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

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 their combined effect on the stoichiometry, dynamics, and stability of ecological communities remains largely unexplored. To fill this gap, we extended the Rosenzweig-MacArthur consumer-resource model by including thermal dependencies, nutrient dynamics, and stoichiometric constraints on both the primary producer and the consumer. We found that stoichiometric constraints dampen the paradox of enrichment and increased persistence at high nutrient levels. Nevertheless, they also reduced consumer persistence at extreme temperatures. Finally, we also found that stoichiometric constraints can strongly influence biomass distribution across trophic levels by modulating consumer assimilation efficiency and resource growth rates along the environmental 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.

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, CO_2, 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 (g.m^{-3}):

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

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

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 (gC.m^{-3}), except that the resource population growth rate follows the Droop equation (Droop

210   1974) given by $r(1-Q_{min}/Q_R)R$ and is now limited by Q_R relative to the minimum nutrient quota

211   Q_{min}:

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

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

214    $\dot{C} = (e\frac{aR}{1+ahR} - m)C$ (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    $e(Q_R) = e_{max}\frac{Q_R}{Q_R+Q_C}$ (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    $$m(T) = m_0 e^{\frac{-E_m}{kT}}$$ (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 $k=8.62\times10^{-5}$ 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    $$g(T) = g_0 e^{\pm\frac{(T-T_{opt})^2}{2s^2}}$$ (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

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^{-}

267   ^{3}, 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. $K = N_{tot}/Q_{min}$). 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

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.

294

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

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 $Q_R = (N_{tot} - Q_C C)/R$. 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 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/m^{3}). 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;
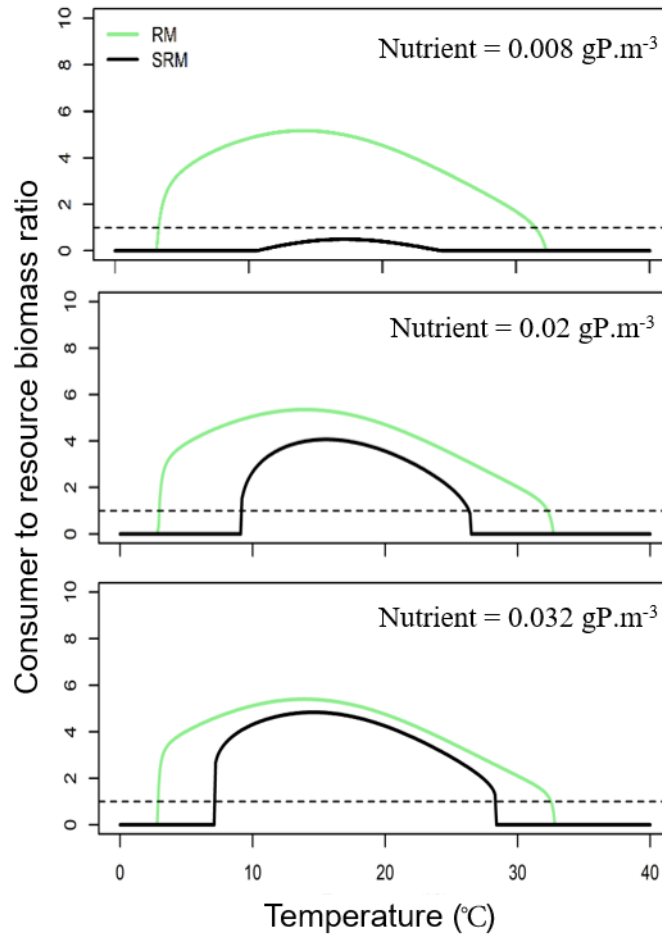
754   panel *c*) models.

