Plant flexible stoichiometry and herbivore compensatory feeding drive population dynamics across temperature and nutrient gradients

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Abstract

Global change drivers like warming and changing nutrient cycles have a substantial impact on ecosystem functioning. In most modelling studies, organism responses to warming are described through the temperature dependence of their biological rates. In nature, however, organisms are more than their biological rates. Plants are

33 flexible in their elemental composition (stoichiometry) and respond to variance in nutrient availability and
34 temperature. An increase in plant carbon-to-nutrient content means a decrease in food quality for herbivores.
35 Herbivores can react to this decrease by compensatory feeding, which implies higher feeding rates and higher
36 carbon excretion to optimize nutrient acquisition. In a novel model of a nutrient-plant-herbivore system, we explored
37 the consequences of flexible stoichiometry and compensatory feeding for plant and herbivore biomass production
38 and survival across gradients in temperature and nutrient availability. We found that flexible stoichiometry increases
39 plant and herbivore biomasses, which results from increased food availability due to higher plant growth.
40 Surprisingly, compensatory feeding decreased plant and herbivore biomasses as overfeeding by the herbivore
41 reduced plants to low densities and depleted their resource. Across a temperature gradient, compensatory feeding
42 caused herbivore extinction at a lower temperature, while flexible stoichiometry increased its extinction threshold.
43 Our results suggest that compensatory feeding can become critical under warm conditions. In contrast, flexible
44 stoichiometry is beneficial for plants up to a certain temperature threshold. These findings demonstrate the
45 importance of accounting for adaptive and behavioural organismal responses to nutrient and temperature gradients
46 when predicting the consequences of warming and eutrophication for population dynamics and survival.

47

Introduction

Global warming and changes in nutrient cycles are two of the major global change drivers impacting ecosystem functioning. Since the start of temperature records in 1850, the world has continuously warmed (0.85°C between 1880 and 2012). The IPCC predicts global average temperature to rise by 0.3 to 4.8°C (compared to 1986-2005 baseline) by 2100, depending on the mitigation scenario (IPCC 2014). Simultaneously, other anthropogenic drivers such as agriculture and land-use changes influence nutrient availability, e.g., by increasing nitrogen (N) deposition through fertilizers (Falkowski 2000; Sala et al. 2000; Galloway et al. 2008; Sentis et al. 2015). Despite growing scientific interest in the ecological consequences of global warming (Peters 1991; Hughes 2000; Scheffers et al. 2016) and nutrient eutrophication (Ball et al. 2000; Dokulil and Teubner 2010; Johnson and McNicol 2010; Hwang 2020), mechanistic knowledge on their interactions is only beginning to emerge (Binzer et al. 2012, 2015; Cross et al. 2014; Schmitz and Rosenblatt 2017; Rho and Lee 2017; Ruiz et al. 2020).

While warming tends to stabilize population dynamics and increase primary productivity (O'Connor et al. 2009; Fussmann et al. 2014), it can also decrease biomass standing stocks through increased consumer control of primary production, ultimately leading to consumer starvation (O'Connor et al. 2009; Rall et al. 2012; Fussmann et al. 2014; Uszko et al. 2017; Marx et al. 2019). Increases in nutrient availability may help buffer this effect by increasing the energy entering the system (Binzer et al. 2012, 2015). A prior study found that temperature directly affects plant nutrient uptake rate by increasing the maximum uptake rate and half-saturation density of N and phosphorus (P) uptake (Marx et al. 2019).

Increasing nutrient availability has been studied mostly as a factor that increases the quantity of plant primary production. Low nutrient supply can cause starvation of higher trophic levels due to low plant biomass (Fussmann et al. 2014). High nutrient supply is not necessarily better – it can also cause consumer extinction due to unstable oscillations (Rosenzweig 1971; Rall et al. 2008). In addition to these effects on population dynamics, nutrient availability changes can also trigger variation in plant stoichiometry and thus resource quality for herbivores (Persson et al. 2010; Sardans et al. 2012).

Several lines of evidence have shown large differences in plant stoichiometry among and within species due to genetic and physiological mechanisms, and to the heterogeneity in the availability of nutrients in the environment. Plants display variable stoichiometric homeostasis, adjusting their elemental content in response to that of the environment. Stoichiometric homeostasis (from flexible/plastic to strict homeostasis) can vary widely among plant types. For example, vascular plants appear to be less flexible than algae (Yu et al. 2011). Furthermore, the degree of homeostasis is related to the heterogeneity of the environment. Plants that face variable nutrient availability in their habitat show a higher capacity to store nutrients, and therefore have higher plasticity (Meunier et al. 2014; Puche et al. 2018). Meunier et al. (2014) found that responding to varying environmental conditions by storing nutrients when available (i.e., flexible stoichiometry) is advantageous. In addition, homeostatic regulation can vary between nutrients. Yu et al. (2011) found variations of ±22-25% in N and ±30-50% in P content in aboveground plant tissue

82   across different levels of nutrient availability. Together, these studies indicate considerable variation in the tissue
83   stoichiometry of plants across sites and species.

84   Nutrient content in plant tissue is likely to be impacted by global changes such as rising temperatures and increasing
85   nutrient deposition (Rosenblatt and Schmitz 2016). Changing nutrient content means changes in the food quality that
86   plants provide for higher trophic levels (Johnson and McNicol 2010). In this way, the effects of global change
87   drivers on plants will propagate upwards to affect higher trophic levels. Compared to plants, animals have low to no
88   flexibility in their stoichiometric composition, likely due to their more complex body architecture and lack of
89   nutrient storage mechanisms (Sterner et al. 2002; Persson et al. 2010; Yu et al. 2011; Meunier et al. 2014). The
90   difference between plant and herbivore elemental ratios and the potential, unpredictable variation in plant
91   stoichiometry can be problematic for herbivores (Logan et al. 2004). Herbivores can mediate this stoichiometric
92   mismatch and maintain homeostasis by changing their feeding decisions and increasing their food intake through
93   compensatory feeding (Logan et al. 2004; Johnson and McNicol 2010; Jochum et al. 2017). This compensatory
94   behaviour by herbivores in reaction to changing plant nutrient content may, in turn, have effects on plants (Johnson
95   and McNicol 2010). It is, therefore, necessary to consider both bottom-up (flexible stoichiometry) and top-down
96   (compensatory feeding) effects to predict how ecosystems may respond to changing conditions (Rosenblatt and
97   Schmitz 2016).

98   Theoretical and empirical evidence has shown that the parallel change in temperature and nutrient availability
99   interactively affects communities (O'Connor et al. 2009; Binzer et al. 2012, 2015; Sentis et al. 2014, 2017; Malzahn
100   and Doerfler 2016; Ruiz et al. 2020). However, previous models of population dynamics under global change have
101   neither included flexible stoichiometry in plants nor compensatory feeding in herbivores. Flexible stoichiometry can
102   increase or decrease the stoichiometric mismatch between plants and herbivores and, therefore, may buffer or
103   aggravate the effects of changing temperature and nutrient availability. Similarly, compensatory feeding could help
104   herbivores to buffer the adverse effects of an increasing mismatch. Consequently, we should explore the impact of
105   flexible stoichiometry in plants and compensatory feeding in herbivores along gradients in temperature and nutrient
106   availability.

