Stoichiometric constraints modulate the effects of temperature and nutrients on biomass distribution and community stability

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Abstract

Temperature and nutrients are two of the most important drivers of global change. Both can modify the elemental composition (i.e. stoichiometry) of primary producers and consumers. Yet the combined effect of temperature and nutrients on the stoichiometry, dynamics, and stability of ecological communities remains largely unexplored. In particular, we lack theory on temperature and stoichiometry as drivers of biomass and stability patterns. To fill this gap, we extended the well-known Rosenzweig-MacArthur consumer-resource model by including thermal dependencies, nutrient dynamics, and stoichiometric constraints on both the primary producer and the consumer. We next investigated the effects of temperature and nutrients on consumer-resource stability and biomass distribution across trophic levels. We found that stoichiometric constraints dampen the paradox of enrichment and thus increase persistence at high nutrient levels. Nevertheless, stoichiometric constraints also reduced the persistence of the consumer at low and high temperatures. As a result, the overall effect of stoichiometric constraints on system stability depends on its relative influence on population fluctuations versus consumer persistence. We also found that stoichiometric constraints can reverse biomass distribution across trophic levels by modulating consumer assimilation efficiency and resource growth rate along the temperature and nutrient gradients. Our findings highlight the importance of accounting for stoichiometric constraints as they can mediate the temperature and nutrient impact on the dynamics and functioning of ecological communities.

Key words: temperature, stoichiometry, temporal variability, paradox of enrichment, trophic interactions, nutrient quota, consumer-resource dynamics, biomass structure.

Introduction

Temperature and nutrients regulate many biological processes, including species geographical distribution, primary production, species interactions, and energy and material fluxes (Falkowski *et al.* 1998; Enquist *et al.* 1999; Elser *et al.* 2007; Thomas *et al.* 2017). Not surprisingly, they are at the core of several ecological theories. While temperature is a fundamental component of the metabolic scaling theory (Brown *et al.* 2004), nutrients are at the core of resource competition theory (Tilman 1982) and ecological stoichiometry theory (Sterner & Elser 2002). Nevertheless, we lack an integrative theory that links stoichiometry (i.e. the element composition of organisms), nutrient enrichment, and temperature in multispecies communities. Such a theory will allow us to understand how and when stoichiometric variation modulates the consequences of global changes on trophic interactions, community dynamics, and ecosystem functioning.

Nutrients can modulate the effects of warming on communities directly by altering primary production, and/or indirectly by changing the elemental composition of primary producers. Conversely, thermal effects on trophic interaction strengths (i.e. the *per capita* effect of predators on prey population densities) and on consumer energetic efficiency (i.e. ingestion relative to metabolic demand) depend on both the quantity and quality of their resources. Thus, to understand the combined effects of temperature and nutrients on ecosystems we need a theory that includes both thermal and stoichiometric dependencies that regulate species interactions and community dynamics.

Predicting the effects of global warming and nutrient changes on ecosystems is challenging as species are embedded within communities of multiple interacting species (Petchey *et al.* 1999; Tylianakis *et al.* 2008; Montoya & Raffaelli 2010; Gilbert *et al.* 2014). Increased resource availability (hereafter: enrichment) and warming can jointly affect food-web stability and structure by modifying the strength of trophic interactions (O'Connor *et al.* 2009; Binzer *et al.* 2012; Kratina *et al.* 2012; Sentis *et al.* 2014; Binzer *et al.* 2016). Enrichment typically increases energy flux from resources to higher trophic levels which often leads to the well-known paradox of enrichment where the amplitude of population fluctuations increase with nutrients, leading to extinctions at high nutrient concentrations (Rosenzweig 1971; Rip & McCann 2011; Gilbert *et al.* 2014). Nevertheless, most consumer species become less energetically efficient at warmer temperatures as their metabolic rates often increase faster with temperature than their feeding rates (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Iles 2014). This reduction of energetic efficiency lessens energy flow between trophic levels and hence stabilizes food-web dynamics by reducing population fluctuations (Rip & McCann 2011; Binzer *et al.* 2012; Gilbert *et al.* 2014). As a result, mild warming may alleviate the paradox of enrichment by decreasing consumer energetic efficiency (Binzer *et al.* 2012; Sentis *et al.* 2017).

The theoretical expectations and results described above have already improved our ability to understand and predict the effects of temperature and enrichment on food webs. However, most previous studies using metabolic scaling theory assumed that nutrient enrichment lead to an increase in resource carrying capacity (Vasseur & McCann 2005; Binzer *et al.* 2012; Gilbert *et al.* 2014; Binzer *et al.* 2016; Sentis *et al.* 2017). Yet nutrient enrichment effects are more complex. The elemental composition of primary producers is likely to be altered, in response to the relative supplies of energy and materials (Rastetter et al. 1997, Sterner et al. 1997). This, in turn, can affect the dynamics of the producer population and the herbivores feeding on it. More generally, the stoichiometric flexibility of primary producers, in particular the flexibility in carbon to nutrient ratios, has important implications for animal feeding behaviour (White 1993), consumer population stability (White 1993; Sterner & Hessen 1994; Hessen *et al.* 2002), community structure (Andersen 1997), and ecosystem processes such as biogeochemical cycling (Andersen 1997; Hessen *et al.* 2004).

Previous theoretical and empirical studies reported that stoichiometric variations can have a strong influence on the stability of consumer-resource interactions (Andersen 1997; Andersen *et al.* 2004; Diehl *et al.* 2005; Elser *et al.* 2012). For instance, crustacean Daphnia feeding on low quality (i.e. low nutrient: carbon ratio) algae cannot persist even when resource quantity is not a limiting factor (Elser *et al.* 2007). Consumer extinction is explained by the fact that the consumer assimilation efficiency is, for most organisms, a function of resource quality (Elser *et al.* 2000). When the resource quality is low, the consumers assimilate only few nutrients relative to the biomass they ingest, which limits their growth and reproduction (Elser *et al.* 2000; Elser *et al.* 2012). Temporal variations in resource quality can stabilize the system by weakening interaction strength and dampening population fluctuations (Andersen *et al.* 2004; Diehl *et al.* 2005). However, it remains unclear whether and how temporal variations in the elemental composition of primary producers and consumers can modulate the effects of temperature and nutrient on important

community features such as stability and biomass distribution across trophic levels. Previous studies indicated that the variations in the elemental composition of primary producers are expected to increase in response to global change drivers such as temperature, CO_2, and nutrient availability (Bezemer & Jones 1998). This increased variation can be of importance for both primary producer and consumer populations as the growth rate of primary producers is well known to depend on their elemental composition (Droop 1974) as is the assimilation efficiency of the consumers (Sterner & Elser 2002).

Altogether, previous studies indicated that both temperature and stoichiometric variations can have important effects on species interactions and community dynamics (Andersen *et al.* 2004; Diehl *et al.* 2005; Fussmann *et al.* 2014; Binzer *et al.* 2016; Sentis *et al.* 2017). However, the effects of temperature and nutrient stoichiometry have only been studied in isolation. Here we focus on the combined effects of temperature and nutrients on the stoichiometry of primary producers and consumers and how this affects community stability and biomass distribution across trophic levels. Understanding the determinants of stability and biomass distribution has been at the core of ecology for a long time (Elton (1927), Lindeman (1942). Recent theory aims at explaining empirical observations of trophic pyramids, inverted trophic pyramids, trophic cascades and the link between biomass distribution and stability (McCauley *et al.* 2018; Barbier & Loreau 2019). However, we lack theory on temperature and stoichiometry as drivers of biomass and stability patterns. We developed that theory here.

