1   **Stoichiometric constraints modulate the effects of temperature and nutrients on biomass**

2   **distribution and community stability**

3

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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

28   modify the elemental composition (i.e. stoichiometry) of primary producers and consumers. Yet

29   their combined effect on the stoichiometry, dynamics, and stability of ecological communities

30   remains largely unexplored. To fill this gap, we extended the Rosenzweig-MacArthur consumer-

31   resource model by including thermal dependencies, nutrient dynamics, and stoichiometric

32   constraints on both the primary producer and the consumer. We found that stoichiometric

33   constraints dampen the paradox of enrichment and increased persistence at high nutrient levels.

34   Nevertheless, they also reduced consumer persistence at extreme temperatures. Finally, we also

35   found that stoichiometric constraints can strongly influence biomass distribution across trophic

36   levels by modulating consumer assimilation efficiency and resource growth rates along the

37   environmental gradients. Our findings highlight the importance of accounting for stoichiometric

38   constraints as they can mediate the temperature and nutrient impact on the dynamics and

39   functioning of ecological communities.

40

41   **Key words:** temperature, stoichiometry, temporal variability, paradox of enrichment, trophic

42   interactions, nutrient quota, consumer-resource dynamics, biomass structure.

43   **Introduction**

44   Temperature and nutrients regulate many biological processes, including species geographical

45   distribution, primary production, species interactions, and energy and material fluxes (Falkowski

46   *et al.* 1998; Enquist *et al.* 1999; Elser *et al.* 2007; Thomas *et al.* 2017). They are at the core of

47   several ecological theories. While temperature is a fundamental component of metabolic scaling

48   theory (Brown *et al.* 2004), nutrients are at the core of resource competition theory (Tilman 1982)

49   and ecological stoichiometry (i.e. the element composition of organisms) theory (Sterner & Elser

50   2002). Cross et al. (2015) suggested that a better understanding of the interactions between

51   temperature and nutrients is crucial for developing realistic predictions about ecological

52   responses to multiple drivers of global change, including climate warming and elevated nutrient

53   supply. Nutrients can modulate the effects of warming on communities directly by altering

54   primary production, and/or indirectly by changing the elemental composition of primary

55   producers. Conversely, thermal effects on trophic interaction strengths (i.e. the *per capita* effect

56   of predators on prey population densities) and on consumer energetic efficiencies (i.e. ingestion

57   relative to metabolic demand) depend on both the quantity and quality of their resources. While

58   Cross et al. (2015) provided a road map on how to investigate the combined effects of

59   temperature and nutrient on ecological processes, we still lack an integrative theory to better

60   understand how the links between stoichiometry, nutrient enrichment, and temperature influence

61   the dynamics and stability of multispecies communities. Such a theory will allow us to

62   understand how and when stoichiometric variation modulates the consequences of single and

63   combined components of global change on trophic interactions, community dynamics, and

64   ecosystem functioning.

65

66

67   Predicting the effects of global warming and nutrient changes on ecosystems is challenging as

68   species are embedded within communities of multiple interacting species (Petchey *et al.* 1999;

69   Tylianakis *et al.* 2008; Montoya & Raffaelli 2010; Gilbert *et al.* 2014). Increased resource

70   availability (hereafter: enrichment) and warming can jointly affect food-web stability and

71   structure by modifying the strength of trophic interactions (O'Connor *et al.* 2009; Binzer *et al.*

72   2012; Kratina *et al.* 2012; Sentis *et al.* 2014; Binzer *et al.* 2016). Enrichment typically increases

73   energy flux from resources to higher trophic levels which often leads to the well-known paradox

74   of enrichment where the amplitude of population fluctuations increase with nutrients, leading to

75   extinctions at high nutrient concentrations (Rosenzweig 1971; Rip & McCann 2011; Gilbert *et al.*

76   2014). Nevertheless, most consumer species become less efficient at processing matter and

77   energy at warmer temperatures as their metabolic rates often increase faster with temperature

78   than their feeding rates (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Iles 2014). This

79   reduction of energetic efficiency lessens energy flow between trophic levels and hence stabilizes

80   food-web dynamics by reducing population fluctuations (Rip & McCann 2011; Binzer *et al.*

81   2012; Gilbert *et al.* 2014). As a result, mild warming may alleviate the paradox of enrichment by

82   decreasing consumer energetic efficiency (Binzer *et al.* 2012; Sentis *et al.* 2017).

83

84   The theoretical expectations and results described above have already improved our ability to

85   understand and predict the effects of temperature and enrichment on food webs (Boit *et al.* 2012;

86   Tabi *et al.* 2019). However, most previous studies using metabolic scaling theory assumed that

87   nutrient enrichment lead to an increase in resource carrying capacity without influencing resource

88   elemental composition (Vasseur & McCann 2005; Binzer *et al.* 2012; Gilbert *et al.* 2014; Binzer

89   *et al.* 2016; Sentis *et al.* 2017). Yet nutrient enrichment effects are more complex. The elemental

90   composition of primary producers is likely to be altered, in response to the supplies of energy and

91   materials relative to their growth and nutrient intake rates (Rastetter *et al.* 1997;

92   Robert W. Sterner *et al.* 1997; Finkel *et al.* 2009) Sterner et al. 1997). This, in turn, can affect the

93   dynamics of the producer population and the herbivores feeding on it. For instance, previous

94   modelling studies showed that introducing stoichiometric heterogeneity in predator-prey

95   population dynamic models can dampen the negative effect of nutrient enrichment on system

96   persistence by reducing population biomass fluctuations (Andersen 1997; Loladze *et al.* 2000;

97   Andersen *et al.* 2004; Elser *et al.* 2012). More generally, the stoichiometric flexibility of primary

98   producers, in particular the flexibility in carbon to nutrient ratios (e.g. C:N or C:P), has important

99   implications for animal feeding behaviour (White 1993), consumer population stability (White

100   1993; Sterner & Hessen 1994; Hessen *et al.* 2002), community structure (Andersen 1997), and

101   ecosystem processes such as biogeochemical cycling (Andersen 1997; Hessen *et al.* 2004).

102

103   Previous theoretical and empirical studies reported that stoichiometric variations can have a

104   strong influence on the stability of consumer-resource interactions (Andersen 1997; Andersen *et*

105   *al.* 2004; Diehl *et al.* 2005; Elser *et al.* 2012). For instance, populations of crustacean *Daphnia*

106   feeding on low quality (i.e. low nutrient: carbon ratio) algae cannot persist even when resource

107   quantity is not a limiting factor (Elser *et al.* 2007). Consumer extinction is explained by the fact

108   that the consumer assimilation efficiency is, for most organisms, a function of resource quality

109   (Elser *et al.* 2000). When resource quality is low, the consumers assimilate only few nutrients

110   relative to the biomass they ingest, which limits their growth and reproduction (Elser *et al.* 2000;

111   Elser *et al.* 2012). Temporal variations in resource quality can stabilize the system by weakening

112   interaction strength and dampening population fluctuations (Andersen *et al.* 2004; Diehl *et al.*

113   2005)but see(Loladze *et al.* 2000; Elser *et al.* 2012). However, it remains unclear whether and

114   how temporal variations in the elemental composition of primary producers and consumers can

115   modulate the effects of temperature and nutrients on important community features such as

116   stability and biomass distribution across trophic levels. Previous studies indicated that the spatial

117   and temporal intraspecific variations in the elemental composition of primary producers are

118   expected to increase in response to global change drivers such as temperature, CO_2, and nutrient

119   availability (Bezemer & Jones 1998; Woods *et al.* 2003; Finkel *et al.* 2009). This increased

120   variation can be of importance for both primary producer and consumer populations as the

121   growth rate of primary producers is well known to depend on their elemental composition (Droop

122   1974) as is the assimilation efficiency of the consumers (Sterner & Elser 2002).

123

124   Altogether, previous studies indicated that both temperature and stoichiometric variations can

125   have important effects on species interactions and community dynamics (Andersen *et al.* 2004;

126   Diehl *et al.* 2005; Fussmann *et al.* 2014; Binzer *et al.* 2016; Sentis *et al.* 2017). However, the

127   effects of temperature and nutrient stoichiometry on food web dynamics and stability have only

128   been studied in isolation. Recent theory by Uszko et al. (2017) showed that considering nutrient

129   dynamics can help to better understand the influence of temperature on consumer-resource

130   population dynamics and resource carrying capacity. Nevertheless, they considered that the

131   elemental composition of both the resource and the consumer are constant and independent of

132   temperature and nutrient dynamics. This contrasts with the empirical observation that resource

133   elemental composition is flexible and can vary with both temperature and nutrient dynamics

134   (Droop 1974; Elser *et al.* 2000; Woods *et al.* 2003). Here we thus focused on the combined

135   effects of temperature and nutrients on the stoichiometry of primary producers and how this

136   affects community stability and biomass distribution across trophic levels in a consumer-resource

137   system. Understanding the determinants of stability and biomass distribution has been at the core

138   of ecology for a long time (Elton (1927), Lindeman (1942)). Recent theory aims at explaining

139   empirical observations of trophic pyramids (i.e. population biomass decreases with trophic

140   levels), inverted trophic pyramids (i.e. population biomass increases with trophic levels), trophic

141   cascades and the link between biomass distribution and stability (McCauley *et al.* 2018; Barbier

142   & Loreau 2019).