107   In this study, we use a population-dynamics model integrating nutrient-plant and plant-herbivore interactions to
108   address (1) how flexible stoichiometry and compensatory feeding affect population dynamics, stoichiometric
109   mismatch, and carbon (C) storage in a tri-trophic nutrient-plant-herbivore system and (2) how these strategies affect
110   the survival and biomass of plants and herbivores in a world faced with warming and changes in nutrient
111   availability. We simulate the nutrient-plant-herbivore system (N represents the nutrients) using three models (Figure
112   1). We start from a baseline model, including the temperature dependencies of (1) plant nutrient uptake, (2) the
113   herbivore feeding rate, and (3) the plant and herbivore metabolic rates. In the second model, we allow plants to
114   adjust their N:C ratio by changing their C uptake as a function of N uptake, depending on nutrient availability
115   (flexible stoichiometry model). In the third model, in addition to flexible stoichiometry, we give our herbivores the
116   ability to adapt their feeding rate to the N:C ratio of their plant resource (compensatory feeding model). As
117   compensatory feeding is a direct reaction to the varying plant N:C ratios, we refrained from running a model with

118 compensatory feeding but without flexible stoichiometry, which would yield the same dynamics as the baseline
119 model. We hypothesize that flexible plant stoichiometry should allow for higher biomass production even at low
120 nutrient supply, along with a decrease in the plant N:C, as plants consume more C relative to N (compared to the
121 baseline model).

122 Consequently, we expect a reduction in herbivore biomass as the stoichiometric mismatch between them and their
123 food increases. Compensatory feeding should help alleviate this effect and lead to an increase in herbivore biomass.
124 We also expect warming to decrease plant and herbivore biomasses, while higher nutrient availability should lead to
125 higher biomasses. If both vary simultaneously, we expect interactive effects, with the adverse effects of warming
126 being more severe in systems facing pressure from nutrient limitation. Flexible stoichiometry and compensatory
127 feeding are likely to counteract the warming and nutrient effects under certain conditions but may aggravate them in
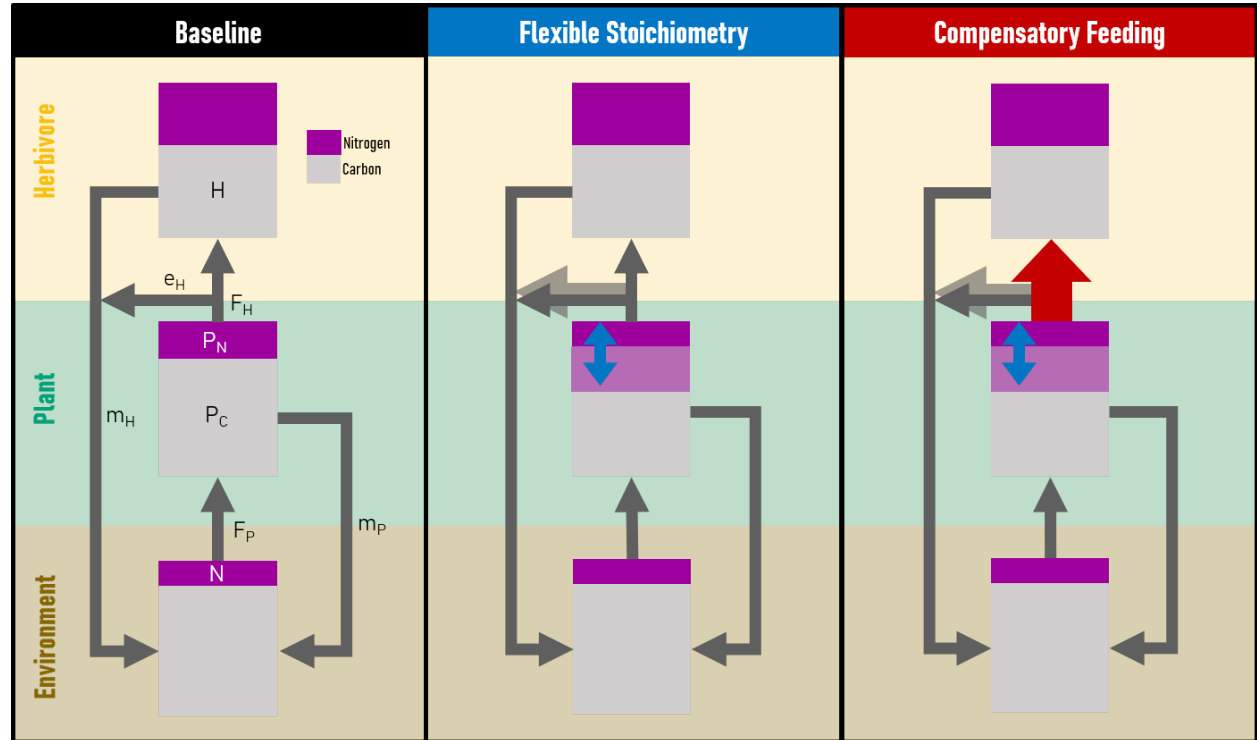128 more extreme cases.

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131 *Figure 1: Conceptual figure showing the structure of our three models: baseline (left), flexible stoichiometry*
132 *(middle) and compensatory feeding (right). The model terms are shown in the baseline panel with N as the*
133 *environmental nitrogen pool, P_C and P_N as plant nitrogen and carbon respectively, and H as the herbivore pool. The*
134 *pools interact by plant nutrient uptake F_P, herbivore feeding F_H, assimilation efficiency e_H and plant and herbivore*
135 *metabolism m_P and m_H. The environmental carbon pool and the herbivore nitrogen pool are included here for*
136 *clarity, even though we do not explicitly model them. The blue arrow shows the flexibility in plant N:C ratio in the*
137 *flexible stoichiometry model, the red arrow represents the potential increase in herbivore feeding in the*
138 *compensatory feeding model.*

139

Methods

Carbon-Flow Models

This study explores the role of flexible stoichiometry and compensatory feeding for plant and herbivore growth under various temperatures and nutrient supplies. We simulate a tri-trophic system consisting of a nutrient, a plant, and a herbivore pool across three different carbon-flow models and a range of temperature and nutrient conditions. As one of the more abundant elements in plant and animal tissue, our model uses nitrogen (N) to represent the nutrients. All other elements are pooled together with carbon (C) for the sake of simplicity in this model. We use C as a proxy for total biomass in this study, as it is the most abundant element in both plant and animal tissue.

The first model is our baseline (Fig. 1 left, Eqs. 1-4), where plants have a fixed stoichiometry, and herbivores cannot vary their feeding rate. It is similar to many prior models (Ceulemans et al. 2019), but it adds the temperature-dependent plant nutrient uptake, simplified from the model in Marx et al. (2019). In this model, the temperature-dependent uptake of N regulates plant growth. Since the plant is simplified to consist of only N and C, the plant C uptake is given by multiplying N uptake with the inverse of the N:C ratio. We use this model as a starting point to which we compare the models including flexible stoichiometry and compensatory feeding as strategies. Our second model adds flexible stoichiometry (Fig. 1 middle, Eq.5). In this model, the N:C ratio of the plant, which regulates the C uptake, varies depending on the N availability (Figure 2a). We also add a more realistic herbivore assimilation efficiency dependent on plant N:C ratio (Figure 2b; Eq. 6). The third model adds compensatory feeding by the herbivore (Fig. 1 right), allowing the herbivore to take in more plant material as the plant N:C ratio decreases. In this model, the herbivore feeding rate is directly dependent on the plant N:C ratio (Figure 2c; Eq. 7). As compensatory feeding is directly dependent on the plant N:C ratio, our compensatory feeding also includes flexible stoichiometry in the plant.