We used the Rosenzweig-MacArthur model as a baseline nonstoichiometric model because this model is one of the most popular models used to investigate the effects of temperature and nutrient enrichment on community dynamics (Vasseur & McCann 2005; Binzer *et al.* 2012; Fussmann *et al.* 2014; Sentis *et al.* 2017). We then extended this model to account for nutrient dynamics as well as for the simultaneous dependence of community dynamics on temperature and flexible resource stoichiometry. We next used this model to predict the effects of warming and nutrient enrichment on population dynamics and biomass distribution across trophic levels and compared these predictions with the predictions of the nonstoichiometric Rosenzweig-MacArthur model. We particularly addressed two questions: (i) How do stoichiometric constraints modulate the effects of enrichment and warming on community stability and persistence? and (ii) How do stoichiometric constraints modulate the effects of enrichment and warming on biomass distribution across trophic levels?

Population dynamic models

The Rosenzweig-MacArthur (RM) model.
Rates of change of the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$ depend on their respective biomass densities C and R (g.m^{-3}):

$$\dot{R} = r(1 - \frac{R}{K})R - \frac{aR}{1+ahR}C \quad (1)$$

$$\dot{C} = (e\frac{aR}{1+ahR} - m)C \quad (2)$$

The population growth rate of the resource is given by the logistic equation where r is the resource maximum growth rate and K is the resource carrying capacity. The population growth rate of the consumer is equal to its feeding rate multiplied by its assimilation efficiency e (i.e. the fraction of resource biomass converted into consumer biomass) minus a loss term associated to metabolic losses m. The feeding rate of the consumer C depends on the density of its resource R and follows a Holling type II functional response, with consumer-resource attack rate a and handling time h. Our choice for a type II functional response is motivated by a meta-analysis reporting that most consumers feed on their prey following a saturating type II functional response rather than a linear type I or a sigmoidal type III functional response (Jeschke *et al.* 2004).

In the RM model, consumer and resource population growth rates are only limited by nutrient or resource density. Nutrient enrichment is assumed to increase resource carrying capacity, which often leads to the well-known paradox of enrichment where

populations fluctuates up to extinctions (Rosenzweig 1971). Nevertheless, this model neither considers nutrient dynamics nor temporal variations of resource stoichiometry and their consequences on population dynamics. To circumvent these limitations of the RM model, we extended it to better consider nutrient dynamics, resource stoichiometry and the way they can affect resource and consumer population dynamics.

The Stoichiometric Rosenzweig-MacArthur (SRM) model.

We derived a stoichiometric extension of the Rosenzweig-MacArthur consumer–resource model with additional stoichiometric and temperature dependencies of several biological rates. We considered two stoichiometric constraints: one on the resource population growth rate, and the other on the consumer assimilation efficiency (see below for more details). These stoichiometric constraints have been observed for several consumer-resource pairs suggesting that they are core components of species growth and interactions (Sterner & Elser 2002).

Stoichiometric constraint on the resource population growth rate

We extended the RM model by considering explicit nutrient dynamics and nutrient effects on resource population growth rate. The system is assumed to be closed for nutrients. Thus, nutrient supply originates exclusively from biomass excretion and remineralization. The total amount of nutrients in the system (N_{tot}) is then a measure of nutrient enrichment. As elemental homeostasis is much stronger for consumers compared to primary producers (Andersen 1997), we assumed the nutrient quota of the consumer Q_C to be conserved whereas the one of the resource Q_R is flexible over time. As in the RM model, rates of change of the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$ depend on their respective carbon biomass densities C and R (gC.m^{-3}), except that the resource population growth rate follows the Droop equation (Droop 1974) given by $r(1-Q_{min}/Q_R)R$ and is now limited by Q_R relative to the minimum nutrient quota Q_{min}:

$$N_{tot} = Q_R R + Q_C C \quad (3)$$

$$\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C \quad (4)$$

$$\dot{C} = (e\frac{aR}{1+ahR} - m)C \quad (5)$$

From the nutrient conservation equation (eqn 3) we obtain that $Q_R = \frac{N_{tot}-Q_C C}{R}$. The intuitive interpretation is that the resource nutrient quota Q_R changes instantaneously with the density of the resource population R and with the density of the nutrient stored in the consumer biomass $Q_C C$, to maintain nutrient balance (see Text S1 for details).

Stoichiometric constraint on the consumer population growth rate

In the RM model, the growth rate of the consumer population only depends on resource density. We relaxed this assumption by making the population growth rate of the consumer dependent on both resource quality (i.e. nutrient quota) and quantity (i.e. biomass density). In the SRM model, consumer production is also limited by resource quality as the consumer assimilation efficiency e is a saturating function of resource nutrient quota Q_R:

$$e(Q_R) = e_{max}\frac{Q_R}{Q_R+Q_C} \quad (6)$$

The intuitive interpretation of eqn. 6 is that resource quality is not a limiting factor for consumer growth as long as the nutrient content of the resource is superior to the nutrient content of the consumer (i.e. $Q_R > Q_C$). In other words, $e(Q_R)$ is at its maximum for $Q_R > Q_C$ and proportional to Q_R for $Q_R < Q_C$. By replacing e by $e(Q_R)$ in eqn. 5, we obtain the SRM model.

Temperature dependence of model parameters

To investigate the effect of temperature and stoichiometric constraints on consumer-resource dynamics, we next extended the RM and SRM models described above by adding thermal dependencies of the parameters. Following Uszko et al. (2017), we assumed that the total amount of nutrient N_{tot}, the maximum food conversion efficiency e_{max}, and fixed stoichiometric traits (Q_C) are independent of temperature, as there is no evidence of systematic temperature dependence for any of them (Peters 1983; Ahlgren 1987; Borer *et al.* 2013; Yvon-Durocher *et al.* 2015). Rate of maintenance respiration and natural background mortality m typically increases exponentially with temperature (Fig. S1a and b). We thus used the Arrhenius equation to describe the effect of temperature T (in Kelvin) on m:

$$m(T) = m_0 e^{\frac{-E_m}{kT}} \quad (7)$$

where m_0 is a parameter-specific constant calculated at temperature of 0°C (= 273.15 K). The temperature dependence is characterized by the respective activation energy E_m (eV) and the Boltzmann constant k=8.62×10^{-5} eVK^{-1}. As the temperature dependencies of resource intrinsic growth rate r and functional response parameters (a, 1/h) are often unimodal rather than exponential (Englund *et al.* 2011; Rall *et al.* 2012; Sentis *et al.* 2012; Thomas *et al.* 2012), we used Gaussian functions for r and a and an inverted Gaussian function for h:

$$g(T) = g_0 e^{\pm\frac{(T-Topt)^2}{2s^2}} \quad (8)$$

where T_{opt} is the temperature at which the rate g reaches its minimum or maximum, s is the function width and g_0 is a parameter-specific constant calculated at T_{opt}. The minus-sign corresponds to Gaussian functions and the plus-sign to inverted Gaussian functions.