143

144   Here, we used the Rosenzweig-MacArthur model as a baseline non-stoichiometric model because

145   this model is one of the most studied models used to investigate the effects of temperature and

146   nutrient enrichment on community dynamics (Vasseur & McCann 2005; Binzer *et al.* 2012;

147   Fussmann *et al.* 2014; Sentis *et al.* 2017). Inspired by previous temperature-independent

148   stoichiometric consumer-resource models (Andersen 1997; Andersen *et al.* 2004; Diehl *et al.*

149   2005), we then extended the Rosenzweig-MacArthur model to account for nutrient dynamics as

150   well as for the simultaneous dependence of community dynamics on temperature and flexible

151   resource stoichiometry. Our objective here was not to develop a complex and very realistic

152   stoichiometric model that would include additional important abiotic and biotic features such as

153   light intensity (Diehl 2007) or compensatory feeding (Cruz-Rivera & Hay 2000). Instead, we

154   aimed at introducing two fundamental stoichiometric features (i.e. stoichiometric flexibility and

155   stoichiometric imbalance) and investigate how these stoichiometric considerations can change

156   predictions of the Rosenzweig-MacArthur model. We thus used our extended Rosenzweig-

157   MacArthur model to predict the effects of warming and nutrient enrichment on population

158   dynamics and biomass distribution across trophic levels and compared these predictions with the

159   predictions of the nonstoichiometric Rosenzweig-MacArthur model. We particularly addressed

160   two questions: (i) How do stoichiometric constraints modulate the effects of enrichment and

161   warming on community stability and persistence? and (ii) How do stoichiometric constraints

162   modulate the effects of enrichment and warming on biomass distribution across multiple trophic

163   levels?

164   **Methods: Population dynamic models**

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

166   Rates of change of the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$ depend on their

167   respective biomass densities C and R (g.m^{-3}):

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

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

170   The population growth rate of the resource is given by the logistic equation where r is the

171   resource maximum growth rate and K is the resource carrying capacity. The population growth

172   rate of the consumer is equal to its feeding rate multiplied by its assimilation efficiency e (i.e. the

173   fraction of resource biomass converted into consumer biomass) minus a loss term associated to

174   metabolic losses m. The feeding rate of the consumer C depends on the density of its resource R

175   and follows a Holling type II functional response, with consumer-resource attack rate a and

176   handling time h. Our choice for a type II functional response is motivated by a meta-analysis

177   reporting that most consumers feed on their prey following a saturating type II functional

178   response rather than a linear type I or a sigmoidal type III functional response (Jeschke *et al.*

179   2004).

180

181   In the RM model, consumer and resource population growth rates are only limited by nutrient or

182   resource density. Nutrient enrichment is assumed to increase resource carrying capacity, which

183   often leads to the well-known paradox of enrichment where populations fluctuates up to

184   extinctions (Rosenzweig 1971). Nevertheless, this model neither considers nutrient dynamics nor

185   temporal variations of resource stoichiometry and their consequences on population dynamics.

186   To circumvent these limitations of the RM model, we extended it to better consider nutrient

187   dynamics, resource stoichiometry and the way they can affect resource and consumer population

188   dynamics.

189

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

191   We derived a stoichiometric extension of the Rosenzweig-MacArthur consumer–resource model

192   with additional stoichiometric and temperature dependencies of several biological rates. We

193   considered two stoichiometric constraints: one on the resource population growth rate, and the

194   other on the consumer assimilation efficiency (see below for more details). These stoichiometric

195   constraints have been observed for several consumer-resource pairs suggesting that they are core

196   components of species growth and interactions (Sterner & Elser 2002).

197

198   *Stoichiometric constraint on the resource population growth rate*

199   Inspired by previous stoichiometric models (Andersen 1997; Loladze *et al.* 2000; Andersen *et al.*

200   2004; Diehl *et al.* 2005), we extended the RM model by considering explicit nutrient dynamics

201   and nutrient effects on resource population growth rate. The system is assumed to be closed for

202   nutrients. Thus, nutrient supply originates exclusively from biomass excretion and

203   remineralization. The total amount of nutrients in the system (N_{tot}) is then a measure of nutrient

204   enrichment. In contrast to the very high plasticity in C:N or C:P exhibited by autotrophs,

205   heterotrophs regulate elemental composition within narrower bounds, even when consuming food

206   with large variation in elemental composition (Andersen & Hessen 1991; Sterner & Hessen 1994;

207   Andersen 1997; Elser *et al.* 2000). In other words, the elemental homeostasis is much stronger for

208   consumers compared to primary producers. We thus assumed the nutrient quota (i.e. the nutrient

209   to carbon ratio) of the consumer Q_C to be conserved whereas the one of the resource Q_R is

210   flexible over time with the only constraint that $Q_R > 0$. As in the RM model, rates of change of

211   the consumer and resource biomass densities $\dot{C}$ and $\dot{R}$ depend on their respective carbon biomass

212   densities C and R (gC.m^{-3}), except that the resource population growth rate follows the Droop

213   equation (Droop 1974) given by $r(1-Q_{min}/Q_R)R$ and is now limited by Q_R relative to the

214   minimum nutrient quota Q_{min}:

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

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

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

218   From the nutrient conservation equation (eqn 3) we obtain that $Q_R = \frac{N_{tot} - Q_C C}{R}$. The intuitive

219   interpretation is that the resource nutrient quota Q_R changes instantaneously with the density of

220   the resource population R and with the density of the nutrient stored in the consumer biomass

221    $Q_C C$, to maintain nutrient balance (see Text S1 for details).

222

223   *Stoichiometric constraint on the consumer population growth rate*

224   In the RM model, the growth rate of the consumer population only depends on resource density.

225   We relaxed this assumption by making the population growth rate of the consumer dependent on

226   both resource quality (i.e. nutrient quota) and quantity (i.e. biomass density). In the SRM model,

227   consumer production is also limited by resource quality as the consumer assimilation efficiency e

228   is a saturating function of resource nutrient quota Q_R:

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

230   The intuitive interpretation of eqn. 6 is that resource quality is not a limiting factor for consumer

231   growth as long as the nutrient content of the resource is superior to the nutrient content of the

232   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

233   Q_R for $Q_R < Q_C$. By replacing e by $e(Q_R)$ in eqn. 5, we obtain the SRM model.

234

235   **Temperature dependence of model parameters**

236   To investigate the effect of temperature and stoichiometric constraints on consumer-resource

237   dynamics, we next extended the RM and SRM models described above by adding thermal

238   dependencies of the parameters. Following Uszko et al. (2017), we assumed that the total amount

239   of nutrient N_{tot}, the maximum food conversion efficiency e_{max}, and fixed stoichiometric traits

240   (Q_C) are independent of temperature, as there is no evidence of systematic temperature

241   dependence for any of them (Peters 1983; Ahlgren 1987; Borer *et al.* 2013; Yvon-Durocher *et al.*

242   2015). Rate of maintenance respiration and natural background mortality *m* typically increases

243   exponentially with temperature (Fig. S1a and b). We thus used the Arrhenius equation to describe

244   the effect of temperature *T* (in Kelvin) on *m*:

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

246   where m_0 is a parameter-specific constant calculated at temperature of 0°C (= 273.15 K). The

247   temperature dependence is characterized by the respective activation energy E_m (eV) and the

248   Boltzmann constant $k=8.62\times10^{-5}$ eVK^{-1}. As the temperature dependencies of resource intrinsic

249   growth rate *r* and functional response parameters (*a*, 1/*h*) are often unimodal rather than

250   exponential (Englund *et al.* 2011; Rall *et al.* 2012; Sentis *et al.* 2012; Thomas *et al.* 2012), we

251   used Gaussian functions for *r* and *a* and an inverted Gaussian function for *h*:

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

253

254   where T_{opt} is the temperature at which the rate *g* reaches its minimum or maximum, *s* is the

255   function width and g_0 is a parameter-specific constant calculated at T_{opt}. The minus-sign

256   corresponds to Gaussian functions and the plus-sign to inverted Gaussian functions.

257

258   **Model parameterisation and simulations**

259   To parameterise the models we assumed the resource and consumer species to be a unicellular

260   freshwater algae and a *Daphnia* grazer, respectively. The choice for this system was motivated by

261   the good characterization of both the stoichiometric parameters and thermal dependencies for this

262   system (Andersen 1997; Uszko *et al.* 2017). Uszko *et al.* (2017) recently estimated the thermal

263   dependencies for biological rates of the green algae *Monoraphidium minutum* and the grazer

264   *Daphnia hyalina*. We thus used their estimates of stoichiometric parameters and thermal

265   dependencies (See Table S1 and Fig. S1 for further details).

