

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

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15 **Author contributions**

16 A.S., B.H., and J.M.M. conceived the study. B.H. and A.S. developed and analysed the models.

17 A.S. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

18

19 **Running title:** Stoichiometry alters thermal effects in food webs

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

22

23 **Legal and ethical requirements**

24 The authors declare that they have no conflict of interest.

25

26 **Abstract**

27 Temperature and nutrients are two of the most important drivers of global change. Both can modify
28 the elemental composition (i.e. stoichiometry) of primary producers and consumers. Yet their
29 combined effect on the stoichiometry, dynamics, and stability of ecological communities remains
30 largely unexplored. To fill this gap, we extended the Rosenzweig-MacArthur consumer-resource
31 model by including thermal dependencies, nutrient dynamics, and stoichiometric constraints on
32 both the primary producer and the consumer. We found that stoichiometric constraints dampen the
33 paradox of enrichment and increased persistence at high nutrient levels. Nevertheless, they also
34 reduced consumer persistence at extreme temperatures. Finally, we also found that stoichiometric
35 constraints can strongly influence biomass distribution across trophic levels by modulating
36 consumer assimilation efficiency and resource growth rates along the environmental gradients. Our
37 findings highlight the importance of accounting for stoichiometric constraints as they can mediate
38 the temperature and nutrient impact on the dynamics and functioning of ecological communities.

39
40 **Key words:** temperature, stoichiometry, temporal variability, paradox of enrichment, trophic
41 interactions, nutrient quota, consumer-resource dynamics, biomass structure.

42 **Introduction**

43 Temperature and nutrients regulate many biological processes, including species geographical
44 distribution, primary production, species interactions, and energy and material fluxes (Falkowski
45 *et al.* 1998; Enquist *et al.* 1999; Elser *et al.* 2007; Thomas *et al.* 2017). They are at the core of
46 several ecological theories. While temperature is a fundamental component of metabolic scaling
47 theory (Brown *et al.* 2004), nutrients are at the core of resource competition theory (Tilman 1982)
48 and ecological stoichiometry theory (Sterner & Elser 2002). Nevertheless, less is known about how
49 temperature and stoichiometry (i.e. the element composition of organisms) interact to influence
50 ecological processes across level of organisation (but see Cross *et al.* 2015, Woods *et al.* 2003).
51 Cross *et al.* (2015) reviewed the evidence and suggested that a better understanding of the
52 interactions between temperature and nutrients is crucial for developing realistic predictions about
53 ecological responses to multiple drivers of global change, including climate warming and elevated
54 nutrient supply. While they provided a road map on how to investigate the combined effects of
55 temperature and nutrient on ecological processes, we still lack an integrative theory to understand
56 better how the links between stoichiometry, nutrient enrichment, and temperature influence the
57 dynamics and stability of multispecies communities. Such a theory will allow us to understand how
58 and when stoichiometric variation modulates the consequences of single and combined
59 components of global change on trophic interactions, community dynamics, and ecosystem
60 functioning.

61
62 Nutrients can modulate the effects of warming on communities directly by altering primary
63 production, and/or indirectly by changing the elemental composition of primary producers.
64 Conversely, thermal effects on trophic interaction strengths (i.e. the *per capita* effect of predators
65 on prey population densities) and on consumer energetic efficiencies (i.e. ingestion relative to
66 metabolic demand) depend on both the quantity and quality of their resources. Thus, to understand

67 the combined effects of temperature and nutrients on ecosystems we need a theory that includes
68 both thermal and stoichiometric dependencies that regulate species interactions and community
69 dynamics.

70
71
72 Predicting the effects of global warming and nutrient changes on ecosystems is challenging as
73 species are embedded within communities of multiple interacting species (Petchey *et al.* 1999;
74 Tylianakis *et al.* 2008; Montoya & Raffaelli 2010; Gilbert *et al.* 2014). Increased resource
75 availability (hereafter: enrichment) and warming can jointly affect food-web stability and structure
76 by modifying the strength of trophic interactions (O'Connor *et al.* 2009; Binzer *et al.* 2012; Kratina
77 *et al.* 2012; Sentis *et al.* 2014; Binzer *et al.* 2016). Enrichment typically increases energy flux from
78 resources to higher trophic levels which often leads to the well-known paradox of enrichment
79 where the amplitude of population fluctuations increase with nutrients, leading to extinctions at
80 high nutrient concentrations (Rosenzweig 1971; Rip & McCann 2011; Gilbert *et al.* 2014).
81 Nevertheless, most consumer species become less efficient at processing matter and energy at
82 warmer temperatures as their metabolic rates often increase faster with temperature than their
83 feeding rates (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Iles 2014). This reduction of
84 energetic efficiency lessens energy flow between trophic levels and hence stabilizes food-web
85 dynamics by reducing population fluctuations (Rip & McCann 2011; Binzer *et al.* 2012; Gilbert *et*
86 *al.* 2014). As a result, mild warming may alleviate the paradox of enrichment by decreasing
87 consumer energetic efficiency (Binzer *et al.* 2012; Sentis *et al.* 2017).

88
89 The theoretical expectations and results described above have already improved our ability to
90 understand and predict the effects of temperature and enrichment on food webs (Boit *et al.* 2012;
91 Tabi *et al.* 2019). However, most previous studies using metabolic scaling theory assumed that
92 nutrient enrichment lead to an increase in resource carrying capacity without influencing resource

93 elemental composition (Vasseur & McCann 2005; Binzer *et al.* 2012; Gilbert *et al.* 2014; Binzer
94 *et al.* 2016; Sentis *et al.* 2017). Yet nutrient enrichment effects are more complex. The elemental
95 composition of primary producers is likely to be altered, in response to the supplies of energy and
96 materials relative to their growth and nutrient intake rates (Rastetter *et al.* 1997; Robert W. Sterner
97 *et al.* 1997; Finkel *et al.* 2009) Sterner *et al.* 1997). This, in turn, can affect the dynamics of the
98 producer population and the herbivores feeding on it. For instance, previous modelling studies
99 showed that introducing stoichiometric heterogeneity in predator-prey population dynamic models
100 can dampen the negative effect of nutrient enrichment on system persistence by reducing
101 population biomass fluctuations (Andersen 1997; Loladze *et al.* 2000; Andersen *et al.* 2004; Elser
102 *et al.* 2012). More generally, the stoichiometric flexibility of primary producers, in particular the
103 flexibility in carbon to nutrient ratios (e.g. C:N or C:P), has important implications for animal
104 feeding behaviour (White 1993), consumer population stability (White 1993; Sterner & Hessen
105 1994; Hessen *et al.* 2002), community structure (Andersen 1997), and ecosystem processes such
106 as biogeochemical cycling (Andersen 1997; Hessen *et al.* 2004).

107
108 Previous theoretical and empirical studies reported that stoichiometric variations can have a strong
109 influence on the stability of consumer-resource interactions (Andersen 1997; Andersen *et al.* 2004;
110 Diehl *et al.* 2005; Elser *et al.* 2012). For instance, populations of crustacean *Daphnia* feeding on
111 low quality (i.e. low nutrient: carbon ratio) algae cannot persist even when resource quantity is not
112 a limiting factor (Elser *et al.* 2007). Consumer extinction is explained by the fact that the consumer
113 assimilation efficiency is, for most organisms, a function of resource quality (Elser *et al.* 2000).
114 When resource quality is low, the consumers assimilate only few nutrients relative to the biomass
115 they ingest, which limits their growth and reproduction (Elser *et al.* 2000; Elser *et al.* 2012).
116 Temporal variations in resource quality can stabilize the system by weakening interaction strength
117 and dampening population fluctuations (Andersen *et al.* 2004; Diehl *et al.* 2005)but see(Loladze *et*

118 *al.* 2000; Elser *et al.* 2012). However, it remains unclear whether and how temporal variations in
119 the elemental composition of primary producers and consumers can modulate the effects of
120 temperature and nutrients on important community features such as stability and biomass
121 distribution across trophic levels. Previous studies indicated that the spatial and temporal
122 intraspecific variations in the elemental composition of primary producers are expected to increase
123 in response to global change drivers such as temperature, CO₂, and nutrient availability (Bezemer
124 & Jones 1998; Woods *et al.* 2003; Finkel *et al.* 2009). This increased variation can be of importance
125 for both primary producer and consumer populations as the growth rate of primary producers is
126 well known to depend on their elemental composition (Droop 1974) as is the assimilation efficiency
127 of the consumers (Sterner & Elser 2002).