Model parameterisations and simulations

To parameterise the models we assumed the resource and consumer species to be a unicellular freshwater algae and a grazer (e.g. Rotifera or Cladocera), respectively. The choice for this system was motivated by the good characterization of both the stoichiometric parameters and thermal dependencies for this system. We used the same parameters and thermal dependencies as in Uszko *et al.* (2017). See Table S1 and Fig. S1 for further details.

To investigate the individual and combined effects of enrichment, warming, and stoichiometric constraints, we varied temperature (401 values ranging from 0 to 40°C by 0.1°C) and total amount of nutrients (parameter N_{tot} in eqn. 10; 60 values ranging from 0.001 to 0.06 gP.m^{-3} by 0.001 gP.m^{-3}, overlapping with reported mean phosphorus concentration in European peri-alpine lakes (Anneville *et al.* 2005)). For the RM model, we used the minimum nutrient quota to convert nutrients into resource (i.e. $K = N_{tot}/Q_{min}$). We then simulated the consumer-resource dynamics for 1000 days to enable the system to reach an attractor (either an equilibrium point or a limit cycle) before we assessed the final state. Therefore, for each model, we simulated 24060 combinations of environmental conditions (401 temperatures by 60 nutrient concentrations). Initial biomass density of each species was set to 0.98 times its equilibrium density in the two-species system (calculated by solving for the two-species equilibrium, using either eqns 1-2 for model RM or eqns 3-5 for model SRM). The value of 0.98 was chosen to be (1) close enough to equilibria to avoid extinctions caused solely by transient dynamics and (2) not exactly the equilibrium value to probe the stability of the equilibrium. Any population falling below the extinction threshold of 10^{-9} g.m^{-3} during the simulation was deemed extinct and its biomass set to zero to exclude ecologically unrealistic limit cycles. For each model, we calculated system persistence as the percentage of simulations with the two species remaining extant at the end of the simulations.

Results

Stability: population fluctuations and persistence

Stoichiometric constraints dampened the paradox of enrichment, reducing fluctuations at high nutrient levels and hence increasing persistence. However, stoichiometric constraints also reduced the persistence of the consumer at low and high temperatures. As a result, the overall effect of stoichiometric constraints on stability depends on its relative influence on population fluctuations versus consumer persistence. In the two following paragraphs, we explain in more detail these results and highlight key differences between the outcomes from RM and SRM models.

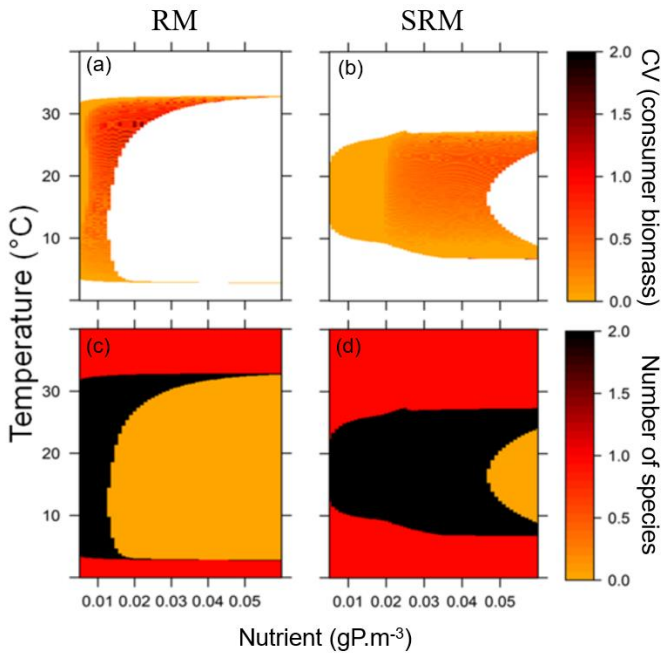

Fig. 1. Population fluctuations (consumer biomass coefficient of variation; panels *a* and *b*) and species persistence (number of species; panels *c* and *d*) across the temperature (*y* axis) and nutrient (*x* axis) gradients as predicted by the Rosenzweig-MacArthur (RM; panels *a* and *c*) and by the Stoichiometric Rosenzweig-MacArthur (SRM; panels *b* and *d*) models. In panels *a* and *b*, the white colour corresponds to the temperature-nutrient scenario for which the consumer has gone extinct whereas the orange to red to dark red represent population fluctuations of increasing amplitude. In panels *c* and *d*, in black: both consumer and resource persist; in red: only the resource persists; in orange: none persists. Resource biomass CV is not shown; it is qualitatively similar to the consumer biomass CV as resource and consumer biomass fluctuation are strongly coupled.

The RM model predicts that increasing nutrient concentration is strongly destabilizing: the system shifts from a stable equilibrium point to limit cycles (i.e. the system crosses a Hopf bifurcation). This agrees with the paradox of enrichment. As population biomass fluctuations (i.e. cycle amplitude) increase with nutrient concentration, minimal population densities are very low at high nutrient concentrations leading to the extinction of both the consumer and resource once the extinction threshold is crossed (Fig. 1). In the range of temperatures where the consumer persists, warming does not have a strong influence on the nutrient concentration at which the system shifts from the stable equilibrium point to limit cycles, although this qualitative shift is absent at very high temperatures (i.e. 32°C) when the consumer is close to extinction. Warming decreases fluctuation amplitude and thus dampens extinctions driven by the paradox of enrichment, which results in warming enhancing the persistence of the consumer-resource system at high nutrient concentrations. However, very warm and cold temperatures cause the extinction of the consumer (see below for the mechanisms underlying extinctions), releasing resources from top-down control. Overall, we found that, without considering extinctions driven by fluctuations, both the consumer and the resource can persist in 74% of the temperature-nutrient concentration scenarios (i.e. black + orange areas in Fig 1C). Nevertheless, when considering extinctions driven by fluctuations, they persist in only 21% of the temperature-nutrient scenarios (i.e. black area in Fig. 1c) indicating that extinctions driven by population fluctuations are highly prevalent in the RM model.

In contrast, the SRM model shows that increasing nutrient concentrations causes fewer fluctuations than those observed for the RM model (Fig. 1). This is because: (1) more nutrients are needed to shift the system from a stable equilibrium point to limit cycles—the system can indeed persist without fluctuations up to 0.02 $gP.m^{-3}$ whereas it was only up to 0.0005 $gP.m^{-3}$ in the RM model—and (2) when the system fluctuates, the amplitude of the fluctuations is smaller in the SRM than in the RM model. As a result, stoichiometric constraints dampen the amplitude of population fluctuations (i.e. the paradox of enrichment) and hence increase system persistence at high nutrient levels. While the qualitative effect of temperature is similar to that observed in the RM model, the thermal thresholds for consumer persistence are reduced at low and high temperatures. Moreover, thermal thresholds are reduced by up to 5°C at low nutrient concentrations with the SRM model whereas they are mostly independent of nutrient level with the RM model (Fig. 1). The consumer is thus more likely to go extinct at low nutrient concentrations and extreme temperatures in the SRM model than in the RM model. Overall, system persistence for the SRM model was 44% without considering extinctions driven by fluctuations and 37% when considering them. In other words, without considering extinctions driven by fluctuations, the

SRM model predicts lower persistence of the consumer compared to RM model but it is the opposite pattern when considering extinctions driven by fluctuations. We thus conclude that the RM model predicts larger population fluctuations leading to high probabilities of populations extinctions in comparison to the SRM model.