266

267   To investigate the individual and combined effects of enrichment, warming, and stoichiometric

268   constraints, we varied temperature (401 values ranging from 0 to 40°C by 0.1°C) and total

269   amount of nutrients (parameter N_{tot} in eqn. 10; 60 values ranging from 0.001 to 0.06 gP.m^{-3} by

270   0.001 gP.m^{-3}, overlapping with reported mean phosphorus concentration in European peri-alpine

271   lakes (Anneville *et al.* 2005)). For the RM model, we used the minimum nutrient quota to convert

272   nutrients into resource (i.e. $K = N_{tot}/Q_{min}$). This implies that carrying capacity is independent of

273   temperature which is expected for closed, nutrient-limited systems (Uszko *et al.* 2017) although

274   more experimental evidence are needed to verify this assumption. We then simulated the

275   consumer-resource dynamics for 1000 days to enable the system to reach an attractor (either an

276   equilibrium point or a limit cycle) before we assessed the final state. Therefore, for each model,

277   we simulated 24060 combinations of environmental conditions (401 temperatures by 60 nutrient

278   concentrations). Initial biomass density of each species was set to 0.98 times its equilibrium

279   density in the two-species system (calculated by solving for the two-species equilibrium, using

280   either eqns 1-2 for model RM or eqns 3-5 for model SRM). The value of 0.98 was chosen to be

281   (1) close enough to equilibria to avoid extinctions caused solely by transient dynamics and (2) not

282   exactly the equilibrium value to probe the stability of the equilibrium. Any population falling

283   below the extinction threshold of 10^{-9} g.m^{-3} during the simulation was deemed extinct and its

284   biomass set to zero to exclude ecologically unrealistic low biomass densities. For each model, we

285   calculated system persistence as the percentage of simulations with the two species remaining

286   extant at the end of the simulations. Population dynamics were simulated with R version 3.4.3 (R

287   Development Core Team 2017) using the "deSolve" package (Soetaert *et al.* 2012) with an

288   absolute error tolerance of 10^{-10} and a relative error tolerance of 10^{-6}.

289

290   **Results**

291   *Stability: population fluctuations and persistence*

292   Stoichiometric constraints dampened the paradox of enrichment, reducing fluctuations at high

293   nutrient levels and hence increasing persistence. However, stoichiometric constraints also

294   reduced the persistence of the consumer at low and high temperatures. As a result, the overall

295   effect of stoichiometric constraints on stability depends on its relative influence on population

296   fluctuations versus consumer persistence. In the two following paragraphs, we explain in more

297   detail these results and highlight key differences between the outcomes from RM and SRM

298   models.

299

300   The RM model predicts that increasing nutrient concentration is strongly destabilizing: the

301   system shifts from a stable equilibrium point to limit cycles (i.e. the system crosses a Hopf

302   bifurcation). This agrees with the paradox of enrichment. As population biomass fluctuations (i.e.

303   cycle amplitude) increase with nutrient concentration, minimal population densities are very low

304   at high nutrient concentrations leading to the extinction of both the consumer and resource once

305   the extinction threshold is crossed (Fig. 1). In the range of temperatures where the consumer

306   persists, warming does not have a strong influence on the nutrient concentration at which the

307   system shifts from the stable equilibrium point to limit cycles, although this qualitative shift is

308   absent at very high temperatures (i.e. 32°C) when the consumer is close to extinction. Warming

309   decreases fluctuation amplitude and thus dampens extinctions driven by the paradox of

310   enrichment, which results in warming enhancing the persistence of the consumer-resource system

311   at high nutrient concentrations. However, very warm and cold temperatures cause the extinction

312   of the consumer (see below for the mechanisms underlying extinctions), releasing resources from

313   top-down control. Overall, we found that, without considering the extinction threshold of 10^{-9}

314    $g.m^{-3}$ (see Model parametrisation and simulations), both the consumer and the resource can

315   persist in 74% of the temperature-nutrient concentration scenarios (i.e. black + orange areas in

316   Fig 1C). Nevertheless, when considering the extinction threshold, they persist in only 21% of the

317   temperature-nutrient scenarios (i.e. black area in Fig. 1c) indicating that extinctions driven by

318   population fluctuations are highly prevalent in the RM model.

319

320   In contrast, the SRM model shows that increasing nutrient concentrations causes fewer

321   fluctuations than those observed for the RM model (Fig. 1). This is because: (1) more nutrients

322   are needed to shift the system from a stable equilibrium point to limit cycles—the system can

323   indeed persist without fluctuations up to 0.02 $gP.m^{-3}$ whereas it was only up to 0.0005 $gP.m^{-3}$ in

324   the RM model—and (2) when the system fluctuates, the amplitude of the fluctuations is smaller

325   in the SRM than in the RM model. As a result, stoichiometric constraints dampen the amplitude

326   of population fluctuations (i.e. the paradox of enrichment) and hence increase system persistence

327   at high nutrient levels. While the qualitative effect of temperature is similar to that observed in

328   the RM model, the thermal thresholds for consumer persistence are reduced at low and high

329   temperatures in the SRM predictions. Moreover, thermal thresholds remain almost constant along

330   the nutrient gradient in the RM model, whereas in the SRM model they depend on nutrient

331   concentration, with a smaller thermal range at low nutrient levels compared to high nutrient

332   levels (Fig. 1). The consumer is thus more likely to go extinct at low nutrient concentrations and

333   extreme temperatures in the SRM model than in the RM model. Overall, system persistence for

334   the SRM model was 44% without considering the extinction threshold and 37% when

335   considering it. In other words, without considering extinctions driven by very low biomass

336   densities, the SRM model predicts lower persistence of the consumer compared to RM model but

337   it is the opposite pattern when considering extinctions driven by very low biomass densities. We

338   thus conclude that the RM model predicts larger population fluctuations leading to high

339   probabilities of populations extinctions in comparison to the SRM model.

340

341   *Biomass distribution*

342   We next compared the predictions of both models for consumer-resource biomass ratios along the

343   temperature and nutrient gradients (Fig. 2). We found that the RM model systematically predicts

344   biomass ratio > 1 (i.e. consumer biomass is larger than resource biomass). In contrast, the SRM

345   model predicts biomass ratios both > or < than 1 depending on temperature and nutrient levels.

346   The RM model predicts that, as soon as the consumer can persist, its population biomass density

347   always exceeds the resource population biomass density (Fig. 2). With the SRM model, the

348   biomass ratios are below one at low nutrient levels (Fig. 2). However, at medium and high

349   nutrient levels, the ratios are above one as soon as the consumer can persist. We found

350   qualitatively similar results when considering unstable equilibrium points (Fig. S2). Finally, we

351   showed that, for equivalent parameter values, the RM model predicts biomass ratio that are

352   superior or equal to the ones predicted by the SRM model (text S2). This difference between the

353   two models is independent of the shape and position of the temperature function used to

354   parametrise the models.

355

356   *Mechanisms underlying stability and biomass distribution patterns*

357 Here, we detail the mechanisms underlying the stability and biomass distribution patterns to

358 better understand how and when stoichiometric constraints modulate the effects of temperature

359 and nutrients on consumer-resource dynamics. The first mechanism corresponds to the effect of

360 stoichiometric constraints on the consumer energetic efficiency that determines the consumer

361 persistence at extreme low and high temperatures. The second mechanism relates to the influence

362 of the stoichiometric constraints on population dynamical feedback that explains why the

363 stoichiometric model predicts more stability at high nutrient levels compared to the non-

364 stoichiometric model.

365

366 *Consumer energetic efficiency*

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

368 efficiency *EE* of the consumer (i.e. its feeding rate relative to metabolic losses) calculated as

369 follows:

370 $$EE = \frac{e f(R^*)}{m} \tag{9}$$

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

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

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

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

375 grow and persist.

376

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

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

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

380 models, energetic efficiency at equilibrium has a hump-shaped relationship with temperature with

381   maximal efficiency values at medium temperatures. While this unimodal shape is conserved

382   across nutrient levels and models, the RM model systematically predicts higher consumer

383   energetic efficiency values than the SRM model because consumer assimilation efficiency is

384   lower in the SRM than in the RM model (Fig. S3). As a result, the temperatures at which

385   energetic efficiency falls below one and drives consumers extinct are more extreme in the RM

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

387   a narrower thermal range in the SRM model.

388

389   *Dynamical feedbacks due to the stoichiometric constraints*

390   The second mechanism by which stoichiometric constraints influence consumer-resource stability

391   and biomass distribution are the dynamical feedbacks due to stoichiometric constraints on the

392   resource population growth rate and on the consumer energetic efficiency. In the SRM model, the

393   growth rate of the resource population depends on both the total nutrient load and the consumer

394   population density as $Q_R = (N_{tot} - Q_C C)/R$. In other words, when consumer population increases,

395   this decreases resource population growth by reducing both resource density (through predation)

396   and quality (through the total nutrient load) leading to a negative feedback on consumer

397   population growth rate. In contrast, for the RM model, the negative consumer feedback is only

398   driven by the reduction in resource density as resource quality is not considered. In addition to

399   this first dynamical feedback, there is a second dynamical feedback as the consumer population

400   growth rate also depends on Q_R and thus on its own biomass density. Thus, also this second

401   negative feedback loop limits the consumer population growth rate when its density increases.