128
129 Altogether, previous studies indicated that both temperature and stoichiometric variations can have
130 important effects on species interactions and community dynamics (Andersen *et al.* 2004; Diehl *et*
131 *al.* 2005; Fussmann *et al.* 2014; Binzer *et al.* 2016; Sentis *et al.* 2017). However, the effects of
132 temperature and nutrient stoichiometry on food web dynamics and stability have only been studied
133 in isolation. Here we focus on the combined effects of temperature and nutrients on the
134 stoichiometry of primary producers and consumers and how this affects community stability and
135 biomass distribution across trophic levels in a consumer-resource system. Understanding the
136 determinants of stability and biomass distribution has been at the core of ecology for a long time
137 (Elton (1927), Lindeman (1942)). Recent theory aims at explaining empirical observations of
138 trophic pyramids (i.e. population biomass decreases with trophic levels), inverted trophic pyramids
139 (i.e. population biomass increases with trophic levels), trophic cascades and the link between
140 biomass distribution and stability (McCauley *et al.* 2018; Barbier & Loreau 2019). However, we
141 lack theory on temperature and stoichiometry as drivers of biomass and stability patterns.

142

143 Here, we used the Rosenzweig-MacArthur model as a baseline **nonstoichiometric** model because
144 this model is one of the most studied models used to investigate the effects of temperature and
145 nutrient enrichment on community dynamics (Vasseur & McCann 2005; Binzer *et al.* 2012;
146 Fussmann *et al.* 2014; Sentis *et al.* 2017). Inspired by previous temperature-independent
147 stoichiometric consumer-resource models (Andersen 1997; Andersen *et al.* 2004; Diehl *et al.*
148 2005), we then extended the Rosenzweig-MacArthur model to account for nutrient dynamics as
149 well as for the simultaneous dependence of community dynamics on temperature and flexible
150 resource stoichiometry. Our objective here was not to develop a complex and very realistic
151 stoichiometric model that would include additional important abiotic and biotic features such as
152 light intensity (Diehl 2007) or compensatory feeding (Cruz-Rivera & Hay 2000). Instead, we aimed
153 at introducing two fundamental stoichiometric features (i.e. stoichiometric flexibility and
154 stoichiometric imbalance) and investigating how these stoichiometric considerations can change
155 predictions of the Rosenzweig-MacArthur model. We thus used our extended Rosenzweig-
156 MacArthur model to predict the effects of warming and nutrient enrichment on population
157 dynamics and biomass distribution across trophic levels and compared these predictions with the
158 predictions of the nonstoichiometric Rosenzweig-MacArthur model. We particularly addressed
159 two questions: (i) How do stoichiometric constraints modulate the effects of enrichment and
160 warming on community stability and persistence? and (ii) How do stoichiometric constraints
161 modulate the effects of enrichment and warming on biomass distribution across multiple trophic
162 levels?

163 **Methods: Population dynamic models**

164 **The Rosenzweig-MacArthur (RM) model.**

165 Rates of change of the consumer and resource biomass densities \dot{C} and \dot{R} depend on their respective
166 biomass densities C and R ($\text{g}\cdot\text{m}^{-3}$):

167
$$\dot{R} = r\left(1 - \frac{R}{K}\right)R - \frac{aR}{1+ahR}C \quad (1)$$

168
$$\dot{C} = \left(e\frac{aR}{1+ahR} - m\right)C \quad (2)$$

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

178
179 In the RM model, consumer and resource population growth rates are only limited by nutrient or
180 resource density. Nutrient enrichment is assumed to increase resource carrying capacity, which
181 often leads to the well-known paradox of enrichment where populations fluctuates up to extinctions
182 (Rosenzweig 1971). Nevertheless, this model considers neither nutrient dynamics nor temporal
183 variations of resource stoichiometry and their consequences on population dynamics. To
184 circumvent these limitations of the RM model, we extended it to ~~better~~ consider nutrient dynamics,
185 resource stoichiometry and the way they can affect resource and consumer population dynamics.

186

187 **The Stoichiometric Rosenzweig-MacArthur (SRM) model.**

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

194

195 *Stoichiometric constraint on the resource population growth rate*

196 Inspired by previous stoichiometric models (Andersen 1997; Loladze *et al.* 2000; Andersen *et al.*
197 2004; Diehl *et al.* 2005), we extended the RM model by considering explicit nutrient dynamics and
198 nutrient effects on resource population growth rate. The system is assumed to be closed for
199 nutrients. Thus, nutrient supply originates exclusively from biomass excretion and
200 remineralisation. The total amount of nutrients in the system (N_{tot}) is then a measure of nutrient
201 enrichment. In contrast to the very high plasticity in C:N or C:P exhibited by autotrophs,
202 heterotrophs regulate elemental composition within narrower bounds, even when consuming food
203 with large variation in elemental composition (Andersen & Hessen 1991; Sterner & Hessen 1994;
204 Andersen 1997; Elser *et al.* 2000). In other words, the elemental homeostasis is much stronger for
205 consumers compared to primary producers. We thus assumed the nutrient quota (i.e. the nutrient
206 to carbon ratio) of the consumer Q_C to be conserved whereas the one of the resource Q_R is flexible
207 over time with the only constraint that $Q_R > 0$. As in the RM model, rates of change of the consumer
208 and resource biomass densities \dot{C} and \dot{R} depend on their respective carbon biomass densities C and
209 R ($\text{gC}\cdot\text{m}^{-3}$), except that the resource population growth rate follows the Droop equation (Droop
210 1974) given by $r(1-Q_{\text{min}}/Q_R)R$ and is now limited by Q_R relative to the minimum nutrient quota
211 Q_{min} :

212
$$N_{tot} = Q_R R + Q_C C \quad (3)$$

213
$$\dot{R} = r \left(1 - \frac{Q_{min}}{Q_R}\right) R - \frac{aR}{1+ahR} C \quad (4)$$

214
$$\dot{C} = \left(e \frac{aR}{1+ahR} - m\right) C \quad (5)$$

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

219

220 *Stoichiometric constraint on the consumer population growth rate*

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

226
$$e(Q_R) = e_{max} \frac{Q_R}{Q_R + Q_C} \quad (6)$$

227 The intuitive interpretation of eqn. 6 is that resource quality is not a limiting factor for consumer
228 growth as long as the nutrient content of the resource is superior to the nutrient content of the
229 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
230 Q_R for $Q_R < Q_C$. By replacing e by $e(Q_R)$ in eqn. 5, we obtain the SRM model.

231

232 **Temperature dependence of model parameters**

233 To investigate the effect of temperature and stoichiometric constraints on consumer-resource
234 dynamics, we next extended the RM and SRM models described above by adding thermal
235 dependencies of the parameters. Following Uszko et al. (2017), we assumed that the total amount

236 of nutrient N_{tot} , the maximum food conversion efficiency e_{max} , and fixed stoichiometric traits (Q_C)
237 are independent of temperature, as there is no evidence of systematic temperature dependence for
238 any of them (Peters 1983; Ahlgren 1987; Borer *et al.* 2013; Yvon-Durocher *et al.* 2015). Rate of
239 maintenance respiration and natural background mortality m typically increases exponentially with
240 temperature (Fig. S1a and b). We thus used the Arrhenius equation to describe the effect of
241 temperature T (in Kelvin) on m :

$$242 \quad m(T) = m_0 e^{\frac{-E_m}{kT}} \quad (7)$$

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

$$249 \quad g(T) = g_0 e^{\pm \frac{(T-T_{\text{opt}})^2}{2s^2}} \quad (8)$$

250
251 where T_{opt} is the temperature at which the rate g reaches its minimum or maximum, s is the function
252 width and g_0 is a parameter-specific constant calculated at T_{opt} . The minus-sign corresponds to
253 Gaussian functions and the plus-sign to inverted Gaussian functions.

