1$ (rare mutant). Hence: $c_{1'1'}B_{1'} \ll c_{1'1}B_1$ and $(1-e)a_{1'1'}B_{1'} \ll a_{11'}B_1$

All in all, we deduce:

$$\frac{1}{B_{1'}}\frac{dB_{1'}}{dt} = ea_{1'0}B_0 - c_0B_1 - a_{11'}B_1 + ea_{1'1}B_1 - d_{1'}$$

Which leads to:

$$w(M_{1'}, M_1) \stackrel{\text{def}}{=} \left[\frac{1}{B_{1'}}\frac{dB_{1'}}{dt}\right]_{\substack{B_{1'} \ll B_1 \\ B_0^*, B_1^*}} = ea_{1'0}B_0^* - c_0B_1^* - a_{11'}B_1^* + ea_{1'1}B_1^* - d_{1'}$$

b. Evolutionary singularities (proof of equation (15))

We first need to determine the derivative of the fitness invasion function with respect to the mutant body mass (first variable):

$$\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}} = eB_0^*\frac{\partial a_{1'0}}{\partial M_{1'}} - \underbrace{\frac{\partial c_0B_1^*}{\partial M_{1'}}}_{0} - B_1^*\frac{\partial a_{11'}}{\partial M_{1'}} + eB_1^*\frac{\partial a_{1'1}}{\partial M_{1'}} - \frac{\partial d_{1'}}{\partial M_{1'}}$$

$$= -\frac{\ln(10)}{4}\, ea_{1'0}B_0^* - \frac{(F_1 - M_{1'})}{s^2}a_{11'} - \frac{\ln(10)}{4}ea_{1'1}B_1^* - \frac{\ln(10)}{4}d_{1'}$$

Thus:

$$\left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}}\right]_{M_{1'}=M_1} = -\frac{\ln(10)}{4}(ea_{10}B_0^* + ea_{11}B_1^* - d_1) - \frac{(F_1 - M_1)}{s^2}a_{11}B_1^*$$

At ecological equilibrium $\frac{dB_1}{dt} = 0$ gives $ea_{10}B_0^* + ea_{11}B_1^* - d_1 = c_0B_1^* + a_{11}B_1^*$ and hence:

$$\left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}}\right]_{M_{1'}=M_1} = B_1^*\left(-\frac{\ln(10)}{4}(c_0 + a_{11}) - \frac{(F_1 - M_1)}{s^2}a_{11}\right)$$

Evolutionary singularities occur when the selection gradient vanishes:

$$\left[\frac{\partial w(M_{1'}, M_1)}{\partial M_{1'}}\right]_{M_{1'}=M_1} = 0 \Leftrightarrow -\frac{\ln(10)}{4}(c_0 + a_{11}) - \frac{(F_1 - M_1^*)}{s^2} a_{11} = 0$$

$$\Leftrightarrow c_0 + a_{11}\left(1 - \frac{4(M_1 - F_1)}{s^2 \ln(10)}\right) = 0$$

Noting explicitly the dependence of a_{11} on M_1, we deduce evolutionary singularities M_1^* verify:

$$\boxed{c_0 + a_{11}(M_1^*) * \left(1 - \frac{4(M_1^* - F_1)}{s^2 \ln(10)}\right) = 0 \qquad (15)}$$

This ends the proof of equation (15).

2. How does the selected foraging strategy depend on temperature?

a. Fitness of invasion

Here, the evolving trait is f_1 or equivalently F_1. As we did before, we consider the appearance of a new morph 1' issued from 1 by a random small mutation.