402   Altogether, dynamical feedbacks reduce strongly the amplitude of population fluctuations, which

403   in turn increases resource and consumer persistence.

404

405   To reveal the dynamic effects of the stoichiometric constraints, we calculated the values of

406   assimilation efficiencies and carrying capacities predicted by the SRM model for each

407   temperature-nutrient scenario (Fig. S3) and used these effective parameter values to replace the

408   values of parameters e and K in the RM model for each temperature-nutrient scenario. In other

409   words, we calculated average values of e and K in the dynamic SRM model and used them as

410   constant input parameters in the RM model. The objective of using these effective parameter

411   values was to disentangle the static effect of stoichiometric constraints (i.e. changing the average

412   parameter values of consumer assimilation efficiency and of the resource carrying capacity) from

413   their population dynamical effect (i.e. the two dynamical feedback described above). We thus

414   simulated population dynamics along the temperature-nutrient gradient using the RM model with

415   these effective parameters; referred hereafter as effective RM model (Fig. 4). Comparing

416   predictions from the RM, effective RM, and SRM models allowed to disentangle the static

417   stoichiometric effects when going from the RM to the effective RM predictions (Fig. 4, panels a

418   to b) from the dynamical stoichiometric effects when going from the effective RM to the SRM

419   predictions (Fig. 4, panels b to c). In other words, the RM and effective RM only differ in their

420   parameter values because the effective RM takes into account the effect of stoichiometric

421   constraints on the average parameter values. On the other hand, the effective RM and SRM have

422   similar parameter values but different population dynamics, which helps understanding the

423   dynamical feedback induced by stoichiometric constraints.

424

425   We found that, at low nutrient concentrations, population fluctuations and consumer persistence

426   predicted by the effective RM model agreed with predictions of the SRM model. However, the

427   system shifted from a stable equilibrium point to a limit cycle at lower nutrient concentrations for

428   the effective RM model than for the SRM model. This suggests that more nutrients are needed to

429   destabilize the system with the SRM model. Moreover, the effective RM model predicts ampler

430   population fluctuations than the SRM model. As a result, the effective RM predicts high

431   extinction rates at high nutrient concentrations compared to the SRM model. Overall, we found

432   that the effective RM model cannot fully reproduce the dynamics predicted by the SRM, which

433   indicates that including stoichiometric constraints in the RM model involves more than only

434   changing parameter values.

435

436

437

438

439   **Discussion**

440   Temperature and nutrient enrichment are two of the most important drivers of global change

441   (Nelson 2005). However, most research on the effects of temperature and nutrients on community

442   dynamics assumes that the elemental composition of primary producers and consumers are

443   constant and independent of changes on energy and material fluxes (Binzer *et al.* 2012; Boit *et al.*

444   2012; Amarasekare & Coutinho 2014; Gilbert *et al.* 2014; Amarasekare 2015; Binzer *et al.* 2016;

445   Gilarranz *et al.* 2016). Yet, the elemental composition of primary producers is known to be

446   flexible, which can have important consequences for community dynamics and ecosystem

447   processes (Elser *et al.* 2000). We have shown how stoichiometric constraints that account for

448   flexible stoichiometry can affect predictions on how temperature and nutrients influence

449   community stability and biomass distribution across trophic levels. We thus argue that

450   considering stoichiometric constraints is an important step toward a better understanding of the

451   effects of global change on ecosystems.

452

453

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

455 We showed that both stoichiometric constraints and temperature dampen the negative effect of

456 nutrient enrichment on consumer-resource fluctuations and increase system persistence at high

457 nutrient levels. Temperature effects are driven by physiological mechanisms. In agreement with

458 previous empirical studies, our model parametrization reflects the observation that metabolic loss

459 rates increase faster with warming than consumer feeding rates (Vucic-Pestic *et al.* 2011; Sentis

460 *et al.* 2012; Fussmann *et al.* 2014; Iles 2014). Consumers are thereby less energetically efficient

461 at higher temperatures which stabilizes food-web dynamics by reducing energy flow between

462 trophic levels (Binzer *et al.* 2012; Kratina *et al.* 2012; Fussmann *et al.* 2014; Sentis *et al.* 2017).

463 In contrast, the effect of stoichiometric constraints is mainly linked to two mechanisms: a shift in

464 the position of the Hopf bifurcation and negative dynamical feedbacks of the consumer and

465 resource on their population growth rates. Both resources and consumers are composed of the

466 same essential elements (N, P, and C), which implies that, when consumer or resource population

467 biomass increases, it reduces the pool of free nutrients available for the growth of the resource

468 population. Therefore, more nutrients are needed to shift the system from a stable equilibrium to

469 population cycles. In other words, the paradox of enrichment is displaced to higher nutrient

470 concentrations (i.e., the position of the Hopf bifurcation is shifted to higher nutrient levels. In

471 contrast, the RM model does not take into account the storage of nutrients in both the resource

472 and consumer biomasses (i.e. the carrying capacity only depends on the total nutrient load). Less

473 enrichment is thus required to shift the system from a stable equilibrium point to limit cycles.

474

475 We found two dynamic effects that correspond to negative dynamical feedbacks of the consumer

476 and the resource on themselves. When consumer population increases, it decreases the population

477 growth rate of the resource by limiting nutrient availability, diminishing resource biomass, which,

478 in turn, decreases the consumer population growth rate. Conversely, when the resource biomass

479 increases, this decreases the nutrient content of the resource, which, in turn, limits the growth

480 rates of both the resource and consumer populations. These stoichiometric negative feedback

481 loops strongly decrease the amplitude of population fluctuations and thus dampen the paradox of

482 enrichment. Interestingly, our comparisons of the RM, effective RM and SRM model predictions

483 indicate that the dynamical effects contribute more to the reduction of fluctuations than the static

484 effects: population fluctuations are large in the effective RM model accounting for the static

485 effect only, whereas they are much smaller in SRM model accounting for both static and

486 dynamical effects (Fig. 4). This implies that the impact of stoichiometric constraints on

487 community dynamics goes beyond a simple modification of parameter values and encompass

488 more complex population feedbacks between the consumer and the resource.

489

490 Overall, these results demonstrate that both flexible stoichiometry and temperature can

491 synergistically dampen the paradox of enrichment by two different mechanisms: population

492 dynamic feedbacks and physiological constraints. Our consumer-resource model is simplified

493 compared to natural communities composed of numerous species. Moreover, in natural systems,

494 a large amount of nutrient can be stored in abiotic and slow biotic pools that have long turnover

495 times which, in turn, can influence the population dynamics. In particular, the amplitude of the

496 population fluctuations is expected to be smaller as abiotic pools can buffer the population

497 feedback. Nevertheless, considering the nutrient held in slow abiotic or biotic pools would not

498 change the equilibrium densities of primary producers and grazer if nutrients are released in the

499 environment proportionally to their density stored in the abiotic pool. Moreover, the predictions

500 of the stoichiometric model fit with empirical observations. In eutrophic lakes and experimental

501 mesocosms, populations can persist at relatively high nutrient concentrations even if fertilisation

502 enhance population fluctuations (O'Connor *et al.* 2009; Boit *et al.* 2012; Kratina *et al.* 2012), as

503 our stoichiometric model predicts. In contrast, the Rosenzweig-MacArthur model tends to

504   produce very large population fluctuations and extinctions at low nutrient concentrations which

505   can explain why these predictions are not well supported by empirical observations (McAllister *et*

506   *al.* 1972; Jensen & Ginzburg 2005).

507

508   *Effects of stoichiometric constraints on system persistence across environmental gradients*

509   While stoichiometric constraints dampen the paradox of enrichment and thus increase persistence

510   at high nutrient levels, they also reduce the persistence of the consumer at low and high

511   temperatures. Stoichiometric constraints affect the thermal thresholds for consumer extinctions.

512   Consumers can only persist over a narrower range of intermediate temperatures when they are

513   constrained by stoichiometry. This is due to the reduced biomass assimilation of the consumer at

514   low and high temperatures that, in turn, decreases its energetic efficiency and thus fastens

515   consumer extinction. In our stoichiometric model, the reduction of biomass assimilation

516   efficiency emerges from the effect of temperature on resource quality: extreme high and low

517   temperatures decrease resource quality and thus less resource biomass can be converted in

518   consumer biomass at these temperatures. The emergence of a thermal dependency for

519   assimilation efficiency contrasts with previous theoretical studies that used the RM model and

520   assumed that the assimilation efficiency is temperature independent as resource quality is

521   assumed constant (Binzer *et al.* 2012; Gilbert *et al.* 2014; Sentis *et al.* 2017; Uszko *et al.* 2017).