254

255 **Model parameterisation and simulations**

256 To parameterise the models we assumed the resource and consumer species to be a unicellular
257 freshwater algae and a *Daphnia* grazer, respectively. The choice for this system was motivated by
258 the good characterization of both the stoichiometric parameters and thermal dependencies for this
259 system (Andersen 1997; Uszko *et al.* 2017). Uszko *et al.* (2017) recently estimated the thermal

260 dependencies for biological rates of the green algae *Monoraphidium minutum* and the grazer
261 *Daphnia hyalina*. We thus used their estimates of stoichiometric parameters and thermal
262 dependencies (See Table S1 and Fig. S1 for further details).

263
264 To investigate the individual and combined effects of enrichment, warming, and stoichiometric
265 constraints, we varied temperature (401 values ranging from 0 to 40°C by 0.1°C) and total amount
266 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,
267 overlapping with reported mean phosphorus concentration in European peri-alpine lakes
268 (Anneville *et al.* 2005)). For the RM model, we used the minimum nutrient quota to convert
269 nutrients into resource (i.e. $K = N_{\text{tot}}/Q_{\text{min}}$). This implies that carrying capacity is independent of
270 temperature which is expected for closed, nutrient-limited systems (Uszko *et al.* 2017) although
271 more experimental evidence are needed to verify this assumption. We then simulated the consumer-
272 resource dynamics for 1000 days to enable the system to reach an attractor (either an equilibrium
273 point or a limit cycle) before we assessed the final state. Therefore, for each model, we simulated
274 24060 combinations of environmental conditions (401 temperatures by 60 nutrient concentrations).
275 Initial biomass density of each species was set to 0.98 times its equilibrium density in the two-
276 species system (calculated by solving for the two-species equilibrium, using either eqns 1-2 for
277 model RM or eqns 3-5 for model SRM). The value of 0.98 was chosen to be (1) close enough to
278 equilibria to avoid extinctions caused solely by transient dynamics and (2) not exactly the
279 equilibrium value to probe the stability of the equilibrium. Any population falling below the
280 extinction threshold of 10⁻⁹ g.m⁻³ during the simulation was deemed extinct and its biomass set to
281 zero to exclude ecologically unrealistic limit cycles. For each model, we calculated system
282 persistence as the percentage of simulations with the two species remaining extant at the end of the
283 simulations.

284

285

286 **Results**

287 *Stability: population fluctuations and persistence*

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

294

295 The RM model predicts that increasing nutrient concentration is strongly destabilizing: the system
296 shifts from a stable equilibrium point to limit cycles (i.e. the system crosses a Hopf bifurcation).
297 This agrees with the paradox of enrichment. As population biomass fluctuations (i.e. cycle
298 amplitude) increase with nutrient concentration, minimal population densities are very low at high
299 nutrient concentrations leading to the extinction of both the consumer and resource once the
300 extinction threshold is crossed (Fig. 1). In the range of temperatures where the consumer persists,
301 warming does not have a strong influence on the nutrient concentration at which the system shifts
302 from the stable equilibrium point to limit cycles, although this qualitative shift is absent at very
303 high temperatures (i.e. 32°C) when the consumer is close to extinction. Warming decreases
304 fluctuation amplitude and thus dampens extinctions driven by the paradox of enrichment, which
305 results in warming enhancing the persistence of the consumer-resource system at high nutrient
306 concentrations. However, very warm and cold temperatures cause the extinction of the consumer
307 (see below for the mechanisms underlying extinctions), releasing resources from top-down control.
308 Overall, we found that, without considering the extinction threshold of 10^{-9} g.m⁻³ (see Model

309 parametrisation and simulations), both the consumer and the resource can persist in 74% of the
310 temperature-nutrient concentration scenarios (i.e. black + orange areas in Fig 1C). Nevertheless,
311 when considering the extinction threshold, they persist in only 21% of the temperature-nutrient
312 scenarios (i.e. black area in Fig. 1c) indicating that extinctions driven by population fluctuations
313 are highly prevalent in the RM model.

314
315 In contrast, the SRM model shows that increasing nutrient concentrations causes fewer fluctuations
316 than those observed for the RM model (Fig. 1). This is because: (1) more nutrients are needed to
317 shift the system from a stable equilibrium point to limit cycles—the system can indeed persist
318 without fluctuations up to 0.02 gP.m^{-3} whereas it was only up to 0.0005 gP.m^{-3} in the RM model—
319 and (2) when the system fluctuates, the amplitude of the fluctuations is smaller in the SRM than in
320 the RM model. As a result, stoichiometric constraints dampen the amplitude of population
321 fluctuations (i.e. the paradox of enrichment) and hence increase system persistence at high nutrient
322 levels. While the qualitative effect of temperature is similar to that observed in the RM model, the
323 thermal thresholds for consumer persistence are reduced at low and high temperatures in the SRM
324 predictions. Moreover, thermal thresholds remain almost constant along the nutrient gradient in the
325 RM model, whereas in the SRM model they depend on nutrient concentration, with a smaller
326 thermal range at low nutrient levels compared to high nutrient levels (Fig. 1). The consumer is thus
327 more likely to go extinct at low nutrient concentrations and extreme temperatures in the SRM
328 model than in the RM model. Overall, system persistence for the SRM model was 44% without
329 considering the extinction threshold and 37% when considering it. In other words, without
330 considering extinctions driven by very low biomass densities, the SRM model predicts lower
331 persistence of the consumer compared to RM model but it is the opposite pattern when considering
332 extinctions driven by very low biomass densities. We thus conclude that the RM model predicts

333 larger population fluctuations leading to high probabilities of populations extinctions in
334 comparison to the SRM model.

335

336 *Biomass distribution*

337 We next compared the predictions of both models for consumer-resource biomass ratios along the
338 temperature and nutrient gradients (Fig. 2). We found that the RM model systematically predicts
339 inverted biomass pyramids. In contrast, the SRM model predicts both biomass pyramids and
340 inverted pyramids depending on temperature and nutrient levels. The RM model **systemically**
341 predicts that, as soon as the consumer can persist, its population biomass density systematically
342 exceeds the resource population biomass density (Fig. 2). With the SRM model, the biomass ratios
343 are below one at low nutrient levels (Fig. 2). However, at medium and high nutrient levels, the
344 ratios are above one as soon as the consumer can persist. We found qualitatively similar results
345 when considering unstable equilibrium points (Fig. S2).

346

347 *Mechanisms underlying stability and biomass distribution patterns*

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

355

356

357

358 *Consumer energetic efficiency of the consumer and assimilation efficiency*

359 The persistence of the consumer at low and high temperatures is driven by the energetic efficiency

360 *EE* of the consumer (i.e. its feeding rate relative to metabolic losses) calculated as follows:

361
$$EE = \frac{ef(R^*)}{m} \quad (9)$$

362 Where $f(R^*)$ is the functional response of the consumer at resource density R^* (i.e. the resource

363 equilibrium density in absence of the consumer). We recall that the assimilation efficiency e is a

364 function of resource quality Q_R in the SRM model whereas it is constant in the RM model. The

365 intuitive interpretation of eqn. 9 is that *EE* should be above one for the consumer population to

366 **growth** and persist.