Our carbon-flow models consist of an environmental N pool (N), a plant N pool (P_N), a plant C pool (P_C), and a herbivore pool (H), also expressed in terms of C units We do not explicitly model the environmental C pool, assuming that C is always available in sufficient amounts. The plants' N uptake depends on their biomass (expressed as plant C). We do not explicitly model herbivore N, as, due to the fixed body stoichiometry, it can be directly inferred from the C content. N is recycled from plant and herbivore metabolism. We assume that the biomass lost through metabolism has the same N:C ratio, as is found in the organisms. We also assume that N is perfectly assimilated, and only C is lost due to low assimilation efficiency.

In the baseline model, environmental N is expressed by:

$$\frac{dN}{dt} = D\left(S_N - N\right) - F + \frac{P_N}{P_C} m_P P_C + r_H m_H H \tag{1}$$

170   where D stands for the system turnover rate, S_N is the N supply rate. m_P and m_H are the metabolic rates of plant and

171   herbivore, respectively. r_H is the N:C ratio in herbivore tissue. F is the functional response for the plant N uptake

172   given by:

173    $$F_P = \frac{V_N N}{K_N + N} P_C$$

174   (2)

175   where V_N refers to the maximum N uptake rate, and K_N is the half-saturation density. Here, the N uptake directly

176   relates to plant biomass (P_C). This equation is equivalent to a type II functional response. The herbivore feeding

177   follows a type III functional response and is given by:

178    $$F_H = \frac{f_H P_C^h}{K_H^h + P_C^h} H$$

179   (3)

180   The plant C uptake is given by multiplying plant C:N with the N uptake. The equations for the plant N and C

181   compartments write:

182    $$\frac{dP_N}{dt} = F_P - \frac{P_N}{P_C} F_H - \frac{P_N}{P_C} m_P P_C$$

183   (4)

184    $$\frac{dP_C}{dt} = \frac{P_C}{P_N} F_P - F_H - m_P * P_C \qquad\qquad (5)$$

185   Then, the growth rate of the C biomass of the herbivore is defined as

186    $$\frac{dH}{dt} = e_H F_H - m_H H \qquad\qquad (6)$$

187   Where e_H stands for the assimilation efficiency of the herbivore. f_H is their feeding rate, and K_H the half-saturation

188   density. h is the Hill-exponent, which shapes the functional response of the consumer. The loss from the plant N

189   pool to the herbivore is given by multiplying herbivore feeding with the plant N:C ratio. We assume the proportion

190   of N and C transferred from the plant to the herbivore to be equivalent to the plant N:C ratio.

191   In the flexible stoichiometry model, the plant N:C ratio is related to N availability. Higher environmental N

192   availability will increase N:C ratio, following a saturating hyperbolic curve up to the maximum N:C ratio (Figure

193   2a). The result is a decrease in the C uptake relative to the N uptake, as expressed by:

194 $$\frac{dP_C}{dt} = \frac{1}{\left(\dfrac{(maxNC-minNC)*F}{K_N+F}\right)+minNC} * F_P - F_H - m_P * P_C$$

195   (7)

196 here *maxNC* and *minNC* are the minimum and maximum N:C ratio of the plant, respectively. In this model, the

197 herbivore assimilation efficiency is dependent on their plant N content (Jochum et al. 2017) and given by:

198 $$logit(e_H) = a\left(\frac{P_N}{P_C+P_N} * 100\right) + b$$

199   (8)

200 *a* and *b* are constants standing respectively for the slope and intercept of this relation.

201 In the compensatory feeding model, herbivore feeding rate is also related to the plant N:C ratio:

202 $$f_H = s\left(\frac{P_C}{P_N}\right)m_H + y \qquad\qquad (9)$$

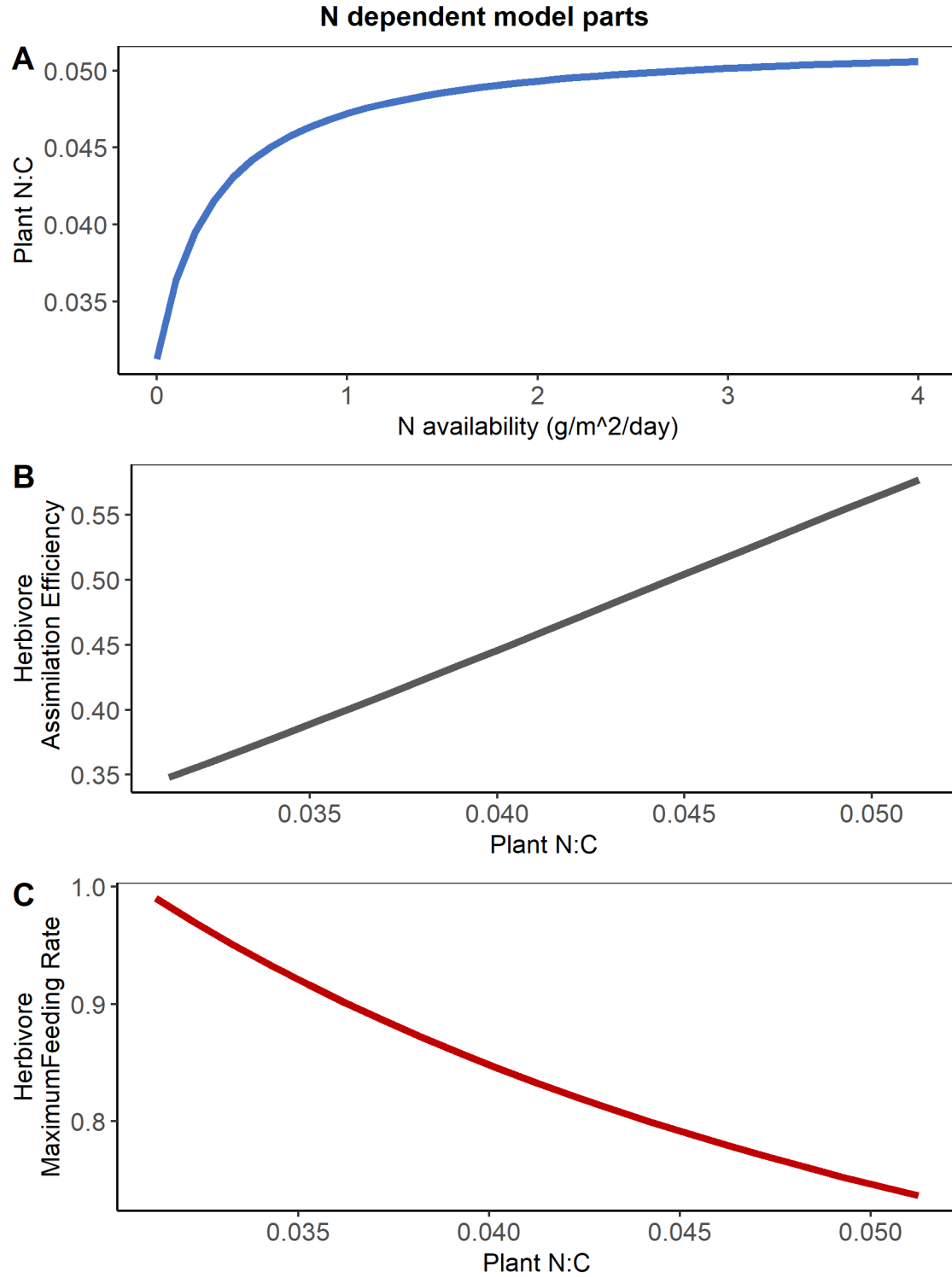203 *s* and *y* respectively being the slope and intercept of this relation.

