Elements & Energy

Modelling nutrient and population dynamics under global change

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Summary

Global change is affecting the world's ecosystems through a range of drivers. Biomass production and the functioning of biological systems are essential for the provision of ecosystem services. As ecosystem services are essential for human survival and quality of life, we must understand the impacts of global change on the processes and mechanisms relevant to the functioning of ecosystems. It is also vital for us to gain insight into the additive or interactive effects of global change drivers, as they tend to vary simultaneously. Two of the global change drivers that have a strong influence on plant growth, and therefore biomass production of the whole ecosystem, are global warming and changes in nutrient cycles.

To improve our understanding of the pathways through which these drivers influence plant growth, I investigated the temperature-dependency of plant nutrient uptake and developed a nutrient-explicit model. In this model, the flow of carbon (energy) is coupled with the flow of nutrients (elements) between populations, giving us insight into the effect of warming and changing nutrient supply on population dynamics.

Organisms are not just passively affected by global change but can respond to environmental pressures to varying degrees. Static models that do not take any plasticity into account may under- or overestimate the effect of global change drivers. To broaden our knowledge on the importance of flexibility in the response of populations to global change, I developed models that included realistic flexibility in the stoichiometry (elemental balance) of the plant and gave the herbivore the ability to react to changing food quality by adjusting their feeding rate.

In my first chapter, I show that plant uptake of the vital nutrients nitrogen and phosphorus is indeed dependent on temperature. For both nutrients, I found an increase in maximum uptake rate with temperature, as well as an increase in half-saturation density. In other words, with rising temperature, the amount of nutrients that plants can take up at high nutrient supply increases. At low nutrient supply, however, their uptake efficiency decreases. This finding points to the importance of looking at the global change drivers warming and nutrient supply in parallel. With my population dynamics model, I show that including temperature-dependent nutrient uptake by the plant results in decreased community biomass with temperature. The biomass increase achieved through fertilization cannot fully compensate for the loss with warming.

My second chapter focusses on the adaptive abilities of populations. Investigating the effect of flexible stoichiometry on populations facing the pressures of global warming and changes in nutrient supply, I show that allowing plants to vary their carbon uptake dependent on the nitrogen supply results in an increase in community biomass. The herbivore benefits from the higher quantity of plant tissue available. This increase fully compensates the decrease in food quality for the herbivore. Compensatory feeding as a reaction to decreased food quality does not appear to be a beneficial strategy for the herbivore as it causes depletion of their resource through 'overfeeding'.

Through these studies, I show how important it is to consider the interaction of several global change drivers as they can aggravate or mitigate each other. Furthermore, it is crucial to consider adaptive strategies available to the different organisms, as they can modulate the impact of global change on the ecosystem functioning. Assuming static responses to temperature and nutrient supply changes may cause severe under-or overestimation of changes in ecosystem service provision.

Zusammenfassung

Der globale Wandel beeinflusst die Ökosysteme unseres Planeten durch verschiedene Veränderungsprozesse. Die Produktion von Biomasse und die Funktion von biologischen Systemen sind die Basis für viele Ökosystemdienstleistungen. Da diese Dienstleistungen unfassbar wichtig für das Überleben und die Lebensqualität von uns Menschen sind, müssen wir verstehen wie der globale Wandel die Prozesse und Mechanismen hinter der Funktion der Ökosysteme beeinflusst. Da die verschiedenen Veränderungsprozesse des globalen Wandels zeitgleich ablaufen, ist es außerdem entscheidend zu verstehen, ob und wie sie sich gegenseitig verstärken oder abschwächen – wie sie also interagieren. Zwei dieser Prozesse, haben einen besonders starken Einfluss auf das Wachstum der Pflanzen, und dadurch auf die Gesamtproduktion von Biomasse: die Erderwärmung und sich verändernde Nährstoffzyklen.