367

368 To better understand the influence of stoichiometric constraints on consumer persistence, we thus

369 investigated differences in the RM and SRM model predictions regarding the consumer energetic

370 efficiency *EE* along the temperature gradient at two nutrient concentrations (Fig. 3). For both

371 models, energetic efficiency at equilibrium (i.e. static effect) has a hump-shaped relationship with

372 temperature with maximal efficiency values at medium temperatures. While this unimodal shape

373 is conserved across nutrient levels and models, the RM model systematically predicts higher

374 consumer energetic efficiency values than the SRM model because consumer assimilation

375 efficiency is lower in the SRM than in the RM model (Fig. S3). As a result, the temperatures at

376 which energetic efficiency falls below one and drives consumers extinct are more extreme in the

377 RM model compared to the SRM model (Fig. 3). In other words, energetic efficiency is above one

378 for a narrower thermal range in the SRM model.

379

380

381

382 *Dynamical feedbacks due to the stoichiometric constraints*

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

394
395 To separate the static and dynamic effects of the stoichiometric constraints, we calculated the
396 values of assimilation efficiencies and carrying capacities predicted by the SRM model for each
397 temperature-nutrient scenario (Fig. S3) and used these effective parameter values to replace the
398 values of parameters e and K in the RM model for each temperature-nutrient scenario. In other
399 words, we calculated average values of e and K in the dynamic SRM model and used them as
400 constant input parameters in the RM model. We then simulated population dynamics along the
401 temperature-nutrient gradient using the RM model with these effective parameters; referred
402 hereafter as effective RM model (Fig. 4). Comparing predictions from the RM, effective RM, and
403 SRM models allowed to disentangle the static stoichiometric effects (when going from the RM to
404 the effective RM predictions; Fig. 4, panels a to b) from the dynamical stoichiometric effects (when
405 going from the effective RM to the SRM predictions; Fig. 4, panels b to c). We found that, at low
406 nutrient concentrations, population fluctuations and consumer persistence predicted by the

407 effective RM model agreed with predictions of the SRM model. However, the system shifted from
408 a stable equilibrium point to a limit cycle at lower nutrient concentrations for the effective RM
409 model than for the SRM model. This suggests that more nutrients are needed to destabilize the
410 system with the SRM model. Moreover, the effective RM model predicts ampler population
411 fluctuations than the SRM model. As a result, the effective RM predicts high extinction rates at
412 high nutrient concentrations compared to the SRM model. Overall, we found that the effective RM
413 model cannot fully reproduce the dynamics predicted by the SRM, which indicates that including
414 stoichiometric constraints in the RM model involves more than only changing parameter values.

415

416

417 **Discussion**

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

429

430

431 *Stoichiometric constraints and temperature can dampen the paradox of enrichment*

432 We showed that both stoichiometric constraints and temperature dampen the negative effect of
433 nutrient enrichment on consumer-resource fluctuations and increase system persistence at high
434 nutrient levels. Temperature effects are driven by physiological mechanisms. In agreement with
435 previous empirical studies, our model parametrization reflects the observation **we found** that
436 metabolic loss rates increase faster with warming than consumer feeding rates (Vucic-Pestic *et al.*
437 2011; Sentis *et al.* 2012; Fussmann *et al.* 2014; Iles 2014). Consumers are thereby less energetically
438 efficient at higher temperatures which stabilizes food-web dynamics by reducing energy flow
439 between trophic levels (Binzer *et al.* 2012; Kratina *et al.* 2012; Fussmann *et al.* 2014; Sentis *et al.*
440 2017). In contrast, the effect of stoichiometric constraints is mainly linked to two mechanisms: a
441 **static** shift in the position of the Hopf bifurcation and negative dynamical feedbacks of the
442 consumer and resource on their population growth rates. Both resources and consumers are
443 composed of the same essential elements (N, P, and C), which implies that, when consumer or
444 resource population biomass increases, it reduces the pool of free nutrients available for the growth
445 of the resource population. **Therefore, more nutrients are needed to shift the system from a stable**
446 **equilibrium to population cycles**. In other words, the paradox of enrichment is displaced to higher
447 nutrient concentrations (i.e., the position of the Hopf bifurcation is shifted to higher nutrient levels).
448
449 In addition to the static effect above, we found two dynamic effects that correspond to negative
450 dynamical feedbacks of the consumer and the resource on themselves. When consumer population
451 increases, it decreases the population growth rate of the resource by limiting nutrient availability,
452 diminishing resource biomass, which, in turn, decreases the consumer population growth rate.
453 Conversely, when the resource biomass increases, this decreases the nutrient content of the
454 resource, which, in turn, limits the growth rates of both the resource and consumer populations.
455 These stoichiometric negative feedback loops strongly decrease the amplitude of population

456 fluctuations and thus dampen the paradox of enrichment. Interestingly, our comparisons of the RM,
457 effective RM and SRM model predictions indicate that the dynamical effects contribute more to
458 the reduction of fluctuations than the static effects: population fluctuations are large in the effective
459 RM model accounting for the static effect only, whereas they are much smaller in SRM model
460 accounting for both static and dynamical effects (Fig. 4). This implies that the impact of
461 stoichiometric constraints on community dynamics goes beyond a simple modification of
462 parameter values and encompass more complex population feedbacks between the consumer and
463 the resource.

464
465 Overall, these results demonstrate that both flexible stoichiometry and temperature can
466 synergistically dampen the paradox of enrichment by two different mechanisms: population
467 dynamic feedbacks and physiological constraints. Our consumer-resource model is simplified
468 compared to natural communities composed of numerous species. Yet, the predictions of the
469 stoichiometric model fit with empirical observations. In eutrophic lakes and experimental
470 mesocosms, populations can persist at relatively high nutrient concentrations even if fertilisation
471 enhance population fluctuations (O'Connor *et al.* 2009; Boit *et al.* 2012; Kratina *et al.* 2012), as
472 our stoichiometric model predicts. In contrast, the Rosenzweig-MacArthur model tends to produce
473 very large population fluctuations and extinctions at low nutrient concentrations which can explain
474 why these predictions are not well supported by empirical observations (McAllister *et al.* 1972;
475 Jensen & Ginzburg 2005).

476
477 *Effects of stoichiometric constraints on system persistence across environmental gradients*
478 While stoichiometric constraints dampen the paradox of enrichment and thus increase persistence
479 at high nutrient levels, they also reduce the persistence of the consumer at low and high
480 temperatures. Stoichiometric constraints affect the thermal thresholds for consumer extinctions.

481 Consumers can only persist over a narrower range of intermediate temperatures when they are
482 constrained by stoichiometry. This is due to the reduced assimilation efficiency of the consumer at
483 low and high temperatures that, in turn, decreases its energetic efficiency and thus fastens consumer
484 extinction. The finding that assimilation efficiency is temperature dependent contrasts with
485 previous theoretical studies that used the RM model and assumed that the assimilation efficiency
486 is temperature independent (Binzer *et al.* 2012; Gilbert *et al.* 2014; Sentis *et al.* 2017; Uszko *et al.*
487 2017). In the SRM model, the thermal dependency of the consumer assimilation efficiency is fully
488 driven by the change in the resource stoichiometry induced by temperature. The SRM model thus
489 predicts an additional mechanism by which temperature can influence trophic interactions:
490 temperature changes resource stoichiometry which, in turn, impacts the consumer assimilation
491 efficiency and its population growth rate. To sum up, the overall effect of stoichiometric constraints
492 on system persistence thus depends on the temperature range considered and on their relative
493 influence on population fluctuations versus consumer persistence.