Figure 2: N-dependent model parameters. A) Plant N:C dependence on N availability; B) Herbivore assimilation efficiency based on plant N:C; C) Herbivore maximum feeding related to plant N:C ratio.

Parameters

209 We parameterized the models using literature data for both temperature-dependent and temperature-independent
210 parameters. We set the temperature-independent parameters to the following values: We use a value of 0.1 [1/day]
211 for the turnover rate D, meaning that the system's nutrients are renewed every ten days (Cebrian 1999). The Hill
212 exponent, h, we set to 1.2, giving the herbivore a type III functional response (Vucic-Pestic et al. 2011; Kalinkat et
213 al. 2013).

214 Plant mean N:C ratio is 0.028 based on Elser et al. (2000a). For the plasticity in the N:C ratio of the plants, we used
215 the values reported by Yu et al. (2011), who found a variation of about 25% for plant N:C, meaning that in the
216 flexible stoichiometry model, min_{NC} is 0.037 and max_{NC} 0.022. The herbivores have a much higher N:C, which we
217 set to 0.154, based on Elser et al. (2000b).

218 We extracted normalization constants and activation energies for the temperature-dependent parameters from
219 previous studies (Table 1). In Marx et al. (2019), we have established the relation between temperature and plant
220 nutrient uptake, providing an alternative to the commonly used logistic plant growth, where the temperature
221 dependence came from temperature-dependent carrying capacity. We use that same temperature-dependent nutrient
222 uptake here (V_N [g m^{-2} day^{-1}] & K_N [g m^{-2}]), in addition to temperature-dependent metabolic rates (m_P [day^{-1}] & m_H
223 [day^{-1}]), herbivore feeding rate (f_H [day^{-1}]), and half-saturation density (K_H [g m^{-2}]). The parameters used for the
224 assimilation efficiency and compensatory feeding are based on Jochum et al. (2017) (Table 2).

225

Table 1: Temperature-dependent parameters

Parameter	Definition	Normalization Constant	Activation Energy	Source
V_N	Nitrogen maximum uptake rate	0.17	0.22	(Marx et al. 2019)
K_N	Nitrogen half-saturation density	0.32	0.08	(Marx et al. 2019)
K_H	Herbivore half-saturation density	1.00	-0.12	(Fussmann et al. 2014; Mulder and Hendriks 2014)
m_P	Plant metabolism	0.01	0.69	(Ryan 1995; Cannell 2000; Brown et al. 2004)
m_H	Herbivore metabolism	2.56	0.67	(Brown et al. 2004; Lang et al. 2017)

Table 2: Parameters for assimilation efficiency and compensatory feeding equations from Jochum et al. (2017)

Parameter	Value
a	0.47
b	-2.10
y	0.48
s	2.28

226

Model runs

228 We ran our models over a temperature gradient of 0° to 40°C. To simulate realistic N supplies, we ran the models
229 over a gradient-based on a literature survey reported by Marx et al. (2019), which ranges from 0.075 mg N/m²/day
230 up to 3.757 mg N/m²/day.

231 The starting densities of our plant N, plant C, and herbivore pools were drawn randomly from values between 4 and
232 6 times the plants' extinction threshold and 2-3 times the extinction threshold for herbivores. We did 50 runs with
233 2000 timesteps (days) each. We performed all of our model-runs and the analysis in R ver. 3.6.1 (www.r-
234 project.org) using the r package "odeintr" (Keitt 2017).

235

Results

With our three models – (1) baseline, (2) flexible stoichiometry, and (3) compensatory feeding (see Fig. 1 for an overview) – we aimed to identify the impact of the strategies on communities under different temperature and nutrient conditions. The biomasses resulting from our model runs give us insight into the mechanisms driving plant and herbivore growth, and interaction rates.

Model comparison

We start our analysis with an example of time series under mesotrophic conditions at 20°C (Figure 3). Compared to the baseline model, flexible stoichiometry increases plant biomass, i.e. the plant carbon (C) pool, substantially (Figure 3A) while it slightly decreases the plant nitrogen (N) pool (Figure 3B). These two patterns cause a significant decrease in plant N:C ratio compared to the baseline (Figure 3C). It seems that under mesotrophic conditions, the plants still tend to a N:C ratio lower than the average used in the baseline model. The low N:C ratio in the flexible stoichiometry model causes a decrease in herbivore food quality. Although this reduction in quality causes a more considerable mismatch between plant and herbivore stoichiometry, the increase in food quantity resulting from the higher plant biomass production increases herbivore biomass under flexible stoichiometry (Figure 3D). Surprisingly, the herbivore's compensatory feeding decreases not only plant biomass (Figure 3A) but also the herbivore's biomass (Figure 3D) relative to the model with flexible stoichiometry.
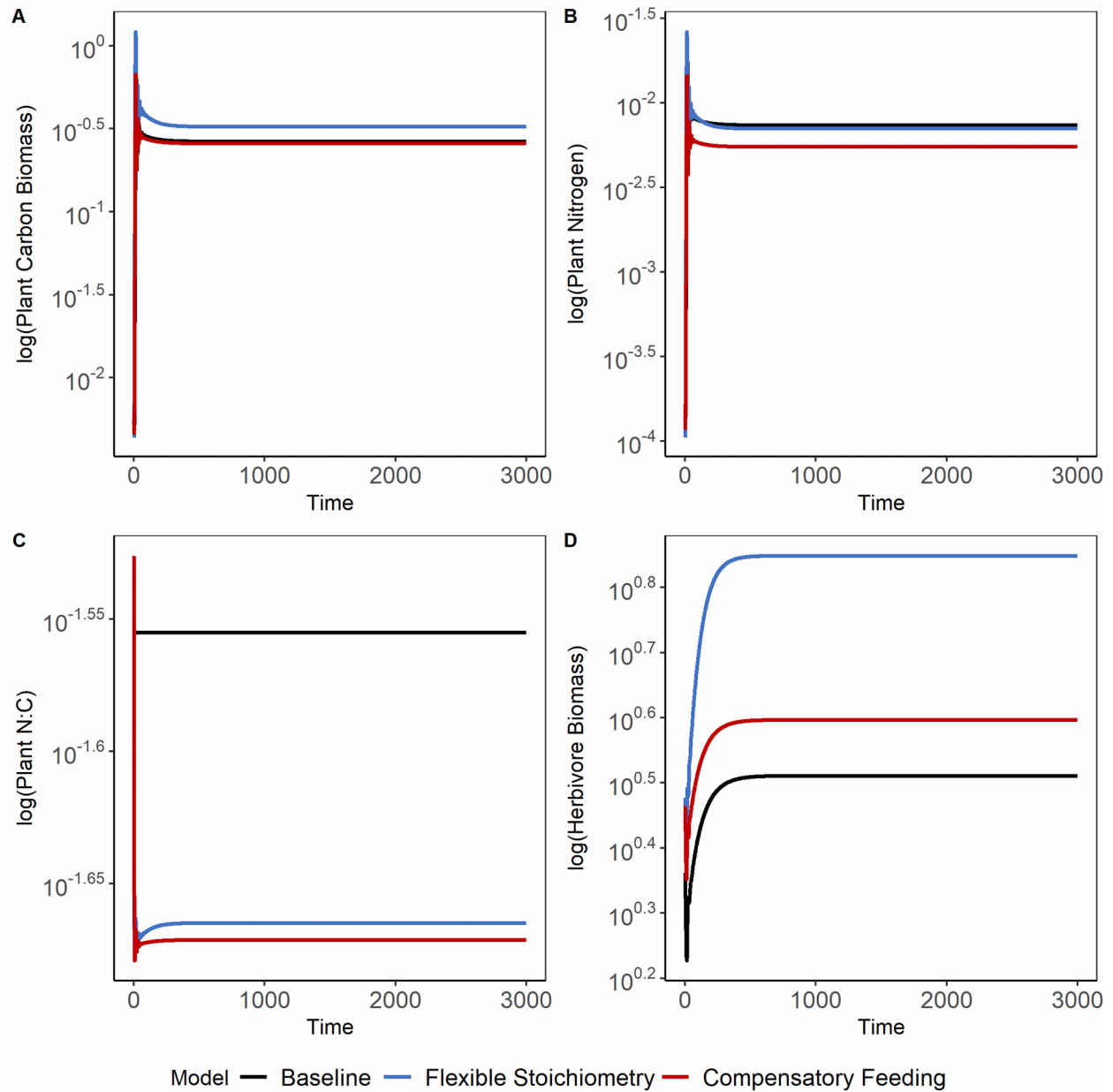
Figure 3: Time-series of the baseline, flexible stoichiometry and compensatory feeding models under mesotrophic conditions at 20°C. A) shows plant carbon biomass, B) plant nitrogen, C) plant N:C ratio, and D) herbivore biomass.