755

756   **Figure 1**
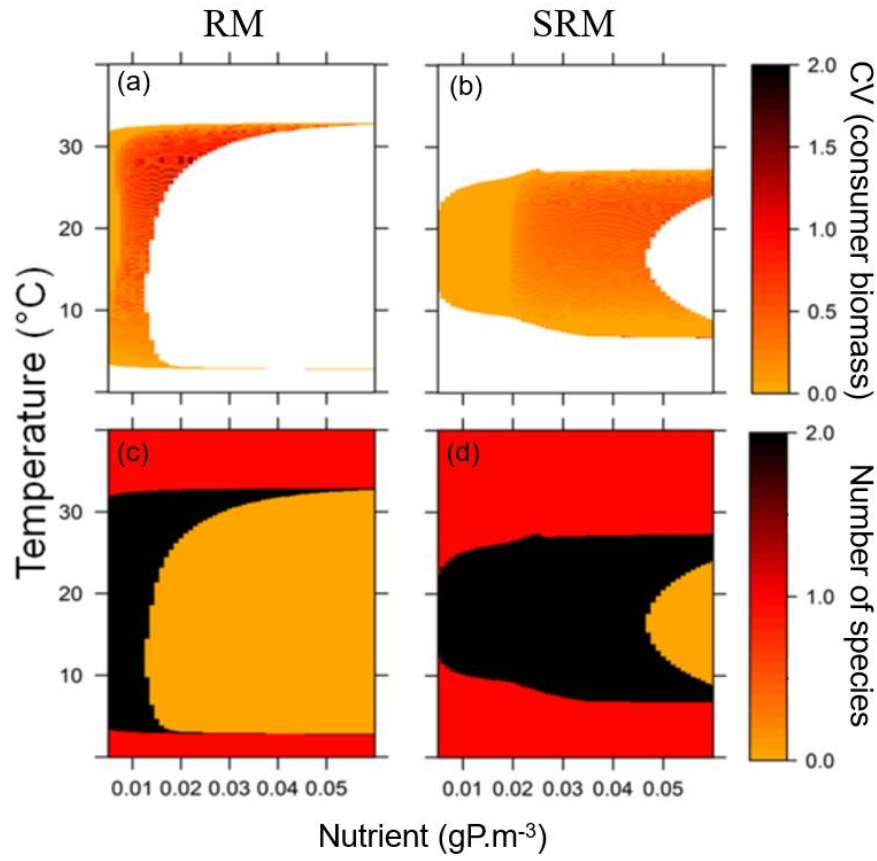
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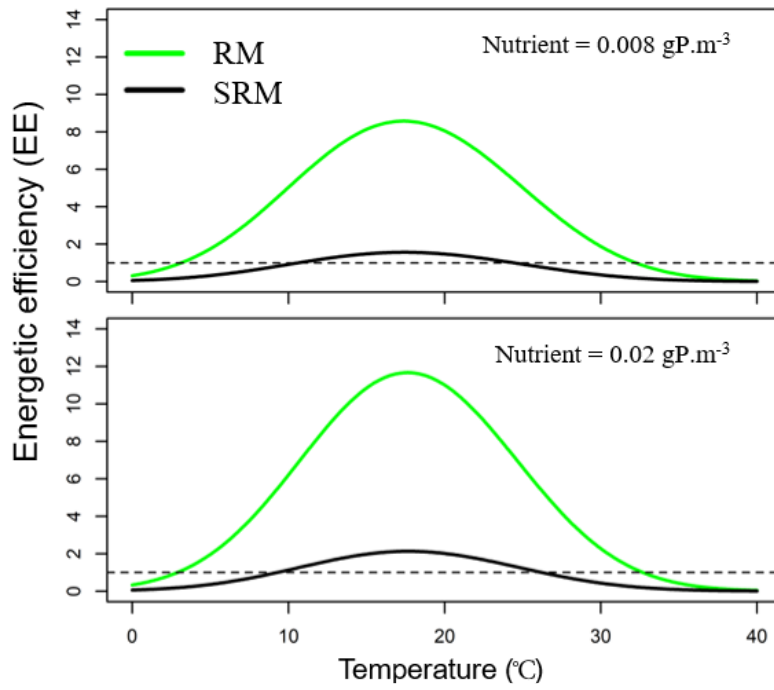
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760   **Figure 2**
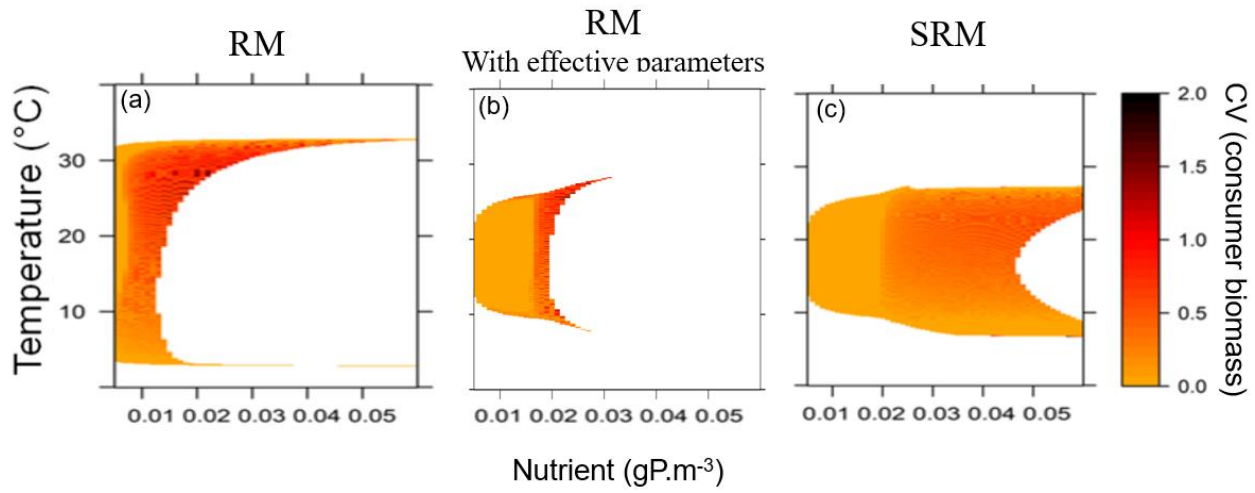