B*iomass distribution*

We next compared the predictions of both models for consumer-resource biomass ratios along the temperature and nutrient gradients (Fig. 2). We found that, at equilibrium, the RM model systematically predicts inverted biomass pyramids (i.e. population biomass increases with trophic levels). In contrast, the SRM model predicts both biomass pyramids and inverted pyramids depending on temperature and nutrient levels. The RM model systemically predicts biomass ratio values above one indicating that, as soon as the consumer can persist, its population biomass density systematically exceeds the resource population biomass density (Fig. 2). With the SRM model, the biomass ratios are below one at low nutrient levels (Fig. 2). However, at medium and high nutrient levels, the ratios are above one as soon as the consumer can persist. We found qualitatively similar results when considering unstable equilibrium points (Fig. S2).

Mechanisms underlying stability and biomass distribution patterns

Here, we detail the mechanisms underlying the stability and biomass distribution patterns to better understand how and when stoichiometric constraints modulate the effects of temperature and nutrients on consumer-resource dynamics. Stoichiometric constraints induce two effects. The first one is a static shift in the parameter values of consumer assimilation efficiency and of the resource carrying capacity. We call this static effect. The second one corresponds to a population dynamical feedback. We call this dynamic effect. Both static and dynamic effects operate through consumer efficiency and resource population growth rate.

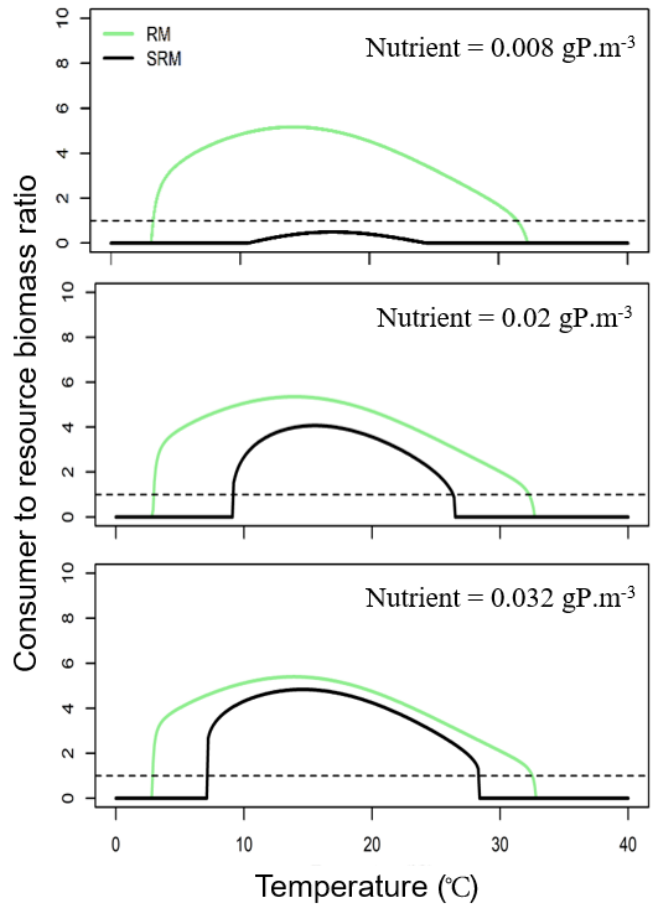

Fig. 2. Consumer-resource biomass ratio along the temperature gradient for the Rosenzweig-MacArthur (RM, green lines) and the Stoichiometric Rosenzweig-MacArthur (SRM, black lines) models at three nutrient concentrations (0.008, 0.02, and 0.032 gP.m^{-3}). In each panel, the dotted line represents biomass ratio of one; i.e. the biomass densities of the resource and the consumer are equal. Biomass values shown at equilibrium points. For unstable equilibrium points (i.e. limit cycles), see Fig. S2.

Consumer energetic efficiency of the consumer and assimilation efficiency

The persistence of the consumer at low and high temperatures is driven by the energetic efficiency *EE* of the consumer (i.e. its feeding rate relative to metabolic losses) calculated as follows:

$$EE = \frac{ef(R^*)}{m} \quad (9)$$

Where $f(R^*)$ is the functional response of the consumer at resource equilibrium density R^* in absence of the consumer. We recall that the assimilation efficiency e is a function of resource quality Q_R in the SRM model whereas it is constant

in the RM model. The intuitive interpretation of eqn. 9 is that *EE* should be above one for the consumer population to growth and persist.

To better understand the influence of stoichiometric constraints on consumer persistence, we thus investigated differences in the RM and SRM model predictions regarding the consumer energetic efficiency *EE* along the temperature gradient at two nutrient concentrations (Fig. 3). We found that, for both models, energetic efficiency at equilibrium (i.e. static effect) has a hump-shaped relationship with temperature with maximal efficiency values at medium temperatures. While this unimodal shape is conserved across nutrient levels and models, the RM model systematically predicts higher consumer energetic efficiency values than the SRM model because consumer assimilation efficiency is lower in the SRM than in the RM model (Fig. S3). As a result, the temperatures at which energetic efficiency falls below one and drives consumers extinct are more extreme in the RM model compared to the SRM model (Fig. 3). In other words, energetic efficiency is above one for a narrower thermal range in the SRM model.

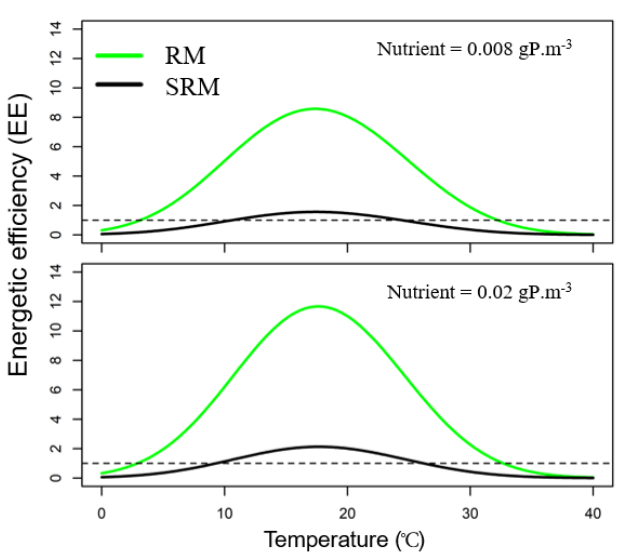

Fig. 3. Consumer energetic efficiency along the temperature gradient for the Rosenzweig-MacArthur (RM, in green) and the Stoichiometric Rosenzweig-MacArthur (SRM, in black) models at two nutrient concentrations (0.008 and 0.02 gP/m^3). In each panel, the dotted line represents energetic efficiency equal to one.

Dynamical feedbacks due to the stoichiometric constraints

The second mechanism by which stoichiometric constraints influence consumer-resource stability and biomass distribution is the dynamical feedbacks due to stoichiometric constraints on the resource population growth rate and on the consumer energetic efficiency. In the SRM model, the growth rate of the resource population depends on both the total nutrient load and the consumer population density as $Q_R = (N_{tot} - Q_C C)/R$. In other words, when consumer population increases, this decreases resource population growth leading to a negative feedback on consumer population growth rate. In addition to this first dynamical feedback, there is a second dynamical feedback as the consumer population growth rate also depends on Q_R and thus on its own biomass density. Thus, also this second negative feedback loop limits the consumer population growth rate when its density increases. Altogether, dynamical feedbacks reduce strongly the amplitude of population fluctuations, which in turn increases resource and consumer persistence.