522   In the SRM model, the thermal dependency of the consumer assimilation efficiency is fully

523   driven by the change in the resource stoichiometry induced by temperature. The SRM model thus

524   predicts an additional mechanism by which temperature can influence trophic interactions:

525   temperature changes resource stoichiometry, which, in turn, impacts the consumer assimilation

526   efficiency and its population growth rate. This prediction matches with empirical results showing

527   that primary producer stoichiometric composition can change with temperature (Woods *et al.*

528   2003) and that consumer assimilation efficiency is sensitive to resource stoichiometric

529   composition (Andersen 1997; Elser *et al.* 2000). To sum up, the overall effect of stoichiometric

530   constraints on system persistence thus depends on the temperature range considered and on their

531   relative influence on population fluctuations versus consumer persistence.

532

533   *Effects of stoichiometric constraints on biomass distribution*

534   We found that stoichiometric constraints can modulate the effects of temperature and nutrients on

535   biomass distribution across trophic levels. Without stoichiometric constraints (i.e. with the

536   Rosenzweig-MacArthur model), biomass ratios are above one for almost all temperatures or

537   nutrient levels as the biomass produced by the resource is efficiently transferred to the consumer

538   level consistently along the environmental gradients. This finding agrees with theoretical studies

539   reporting that Lotka-Volterra and RM models predict biomass ratios above one and fail to

540   reproduce biomass pyramids for a substantial region of parameter values (Jonsson 2017; Barbier

541   & Loreau 2019). However, in nature, consumer-resource biomass ratios are often below one

542   (McCauley & Kalff 1981; Del Giorgio & Gasol 1995; McCauley *et al.* 1999; Irigoien *et al.* 2004)

543   suggesting that additional mechanisms should be included to better understand and predict

544   biomass distribution patterns in natural food webs. Our stoichiometric model agrees with

545   experimental observations. It predicts that, at low nutrient concentrations (i.e. < 0.01 gP.m^{-3}), the

546   biomass ratio never exceeds one along the entire temperature gradient. This is observed in

547   oligotrophic aquatic systems where primary production is too low to sustain high consumer

548   populations (O'Connor *et al.* 2009). In addition, we also found that increasing nutrient levels

549   decreased the temperature ranges within which biomass ratio is below one. This corresponds to

550   results from manipulated nutrient concentrations and temperature in aquatic mesocosms, where

551   zooplankton to phytoplankton biomass ratio only exceeds one in the enriched mesocosms at

552   medium or warm temperatures (i.e. 27°C) (O'Connor *et al.* 2009). This suggests that the models

553   with stoichiometric constraints better reproduce the biomass patterns observed in experimental

554   and natural systems. Nevertheless, further experiments investigating the links between

555   stoichiometric flexibility and consumer-resource dynamics are needed to determine if these

556   stoichiometric mechanisms are underlying patterns of biomass distribution in nature.

557

558   *Implications of our findings for global change*

559   Temperature and nutrients do not act in isolation from each other. Climate warming, for example,

560   causes stronger water stratification which, in turn, can limit nutrient cycling (Sarmiento *et al.*

561   2004; Tranvik *et al.* 2009). Environmental policies such as the European water framework

562   directive (i.e. Directive 2000/60/EC of the European Parliament and of the Council establishing a

563   framework for the Community action in the field of water policy) effectively reduces input of

564   nutrients in aquatic ecosystems (Anneville *et al.* 2005) while the climate keeps warming. With

565   these two phenomena, water will often be warmer and contain fewer nutrients in aquatic systems.

566   Our models consistently predict that warmer temperatures should stabilise consumer-resource

567   dynamics but, if temperature further increases, the consumer goes extinct as energetic efficiency

568   decreases with warming. Moreover, we found that stoichiometric constraints can reduce this

569   thermal extinction threshold (i.e. the consumer persists in a narrower thermal range), especially at

570   low nutrient levels. Our stoichiometric model thus suggests that decreasing nutrient

571   concentrations alongside warmer temperatures should fasten the extinction of consumer

572   populations. This prediction matches empirical observations of consumer extinctions at warm

573   temperatures in oligotrophic aquatic systems (Petchey *et al.* 1999; O'Connor *et al.* 2009).

574   Altogether, these results indicate that considering stoichiometric constraints can be of importance

575   for the management of nutrient inputs and the conservation of natural populations and

576   communities under climate change.

577

578   ***Conclusion***

579   Knowledge of how temperature and nutrient simultaneously influence the elemental composition

580   of primary producers and consumers is crucial to better understand and predict the effects of

581   global change on species interactions, community dynamics and fluxes of energy and material

582   within and among ecosystems. Here we showed that stoichiometric constraints dampen the

583   negative effect of enrichment on stability by reducing population fluctuations through population

584   dynamics feedbacks. However, stoichiometric constraints also decrease consumer energetic

585   efficiency, which increases consumer extinction risk at extreme temperatures and low nutrient

586   concentrations. Finally, stoichiometric constraints can reverse biomass distribution across trophic

587   level by modulating consumer efficiency and resource population growth rate along the

588   temperature and nutrient gradients. Our study provides a first step in the exploration of the

589   consequences of stoichiometric constraints and temperature on ecological communities. It

590   suggests that accounting for stoichiometric constraints can strongly influence our understanding

591   of how global change drivers impact important features of ecological communities such as

592   stability and biomass distribution patterns.

593

597

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767

768 **Figure legends**

769 **Fig. 1.** Population fluctuations (consumer biomass coefficient of variation; panels *a* and *b*) and

770 species persistence (number of species; panels *c* and *d*) across the temperature (*y* axis) and

771 nutrient (*x* axis) gradients as predicted by the Rosenzweig-MacArthur (RM; panels *a* and *c*) and

772 by the Stoichiometric Rosenzweig-MacArthur (SRM; panels *b* and *d*) models. In panels *a* and *b*,

773 the white colour corresponds to the temperature-nutrient scenario for which the consumer has

774 gone extinct whereas the orange to red to dark red represent population fluctuations of increasing

775 amplitude. In panels *c* and *d*, in black: both consumer and resource persist; in red: only the

776 resource persists; in orange: none persists. Resource biomass CV is not shown; it is qualitatively

777 similar to the consumer biomass CV as resource and consumer biomass fluctuation are strongly

778 coupled.

779

780 **Fig. 2.** Consumer-resource biomass ratio along the temperature gradient for the Rosenzweig-

781 MacArthur (RM, green lines) and the Stoichiometric Rosenzweig-MacArthur (SRM, black lines)

782 models at three nutrient concentrations (0.008, 0.02, and 0.032 $gP.m^{-3}$). In each panel, the dotted

783 line represents biomass ratio of one; i.e. the biomass densities of the resource and the consumer

784 are equal. Biomass values shown at equilibrium points. For unstable equilibrium points (i.e. limit

785 cycles), see Fig. S2.

786

787 **Fig. 3.** Consumer energetic efficiency along the temperature gradient for the Rosenzweig-

788 MacArthur (RM, in green) and the Stoichiometric Rosenzweig-MacArthur (SRM, in black)

789 models at two nutrient concentrations (0.008 and 0.02 gP/m^3). In each panel, the dotted line

790 represents energetic efficiency equal to one.

791

Fig. 4. Population fluctuations (consumer biomass coefficient of variation) across the temperature

(y axis) and nutrient (x axis) gradients as predicted by the Rosenzweig-MacArthur (RM; panel *a*),

the RM with effective parameters (panel *b*), and the Stoichiometric Rosenzweig-MacArthur

(SRM; panel *c*) models.