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763   **Figure 3**

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769   **Figure 4**

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775   **Supplementary information**

776   **Stoichiometric constraints modulate the effects of temperature and nutrients on biomass**
777   **distribution and community stability**
778
779   Arnaud Sentis, Bart Haegeman, and José M. Montoya
780

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

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

801    $$\dot{Q}_R = h(N) - r(Q_R - Qmin) \tag{S3}$$

802 $\quad \dot{N} = (Q_R - Q_C e)\dfrac{aR}{1+ahR}C + Q_C mC - h(N)R$ $\hfill$ (S4)

803 $\quad$ As in the RM model, rates of change of the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$

804 $\quad$ depend on their respective carbon biomass densities C and R (gC.m^{-3}), except that the resource

805 $\quad$ population growth rate follows the Droop equation (Droop 1974) and is now limited by its nutrient

806 $\quad$ quota Q_R relative to the minimum nutrient quota Q_{min}. Rate of change of Q_R depends on the nutrient

807 $\quad$ uptake rate by the resource species $h(N)$ and the amount of nutrient invested in growth (eqn S3).

808 $\quad$ $h(N)$ is the specific resource nutrient uptake rate and can be represented by a Michaelis-Menten

809 $\quad$ model where the amount of nutrient uptake saturates at high nutrient concentrations.