To separate the static and dynamic effects of the stoichiometric constraints, we calculated the values of assimilation efficiencies and carrying capacities predicted by the SRM model for each temperature-nutrient scenario (Fig. S3) and used these effective parameter values to replace the values of parameters *e* and *K* in the RM model for each temperature-nutrient scenario. We then simulated population dynamics along the temperature-nutrient gradient using the RM model with these effective parameters; referred hereafter as effective RM model (Fig. 4). Comparing predictions from the RM, effective RM, and SRM models allowed to disentangle the static stoichiometric effects (when going from the RM to the effective RM predictions; Fig. 4, panels a to b) from the dynamical stoichiometric effects (when going from the effective RM to the SRM predictions; Fig. 4, panels b to c). We found that, at low nutrient concentrations, population fluctuations and consumer persistence predicted by the effective RM model agreed with predictions of the SRM model. However, the system shifted from a stable equilibrium point to a limit cycle at lower nutrient

concentrations for the effective RM model than for the SRM model. This suggest that more nutrients are needed to destabilize the system with the SRM model. Moreover, the effective RM model predicts ampler population fluctuations than the SRM model. As a result, the effective RM predicts high extinction rates at high nutrient concentrations compared to the SRM model. Overall, we found that the effective RM model cannot fully reproduce the dynamics predicted by the SRM, which indicates that including stoichiometric constraints in the RM model involves more than only changing parameter values.

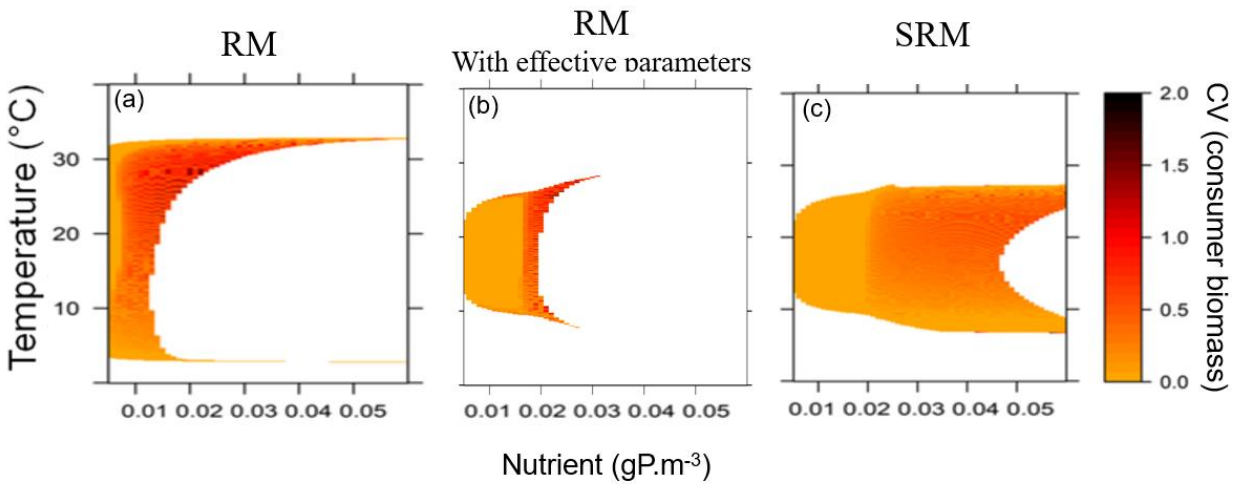

Fig. 4. Population fluctuations (consumer biomass coefficient of variation) across the temperature (*y* axis) and nutrient (*x* axis) gradients as predicted by the Rosenzweig-MacArthur (RM; panel *a*), the RM with effective parameters (panel *b*), and the Stoichiometric Rosenzweig-MacArthur (SRM; panel *c*) models.

Discussion

Temperature and nutrient enrichment are two of the most important drivers of global change (Nelson 2005). However, most research on the effects of temperature and nutrients on community dynamics assumes that the elemental composition of primary producers and consumers are constant and independent of changes on energy and material fluxes (Binzer *et al.* 2012; Boit *et al.* 2012; Amarasekare & Coutinho 2014; Gilbert *et al.* 2014; Amarasekare 2015; Binzer *et al.* 2016; Gilarranz *et al.* 2016). Yet, the elemental composition of primary producers is known to be flexible, which can have important consequences for community dynamics and ecosystem processes (Elser *et al.* 2000). We have shown how stoichiometric constraints that account for flexible stoichiometry can qualitatively affect predictions on how temperature and nutrients influence community stability and biomass distribution across trophic levels. We thus argue that considering stoichiometric constraints is an important step toward a better understanding of the effects of global change on ecosystems.

Stoichiometric constraints and temperature can dampen the paradox of enrichment

We showed that both stoichiometric constraints and temperature dampen the negative effect of nutrient enrichment on consumer-resource fluctuations and increase system persistence at high nutrient levels. Temperature effects are driven by physiological mechanisms. In agreement with previous empirical studies, we found that metabolic loss rates increase

faster with warming than consumer feeding rates (Vucic-Pestic *et al.* 2011; Sentis *et al.* 2012; Fussmann *et al.* 2014; Iles 2014). Consumers are thereby less energetically efficient at higher temperatures which stabilizes food-web dynamics by reducing energy flow between trophic levels (Binzer *et al.* 2012; Kratina *et al.* 2012; Fussmann *et al.* 2014; Sentis *et al.* 2017). In contrast, the effect of stoichiometric constraints is mainly linked to two mechanisms: a static shift in the position of the Hopf bifurcation and negative dynamical feedbacks of the consumer and resource on their population growth rates. Both resources and consumers are composed of the same essential elements (N, P, and C), which implies that, when consumer or resource population biomass increases, it reduces the pool of free nutrients available for the growth of the resource population. As a consequence, more nutrients are needed to shift the system from a stable equilibrium to population cycles. In other words, the paradox of enrichment is displaced to higher nutrient concentrations (i.e., the position of the Hopf bifurcation is shifted to higher nutrient levels).

In addition to the static effect above, we found two dynamic effects that correspond to negative dynamical feedbacks of the consumer and the resource on themselves. When consumer population increases, it decreases the population growth rate of the resource by limiting nutrient availability, diminishing resource biomass, which, in turn, decreases the consumer population growth rate. Conversely, when the resource biomass increases, this decreases the nutrient content if the resource, which, in turn, limits the growth rates of both the resource and consumer populations. These stoichiometric negative feedback loops strongly decrease the amplitude of population fluctuations and thus dampen the paradox of enrichment. Interestingly, our comparisons of the RM, effective RM and SRM model predictions indicate that the dynamical effects contribute more to the reduction of fluctuations than the static effects. This implies that the impact of stoichiometric constraints on community dynamics goes beyond a simple modification of parameter values and encompass more complex population feedbacks between the consumer and the resource.