Temperature

258 Increasing temperature decreases biomasses in nutrient-plant-herbivore systems (Marx et al. 2019). To explore
259 whether flexible stoichiometry and compensatory feeding strategies are beneficial under various temperature
260 conditions, we ran our models over a temperature gradient from 0 to 40°C. While the time series always reach
261 equilibria, we find alternative stable states depending on the starting conditions above a certain temperature
262 threshold. Above this threshold, some starting densities allow for the survival of both plants and herbivores, while
263 others lead to herbivore extinction or extinction of both (Figure 4).

264 Overall, we found our expectation of decreasing plant biomass with temperature confirmed in all models (Figure
265 5A). This decline is nearly linear in all models, up to a certain temperature threshold above which we find the
266 alternative stable states described above. Flexible stoichiometry leads to higher plant biomass under most
267 temperature conditions (up to 37°C). At these temperatures, the compensatory feeding of the herbivore causes a
268 slight decrease in plant biomass compared to the baseline model. Interestingly, at very high temperatures (above
269 38°C), the compensatory feeding model allows for the survival of the plant in some runs where the other models
270 always lead to plant extinction.

271 Herbivores also experience a biomass decline with warming (Figure 5B). Here, too, a temperature threshold can be
272 identified, after which we find alternative stable states. Flexible stoichiometry in plants leads to overall higher
273 herbivore biomass. Increased plant growth under flexible stoichiometry means a higher food availability for the
274 herbivore, buffering the herbivore biomass decline with temperature. The high food supply also allows for herbivore
275 survival up to higher temperatures independent of starting conditions. Surprisingly, compensatory feeding decreases
276 the herbivore biomass compared to the flexible stoichiometry model, at most temperatures, but increases it
277 compared to the baseline, just as we have previously seen in the time series (Figure 3). However, at very high
278 temperatures, compensatory feeding allows the herbivores to survive under some starting conditions, where the
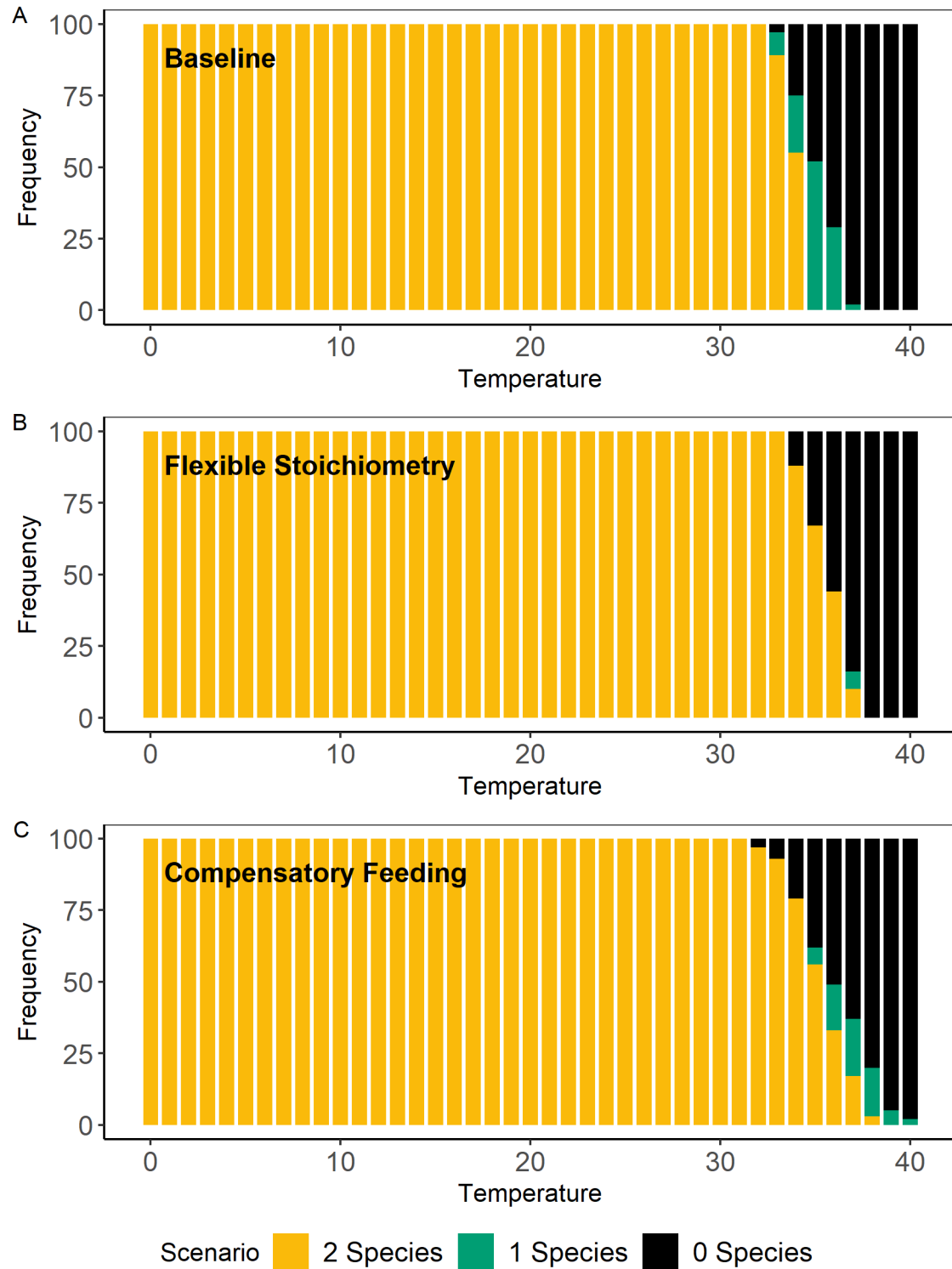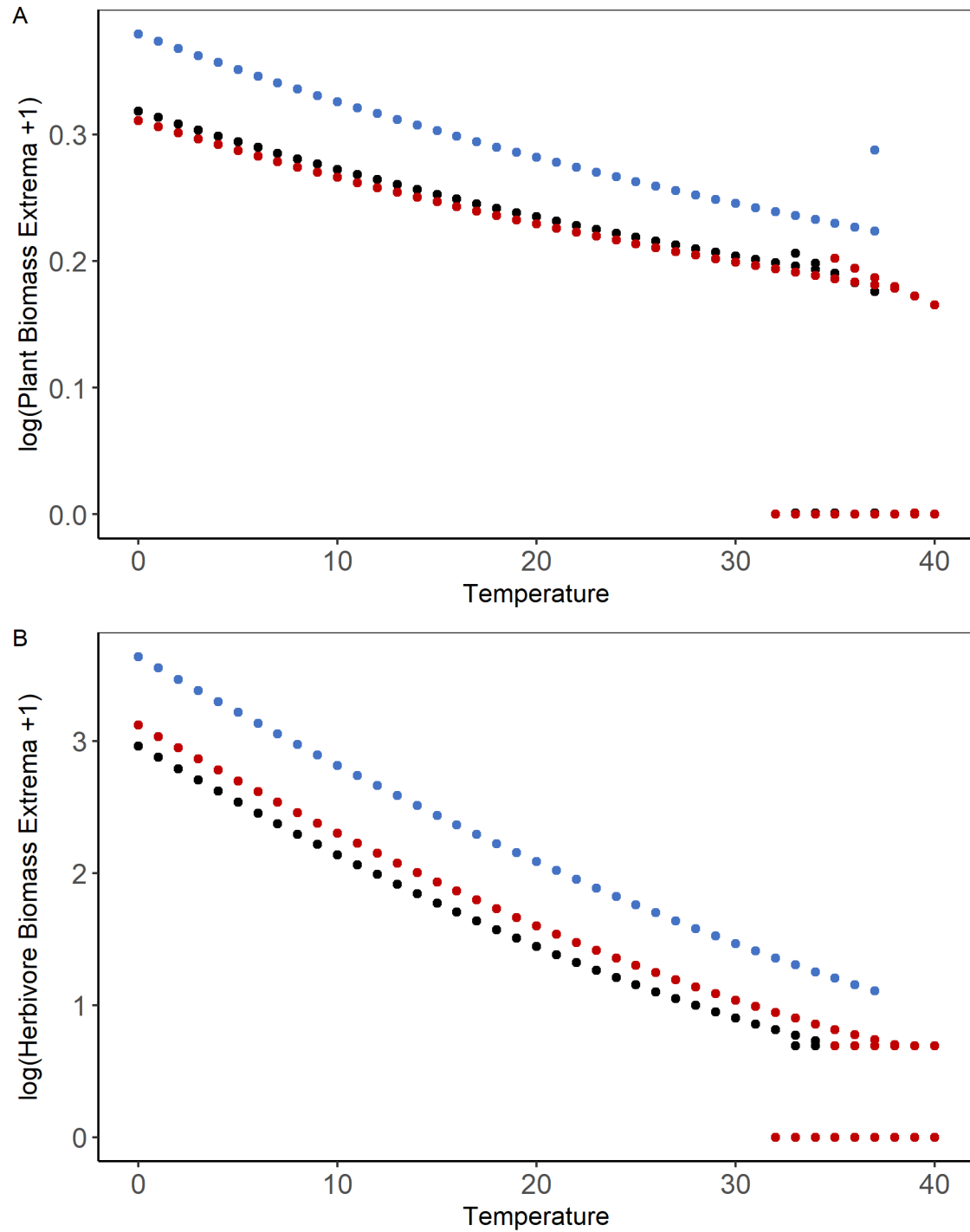279 flexible stoichiometry and baseline model both lead to extinction in all runs.

280

Figure 4: Frequency of survival scenarios across temperature. In yellow are the runs where both plants and herbivore survive, green are the runs where the plant survives, but the herbivore goes extinct and black shows the runs in which both species go extinct. Plot A shows the baseline model, B is the model with flexible stoichiometry, C shows the compensatory feeding model.

Figure 5: Bifurcation diagrams of equilibrium biomasses of plants (A) and herbivores (B) under mesotrophic conditions (0.00197 mg N/m²/day) across a temperature gradient.