Um besser verstehen zu können, auf welchem Wege diese Prozesse das Pflanzenwachstum beeinflussen, habe ich die Temperaturabhängigkeit der Nährstoffaufnahme von Pflanzen untersucht. Außerdem habe ich ein Modell entwickelt, mit dem ich erkunden kann, wie sich diese Temperaturabhängigkeit auf Populationsdynamiken auswirkt.

Organismen werden nicht nur passiv durch den globalen Wandel beeinflusst. Sie können, bis zu einem gewissen Grad, auf Veränderungen in ihrer Umwelt reagieren. Daher ist es möglich, dass statische Modelle den Effekt des globalen Wandels auf Ökosysteme unter- oder überschätzen. Um unser Wissen über die Relevanz der Reaktionen von Populationen auf den globalen Wandel zu erweitern, habe ich Modelle entwickelt die eine realistische Flexibilität in der Stöchiometrie (Nährstoffbalance) der Pflanzen enthalten und es dem Herbivoren erlauben auf Variationen in der Qualität ihrer pflanzlichen Nahrung mit erhöhter Fraßrate zu reagieren.

In meinem ersten Kapitel zeige ich, dass die Aufnahme der lebensnotwendigen Nährstoffe Stickstoff und Phosphor tatsächlich temperaturabhängig ist. Die maximale Aufnahmerate beider Nährstoffe steigt mit der Temperatur an, genauso wie die Halbsättigungsdichte. Wenn es wärmer wird können die Pflanzen also mehr Nährstoffe aufnehmen, vorausgesetzt es stehen genug zur Verfügung. Ist die Nährstoffdichte niedrig, sinkt die Effizienz der Aufnahme. Dieses Resultat zeigt wie wichtig es ist die Veränderungsprozesse der Erderwärmung und der Nährstoffzyklen parallel zu betrachten. In meinem Modell der Populationsdynamik zeige ich, dass die temperaturabhängige Nährstoffaufnahme der Pflanzen eine Verringerung der Gesamtbiomasse mit ansteigender Temperatur zur Folge hat. Durch Düngung steigt die Biomassenproduktion zwar an, jedoch kann dieser Anstieg den Verlust durch die Erwärmung nicht vollständig kompensieren.

Mein zweites Kapitel konzentriert sich auf die Anpassungsfähigkeiten von Populationen. Hier untersuche ich den Effekt von flexibler Stöchiometrie auf Populationen die dem Druck von Erwärmung und Änderungen in der Nährstoffdichte ausgesetzt sind. Dabei zeige ich, dass es zu höherer Gesamtbiomasse führt, wenn die Pflanzen ihre Kohlenstoffaufnahme abhängig von der Verfügbarkeit von Stickstoff variieren können. Der Herbivore profitiert von der höheren Quantität an verfügbarem Pflanzenmaterial, was die verringerte Qualität der Nahrung des Herbivoren vollständig kompensiert. Eine erhöhte Fraßrate als Reaktion auf verringerte Nahrungsqualität, scheint hingegen keine hilfreiche Strategie für den Herbivoren zu sein, da es dazu führt, dass sie ihre Nahrungsquelle durch „Überfraß“ erschöpfen und sich somit der Lebensgrundlage berauben.

Diese Studien zeigen, wie wichtig es ist die Interaktion von verschieden Veränderungsprozessen im Rahmen des globalen Wandels zu untersuchen. Sie können sich gegenseitig verstärken oder abschwächen. Außerdem sollten wir die Anpassungsstrategien der verschiedenen Organismen berücksichtigen. Sie haben das Potential den Effekt des globalen Wandels auf die Funktion von Ökosystem zu beeinflussen. Wenn wir statische Reaktionen auf Veränderungen von Temperatur oder Nährstoffzyklen voraussetzen, führt dies eventuell zu einer ernsthaften Unter- oder Überschätzung der Veränderungen in den Ökosystemdienstleistungen.