Overall, these results demonstrate that both flexible stoichiometry and temperature can synergistically dampen the paradox of enrichment by two different mechanisms: population dynamic feedbacks and physiological constraints. Our consumer-resource model is simplified compared to natural communities composed of numerous species. Yet, the predictions of the stoichiometric model fit with empirical observations. In eutrophic lakes and experimental mesocosms, population fluctuate little and extinctions are seldom at relatively high nutrient concentrations (O'Connor *et al.* 2009; Boit *et al.* 2012; Kratina *et al.* 2012), as our stoichiometric model predicts. In contrast, the Rosenzweig-MacArthur model tends to produce very large population fluctuations and extinctions at low nutrient concentrations which can explain why these predictions are not well supported by empirical observations (McAllister *et al.* 1972; Jensen & Ginzburg 2005).

Effects of stoichiometric constraints on system persistence across environmental gradients

While stoichiometric constraints dampen the paradox of enrichment and thus increase persistence at high nutrient levels, they also reduce the persistence of the consumer at low and high temperatures. Stoichiometric constraints affect the thermal thresholds for consumer extinctions. Consumers can only persist over a narrower range of intermediate temperatures when they are constrained by stoichiometry. This is due to the reduced assimilation efficiency of the consumer at low and high temperatures that, in turn, decreases its energetic efficiency and thus fastens consumer extinction. The finding that assimilation efficiency is temperature dependent contrasts with previous theoretical studies that used the RM model and assumed that the assimilation efficiency is temperature independent (Binzer *et al.* 2012; Gilbert *et al.* 2014; Sentis *et al.* 2017; Uszko *et al.* 2017). In the SRM model, the thermal dependency of the consumer assimilation efficiency is fully driven by the change in the resource stoichiometry induced by temperature. The SRM model thus predicts an additional mechanism by which temperature can influence trophic interactions: temperature changes resource stoichiometry which, in turn, impacts the consumer assimilation efficiency and its population

growth rate. To sum up, the overall effect of stoichiometric constraints on system persistence thus depends on the temperature range considered and on their relative influence on population fluctuations versus consumer persistence.

Effects of stoichiometric constraints on biomass distribution

We found that stoichiometric constraints can modulate the effects of temperature and nutrients on biomass distribution across trophic levels. Without stoichiometric constraints (i.e. with the Rosenzweig-MacArthur model), biomass ratios are above one for almost all temperatures or nutrient levels as the biomass produced by the resource is efficiently transferred to the consumer level consistently along the environmental gradients. This finding agrees with theoretical studies reporting that Lotka-Volterra and RM models predict biomass ratios above one and fail to reproduce biomass pyramids for a substantial region of parameter values (Jonsson 2017; Barbier & Loreau 2019). However, in nature, consumer-resource biomass ratios are often below one (McCauley & Kalff 1981; Del Giorgio & Gasol 1995; McCauley *et al.* 1999; Irigoien *et al.* 2004) suggesting that additional mechanisms should be included to better understand and predict biomass distribution patterns in natural food webs. Our stoichiometric model agrees with experimental observations. It predicts that, at low nutrient concentrations (i.e. < 0.01 $gP.m^{-3}$), the biomass ratio never exceeds one along the entire temperature gradient. This is observed in oligotrophic aquatic systems where primary production is too low to sustain high consumer populations (O'Connor *et al.* 2009). In addition, we also found that increasing nutrient levels decreased the temperature ranges within which biomass ratio is below one. This corresponds to results from manipulated nutrient concentrations and temperature in aquatic mesocosms, where zooplankton to phytoplankton biomass ratio only exceeds one in the enriched mesocosms at medium or warm temperatures (i.e. 27°C) (O'Connor *et al.* 2009). This suggests that the models with stoichiometric constraints better reproduce the biomass patterns observed in experimental and natural systems. Nevertheless, further experiments investigating the links between stoichiometric flexibility and consumer-resource dynamics are needed to determine if these stoichiometric mechanisms are underlying patterns of biomass distribution in nature.

Implications of our findings for global change

Temperature and nutrients are two of the most important drivers of global change (Nelson 2005). They do not act in isolation from each other. Climate warming, for example, causes stronger water stratification which, in turn, can limit nutrient cycling (Sarmiento *et al.* 2004; Tranvik *et al.* 2009). Environmental policies such as the European water framework directive effectively reduces input of nutrients in aquatic ecosystems (Anneville *et al.* 2005) while the climate keeps warming. With these two phenomena, water will be warmer and contain fewer nutrients in most aquatic systems. Our models consistently predict that warmer temperatures should stabilise consumer-resource dynamics but, if temperature further increases, the consumer goes extinct as energetic efficiency decreases with warming. Moreover, we found that stoichiometric constraints can reduce this thermal extinction threshold (i.e. the consumer persists in a narrower thermal range), especially at low nutrient levels. Our stoichiometric model thus suggests that decreasing nutrient concentrations alongside warmer temperatures should fasten the extinction of consumer populations. This prediction matches empirical observations of consumer extinctions at warm temperatures in oligotrophic aquatic systems (Petchey *et al.* 1999; O'Connor *et al.* 2009). Altogether, these results indicate that considering stoichiometric constraints can be of importance for the management of nutrient inputs and the conservation of natural populations and communities under climate change.

Conclusion

Knowledge of how temperature and nutrient simultaneously influence the elemental composition of primary producers and consumers is crucial to better understand and predict the effects of global change on species interactions, community dynamics and fluxes of energy and material within and among ecosystems. Here we showed that stoichiometric constraints dampen the negative effect of enrichment on stability by reducing

population fluctuations through population dynamics feedbacks. However, stoichiometric constraints also decrease consumer energetic efficiency, which increases consumer extinction risk at extreme temperatures and low nutrient concentrations. Finally, stoichiometric constraints can reverse biomass distribution across trophic level by modulating consumer efficiency and resource population growth rate along the temperature and nutrient gradients. Our study provides a first step in the exploration of the consequences of stoichiometric constraints and temperature on ecological communities. It suggests that accounting for stoichiometric constraints can strongly influence our understanding of how global change drivers impact important features of ecological communities such as stability and biomass distribution patterns.

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Supplementary information

Stoichiometric constraints modulate the effects of temperature and nutrients on biomass distribution and community stability

Arnaud Sentis, Bart Haegeman, and José M. Montoya

Text S1. Derivation of the Stoichiometric Rosenzweig-MacArthur (SRM) model

We extended the Rosenzweig-MacArthur (RM) model (Rosenzweig & MacArthur 1963) by considering explicit nutrient dynamics and nutrient effects on resource population growth rate. We assumed that resource and consumer production are limited by energy and a single mineral nutrient. Moreover, we assume the system is closed for nutrients. Thus, nutrient supply originates exclusively from excretion and remineralization of biomass. The total amount of nutrients in the system (N_{tot}) is then a measure of nutrient enrichment. As elemental homeostasis is much stronger for consumers compared to primary producers (Andersen 1997), we assumed the nutrient quota of the consumer Q_C to be constant whereas the nutrient quota of the resource Q_R is flexible. Four differential equations determine the dynamics of four state variables, that is, the concentrations of resource (R) and consumer (C) carbon biomasses and of dissolved mineral nutrients (N), and the nutrient quota of the resource (Q_R):

$$\dot{C} = (e\frac{aR}{1+ahR} - m)C \quad \text{(S1)}$$

$$\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C \quad \text{(S2)}$$

$$\dot{Q_R} = h(N) - r(Q_R - Qmin) \quad \text{(S3)}$$

$$\dot{N} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + Q_C mC - h(N)R \quad \text{(S4)}$$

As in the RM model, rates of change of the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$ depend on their respective carbon biomass densities C and R (gC.m^{-3}), except that the resource population growth rate follows the Droop equation (Droop 1974) and is now limited by its nutrient quota Q_R relative to the minimum nutrient quota Q_{min}. Rate of change of Q_R depends on the nutrient uptake rate by the resource species $h(N)$ and the amount of nutrient invested in growth (eqn S3). $h(N)$ is the specific resource nutrient uptake rate and can be represented by a Michaelis-Menten model where the amount of nutrient uptake saturates at high nutrient concentrations.