796

797   **Figure 1**

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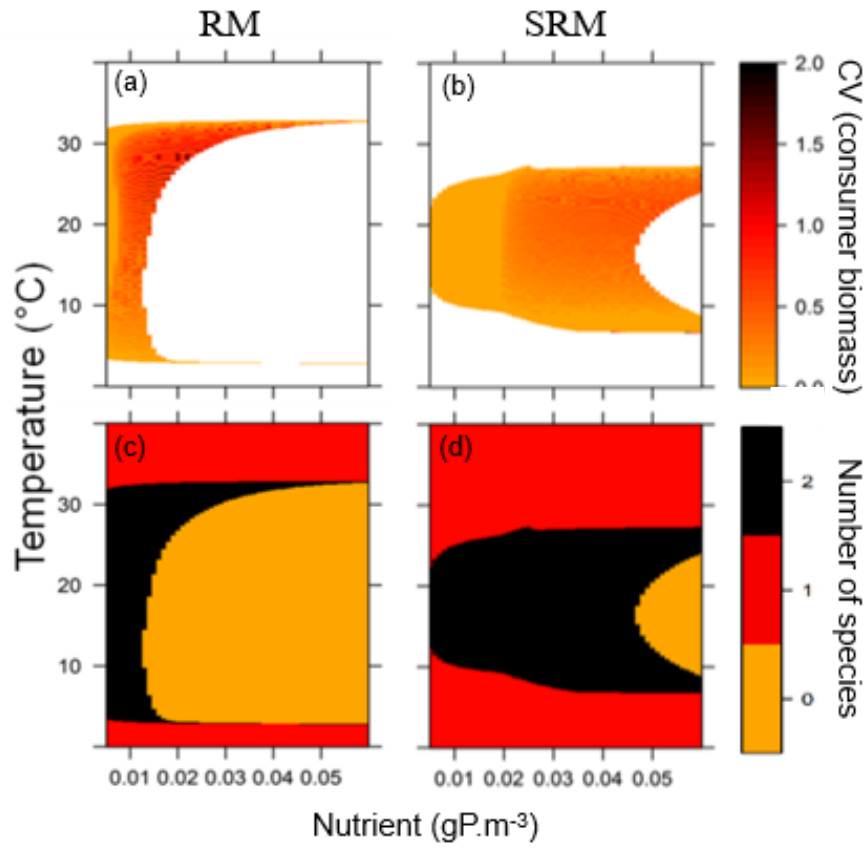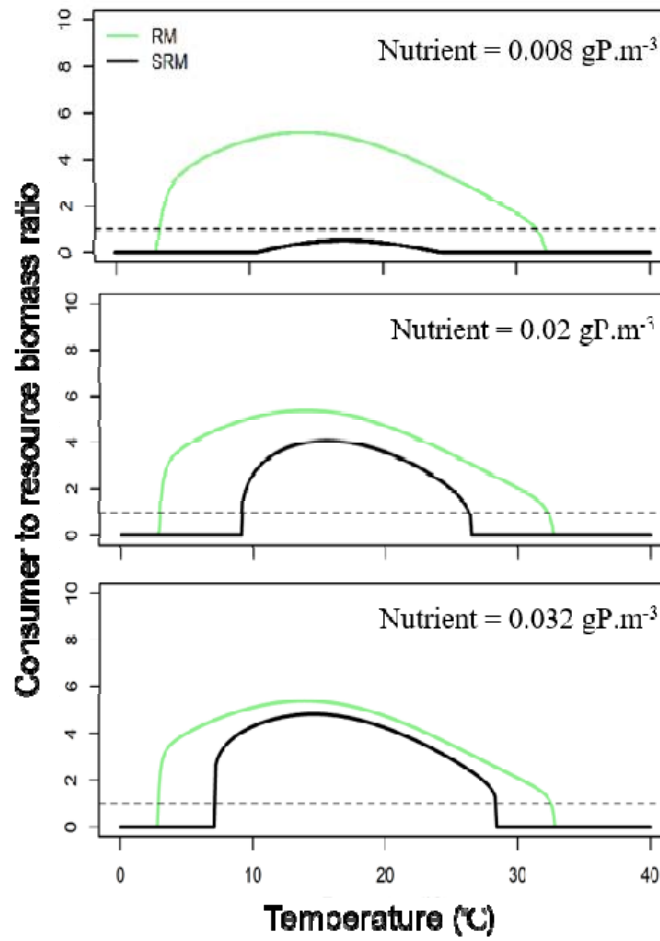

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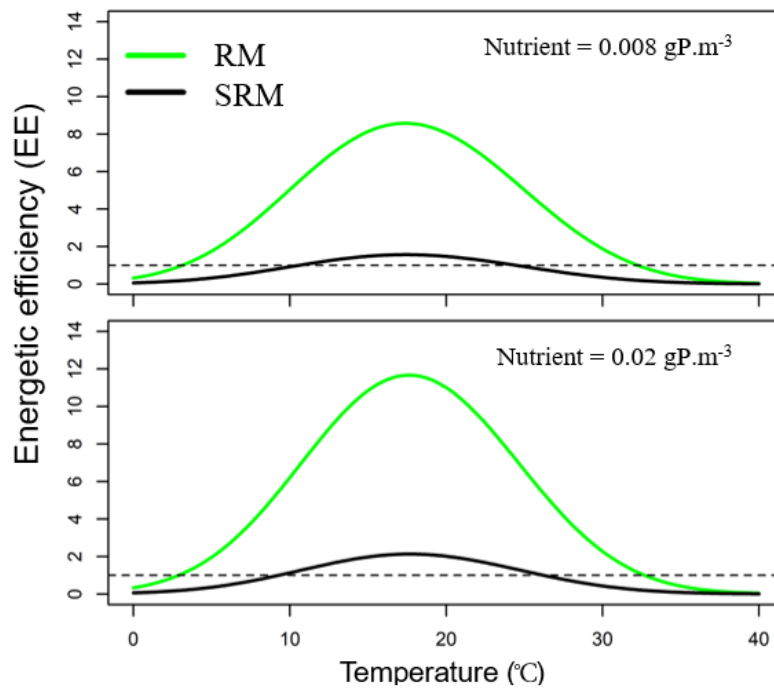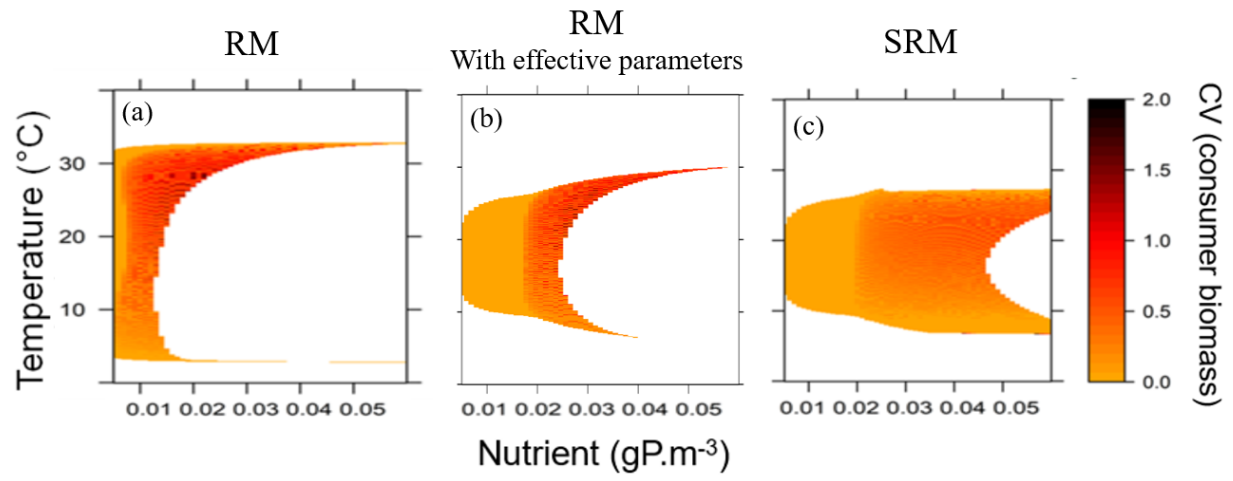802   **Figure 2**

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805   **Figure 3**

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811 **Figure 4**

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817   **Supplementary information**

818   **Stoichiometric constraints modulate the effects of temperature and nutrients on biomass**
819   **distribution and community stability**
820
821   Arnaud Sentis, Bart Haegeman, and José M. Montoya
822

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

824   The model studied in the main text is very similar to previous stoichiometric consumer-resource

825   models (Andersen 1997; Loladze *et al.* 2000; Andersen *et al.* 2004; Diehl *et al.* 2005). To make

826   our paper self-contained, we here present the model assumptions and derive the model equations

827   (eqs. 3-6 in main text). Our objective was not to develop a complex and very realistic

828   stoichiometric model that would include additional important abiotic and biotic features such as

829   light intensity (Diehl 2007) or compensatory feeding (Cruz-Rivera & Hay 2000). Instead, we

830   aimed at introducing two fundamental stoichiometric features (i.e. stoichiometric flexibility and

831   stoichiometric imbalance) and investigate how these stoichiometric considerations can change

832   predictions of the Rosenzweig-MacArthur model. We assumed that resource and consumer

833   production are limited by energy and a single mineral nutrient. Moreover, we assume the system

834   is closed for nutrients. Thus, nutrient supply originates exclusively from excretion and

835   remineralization of biomass. The total amount of nutrients in the system (N_{tot}) is then a measure

836   of nutrient enrichment. As elemental homeostasis is much stronger for consumers compared to

837   primary producers (Andersen 1997), we assumed the nutrient quota of the consumer Q_C to be

838   constant whereas the nutrient quota of the resource Q_R is flexible. Four differential equations

839   determine the dynamics of four state variables, that is, the concentrations of resource (R) and

840   consumer (C) carbon biomasses and of dissolved mineral nutrients (N), and the nutrient quota of

841   the resource (Q_R):

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

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

844 $\dot{Q}_R = h(N) - r(Q_R - Qmin)$ (S3)

845 $\dot{N} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + Q_C mC - h(N)R$ (S4)

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

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

848 population growth rate follows the Droop equation (Droop 1974) and is now limited by its

849 nutrient quota Q_R relative to the minimum nutrient quota Q_{min}. Rate of change of Q_R depends on

850 the nutrient uptake rate by the resource species $h(N)$ and the amount of nutrient invested in

851 growth (eqn S3). $h(N)$ is the specific resource nutrient uptake rate and can be represented by a

852 Michaelis-Menten model where the amount of nutrient uptake saturates at high nutrient

853 concentrations.