Author Contributions

Research Chapter 1 | Opening the black box of plant nutrient uptake under warming predicts global patterns in community biomass and biological carbon storage

Jori M. Marx, Björn C. Rall, Helen R. P. Phillips, Ulrich Brose

JMM, BCR and UB conceived and designed the study. JMM undertook the literature review and analysis of literature data. JMM, BCR and UB developed the model. JMM ran the simulations. All authors interpreted the results. HRPP created the world maps. JMM wrote the first draft and all authors contributed to the writing. Contribution JMM 80%

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Research Chapter 2 | Plant flexible stoichiometry and herbivore compensatory feeding drive population dynamics across temperature and nutrient gradients

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JMM, UB and ALG conceived and designed the study. JMM, UB and BG developed the modelling framework. JMM ran the simulations and JMM, UB and BG discussed and interpreted the results. JMM wrote the first draft of the manuscript, and all authors contributed to the final version. Contribution JMM 70%

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I

General Introduction

1 | Global change and ecosystems

1.1 Studying global change

April 2020: “Dark prospects for the farmers in Saxony due to long-running drought” (MDR 2020a). August 2020: “Swimming advisory! Dangerous blue algae in popular Leipzig lake confirmed” (LVZ 2020). September 2020: “Numerous operations by firefighters – heavy rains in Saxony” (MDR 2020b). These news headlines have something in common: they are the result of global change. As someone living in Leipzig, such headlines serve as a reminder to me of how much global change already affects everyday life here and now.

Global change is not happening far away in time nor space. It is not a problem only for the icecaps at the poles or something we will face 50-100 years from now. It is happening everywhere every day. Increasing temperature, extreme weather, and nutrient runoff into lakes are just a few examples of the changes that biological systems face. These changes, caused by anthropogenic activities, will impact the world’s ecosystems and the ecosystem services they provide (Sala et al. 2000; Walther et al. 2002; Pacifici et al. 2015; IPBES 2019). Humans depend on ecosystem services for basic needs such as food production or water and air quality regulation, as well as cultural and recreational uses (Millennium Ecosystem Assessment 2005). It is up to science to investigate and predict the effect of global change on ecosystems and the services they provide to inform policy to mitigate the adverse effects of global change drivers (Kremen 2005; Montoya and Raffaelli 2010). Countless studies, empirical and theoretical, have investigated warming, eutrophication, or other drivers and often found severe effects on biomass production or other functions relevant to the provision of ecosystem services (e.g. Petchey et al. 1999; Jamieson et al. 2012; Fussmann et al. 2014; Domis et al. 2014; Binzer et al. 2015).

Due to the unavoidable restrictions facing experimental studies, they are often limited to one global change driver, few species or a short time span (e.g. Olsen et al. 2012; Lemoine and Shantz 2016; Wang et al. 2019; Gillis et al. 2019). Nonetheless, these experimental studies are of immense importance, as they provide insights into the effect of global change drivers on ecological processes, needed to inform theory.

There is increasing evidence that different global change drivers interact (Heger et al. 2019). In some cases, one might lessen the other’s adverse impact, while in others, they could reinforce each other (Oliver and Morecroft 2014). For example, increased atmospheric CO_2 negatively affects herbivore performance, while warming (caused by rising CO_2) has positive effects. In this case, these two drivers can mitigate each other (Zvereva and Kozlov 2006).

Furthermore, it is essential to study the effect of global change on species interactions. Varying nutrient cycles caused by land-use change and changing rainfall patterns can alter plant nutrient content (Hessen 2008; Jamieson et al. 2012; Cross et al. 2015; Rosenblatt and Schmitz 2016). Variation in plant nutrient content means fluctuating food quality for herbivores, which may propagate upwards to affect higher trophic levels (Kratina et al. 2012; Rosenblatt and Schmitz 2016). The response of higher trophic levels to changes in their food supply and direct effects of warming on their performance can, in turn, propagate back down to affect the plants (Borer et al. 2006; Rosenblatt and Schmitz 2016; Iannino et al. 2019). Studying species interaction allows us to gain insight into the bottom-up and top-down processes determining the effect of global change on biological systems.