Nutrient availability and temperature

Next to temperature, we also varied nutrients on a realistic gradient of oligotrophic (0.075 mg N/m²/day) to eutrophic (3.757 mg N/m²/day) conditions. The effect of nutrient supply is mostly visible in the herbivore biomass, while plant biomass production is mainly driven by temperature (Figure 6 left side). We find that higher nutrient supply leads to higher herbivore biomass (Figure 6 right side). This pattern is evident at low temperatures, whereas high temperatures lead to overall low biomass even under high nutrient supply. In the baseline model (Figure 6B), nutrient supply is very relevant for herbivore survival even at comparatively low temperatures. The higher the temperature increase, the more nutrient supply is necessary to buffer the negative effect of temperature on herbivore biomass and survival. Adding flexible stoichiometry to the model removes this combined negative effect of high temperature and low nutrient supply (Figure 6D). Here, herbivores survive under all nutrient conditions up to a much higher temperature. With compensatory feeding (Figure 6F), the herbivore biomass pattern resembles the baseline model, but with extinctions starting at higher temperatures. The temperature at which the herbivore goes extinct regardless of nutrient supply increases in the compensatory feeding model compared to the baseline.
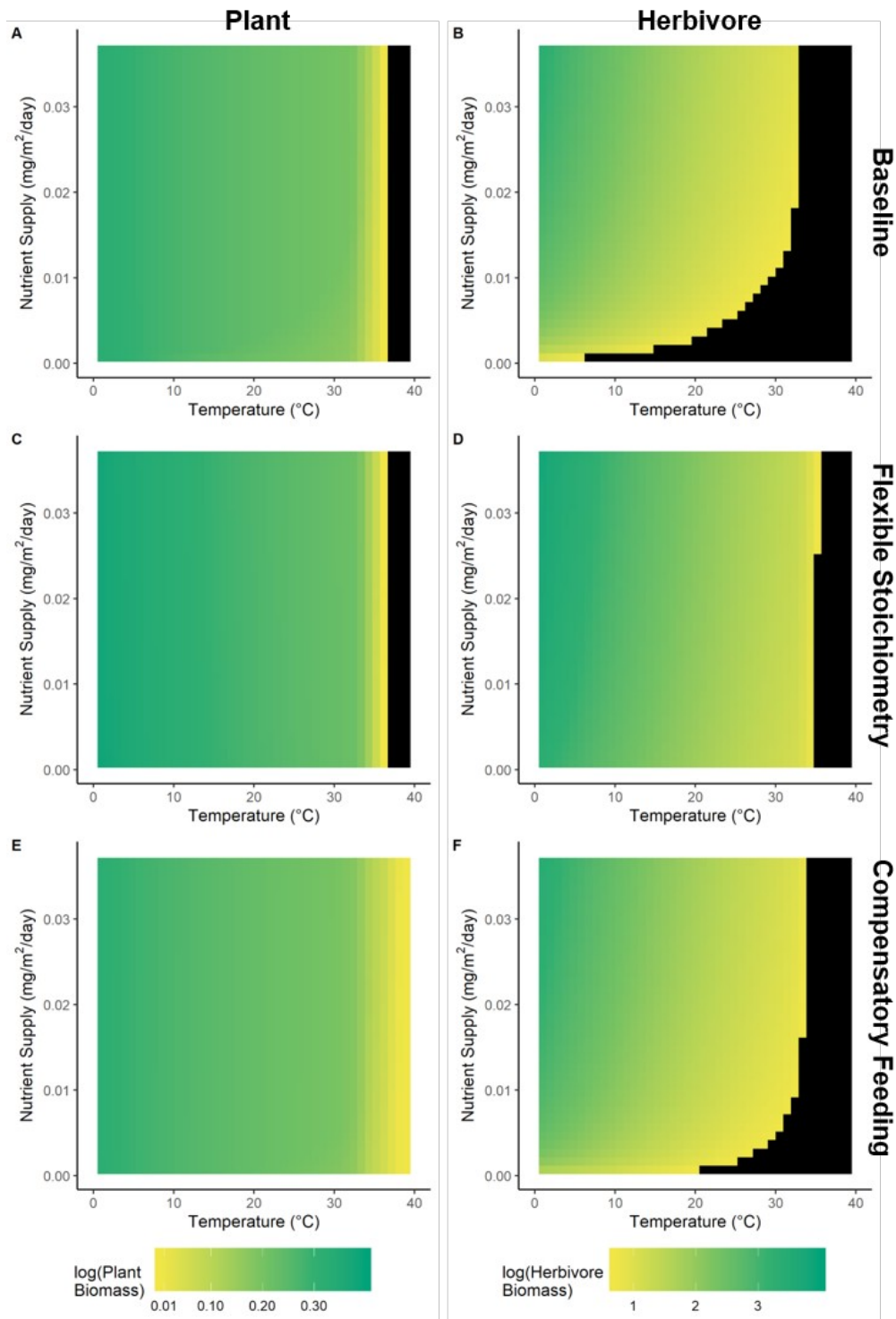
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Figure 6: Heatmaps of the plant (left) and herbivore (right) biomass for the baseline model (A & B), the flexible stoichiometry model (C & D), and the compensatory feeding model (E & F). Black areas mean extinction.

18

Discussion

We explored the effect of flexible plant stoichiometry and herbivore compensatory feeding on a nutrient-plant-herbivore system across various temperatures and nutrient availability levels. We confirmed previous findings that warming tends to decrease biomass, while a higher nutrient supply increases biomass. There are alternative stable states at high temperatures, with some model runs leading to extinctions, while others allow for survival depending on the starting conditions. Adding flexible plant stoichiometry increases both plant and herbivore biomass up to a specific temperature. Flexible stoichiometry also increases plant and herbivore survival under more adverse conditions like low nutrient supply or high temperature. Surprisingly, adding compensatory feeding decreases herbivore biomass as compared to the flexible stoichiometry only model. In the baseline and the compensatory feeding models, the herbivore faces extinction at a combination of high temperature and low nutrient supply, confirming that the level of nutrients sufficient to sustain the populations at a low temperature is not enough at higher temperatures (Klock 1995). However, this effect was removed in the flexible stoichiometry model due to the overall higher primary production.

Warming increases plant growth rate by increasing the maximum nutrient uptake but decreases biomass production by the comparatively higher increase in metabolism (Marx et al. 2019). Allowing the plants to change their stoichiometry increases their biomass production under all conditions, including high temperatures or low nutrient availability. If we allow flexibility in the plant stoichiometry, the resulting lower N:C ratios reduce the food quality for the herbivore. Temperature and food quality can have an interactive effect on herbivore biomass. At low temperatures, higher food quality will likely increase herbivore biomass. However, high-quality food may not be enough to counteract the increased metabolic demand associated with warming (Brown et al. 2004; Malzahn and Doerfler 2016; Lang et al. 2017). Despite the lower food quality, flexible stoichiometry increases herbivore biomass independent of temperature and allows herbivores to survive higher temperatures. Even at high temperatures, low food quality and high herbivore metabolism appear to be counteracted by the increasing food availability resulting from increased plant growth. This increased plant growth at low temperatures and nutrient availability would likely increase unstable dynamics found under such conditions in more complex systems (Binzer et al. 2012). Simultaneously, flexible stoichiometry could reduce the starvation effect at high temperatures, associated with the reduced flow of energy from the basal species to the top consumers (Binzer et al. 2012).

We expected compensatory feeding to be a beneficial strategy for the herbivores, allowing them to compensate for the stoichiometric mismatch by increasing their food intake. However, our results point in the opposite direction. Compensatory feeding led to lower biomasses of plants and herbivores, which caused herbivore extinction at high temperatures and low nutrient supplies. Most likely, the substantial mismatch between plant and herbivore stoichiometry at high temperatures increased the herbivore feeding rates to a level of 'overfeeding.' Thereby, the herbivores deplete their resource to a density that is too low for their survival.

Potential implications

Up to a specific temperature, flexible stoichiometry allows the plants to reach higher biomasses. However, at high temperatures after herbivore extinction, the baseline model without flexible stoichiometry appears to be more beneficial. These results suggest that there might be a tradeoff as the decreasing N:C ratio under flexible stoichiometry could cause the plants to lose their N buffer. Therefore, plants without flexible stoichiometry should benefit and dominate the plant pool if the temperature reaches extremes under global warming.

The effect of warming on plant N:C depends on the climate and the plant type (Sardans et al. 2012; Rosenblatt and Schmitz 2016). Sardans et al. (2012) found no change or a decrease in N:C in dry terrestrial systems, a decrease in plant N:C with warming in temperate and warm-dry systems, and varying results in temperate and cold systems without water limitation. On average, warming decreases autotroph N:C, which could be driven by the direct effects of temperature on nutrient uptake rates (e.g., through the C-enrichment effect, an increase in C-rich compounds relative to the N-rich metabolites, increased N use efficiency, or an increase in C fixed per unit N (Sterner et al. 2002; Sardans et al. 2012). Further, this response could be driven by an indirect effect of communities shifting their composition towards species with more flexible stoichiometry.

Increases in feeding rates as we modelled them in the compensatory feeding model could have implications for plants of economic importance. Higher feeding rates of plant pests could have detrimental effects on crop yields. However, we found that compensatory feeding, as we modelled it, leads to resource depletion starving out the herbivore, after which the plants can recover and increase their biomass. It seems that compensatory feeding is too costly for the herbivore, and we expect to see less compensatory feeding at high temperatures.

Decreases in plant N:C ratio and thereby food quality for the herbivores could lead to local communities of herbivores with a lower optimum N:C ratio. Herbivore communities with a high N:C ratio may collapse due to the homeostatic costs if the mismatch between plant and herbivore N:C reaches a certain threshold (Anderson et al. 2005). In our models, the decreasing food quality did not decrease herbivore biomass, which could mean that we do not reach this mismatch threshold under the conditions that we explore in our models.