Given our model, its biomass follows the equation (note that $d_1 = d_{1'}$):

$$\frac{1}{B_{1'}}\frac{dB_{1'}}{dt} = ea_{1'0}B_0 + ea_{1'1}B_1 - (1-e)a_{1'1'}B_{1'} - a_{11'}B_1 - c_{1'1'}B_{1'} - c_{11'}B_1 - d_1$$

Using $B_{1'} \ll B_1$ and $F_1 \approx F_{1'}$ (small mutation hypothesis), we find:

$$\frac{1}{B_{1'}}\frac{dB_{1'}}{dt} = ea_{1'0}B_0 + (ea_{1'1} - a_{11'})B_1 - c_{11'}B_1 - d_1$$

When considered at ecological equilibrium, the previous expression gives the invasion fitness function:

$$w(F_{1'}, F_1) \stackrel{\text{def}}{=} \left[\frac{1}{B_{1'}}\frac{dB_{1'}}{dt}\right]_{\substack{B_{1'} \ll B_1 \\ B_0^*, B_1^*}} = ea_{1'0}B_0^* + (ea_{1'1} - a_{11'})B_1^* - c_{11'}B_1^* - d_1$$

b. Evolutionary singularities (proof of equation (16)):

When the selection gradient vanishes:

$$\left[\frac{\partial w(F_{1'},F_1)}{\partial F_{1'}}\right]_{F_{1'}=F_1} = 0 \Leftrightarrow \left[eB_0^*\frac{\partial a_{1'0}}{\partial F_{1'}} + eB_1^*\frac{\partial a_{1'1}}{\partial F_{1'}} - B_1^*\underbrace{\frac{\partial a_{11'}}{\partial F_{1'}}}_{0} - B_1^*\frac{\partial c_{11'}}{\partial F_{1'}} - \underbrace{\frac{\partial d_1}{\partial F_{1'}}}_{0}\right]_{F_{1'}=F_1} = 0$$

$$\Leftrightarrow \frac{-eB_0^*}{s^2}a_{10}(F_1 - M_0) - \frac{eB_1^*}{s^2}a_{11}(F_1 - M_1) + \frac{B_1^*}{2s^2}\underbrace{(F_1 - F_1)}_{0}c_0 = 0$$

So that evolutionary singularities F_1^* verify:

$$\boxed{(M_1 - F_1^*)a_{11}B_1^* - (F_1^* - M_0)a_{10}B_0^* = 0 \qquad (16)}$$

This ends the proof of equation (16).

Proof of the existence of at least one singularity:

Here, we proof that equation (16) has at least one solution and that all solutions F_1^*verify: $M_0 < F_1^* < M_1$. For convenience we define:

$$\alpha \text{ such as}: \; F_1 = \alpha M_0 + (1-\alpha)M_1 \qquad ie: \qquad \alpha \stackrel{\text{def}}{=} \frac{M_1 - F_1}{M_1 - M_0}$$

$$L \stackrel{\text{def}}{=} \frac{M_1 - M_0}{s}$$

Equation (16) can be rewritten with these new notations, by noting that $M_1 - M_0 > 0$ (hypothesis of the model):

$$\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)B_1^*(\alpha,T,M_1,L) - (1-\alpha)\exp\left(\frac{-(1-\alpha)^2L^2}{2}\right)B_0^*(\alpha,T,M_1,L) = 0 \qquad \text{(D)}$$

We define:

$$z(\alpha,T,M_1,L) \stackrel{\text{def}}{=} \alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)B_1^*(\alpha,T,M_1,L) - (1-\alpha)\exp\left(\frac{-(1-\alpha)^2L^2}{2}\right)B_0^*(\alpha,T,M_1,L)$$

We have, $z(0,T,M_1,L) < 0, z(1,T,M_1,L) > 0$ and, given $T, M_1, L \quad z_\alpha : \alpha \to z(\alpha,T,M_1,L)$ is a continuous function. So, by the Intermediate Value Theorem, there exists α^* such that $z_\alpha(\alpha^*) = z(\alpha,T,M_1,L) = 0$. This is equivalent to say that equation (D) or (16) has at least one

solution. Moreover, under coexistence (i.e. $B_0^* > 0$ and $B_1^* > 0$) , if $\alpha \leq 0$ $then$ $z(\alpha, T, M_1, L) < 0$ and if $\alpha \geq 1$ $then$ $z(\alpha, T, M_1, L) > 0$ so that we have necessarily $0 < \alpha^* < 1$. This is equivalent to $M_0 < F_1^* < M_1$. This ends the proof.