All of these elements are very difficult to reconcile within the limits of experimental or observational studies. For this reason, this thesis uses theoretical models informed by experimental data to complement and extend our knowledge from experimental studies. With this thesis, I aim to contribute to completing the picture that we have on the mechanisms and pathways through which global change acts on biological systems and establish which of the currently understudied processes are particularly relevant for future research informing policy on global change mitigation and ecosystem service provision.

1.2 Global warming

The IPCC predicts the global average temperature to rise by up to 4.8°C by 2100 relative to the pre-industrial level, without policy strategies to mitigate temperature increases, (IPCC 2014). The current global policies based on the Paris agreement from 2015 aim to limit warming to 1.5°C (Rhodes 2016). A temperature increase of 1.5°C may seem small but, even if this goal can be achieved, we can expect severe impacts on ecosystems, especially as the temperature rise is not evenly distributed (Masson-Delmotte et al. 2018).

Temperature is an essential factor for ecosystem functioning (Gibert 2019). Many biological rates are directly proportional to temperature (Brown et al. 2004). Examples are animal feeding rates, i.e., the amount of food consumed per unit time, and plant and animal metabolic rates, i.e., the amount of biomass lost through maintenance per unit time. These rates are directly impacted by warming (Brown et al. 2004; Binzer et al. 2012; Rall et al. 2012; Rosenblatt and Schmitz 2016). As they play an essential role in shaping ecological interactions, even small changes in any of the rates can carry through entire ecosystems.

Furthermore, these rates respond differently to warming, and the interactions of several rates can change the direction of the effect of warming on populations (Binzer et al. 2012). If, for example, warming increases plant growth rate, we would expect an increase in biomass production. However, if plant metabolism (or respiration rate) increases faster than the growth rate, the interaction of the two causes a reduction in net biomass produced by plants and restricting the amount of energy that is available for the higher trophic levels (Petchey et al. 1999; Yvon-Durocher et al. 2010). Temperature also influences the dynamics of a system (see Figure 1). In a tri-trophic system (e.g. plant, herbivore, predator), warming decreases the amplitude of the oscillations, and above a certain threshold, the system reaches equilibrium dynamics, but with continually decreasing biomasses. At very high temperatures, the reduction in primary production, as described above, leads to the extinction of the highest trophic levels (Binzer et al. 2012). In addition to this limitation from primary production, increased carnivore metabolism causes higher food demand, increasing the feeding pressure from the top. Therefore, warming impacts the ecosystem through bottom-up and top-down processes (Binzer et al. 2012; Kratina et al. 2012; Brose et al. 2012; Rosenblatt and Schmitz 2016).

Overall, these effects of warming can result in decreased biomasses at all trophic levels and decreases in trophic complexity (Vasseur and McCann 2005; Binzer et al. 2012; Olsen et al. 2012). However, warming may also stimulate primary production, indicating that plant growth rates could increase more strongly than respiration (Domis et al. 2014; Robinson et al. 2018). Global warming could also cause species turnover by influencing which plant sizes dominate (Elser et al. 2010). Changes in biomass production, trophic complexity, species composition, and diversity with warming will impact ecosystem service provision.

1.3 Nutrient Cycling

Most ecosystems are naturally adapted to oligotrophic states, with nitrogen (N) or phosphorus (P) limitation (Elser et al. 2010). The use of fossil fuels and the increased use of fertilizers associated with the intensification of agricultural practices have caused a doubling in N supply while P supply quadrupled compared to the natural cycles (Falkowski 2000; Dentener et al. 2006; Mahowald et al. 2008; Elser et al. 2010; Tipping et al. 2014; Sinha et al. 2017). These anthropogenic changes may influence which nutrient is limiting an ecosystem's performance (Güsewell 2004).