With the mass-balance equation, we get that the total amount of nutrient is the sum of the free nutrient plus the nutrient fixed in the resource biomass plus the nutrient fixed in the consumer biomass: $N_{tot} = N + Q_R R + Q_C C$. As Eqns S1-S4 conserve total biomass (the system is closed), the time derivative of N_{tot} is zero. We can thus replace one of the four differential equations S1-S4 with the algebraic equation $N_{tot} = N + Q_R R + Q_C C$:

$$\dot{C} = (e\frac{aR}{1+ahR} - m)C \quad \text{(S5)}$$

$$\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C \quad \text{(S6)}$$

$$\dot{N} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + Q_C mC - h(N)R \quad \text{(S7)}$$

$$N_{tot} = N + Q_R R + Q_C C \quad \text{(S8)}$$

It is possible to derive a simpler model by reducing the number of dimensions in the above model from three to two. This model reduction is based on the assumption that free nutrients are taken up very quickly relative to the dynamics of the consumer and resource biomasses. This corresponds to taking $h(N)$ large, $h(N) = \frac{1}{\varepsilon}\tilde{h}(N)$ for small ε. The fast dynamics (on the timescale t ~ ε) are

$$\dot{N} = -\frac{1}{\varepsilon}\tilde{h}(N)R + (slower\ contributions) \quad \text{(S9)}$$

Which converge to N → 0, and $Q_R \rightarrow \frac{N_{tot}-Q_C C}{R}$ with N_{tot} the total nutrient in the system. In other words, N in dead and excreted matter is immediately recycled and acquired by the resource species. When substituting the quasi-steady-state in eqns. (S5, S6), we get the resulting dynamics (on the timescale t ~1):

$$\dot{C} = (e\frac{aR}{1+ahR} - m)C \quad \text{(S10)}$$

$$\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C \quad \text{(S11)}$$

$$N_{tot} = Q_R R + Q_C C \quad \text{(S12)}$$

From the nutrient conservation equation (eqn. S12) we obtain that $Q_R = \frac{N_{tot}-Q_C C}{R}$. The intuitive interpretation is that the resource nutrient quota Q_R decreases with the density of the resource population and with the density of nutrient stored in the consumer biomass. In contrast to eqns S5-S8, the reduced model has only two differential equations and one algebraic equation. It can be equivalently written as a set of three differential equations with $\dot{C}$ and $\dot{R}$ similar as equations S10 and S11 and with $\dot{Q_R} = \frac{d\frac{N_{tot}-Q_C C}{R}}{dt} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + \frac{Q_C mC}{R} - r(Q_R - Qmin)$.

In the RM model, the growth rate of the consumer population is assumed to depend only on resource density. We relaxed this assumption by making the population growth rate of the consumer dependent on both the resource quality (i.e. nutrient quota) and quantity (i.e. density). In the SRM model, consumer production is also limited by resource quality as the consumer assimilation efficiency e is a saturating function of resource nutrient quota Q_R:

$$e(Q_R) = e_{max}\frac{Q_R}{Q_R+Q_C} \quad \text{(S13)}$$

The intuitive interpretation of eqn. S13 is that resource quality is not a limiting factor for consumer growth as long as the nutrient content of the resource is superior to the nutrient content of the consumer (i.e. $Q_R > Q_C$). In other words, when $Q_R >> Q_C$, $e(Q_R) \rightarrow e_{max}$ and when $Q_R << Q_C$, $e(Q_R) \rightarrow 0$. By replacing e by $e(Q_R)$ in eqn. S10, we obtain the SRM model.

Table S1. Definitions and units of model parameters, from Uszko *et al.* (2017). For temperature-dependent parameters, we list the value of the scaling constant Q_0 (in units of the parameter) and the values of either the activation energy E_Q (eV, when temperature dependence is monotonous, eqn. 7) or of the temperature T_{opt} (Kelvin) at which the parameter value reaches a maximum/minimum and the width s (Kelvin) of this bell-/U-shaped function (when temperature dependence is non-monotonous, eqn. 8). Biomass and nutrients are expressed in units of carbon (C) and phosphorus (P), respectively

Parameter	Temperature independent value Thermal parameters	Unit	Definition	Reference
r	r_0 = 2.2; T_{opt} = 298.15; s = 12.0	1/d	Intrinsic rate of resource net production (gross production – biosynthesis costs)	Uszko et al. 2017
h	h_0 = 0.17; T_{opt} = 294.1; s = 6.4	d	Handling time	Uszko et al. 2017
a	a_0 = 8.9; T_{opt} = 296.0; s = 9.4	m^3/(gC d)	Attack rate	Uszko et al. 2017
m	$m_0 = 4.4 \times 10^8$; E_m = 0.55	1/d	Consumer mortality plus maintenance rate	
e_{max}	0.385	-	Maximum assimilation efficiency	Yodzis
Q_C	0.042	g P/g C	Consumer P:C ratio	Diehl 2005
Q_{min}	0.009	g P/g C	Minimum nutrient quota	Diehl 2005
Q_R	Variable	g P/g C	Resource P:C ratio	
N_{tot}	Variable	g P/m^3	Total nutrients in the system	
T	Variable	K	Temperature	

Fig. S1. Thermal functions used to parametrize the model (adapted from Uszko et al. 2017)