c. Effect of warming on feeding center evolution and emergence of 4 scenarios:

Since do depend on the temperature, equation (16) indicates temperature has an impact on the singularities and consequently on evolutionary dynamics. In order to go further, we rewrite (16) replacing B_0^* and $B_1^*$by their explicit expressions and separating temperature and evolutionary singularity:

$$equation\ (16) \Leftrightarrow equation\ (D) \Leftrightarrow \frac{B_1^*(\alpha, T, M_1, L)}{B_0^*(\alpha, T, M_1, L)} = \frac{(1-\alpha)\exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$$

$$\Leftrightarrow \frac{ea_{10} - \frac{d_\infty 10^{\frac{-M_1}{4}}}{K_\infty} \exp\left(\frac{-2E}{kT}\right)}{a_{11}(1-e) + c_0 + \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} a_{10}} = \frac{(1-\alpha)\exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}$$

$$\Leftrightarrow e \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) - \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) = \left[(1-e)\exp\left(\frac{-\alpha^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} + \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right)\right]\left[\frac{(1-\alpha)\exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right)}{\alpha \exp\left(\frac{-\alpha^2 L^2}{2}\right)}\right]$$

$$\Leftrightarrow e \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) - \frac{\sqrt{2\pi} s d_\infty}{K_\infty} \exp\left(\frac{-2E}{kT}\right) = (1-e)\frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-\alpha)^2 L^2}{2}\right) + \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}} \frac{(1-\alpha)}{\alpha} \exp\left(\frac{-(1-2\alpha) L^2}{2}\right) + \frac{(1-\alpha)}{\alpha} \frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty} \exp\left(\frac{-(2(1-\alpha)^2 - \alpha^2) L^2}{2}\right)$$

We define $C(M_1) = \sqrt{2\pi} s c_0 10^{\frac{M_1}{4}}$ and have the equivalence with:

$$\frac{\sqrt{2\pi}sd_\infty}{K_\infty}\exp\left(\frac{-2E}{kT}\right)$$

$$= \frac{-1}{\alpha}\left[(1-\alpha)C(M_1)\exp\left(\frac{-(1-2\alpha)L^2}{2}\right)\right.$$

$$+ (1-\alpha)\frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty}\exp\left(\frac{-(2(1-\alpha)^2-\alpha^2)L^2}{2}\right)$$

$$\left.+\left[(-\alpha e + (1-e)(1-\alpha))\exp\left(\frac{-(1-\alpha)^2L^2}{2}\right)\right]\right]$$

$$\Leftrightarrow \frac{\sqrt{2\pi}sd_\infty}{K_\infty}\exp\left(\frac{-2E}{kT}\right)$$

$$= \frac{-1}{\alpha}\left[(1-\alpha)C(M_1)\exp\left(\frac{-(1-2\alpha)L^2}{2}\right) + (1-e-\alpha)\exp\left(\frac{-(1-\alpha)^2L^2}{2}\right) + (1\right.$$

$$\left.-\alpha)\frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty}\exp\left(\frac{-(2(1-\alpha)^2-\alpha^2)L^2}{2}\right)\right]$$

$$\boxed{\Leftrightarrow Q(T) = G(\alpha, M_1, L) \qquad \text{(E)}}$$

Where the functions $Q(T)$ and $G(\alpha, M_1, L)$ are defined by:

$$Q(T) \stackrel{\text{def}}{=} \frac{\sqrt{2\pi}sd_\infty}{K_\infty}\exp\left(\frac{-2E}{kT}\right)$$

$$G(\alpha, M_1, L) \stackrel{\text{def}}{=} \frac{-1}{\alpha}\left[(1-\alpha)C(M_1)\exp\left(\frac{-(1-2\alpha)L^2}{2}\right) + (1-e-\alpha)\exp\left(\frac{-(1-\alpha)^2L^2}{2}\right) + (1\right.$$

$$\left.-\alpha)\frac{d_\infty 10^{\frac{-M_1}{4}}}{R_\infty}\exp\left(\frac{-(2(1-\alpha)^2-\alpha^2)L^2}{2}\right)\right]$$