810

811 $\quad$ With the mass-balance equation, we get that the total amount of nutrient is the sum of the free

812 $\quad$ nutrient plus the nutrient fixed in the resource biomass plus the nutrient fixed in the consumer

813 $\quad$ biomass: $N_{tot} = N + Q_R R + Q_C C$. As Eqns S1-S4 conserve total biomass (the system is closed), the

814 $\quad$ time derivative of N_{tot} is zero. We can thus replace one of the four differential equations S1-S4 with

815 $\quad$ the algebraic equation $N_{tot} = N + Q_R R + Q_C C$:

816 $\quad$ $\dot{C} = (e\dfrac{aR}{1+ahR} - m)C$

817 $\quad$ (S5)

818 $\quad$ $\dot{R} = r(1 - \dfrac{Qmin}{Q_R})R - \dfrac{aR}{1+ahR}C$

819 $\quad$ (S6)

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

821 $\quad$ (S7)

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

823

824 $\quad$ It is possible to derive a simpler model by reducing the number of dimensions in the above model

825 $\quad$ 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 ~ ε) are

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

829   (S9)

830   Which converge to N → 0, and $Q_R \to \frac{N_{tot} - Q_C C}{R}$ 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 ~1):

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

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

836     $N_{tot} = Q_R R + Q_C C$ (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 $\dot{Q}_R = \frac{d\frac{N_{tot} - Q_C C}{R}}{dt} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + \frac{Q_C mC}{R} - r(Q_R - Qmin)$.

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 $\quad e(Q_R) = e_{max} \dfrac{Q_R}{Q_R + Q_C}$ $\qquad\qquad$ (S13)

850 $\quad$ The intuitive interpretation of eqn. S13 is that resource quality is not a limiting factor for consumer

851 $\quad$ growth as long as the nutrient content of the resource is superior to the nutrient content of the

852 $\quad$ consumer (i.e. $Q_R > Q_C$). In other words, when $Q_R >> Q_C$, $e(Q_R) \rightarrow e_{max}$ and when $Q_R << Q_C$, $e(Q_R)$

853 $\quad \rightarrow 0$. By replacing e by $e(Q_R)$ in eqn. S10, we obtain the SRM model.