854

855 With the mass-balance equation, we get that the total amount of nutrient is the sum of the free

856 nutrient plus the nutrient fixed in the resource biomass plus the nutrient fixed in the consumer

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

858 time derivative of N_{tot} is zero. We can thus replace one of the four differential equations S1-S4

859 with the algebraic equation $N_{tot} = N + Q_R R + Q_C C$:

860 $\dot{C} = (e\frac{aR}{1+ahR} - m)C$

861 (S5)

862 $\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C$

863 (S6)

864 $\dot{N} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + Q_C mC - h(N)R$

865 (S7)

866 $N_{tot} = N + Q_R R + Q_C C$

867 (S8)

868

869   It is possible to derive a simpler model by reducing the number of dimensions in the above model

870   from three to two. This model reduction is based on the assumption that free nutrients are taken

871   up very quickly relative to the dynamics of the consumer and resource biomasses. This

872   corresponds to taking $h(N)$ large, $h(N) = \frac{1}{\varepsilon}\tilde{h}(N)$ for small ε. The fast dynamics (on the

873   timescale t ~ ε) are

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

875   (S9)

876   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

877   words, N in dead and excreted matter is immediately recycled and acquired by the resource

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

879   (on the timescale t ~1):

880    $\dot{C} = (e\frac{aR}{1+ahR} - m)C$ $\hspace{6cm}$ (S10)

881    $\dot{R} = r(1 - \frac{Qmin}{Q_R})R - \frac{aR}{1+ahR}C$ $\hspace{4.5cm}$ (S11)

882    $N_{tot} = Q_R R + Q_C C$ $\hspace{6.5cm}$ (S12)

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

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

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

886   S5-S8, the reduced model has only two differential equations and one algebraic equation. It can

887   be equivalently written as a set of three differential equations with $\dot{C}$ and $\dot{R}$ similar as equations

888   S10 and S11 and with $\dot{Q}_R = \frac{d\frac{N_{tot}-Q_C C}{R}}{dt} = (Q_R - Q_C e)\frac{aR}{1+ahR}C + \frac{Q_C mC}{R} - r(Q_R - Qmin)$.

889

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

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

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

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

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

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

896   The intuitive interpretation of eqn. S13 is that resource quality is not a limiting factor for

897   consumer growth as long as the nutrient content of the resource is superior to the nutrient content

898   of the consumer (i.e. $Q_R > Q_C$). In other words, when $Q_R \gg Q_C$, $e(Q_R) \rightarrow e_{max}$ and when $Q_R \ll$

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

900

901 **Text S2. Differences in biomass ratios predicted by the two models**

902 Here we show that the equilibrium consumer-to-resource biomass ratio in the model with
903 stoichiometric constraints (SRM model) is always smaller than the one in the model without
904 stoichiometric constraints (RM model), keeping the same parameter values. For simplicity we
905 assume for both models that the consumer and the resource persist at equilibrium, and we do not
906 consider the stability of the equilibrium point (in particular, the equilibrium might be unstable at
907 the center of a limit cycle). We indicate the equilibrium values of the non-stoichiometric model
908 by the superscript "ns" and the equilibrium values of the stoichiometric model by the superscript
909 "s". We use the same superscripts to distinguish the assimilation efficiencies of both models.

910 *Model without stoichiometric constraints*

911 The model is defined as

912 $\dot{R} = r(1 - \frac{R}{K})R - f(R)C$ (S14)

913 $\dot{C} = (e^{ns}f(R) - m)C$ (S15)

914

915 With $f(R) = \frac{aR}{1+ahR}$ and $K = N_{tot}/Q_{min}$.

916 By solving equation (S15) we get the resource biomass at equilibrium:

917 $R^{ns} = \frac{1}{a(\frac{e^{ns}}{m}-h)}$ (S16)

918 From equation (S14) we get the consumer biomass at equilibrium. It follows from $f(R^{ns})C^{ns} =$
919 $r(1 - \frac{R^{ns}}{K})R^{ns}$, or $C^{ns} = r(1 - \frac{R^{ns}}{K})\frac{R^{ns}}{f(R^{ns})}$

920 Hence, the consumer-to-resource biomass ratio is

921 $\frac{C^{ns}}{R^{ns}} = \frac{re^{ns}}{m}(1 - \frac{R^{ns}}{K}) = \frac{re^{ns}}{m}(1 - \frac{Q_{min}R^{ns}}{N_{tot}})$ (S17)

922

923 *Model with stoichiometric constraints*

924 The model is defined as

925 $\dot{R} = r(1 - \frac{Q_{min}}{Q_R})R - f(R)C$ (S18)

926 $\dot{C} = (e^s(Q_R)f(R) - m)C$ (S19)

927

928   With $e^s(Q_R) = e_{max}\frac{Q_R}{Q_C+Q_R}$, $f(R) = \frac{aR}{1+ahR}$ and $N_{tot} = Q_R R + Q_C C$.

929   From equation (S19) we have $e^s(Q_R^s)f(R^s) = m$, or

930    $$R^s = \frac{1}{a(\frac{e^s(Q_R^s)}{m} - h)} \qquad\qquad (S20)$$

931   From equation (S18) we have from $(R^s)C^s = r(1 - \frac{Q_{min}}{Q_R^s})R^s$, or

932    $$C^s = \frac{r e^s(Q_R^s)}{m}(1 - \frac{Q_{min}}{Q_R^s})R^s$$

933   Hence, the consumer-to-resource biomass ratio is

934    $$\frac{C^s}{R^s} = \frac{r e^s(Q_R^s)}{m}(1 - \frac{Q_{min}}{Q_R^s}) = \frac{r e^s(Q_R^s)}{m}(1 - \frac{R^s Q_{min}}{N_{tot} - Q_C C^s}) \qquad (S21)$$

935

936

937   We now compare the biomass ratios of equations (S17) and (S21). We have $e^{ns} = e_{max}$, and hence

938    $$e^{ns} \geq e^s(Q_R^s). \qquad\qquad (S22)$$

939   Using this inequality, we get $a\left(\frac{e^{ns}}{m} - h\right) \geq a(\frac{e^s(Q_R^s)}{m} - h)$, and by equations (S16) and (S20), we

940   see that

941    $R^{ns} \leq R^s \qquad\qquad (S23)$

942   Clearly, we always have $N_{tot} \geq N_{tot} - Q_C C^s$. Combining this with equation (S23), we get

943    $\frac{R^{ns}}{N_{tot}} \leq \frac{R^s}{N_{tot} - Q_C C^s}$ and

944    $$1 - \frac{Q_{min} R^{ns}}{N_{tot}} \geq 1 - \frac{R^s Q_{min}}{N_{tot} - Q_C C^s} \qquad\qquad (S24)$$

945   Finally, from equations (S22) and (S24),

946    $$\frac{r e^{ns}}{m}(1 - \frac{Q_{min} R^{ns}}{N_{tot}}) \geq \frac{r e^s(Q_R^s)}{m}\left(1 - \frac{R^s Q_{min}}{N_{tot} - Q_C C^s}\right), \qquad (S25)$$

947   showing that $\frac{C^{ns}}{R^{ns}} \geq \frac{C^s}{R^s}$.

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

955

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	$a_0 = 8.9$; $T_{opt} = 296.0$; $s = 9.4$	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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958