To investigate the effect of temperature on the evolutionary dynamics, we analyze the functions:

$$T \rightarrow Q(T)$$

$$\alpha \rightarrow G(\alpha, M_1, L)$$

Study of Q as a function of T:

Q is increasing with the temperature T and has the following variation table:

T	0	$+\infty$
$Q(T)$	0 ↗	$\frac{\sqrt{2\pi} s d_\infty}{K_\infty}$

Table A: Table of variation of $\boldsymbol{Q(T)}$. Note that $\boldsymbol{Q(T)}$ is always positive.

Study of G as a function of α, M_1 and L seen as parameters:

Analytically we cannot determine all the possible behaviors of G. Thus, we used the software Python to investigate its variation. **Figure A** shows the allure of G for different values of CR body masses ratio.

For small CR body masses ratios, G is increasing with α (fig A a-d). For big CR body masses ratios, G is not monotonous anymore (fig A-c, A-f). There is a value of the parameter L, M_1-dependant, we refer to as $L^c(M_1)$, around which the switch of behavior from monotonous to not monotonous occurs. We can show by studying the derivative $\frac{\partial G}{\partial \alpha}$ that $\forall M_1 \in \mathbb{R}, L^c(M_1) \geq \sqrt{2}$. Its value is around 2.2 for the values of M_1 we investigated ($M_1 = 0$ and $M_1 = 2$). In addition, just before the change of behavior occurs, the curvature of G changes (fig A-b, A-e) meaning its second derivative switches sign. This can have consequences on the nature of the singularities as this nature depends on the second derivatives of the fitness gradient. This led us to consider scenarios with an intermediate CR body masses ratio.