854

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

Parameter	Temperature independent 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	$a_0 = 8.9$; $T_{opt} = 296.0$; $s = 9.4$	m³/(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/m³	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)
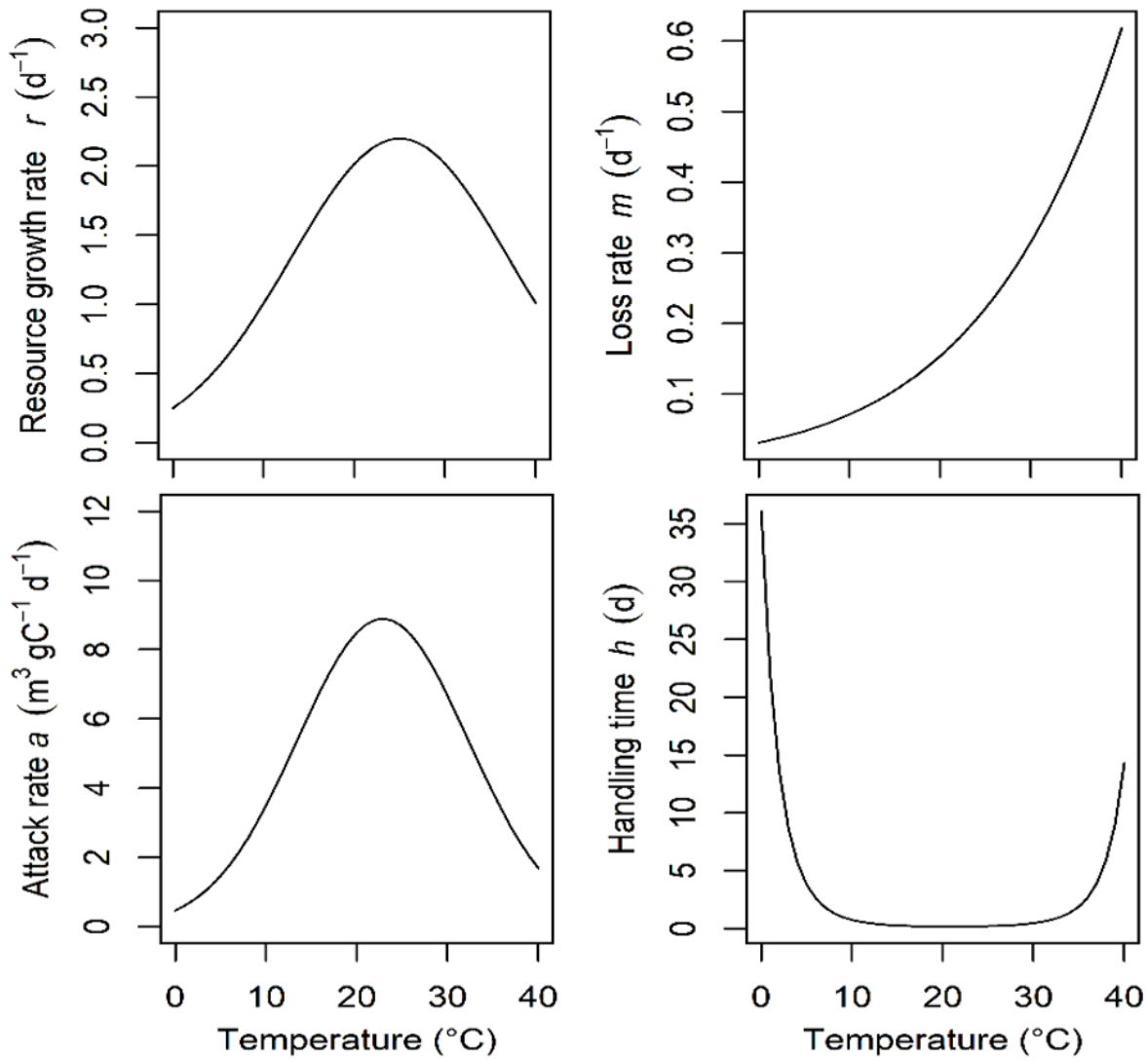
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875   **Fig. S2.** Consumer-resource biomass ratio (log scale) along the temperature gradient for the

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 gP.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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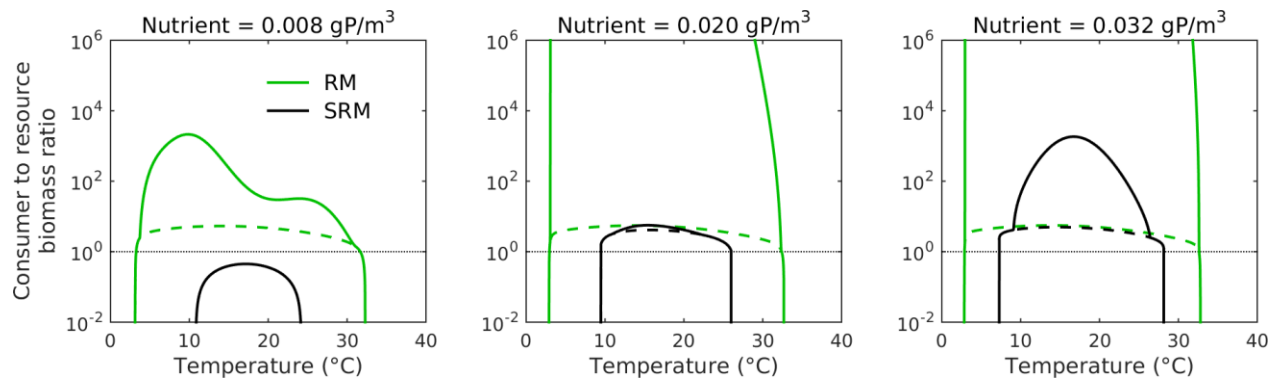
884 **Fig. S3**. Effective assimilation efficiency e_{ef} and carrying capacity K_{ef} from the