494
495 *Effects of stoichiometric constraints on biomass distribution*
496 We found that stoichiometric constraints can modulate the effects of temperature and nutrients on
497 biomass distribution across trophic levels. Without stoichiometric constraints (i.e. with the
498 Rosenzweig-MacArthur model), biomass ratios are above one for almost all temperatures or
499 nutrient levels as the biomass produced by the resource is efficiently transferred to the consumer
500 level consistently along the environmental gradients. This finding agrees with theoretical studies
501 reporting that Lotka-Volterra and RM models predict biomass ratios above one and fail to
502 reproduce biomass pyramids for a substantial region of parameter values (Jonsson 2017; Barbier
503 & Loreau 2019). However, in nature, consumer-resource biomass ratios are often below one
504 (McCauley & Kalff 1981; Del Giorgio & Gasol 1995; McCauley *et al.* 1999; Irigoien *et al.* 2004)
505 suggesting that additional mechanisms should be included to better understand and predict biomass

506 distribution patterns in natural food webs. Our stoichiometric model agrees with experimental
507 observations. It predicts that, at low nutrient concentrations (i.e. $< 0.01 \text{ gP.m}^{-3}$), the biomass ratio
508 never exceeds one along the entire temperature gradient. This is observed in oligotrophic aquatic
509 systems where primary production is too low to sustain high consumer populations (O'Connor *et*
510 *al.* 2009). In addition, we also found that increasing nutrient levels decreased the temperature
511 ranges within which biomass ratio is below one. This corresponds to results from manipulated
512 nutrient concentrations and temperature in aquatic mesocosms, where zooplankton to
513 phytoplankton biomass ratio only exceeds one in the enriched mesocosms at medium or warm
514 temperatures (i.e. 27°C) (O'Connor *et al.* 2009). This suggests that the models with stoichiometric
515 constraints better reproduce the biomass patterns observed in experimental and natural systems.
516 Nevertheless, further experiments investigating the links between stoichiometric flexibility and
517 consumer-resource dynamics are needed to determine if these stoichiometric mechanisms are
518 underlying patterns of biomass distribution in nature.

519
520 *Implications of our findings for global change*
521 Temperature and nutrients do not act in isolation from each other. Climate warming, for example,
522 causes stronger water stratification which, in turn, can limit nutrient cycling (Sarmiento *et al.* 2004;
523 Tranvik *et al.* 2009). Environmental policies such as the European water framework directive (i.e.
524 Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for
525 the Community action in the field of water policy) effectively reduces input of nutrients in aquatic
526 ecosystems (Anneville *et al.* 2005) while the climate keeps warming. With these two phenomena,
527 water will often be warmer and contain fewer nutrients in aquatic systems. Our models consistently
528 predict that warmer temperatures should stabilise consumer-resource dynamics but, if temperature
529 further increases, the consumer goes extinct as energetic efficiency decreases with warming.
530 Moreover, we found that stoichiometric constraints can reduce this thermal extinction threshold

531 (i.e. the consumer persists in a narrower thermal range), especially at low nutrient levels. Our
532 stoichiometric model thus suggests that decreasing nutrient concentrations alongside warmer
533 temperatures should fasten the extinction of consumer populations. This prediction matches
534 empirical observations of consumer extinctions at warm temperatures in oligotrophic aquatic
535 systems (Petchey *et al.* 1999; O'Connor *et al.* 2009). Altogether, these results indicate that
536 considering stoichiometric constraints can be of importance for the management of nutrient inputs
537 and the conservation of natural populations and communities under climate change.

538

539 ***Conclusion***

540 Knowledge of how temperature and nutrient simultaneously influence the elemental composition
541 of primary producers and consumers is crucial to better understand and predict the effects of global
542 change on species interactions, community dynamics and fluxes of energy and material within and
543 among ecosystems. Here we showed that stoichiometric constraints dampen the negative effect of
544 enrichment on stability by reducing population fluctuations through population dynamics
545 feedbacks. However, stoichiometric constraints also decrease consumer energetic efficiency,
546 which increases consumer extinction risk at extreme temperatures and low nutrient concentrations.
547 Finally, stoichiometric constraints can reverse biomass distribution across trophic level by
548 modulating consumer efficiency and resource population growth rate along the temperature and
549 nutrient gradients. Our study provides a first step in the exploration of the consequences of
550 stoichiometric constraints and temperature on ecological communities. It suggests that accounting
551 for stoichiometric constraints can strongly influence our understanding of how global change
552 drivers impact important features of ecological communities such as stability and biomass
553 distribution patterns.

554

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726

727

728 **Figure legends**

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

738

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

745

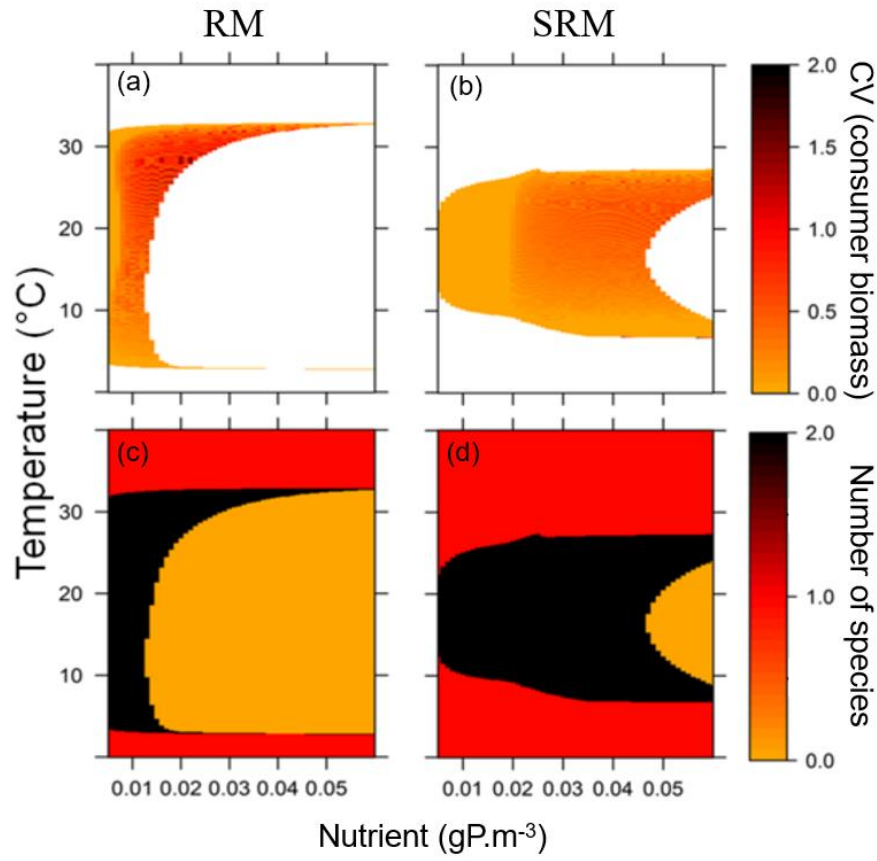
746 **Fig. 3.** Consumer energetic efficiency along the temperature gradient for the Rosenzweig-
747 MacArthur (RM, in green) and the Stoichiometric Rosenzweig-MacArthur (SRM, in black) models
748 at two nutrient concentrations (0.008 and 0.02 gP/m³). In each panel, the dotted line represents
749 energetic efficiency equal to one.