Fertilization increases overall biomass production by increasing plant carrying capacity, primary production, and the resource use efficiency of the consumers (Binzer et al. 2012; Oliver and Morecroft 2014). Increased nitrogen availability will have different impacts on biological systems depending on their initial trophic state (Sistla and Schimel 2012). Oligotrophic systems, with an initially low nutrient supply, may not be much affected. In contrast, already eutrophic systems could be tipped over the edge by additional fertilization, causing a switch from N to P limitation or even harmful excessive growth known from algal blooms (Anderson et al. 2002; Paerl et al. 2016; Gasparini Fernandes Cunha et al. 2017).

The so-called “paradox of enrichment” describes these potentially harmful effects of fertilization (Rosenzweig 1971). All species can coexist in equilibrium at low nutrient levels, but only at low biomass density (see Figure 1). Fertilization increases biomass production but can destabilize the system, causing oscillations with increasing amplitudes. Above a certain threshold, the higher trophic levels are driven to extinction (Binzer et al. 2012). As a result, increasing nutrient availability can increase the provision of ecosystem services related to primary production but may cause a decline in those delivered by species higher up in the trophic chain (Bodirsky et al. 2014; Finney et al. 2016). Increased plant growth resulting from eutrophication may also negatively impact ecosystems by altering the microclimate. Paradoxically, increased canopy cover can cause a sufficient temperature decline to make the area uninhabitable for certain species (Wallisdevries and Van Swaay 2006; Oliver et al. 2012; Oliver and Morecroft 2014).

While many systems face increasing nitrogen levels, others could be facing the opposite. Increased rainfall causes a runoff, which can mean that nutrients are drained from one area and washed into another (Anderson et al. 2002; Lu et al. 2009; Sinha et al. 2017). Again, this can have varying impacts depending on the initial nutrient content of the system. It could lead to a substantial decline in biomass when a system goes from being sufficiently supplied with nutrients to being oligotrophic. Changes in the trophic state of an ecosystem associated with anthropogenic activities will impact the population dynamics of the system, and as a result, influence the biomass production and ecosystem service provision.

1.4 Interaction of warming and nutrient supply

Under global change, ecosystems will frequently face warming in parallel with an increase or decrease in nutrient levels (Jöhnk et al. 2008; Rabalais et al. 2009; Domis et al. 2014). These global change drivers do not act on the ecosystems in isolation but interact with each other. For example, plant carrying capacity is interactively influenced by warming and nutrient supply. Carrying capacity is highest at high nutrient levels combined with low temperature and lowest when nutrient levels are low, and the temperature is high (Binzer et al. 2012). Both low temperatures and high nutrient supply can cause oscillations in population dynamics (Figure 1). If these two happen in parallel, the oscillations may be amplified and cause extinctions. Higher temperature mitigates the negative impact of high nutrient supply and stabilizes the system (Binzer et al. 2015; O’Gorman et al. 2017).

Consumers cannot buffer the increase in metabolism resulting from warming at low nutrient supply due to decreased resource use efficiency. As a result, warming combined with oligotrophy may also cause extinction. In this case, increasing nutrient supply will boost production and improve efficiency, reducing the negative temperature impact (Binzer et al. 2012). Without additional nutrient supply, warming may decrease the amount of N taken up by plants; parallel fertilization could reverse this effect

(Bassirirad 2000). In the example from the previous section, where increased nutrient supply could cause a microclimate cooling, simultaneous warming could have a mitigating effect by pushing the temperature back up (Wallisdevries and Van Swaay 2006).

When temperature and nutrient levels increase in parallel, they might mitigate each other. However, they can also reinforce each other, causing an even more substantial effect together than each on its own. The nutrient supply sufficient to sustain a specific population density at one temperature may not suffice at a different temperature (Klock 1995). These interactions highlight the importance of studying these two global change drivers in parallel. Omitting one of them could lead to an under-or overestimation of the effect of the other (Cross et al. 2015; Atkinson et al. 2017).