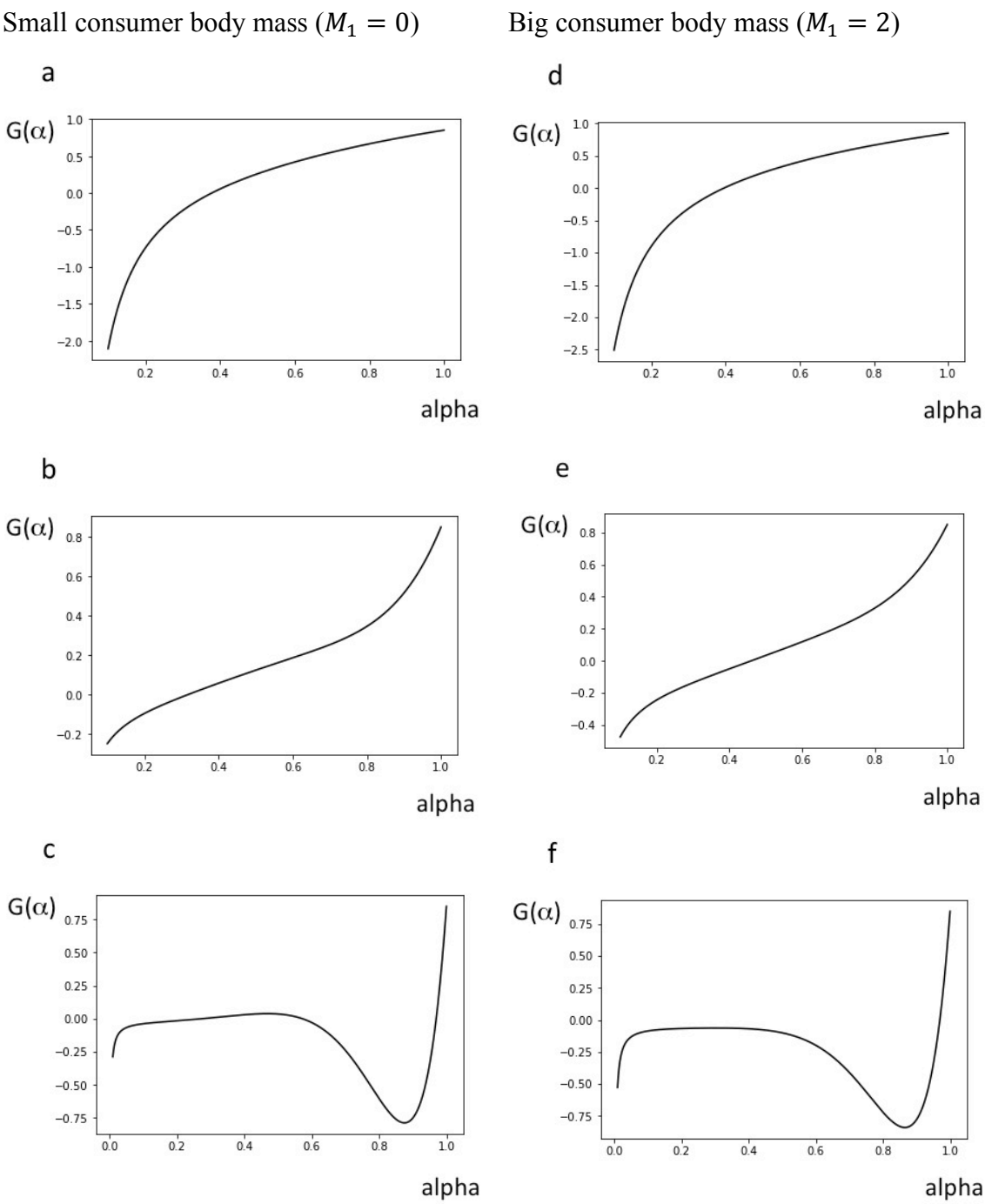


Figure A: Plots of $\boldsymbol{G(\alpha)}$ for various values of $\boldsymbol{L}$ and $\boldsymbol{M_1}$. CR stands for Consumer-Resource.

From the previous analysis, we deduce the following table of variation for G:

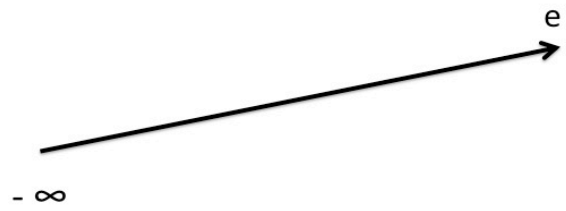
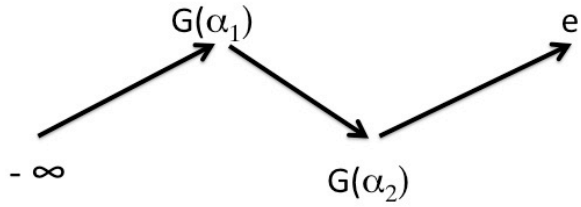
Case	α	0 $\quad\quad$ $\alpha_1(M_1, L)$ $\quad\quad$ $\alpha_2(M_1, L)$ $\quad\quad$ 1
$L \leq L^*(M_1)$	$G(\alpha)$	
$L > L^*(M_1)$	$G(\alpha)$	

Table B: Variation table of function G according to the value of L

If the consumer to resource body mass ratio is small, G is strictly increasing with α so that there is necessarily only one singularity.

If the ratio between consumer and resource body mass is big, the behavior of G indicates the existence of up to three singularities. The coexistence condition on temperature (T_{lim}) implies $Q(T) < e$ so that it is impossible to have two singularities (except one degenerate case) Hence, in this case, there is one or three singularities, depending on $G(\alpha_1(M_1, L)), G(\alpha_2(M_1, L))$ and T.

Finally, while there is no qualitative difference between the case of a small consumer body mass and a big one when the CR body mass ratio is either small (fig A-a, A-d) or intermediate (fig A-b, A-e), there is one in the case it is big. Indeed, in that case, when the consumer body mass is small $G(\alpha_1) > 0$ (fig Ac) while when the consumer body mass is big $G(\alpha_1) < 0$ (fig A-f). This is important since $Q(T)$ is always positive (see Table A). This means there can potentially be 3 singularities in the case of a small consumer body mass while there is only one in the case of a big consumer body mass.