750

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

755

756 **Figure 1**

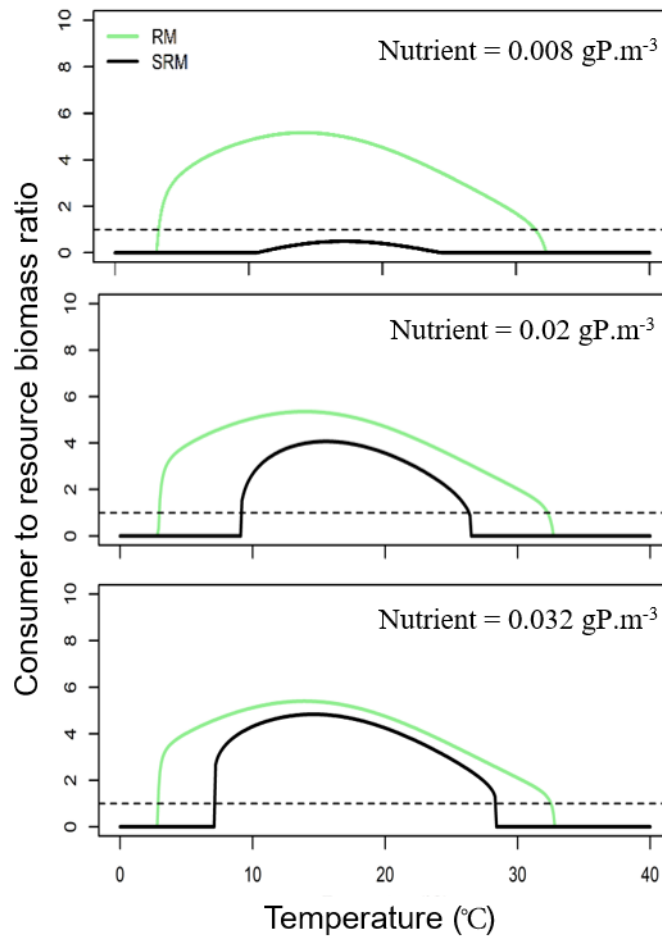


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760 **Figure 2**

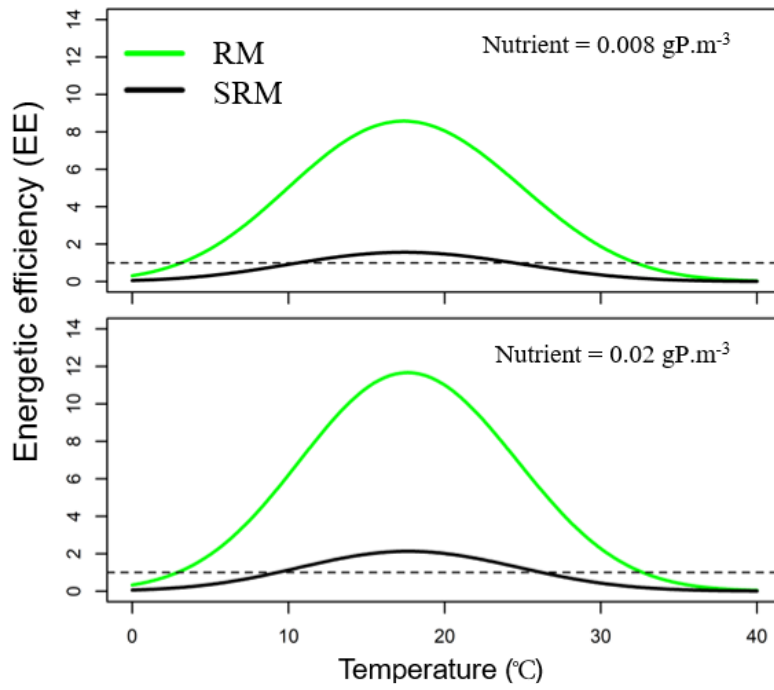


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763 **Figure 3**

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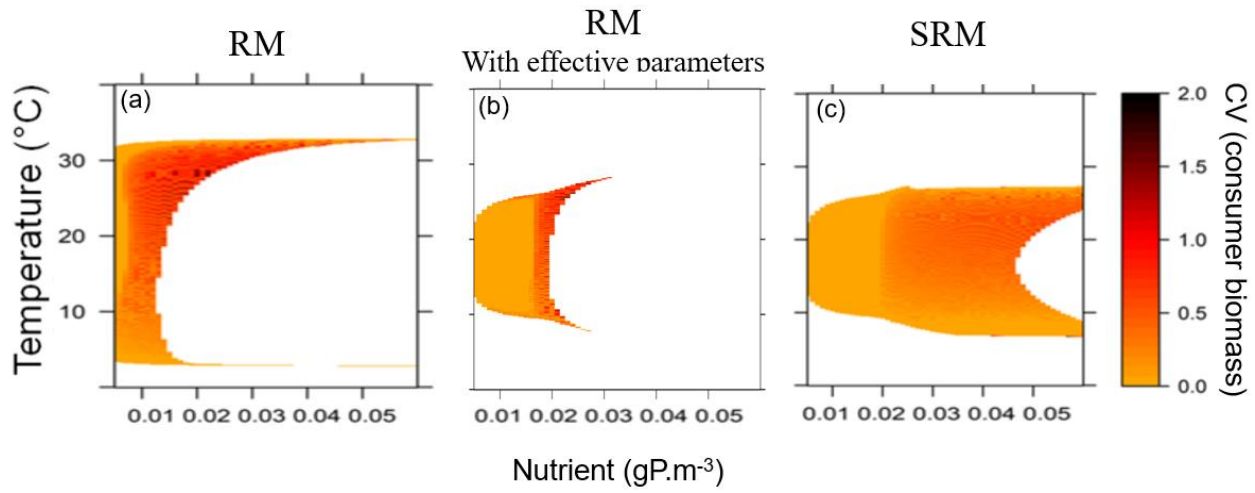
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769 **Figure 4**

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Supplementary information

776 **Stoichiometric constraints modulate the effects of temperature and nutrients on biomass** 777 **distribution and community stability**

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

782 The model studied in the main text is very similar to previous stoichiometric consumer-resource
783 models (Andersen 1997; Loladze *et al.* 2000; Andersen *et al.* 2004; Diehl *et al.* 2005). To make
784 our paper self-contained, we here present the model assumptions and derive the model equations
785 (eqs. 3-6 in main text). Our objective was not to develop a complex and very realistic stoichiometric
786 model that would include additional important abiotic and biotic features such as light intensity
787 (Diehl 2007) or compensatory feeding (Cruz-Rivera & Hay 2000). Instead, we aimed at introducing
788 two fundamental stoichiometric features (i.e. stoichiometric flexibility and stoichiometric
789 imbalance) and investigate how these stoichiometric considerations can change predictions of the
790 Rosenzweig-MacArthur model. We assumed that resource and consumer production are limited by
791 energy and a single mineral nutrient. Moreover, we assume the system is closed for nutrients. Thus,
792 nutrient supply originates exclusively from excretion and remineralization of biomass. The total
793 amount of nutrients in the system (N_{tot}) is then a measure of nutrient enrichment. As elemental
794 homeostasis is much stronger for consumers compared to primary producers (Andersen 1997), we
795 assumed the nutrient quota of the consumer Q_C to be constant whereas the nutrient quota of the
796 resource Q_R is flexible. Four differential equations determine the dynamics of four state variables,
797 that is, the concentrations of resource (R) and consumer (C) carbon biomasses and of dissolved
798 mineral nutrients (N), and the nutrient quota of the resource (Q_R):

$$799 \quad \dot{C} = \left(e \frac{aR}{1+ahR} - m \right) C \quad (\text{S1})$$

$$800 \quad \dot{R} = r \left(1 - \frac{Q_{\text{min}}}{Q_R} \right) R - \frac{aR}{1+ahR} C \quad (\text{S2})$$

$$801 \quad \dot{Q}_R = h(N) - r(Q_R - Q_{\text{min}}) \quad (\text{S3})$$

802
$$\dot{N} = (Q_R - Q_C e) \frac{aR}{1+ahR} C + Q_C m C - h(N)R \quad (\text{S4})$$

803 As in the RM model, rates of change of the consumer and resource biomass densities \dot{C} and \dot{R}
804 depend on their respective carbon biomass densities C and R ($\text{gC}\cdot\text{m}^{-3}$), except that the resource
805 population growth rate follows the Droop equation (Droop 1974) and is now limited by its nutrient
806 quota Q_R relative to the minimum nutrient quota Q_{\min} . Rate of change of Q_R depends on the nutrient
807 uptake rate by the resource species $h(N)$ and the amount of nutrient invested in growth (eqn S3).
808 $h(N)$ is the specific resource nutrient uptake rate and can be represented by a Michaelis-Menten
809 model where the amount of nutrient uptake saturates at high nutrient concentrations.