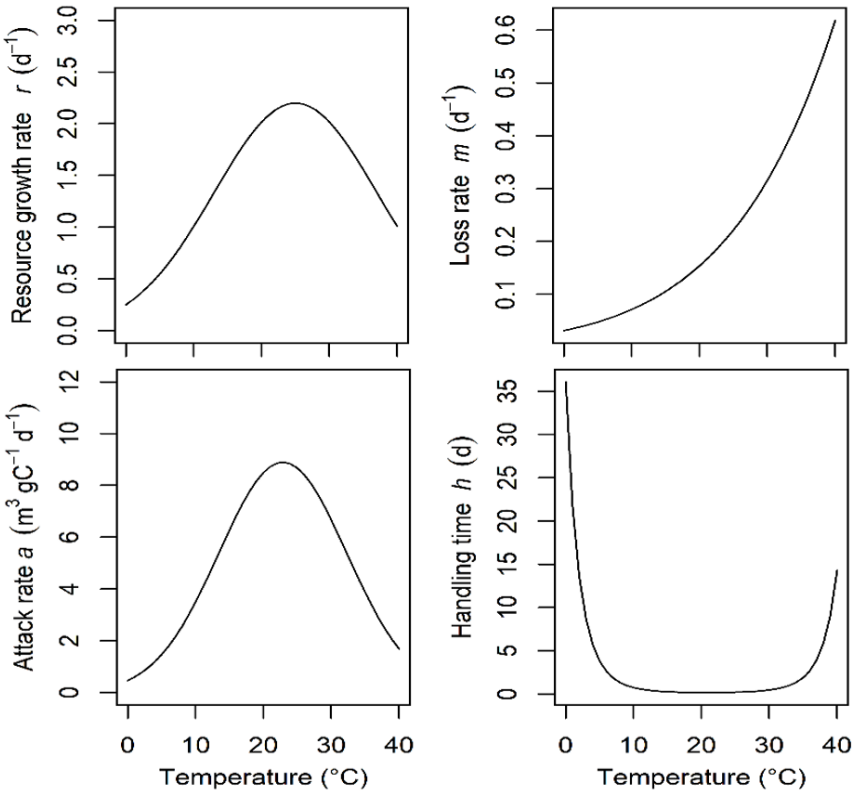

Fig. S2. Consumer-resource biomass ratio (log scale) along the temperature gradient for the Rosenzweig-MacArthur (RM, green lines) and the Stoichiometric Rosenzweig-MacArthur (SRM, black lines) models at three nutrient concentrations (0.008, 0.02, and 0.032 gP.m^{-3}). In each panel, the dotted lines represent unstable solutions whereas full lines represent stable solutions. The thin horizontal dotted line represents biomass ratio of one; i.e. the biomass densities of the resource and the consumer are equal.

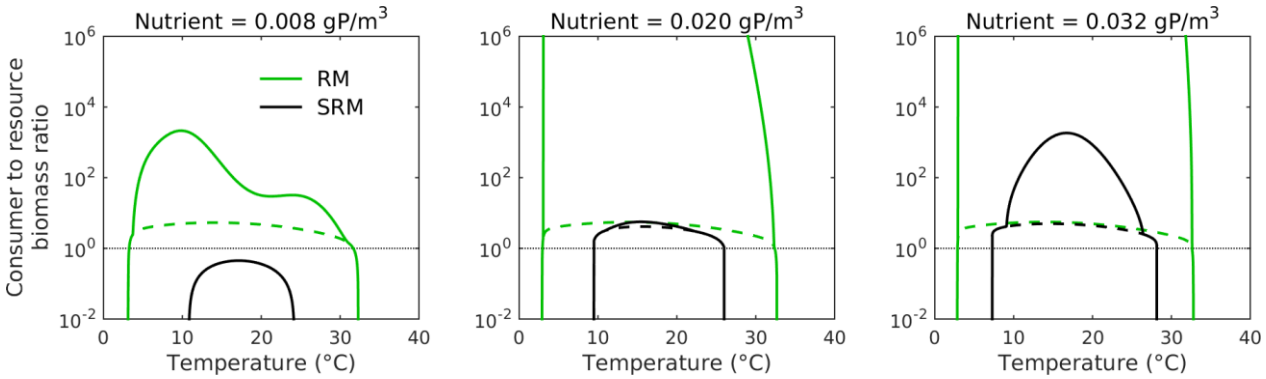
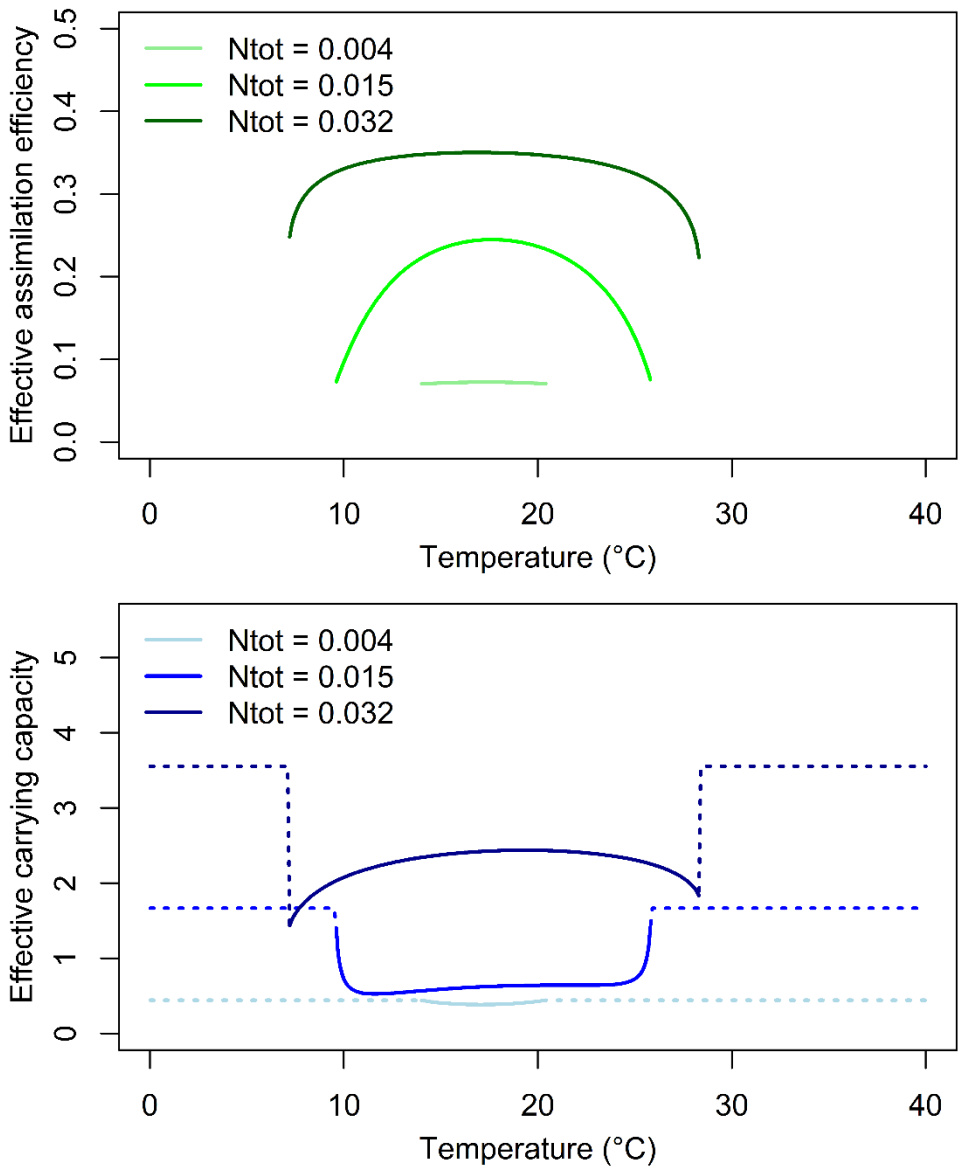
Fig. S3. Effective assimilation efficiency e_{ef} and carrying capacity K_{ef} from the Stoichiometric Rosenzweig-MacArthur (SRM) model along the temperature gradient at three nutrient levels (0.004, 0.015, and 0.032 gP.m^{-3}) with Q_C = 0.042. Full lines represent temperature and nutrient scenarios for which both the resource and consumer persist whereas dotted lines represent scenarios for which only the resource persists. Effective assimilation efficiency was calculated as $e_{ef} = e_{max}Q_R/(Q_R+Q_C)$, with Q_R the equilibrium solution of the SRM model and the effective carrying capacity as $K_{ef} = Q_R R/Q_{min} = (N_{tot}-Q_C C)/Q_{min}$, with Q_R, R and C the equilibrium solutions of the SRM model.