All this analysis of equation (F) leads to distinguish 4 scenarios that differs in the impact of warming on feeding center evolution: small CR body mass ratio **(scenario A)**, intermediate CR body mass ratio **(scenario B)**, big CR body mass ratio and small consumer body mass **(scenario C)**, big CR body mass ratio and big consumer body mass **(scenario D)**. Those are the scenarios presented in **Table 1.**

d. Nature of the evolutionary singularities

Let F_1^* be the evolutionary singularity.

Non-invasibility corresponds mathematically to:

$$\left[\frac{\partial w(F_{1\prime}, F_1)}{\partial F_{1\prime}}\right]_{F_{1\prime}=F_1=F_1^*} < 0$$

Moreover, we have the following expression obtained by derivation:

$$\left[\frac{\partial w(F_{1\prime}, F_1)}{\partial F_{1\prime}}\right]_{F_{1\prime}=F_1} = \frac{e}{s^2} a_{10} B_0^*((1-\alpha)^2 L^2 - 1) + \frac{e}{s^2} a_{11} B_1^*(\alpha^2 L^2 - 1) + \frac{B_1^* c_{11}}{2s^2}$$

We used this expression to determine numerically trough Python software the invasibility properties.

Convergence corresponds mathematically to:

$$\left[\frac{d}{dF_1}\left[\frac{\partial w(F_{1\prime}, F_1)}{\partial F_{1\prime}}_{F_{1\prime}=F_1}\right]\right]_{F_1=F_1^*} < 0$$

In the case of one singularityF_1^*, it can be shown without calculation that the singularity will be convergent stable.

Proof:

Let $F < M_0$ and $0 < \varepsilon < \frac{M_0 - F}{2}$, we have $w(F+\epsilon, F) > 0$ because the mutant with trait $(F + \epsilon)$ has better attack rates on both the resource and the resident $F$and experience less competition with the resident F than experienced by the resident $(c_{11} = c_0)$.

Hence, $\left[\frac{\partial w(F_{1\prime}, F_1)}{\partial F_{1\prime}}_{F_{1\prime}=F_1}\right]_{F_1=F} > 0.$

In a same way, we have: $\forall$ F $> M_1$, $\left[\frac{\partial w(F_{1\prime}, F_1)}{\partial F_{1\prime}}_{F_{1\prime}=F_1}\right]_{F_1=F} < 0$

Moreover, the function:

$$\mathbb{R} \longrightarrow \mathbb{R}$$

$$F_1 \longmapsto \left[\frac{\partial w(F_{1'}, F_1)}{\partial F_{1'}}_{F_{1'}=F_1}\right]$$

is continuous and only vanishes at $F = F_1^* \in]M_0, M_1[$.

Hence, $\forall$ F $< F_1^*$, $\left[\frac{\partial w(F_{1'},F_1)}{\partial F_{1'}}_{F_{1'}=F_1}\right]_{F_1=F} > 0$, $\forall$ F $> F_1^*$, $\left[\frac{\partial w(F_{1'},F_1)}{\partial F_{1'}}_{F_{1'}=F_1}\right]_{F_1=F} < 0$ and $\left[\frac{\partial w(F_{1'},F_1)}{\partial F_{1'}}_{F_{1'}=F_1}\right]_{F_1=F_1^*} = 0$ thus: $\left[\frac{d}{dF_1}\left[\frac{\partial w(F_{1'},F_1)}{\partial F_{1'}}_{F_{1'}=F_1}\right]\right]_{F_1=F_1^*} < 0$

In the case of three singularities $F_1^* < F_2^* < F_3^*$, with the same kind of arguments, we know at least one singularity is convergent stable. It appears numerically that F_1^* and F_3^* are convergent stable while F_2^* is not.

This analysis gives the qualitative outcomes of warming for each scenario presented in **Table 1**.