Caveats

We based our models on the assumption that plants can be flexible in their stoichiometry, whereas animals are homeostatic in their elemental composition. Although animals are certainly less flexible in their stoichiometry, there is still variation in the degree of homeostasis (Persson et al. 2010). Therefore, it is possible that shifts in plant communities towards those with higher flexibility and the resulting lower food N:C ratio would cause shifts in herbivore communities to those with higher flexibility.

We also assumed that if plants are flexible in their uptake, they will maximize their growth, thereby decreasing their N content due to the dilution effect (Sterner et al. 2002). However, Puche et al. (2018) found that the combination of increasing temperature and nutrient availability increased plant N content but not their growth. They suggest that the capacity for luxury consumption and N storage increases with temperature. However, they only found this for plant

373 populations from previously N-rich environments. Hence, the environmental conditions to which plant species are
374 adapted appear to affect their response to elevated temperature and nutrient supply substantially. The consequences
375 of varying initial environmental conditions and different degree of plant stoichiometric flexibility need to be
376 addressed in future studies.

Future directions

Interaction of climate change and nitrogen fertilization

379 Climate change is projected to significantly increase the amount of N ending up in the waterways, due to an increase
380 in the frequency and intensity of rainfalls (Sinha et al. 2017). The negative consequences of higher N availability is
381 already visible in toxic algae blooms further exacerbated by warming (Paerl et al. 2016). Elevated N deposition also
382 has adverse effects on terrestrial ecosystems, for example, by reducing plant diversity (Simkin et al. 2016). An
383 exciting and relevant future application of our model with flexible stoichiometry would be to investigate the effect
384 of such massive increases in N availability on the growth rates of plants and the ability of herbivores to keep the
385 plant biomass in check.

Other nutrients

387 A world consisting of only C and N is severely simplified. Adding other nutrients into the equation - the most
388 prominent of which would be phosphorus (P) - is an obvious extension of this model. With such an extension, we
389 could explore the effect of stoichiometric flexibility under conditions of P limitation. Compared to N, the magnitude
390 of human-driven P deposition is lower (Sardans et al. 2012). As a result, increasing N will not necessarily increase
391 plant growth due to potential P limitation. For phosphorus, Yu et al. (2011) found a variation of up to +- 50% around
392 the mean P:C ratio. We tested the effect of such high flexibility in our model and found similar outcomes (results not
393 shown). In terms of the flexible stoichiometry effect, our model is therefore likely transferable to phosphorus. The
394 material lost through herbivore metabolism currently has the same N:C ratio as the herbivore tissue. This assumption
395 may not be realistic, as consumers can retain specific elements if they become limiting. However, there may be a
396 difference between the retention of P and N. For example, in the model used by Logan et al. (2004), N is excreted by
397 the consumers, while P is sequestered. If herbivores can retain all or most of the P they consume, phosphorus
398 limitation from food would be less challenging than N limitation. It would be interesting to explore whether the
399 ability of herbivores to retain P is enough to counteract P limitation. However, N is most likely the nutrient for
400 which high-quality food, i.e., food with a high nutrient:carbon ratio, is most important.

Elevated CO2 effects

402 Rising levels of atmospheric CO_2 levels could have a further impact on plant N:C ratios. Zvereva et al. (2006)
403 reviewed studies on plant quality as food for herbivores under elevated temperature, elevated CO_2, and a
404 combination of both. They found that N concentration in plant tissue decreased under elevated CO_2 (see Rosenblatt
405 & Schmitz (2016). However, rising temperatures can mitigate this effect, which is also highly species and context-
406 specific (Robinson et al. 2012). Herbivore performance is negatively affected by increases in temperature, but

407 positively if CO_2 rises simultaneously, possibly due to the rise in C demand from higher metabolic rates (Zvereva
408 and Kozlov 2006; Malzahn and Doerfler 2016). The CO_2 level could impact plant chemistry, especially at
409 intermediate N supplies, by influencing the steepness of the curve between the minimum and maximum plant N:C
410 ratios. This finding shows how important it is to look at several global change factors in parallel instead of studying
411 them in an isolated way. It would therefore be an interesting addition to run the three models under a range of CO_2
412 concentrations.

Threshold Elemental Ratio

414 The threshold elemental ratio (TER) is the ratio at which elements should be present in the prey for the consumer to
415 reach their maximum growth (Frost et al. 2006). A food stoichiometry above or below this threshold can induce
416 growth limitation. This so-called 'stoichiometric knife-edge' may also be impacted by temperature (Schmitz and
417 Rosenblatt 2017; Ruiz et al. 2020). The potentially U-shaped relation between TER and temperature would mean
418 that under low or high temperatures, the mismatch between plant and herbivore stoichiometry would have a more
419 substantial adverse effect on the herbivore than at intermediate temperatures (Ruiz et al. 2020). Including the TER
420 into the model and making it temperature-dependent could give us insights into the combined effect of increasing
421 temperatures and nutrient availability on herbivore growth with and without flexible stoichiometry in the plants.

Food webs

423 Of course, plants and herbivores do not live in an isolated system with their nutrients as the basal resource. In
424 reality, they are part of a more complex system consisting of many species arranged in complex food webs with
425 more trophic levels (Brose et al. 2019). Extending our model approach to complex food webs would allow us to
426 explore further the bottom-up and top-down effects of flexible stoichiometry and compensatory feeding. The
427 decreasing N:C ratios we found with flexible stoichiometry could lead to a starvation of the higher trophic levels,
428 especially under adverse conditions like low nutrient supply or high temperature. However, the specific topology of
429 natural food webs can change the biomass dynamics and survival rates under warming substantially (Gauzens et al.
430 2020). In a complex food web, consumers could adapt their diet to variations in food quality by changing the
431 consumption rates over different resource species depending on their needs. Switching prey could decrease the
432 importance of compensatory feeding in natural food webs. Omnivorous consumer species could even shift their
433 preferences to feed more on plants than animals if warming increases their C demand through rising metabolic rates
434 (Boersma et al. 2016; Carreira et al. 2016).

Conclusion

436 We investigated if flexible stoichiometry in plants and compensatory feeding in herbivores are beneficial strategies,
437 especially when faced with warming or changes in nutrient availability. We found that flexible stoichiometry led to
438 higher biomasses and increased survival under most conditions, thereby counteracting some of the negative impacts
439 of moderate warming or low nutrient supply. As a result, we would expect a shift in communities towards plant
440 species that display flexible stoichiometry under warming conditions. However, under very high temperatures,

441 flexible stoichiometry might become too costly and is not necessarily beneficial anymore. Surprisingly,
442 compensatory feeding does not appear to be a good strategy for herbivores under most conditions. Hence, we would
443 expect this strategy to occur at a low frequency in warmer climates. Our findings highlight the importance of
444 integrating adaptive and behavioural plasticity in population-dynamic models that address the consequences of
445 global warming and eutrophication.

446

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Data Accessibility Statement

Should the manuscript be accepted, the code supporting the results will be archived in Github and Zenodo. No data used for this study.

Competing Interest Statement

The authors do not have any competing interest to declare.

Author contributions

JMM, UB, ALG and BG designed the study. JMM performed the simulations and wrote the first draft of the manuscript. All authors contributed to the manuscript.

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