810
811 With the mass-balance equation, we get that the total amount of nutrient is the sum of the free
812 nutrient plus the nutrient fixed in the resource biomass plus the nutrient fixed in the consumer
813 biomass: $N_{\text{tot}} = N + Q_R R + Q_C C$. As Eqns S1-S4 conserve total biomass (the system is closed), the
814 time derivative of N_{tot} is zero. We can thus replace one of the four differential equations S1-S4 with
815 the algebraic equation $N_{\text{tot}} = N + Q_R R + Q_C C$:

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

817 (S5)

818
$$\dot{R} = r(1 - \frac{Q_{\min}}{Q_R})R - \frac{aR}{1+ahR}C$$

819 (S6)

820
$$\dot{N} = (Q_R - Q_C e) \frac{aR}{1+ahR} C + Q_C m C - h(N)R$$

821 (S7)

822
$$N_{\text{tot}} = N + Q_R R + Q_C C \quad (\text{S8})$$

823
824 It is possible to derive a simpler model by reducing the number of dimensions in the above model
825 from three to two. This model reduction is based on the assumption that free nutrients are taken up

826 very quickly relative to the dynamics of the consumer and resource biomasses. This corresponds

827 to taking $h(N)$ large, $h(N) = \frac{1}{\varepsilon} \tilde{h}(N)$ for small ε . The fast dynamics (on the timescale $t \sim \varepsilon$) are

$$828 \quad \dot{N} = -\frac{1}{\varepsilon} \tilde{h}(N)R + (\text{slower contributions})$$

829 (S9)

830 Which converge to $N \rightarrow 0$, and $Q_R \rightarrow \frac{N_{tot} - Q_C C}{R}$ with N_{tot} the total nutrient in the system. In other

831 words, N in dead and excreted matter is immediately recycled and acquired by the resource species.

832 When substituting the quasi-steady-state in eqns. (S5, S6), we get the resulting dynamics (on the

833 timescale $t \sim 1$):

$$834 \quad \dot{C} = (e \frac{aR}{1+ahR} - m)C \tag{S10}$$

$$835 \quad \dot{R} = r(1 - \frac{Q_{min}}{Q_R})R - \frac{aR}{1+ahR} C \tag{S11}$$

$$836 \quad N_{tot} = Q_R R + Q_C C \tag{S12}$$

837 From the nutrient conservation equation (eqn. S12) we obtain that $Q_R = \frac{N_{tot} - Q_C C}{R}$. The intuitive

838 interpretation is that the resource nutrient quota Q_R decreases with the density of the resource

839 population and with the density of nutrient stored in the consumer biomass. In contrast to eqns S5-

840 S8, the reduced model has only two differential equations and one algebraic equation. It can be

841 equivalently written as a set of three differential equations with \dot{C} and \dot{R} similar as equations S10

842 and S11 and with $\dot{Q}_R = \frac{d(N_{tot} - Q_C C)}{dt} = (Q_R - Q_C e) \frac{aR}{1+ahR} C + \frac{Q_C m C}{R} - r(Q_R - Q_{min})$.

843

844 In the RM model, the growth rate of the consumer population is assumed to depend only on

845 resource density. We relaxed this assumption by making the population growth rate of the

846 consumer dependent on both the resource quality (i.e. nutrient quota) and quantity (i.e. density). In

847 the SRM model, consumer production is also limited by resource quality as the consumer

848 assimilation efficiency e is a saturating function of resource nutrient quota Q_R :

849
$$e(Q_R) = e_{max} \frac{Q_R}{Q_R + Q_C} \tag{S13}$$

850 The intuitive interpretation of eqn. S13 is that resource quality is not a limiting factor for consumer
851 growth as long as the nutrient content of the resource is superior to the nutrient content of the
852 consumer (i.e. $Q_R > Q_C$). In other words, when $Q_R \gg Q_C$, $e(Q_R) \rightarrow e_{max}$ and when $Q_R \ll Q_C$, $e(Q_R)$
853 $\rightarrow 0$. By replacing e by $e(Q_R)$ in eqn. S10, we obtain the SRM model.

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855 **Table S1.** Definitions and units of model parameters, from Uszko *et al.* (2017). For temperature-
 856 dependent parameters, we list the value of the scaling constant Q_0 (in units of the parameter) and
 857 the values of either the activation energy E_Q (eV, when temperature dependence is monotonous,
 858 eqn. 7) or of the temperature T_{opt} (Kelvin) at which the parameter value reaches a
 859 maximum/minimum and the width s (Kelvin) of this bell-/U-shaped function (when temperature
 860 dependence is non-monotonous, eqn. 8). Biomass and nutrients are expressed in units of carbon
 861 (C) and phosphorus (P), respectively
 862

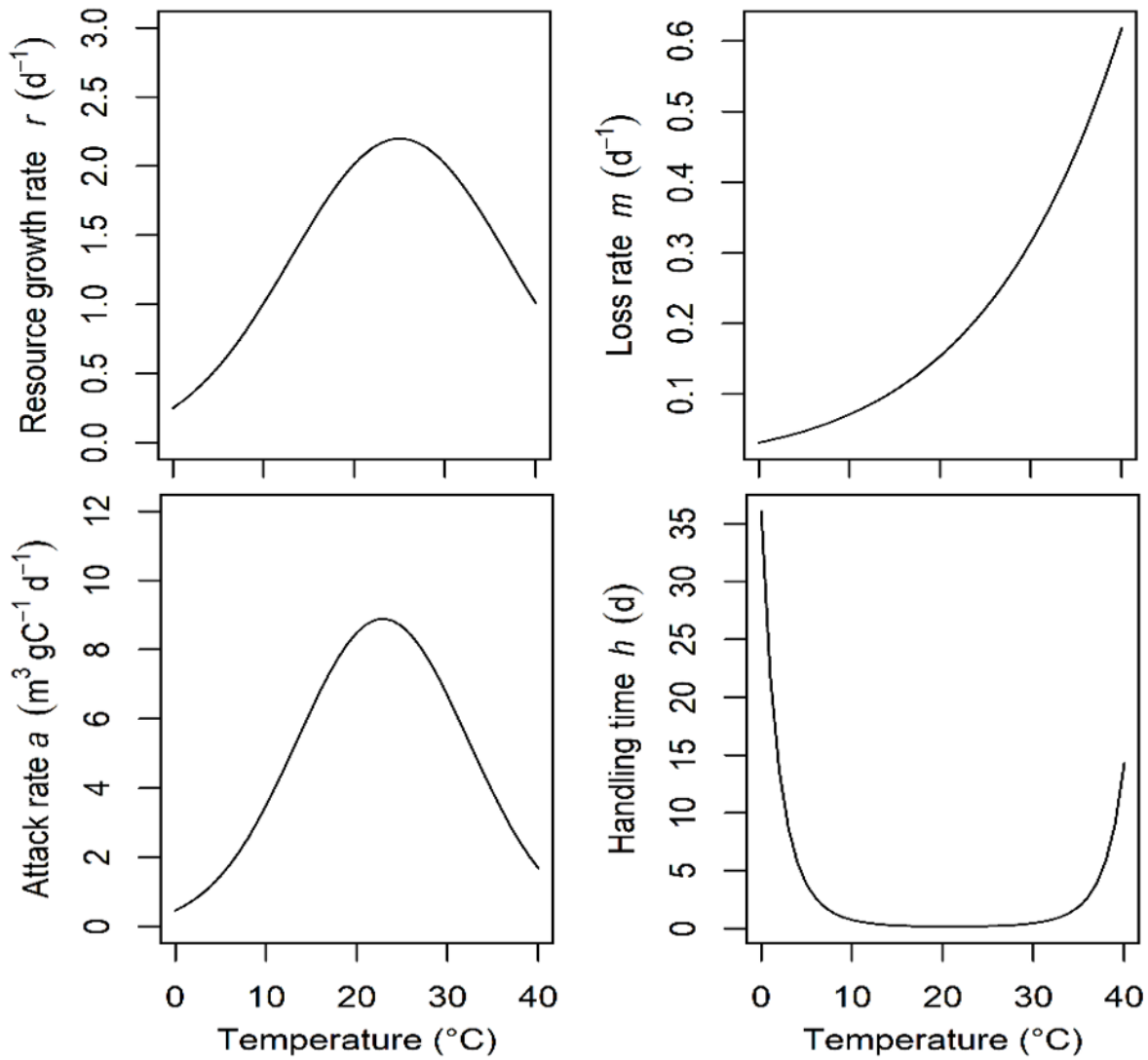
Temperature independent				
Parameter	value	Unit	Definition	Reference
Thermal parameters				
r	$r_0 = 2.2; T_{opt} = 298.15; s = 12.0$	1/d	Intrinsic rate of resource net production (gross production – biosynthesis costs)	Uszko et al. 2017
h	$h_0 = 0.17; T_{opt} = 294.1; s = 6.4$	d	Handling time	Uszko 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	