Appendix S2: Community Evolution Model: species diversity and statistical analysis

Our community evolution model starts with a consumer feeding on an external resource. The evolution of the consumer body mass and foraging strategy (feeding center) follows a mutation/selection process leading to the emergence of a complex multi-trophic network of approximately 30 to 40 morphs and 4 to 5 trophic levels. A morph corresponds to an adaptive phenotype, that is to say, a couple ($body\ mass, feeding\ center$).

<u>**Definition of species diversity:**</u>

At first, we only have one straightforward diversity measure: the trait diversity (i.e. the number of morphs in the trophic network at a given time). Because our model ignores genetic details and focuses on phenotypes, the definition of species is notoriously tricky. For lack of better criteria, we define species as clusters in the phenotypic space. The silhouette method (Rousseeuw, 1987) is used to determine the best number of clusters on the k-means clustering algorithm applied on the set of body masses and feeding centers (m_i, f_i) corresponding to the trait diversity. The number of clusters gives what we define as species diversity.

We consider a set of observations and a clustering. For each observation i, we note C_i the cluster to which i is affected. For each observation i, the silhouette width $S(i)$ is a measure of how much the observation is close its cluster C_i in comparison with other clusters. It is defined as follow:

$$S(i) = \frac{b(i) - a(i)}{\max(a(i), b(i))}$$

Where:

- $a(i)$ is the average dissimilarity between i and the other observations in c_i
- $b(i)$ is the average dissimilarity between i and the observations in the closest cluster to i, C, with $C \neq c_i$ (ie $b(i) = \min_C d(i, C)$)

$S(i)$ is between -1 and 1 and the more it is close to 1, the better is the affectation of i in the

clustering. We use $\underset{i}{\text{mean}}\, S(i)$ as a measure of the performance of a given clustering. We compare the different clustering obtained by the k-means algorithm for different values of k.

We implemented the algorithm in R-software using the packages "Cluster" by Martin Maechler, Peter Rousseeuw Anja Struyf, Mia Hubert, Kurt Hornik, Pierre Roudier, Juan Gonzalez (2017).

Statistical analysis:

We want to compare the diversity response to warming within our multi-trophic network with and without evolution.

For trait and species diversity, three models were fitted ($\mu = 10^{-1}, 10^{-2}, 10^{-3}$) in order to contrast diversity persistence for different evolutionary scenarios (scenario E μ against scenario NE μ). 6 ANCOVAs were fitted with evolution as factor (two levels: "evolution" versus "no evolution") and intensity of warming as quantitative variable (0,2,4,6,8,10,20K). The model is written as follows:

<u>Model:</u> $DiversityPersistence_{ij} = \mu + \alpha_i + (\beta + \gamma_i)WarmingIntensity_{ij} + \varepsilon_{ij}$

As indicated in **table S2**, index 1 (resp. index 2) corresponds to the level "no evolution" (resp. "evolution") so that α_2 corresponds to the direct effect of evolution ($\alpha_1 = 0$) and γ_2 corresponds to the interaction term between evolution and warming or indirect effect of evolution ($\gamma_1 = 0$). β describes the direct effect of warming.

An additional ANCOVA was fitted in order to compare the diversity persistence according to the evolution rate μ (i.e. mutational frequency). Here, diversity persistence is explained by the rate of evolution ($\mu = 10^{-1}, 10^{-2}, 10^{-3}$) as a three-level factor and the intensity of warming (0,2,4,6,8,10,20 K) as a quantitative variable. The model is written as follows:

<u>Model:</u> $DiversityPersistence_{ij} = \mu + \alpha_i + \beta * WarmingIntensity_{ij} + \varepsilon_{ij}$

A graphical visualization showed all hypothesis for ANCOVA were verified for each fitted model. All statistical analyses were conducted using R-software (version 3.5.2). The "Anova" function of the R-package "car" was also used.