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 $K_{ef} = Q_RR/Q_{min} = (N_{tot}-$

891 $Q_CC)/Q_{min}$, with Q_R, R and C the equilibrium solutions of the SRM model.
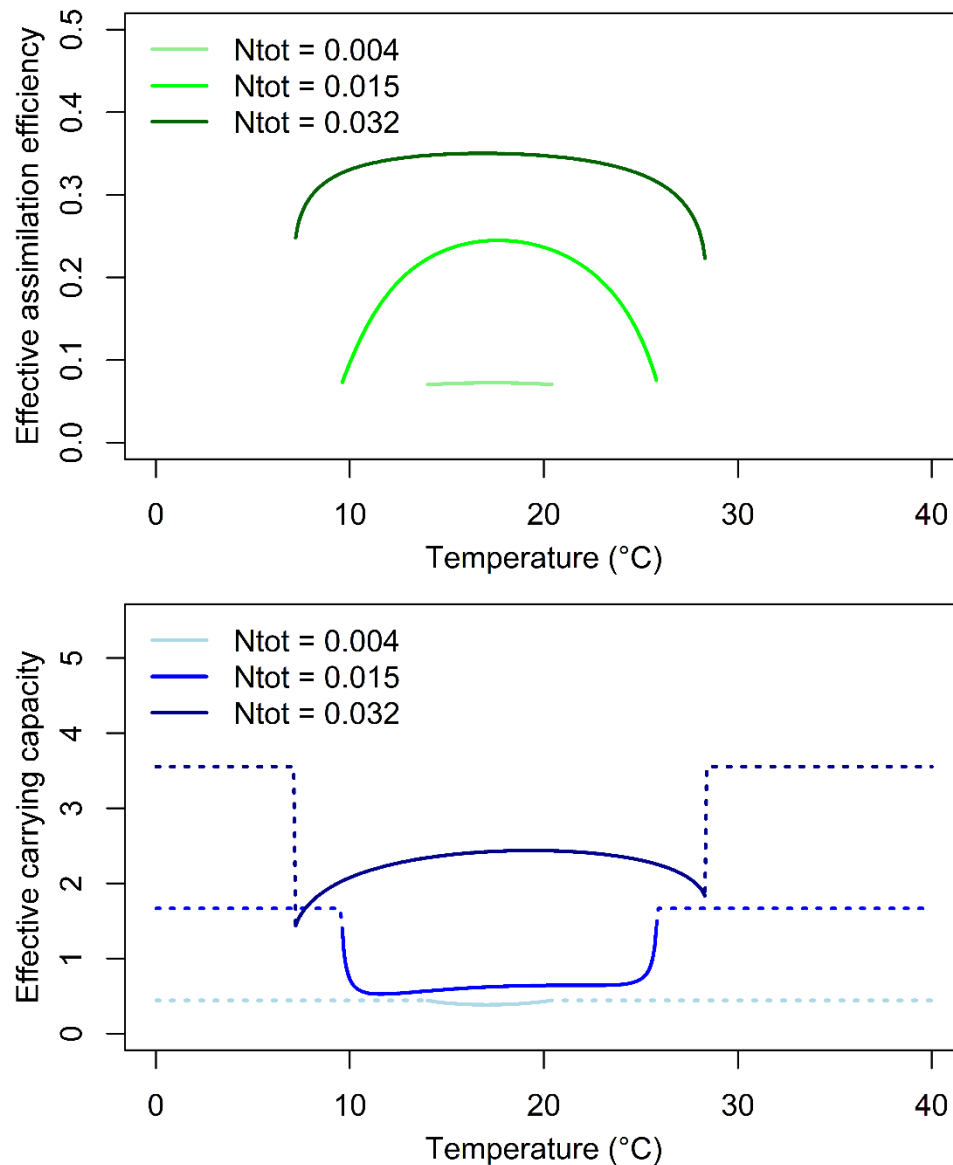
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