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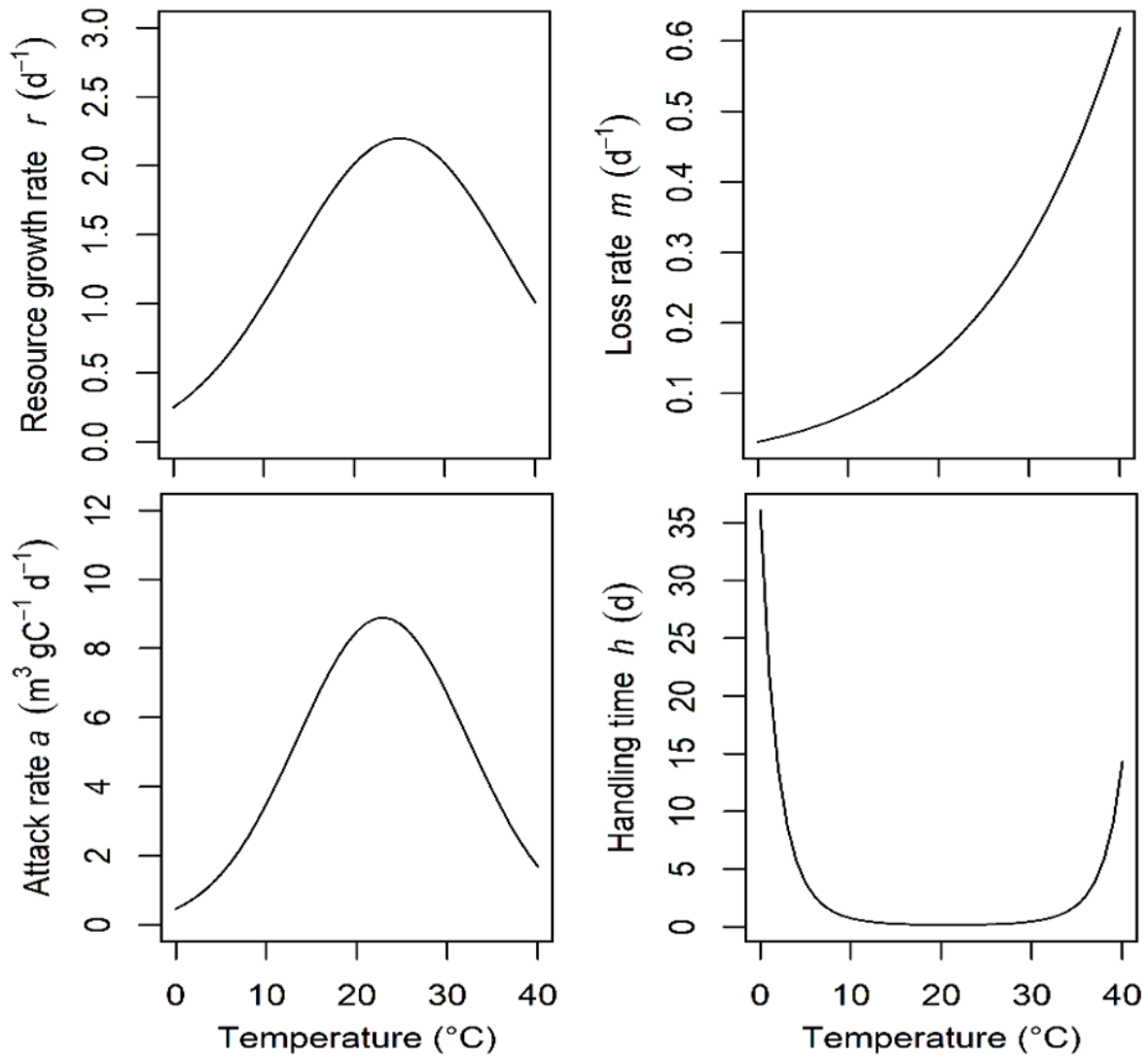

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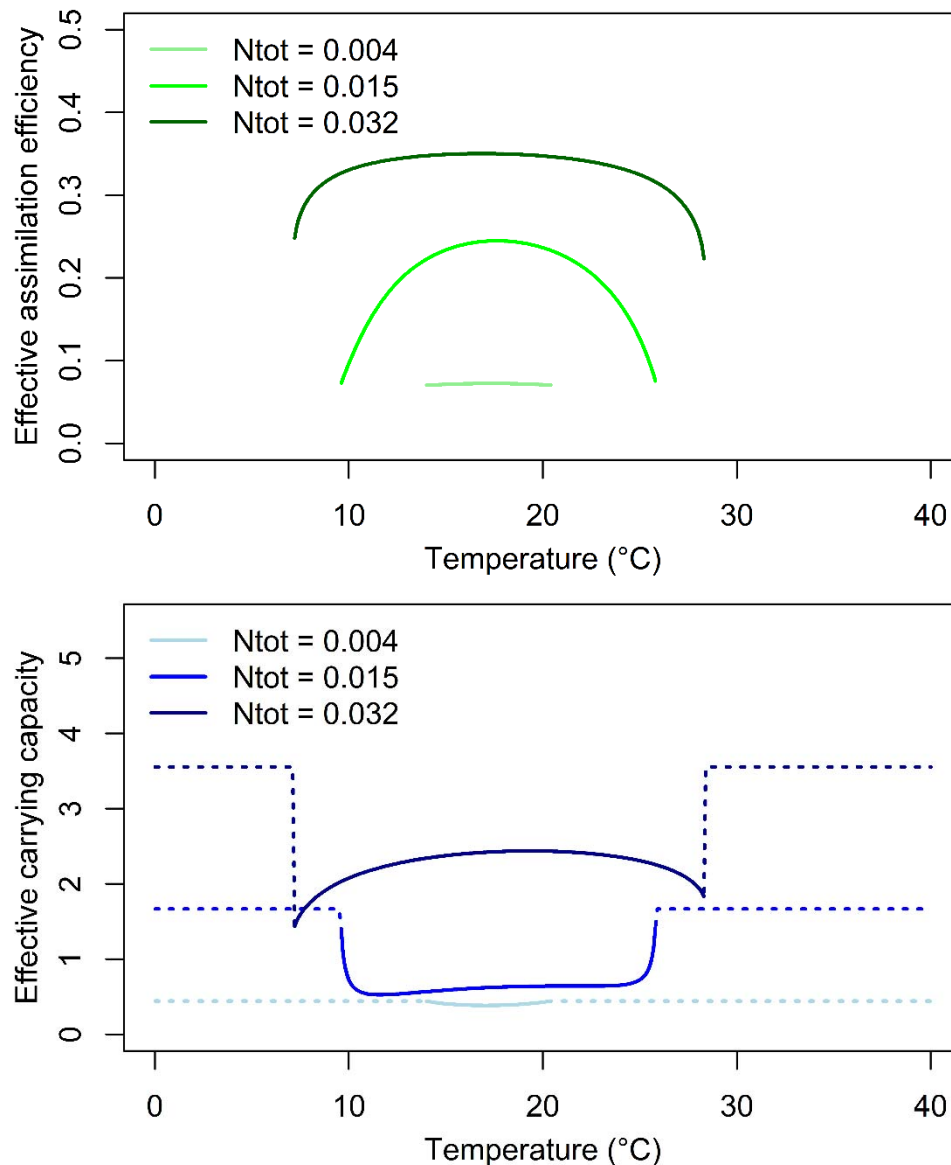
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968   **Fig. S2.** Consumer-resource biomass ratio (log scale) along the temperature gradient for the

969   Rosenzweig-MacArthur (RM, green lines) and the Stoichiometric Rosenzweig-MacArthur (SRM,

970   black lines) models at three nutrient concentrations (0.008, 0.02, and 0.032 $gP.m^{-3}$). In each

971   panel, the dotted lines represent unstable solutions whereas full lines represent stable solutions.

972   The thin horizontal dotted line represents biomass ratio of one; i.e. the biomass densities of the

973   resource and the consumer are equal.

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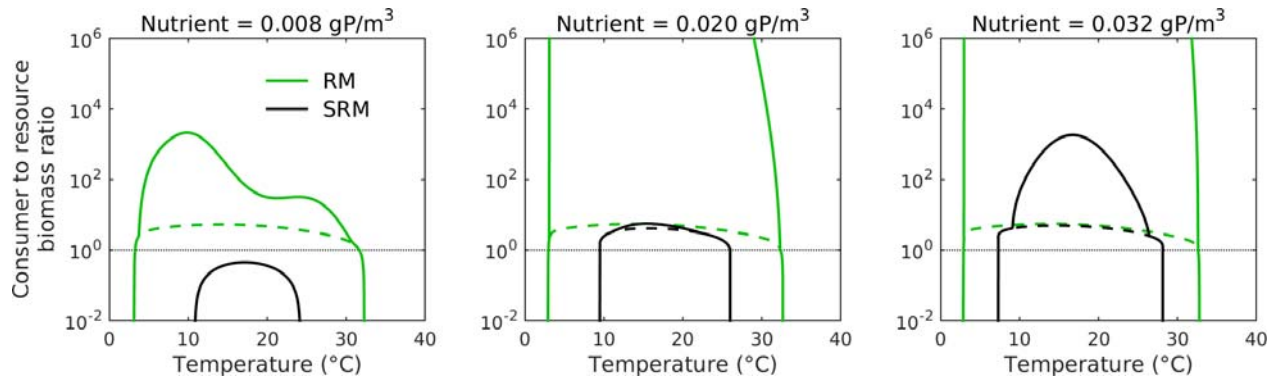
977   **Fig. S3**. Effective assimilation efficiency e_{ef} and carrying capacity K_{ef} from the

978   Stoichiometric Rosenzweig-MacArthur (SRM) model along the temperature gradient at

979   three nutrient levels (0.004, 0.015, and 0.032 gP.m^{-3}) with $Q_C = 0.042$. Full lines represent

980   temperature and nutrient scenarios for which both the resource and consumer persist

981   whereas dotted lines represent scenarios for which only the resource persists. Effective

982   assimilation efficiency was calculated as $e_{ef} = e_{max}Q_R/(Q_R+Q_C)$, with Q_R the equilibrium

983   solution of the SRM model and the effective carrying capacity as $K_{ef} = Q_R R/Q_{min} = (N_{tot}-$

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

985

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