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



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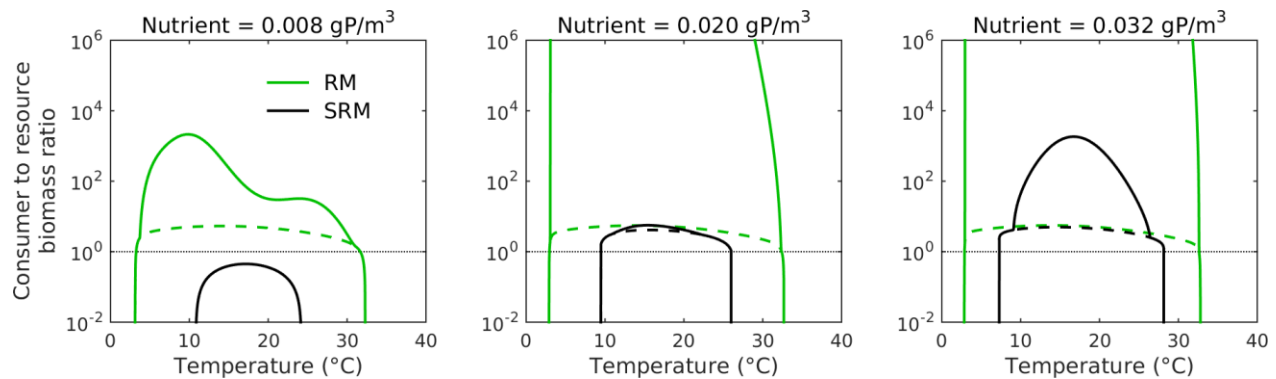
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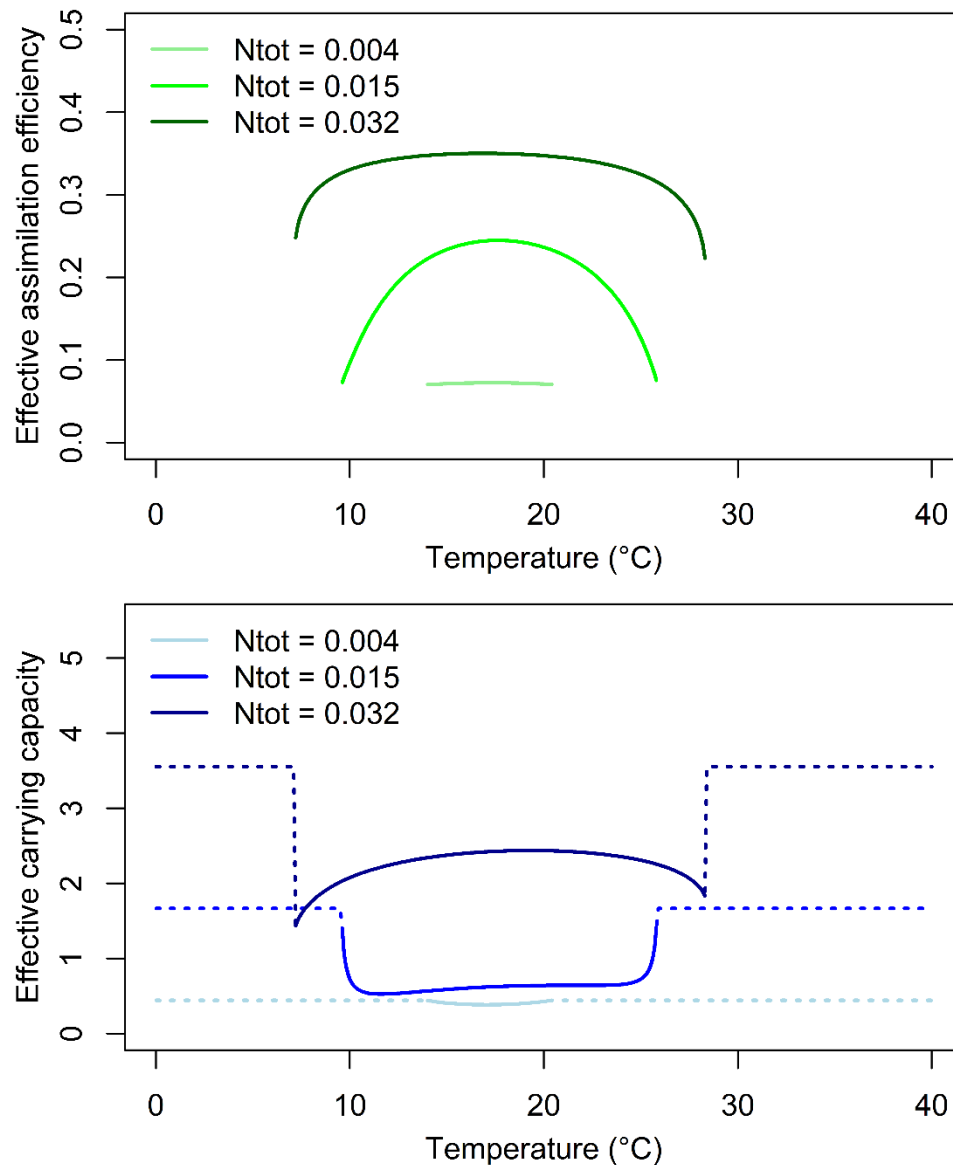
875 **Fig. S2.** Consumer-resource biomass ratio (log scale) along the temperature gradient for the
876 Rosenzweig-MacArthur (RM, green lines) and the Stoichiometric Rosenzweig-MacArthur (SRM,
877 black lines) models at three nutrient concentrations (0.008, 0.02, and 0.032 $\text{gP}\cdot\text{m}^{-3}$).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

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882



884 **Fig. S3.** Effective assimilation efficiency e_{ef} and carrying capacity K_{ef} from the
885 Stoichiometric Rosenzweig-MacArthur (SRM) model along the temperature gradient at
886 three nutrient levels (0.004, 0.015, and 0.032 gP.m⁻³) with $Q_C = 0.042$. Full lines represent
887 temperature and nutrient scenarios for which both the resource and consumer persist
888 whereas dotted lines represent scenarios for which only the resource persists. Effective
889 assimilation efficiency was calculated as $e_{ef} = e_{max}Q_R/(Q_R+Q_C)$, with Q_R the equilibrium
890 solution of the SRM model and the effective carrying capacity as $K_{ef} = Q_R R/Q_{min} = (N_{tot}-$
891 $Q_C C)/Q_{min}$, with Q_R , R and C the equilibrium solutions of the SRM model.



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