Fig. S1: Consumer Resource model: the two-trait coevolution scenario

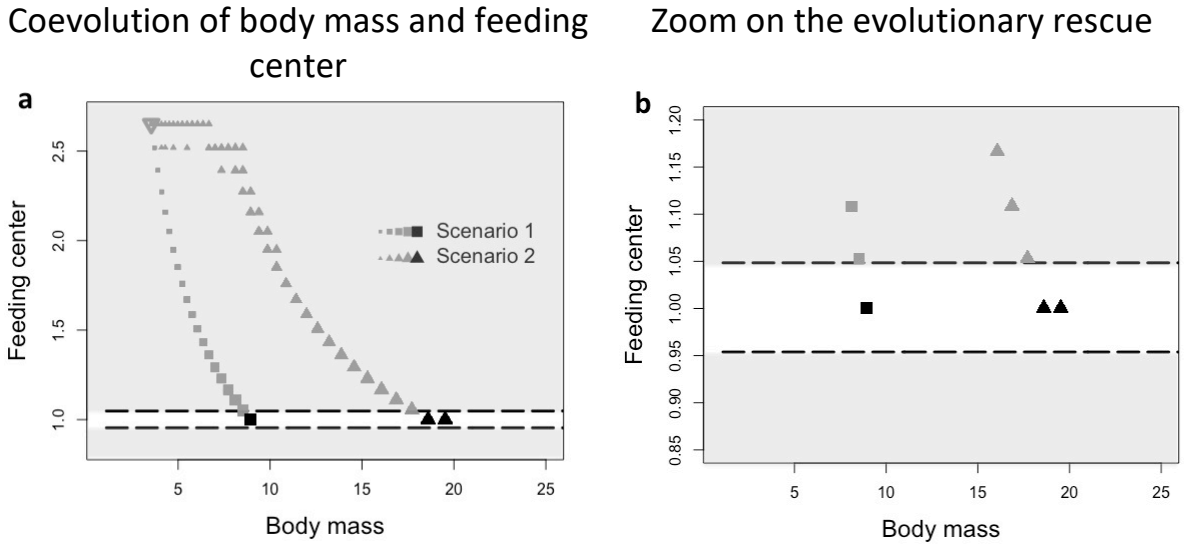


Fig. S1: a. Coevolution of body mass and feeding center under two scenarios. **Scenario 1**: body mass and feeding center evolve at rate $\boldsymbol{\mu = 10^{-2}}$ (squares). **Scenario 2**: body mass evolves at $\boldsymbol{\mu = 10^{-2}}$ while feeding center evolves at $\boldsymbol{\mu = 10^{-3}}$ (triangles). Unfilled grey triangle: initial conditions. The simulations started at 280 K and a warming occurred (switch from grey symbols to black symbols) to 316.4 K (almost maximal sustainable temperature). Light grey area is the non-viability area at 316.4 K. The increase in symbol size indicates time direction. **b.** Zoom to see the evolutionary rescue consecutive to warming. Parameter values are in **table S1**.

Table S2: Diversity persistence in the community evolution model according to evolutionary scenarios: statistical analysis summary

Mutational frequency	Direct effect of evolution		Effect of warming intensity		Interaction term		Adjusted R^2
	α_2	Effect size	β	Effect size	γ_2	Effect size	
$\mu = 10^{-1}$	0.051	32.3%	-0.029***	11.5%	0.031***	15.6%	58.6 %
	-0.026	27.1%	-0.037***	27.9%	0.036***	24.8%	79.4%
$\mu = 10^{-2}$	0.060*	28.4%	-0.024***	30.3%	0.017***	9.5%	67.6%
	0.126**	33.4%	-0.035***	22.6%	0.027***	8.9%	64.1%
$\mu = 10^{-3}$	0.062**	39.8%	-0.019***	18.5%	0.017***	13.1%	70.7%
	0.196***	37.3%	-0.029***	12.2%	0.023***	5.8%	54.4%

Table S2: Outputs of the 6 ANCOVAs. Index 1 $\boldsymbol{(\alpha_1)}$ corresponds to the level « No evolution » while index 2 $\boldsymbol{(\alpha_2)}$ corresponds to the level « Evolution ». All models have a **p-value below 2.10^{-16}.** For each value of mutational frequency, the first line corresponds to trait diversity persistence while the second line corresponds to species diversity persistence. Significance code: $<10^{-3}$ '***', $<10^{-2}$ '**', <0.05 '*