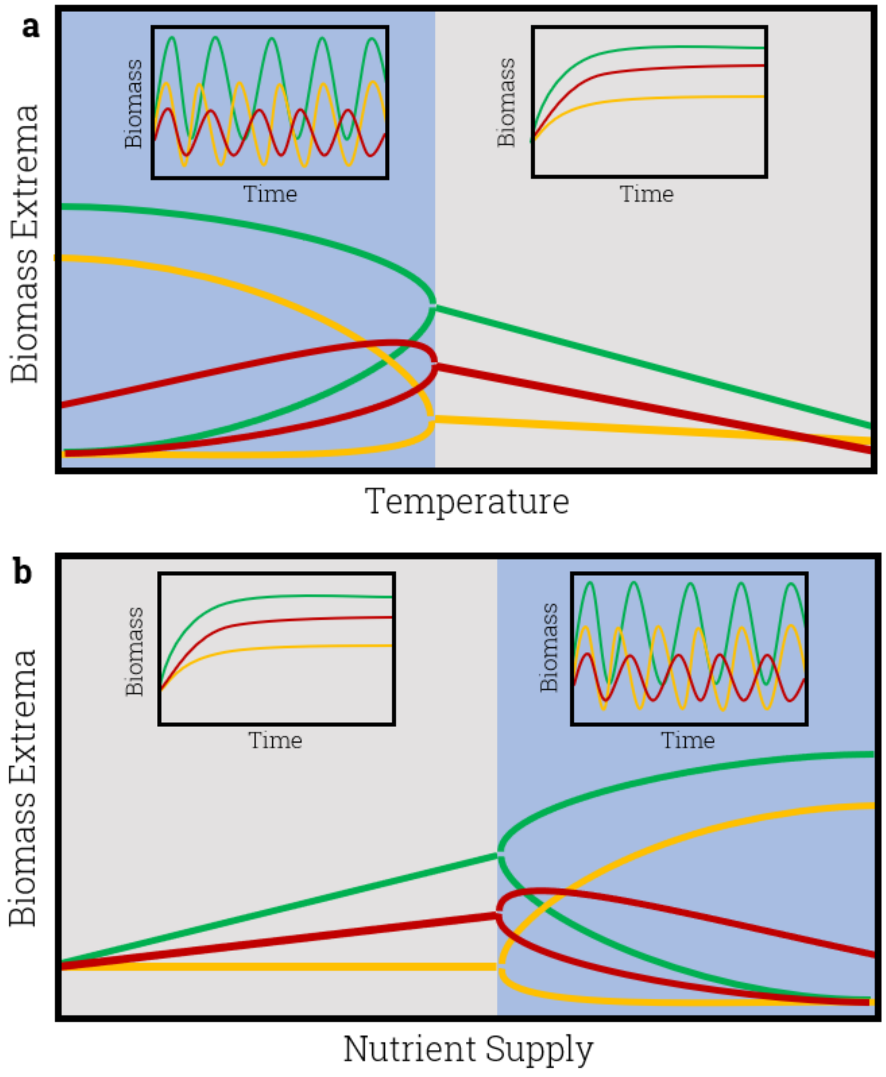

Figure 1: Bifurcation diagrams showing biomass extrema against temperature (a) and nutrient supply (b) adapted from Binzer et al. (2012) with example time series showing the dynamics of a tri-trophic system, e.g., plant (green), herbivore (yellow) and predator (red). In the area shaded in grey, the populations enter into equilibrium; in the blue shaded area the populations face oscillating dynamics.

2 | Carbon-flow models of trophic interactions

If we want to learn more about how global change drivers interact to impact ecosystem function, it is necessary to understand how the mechanisms shaping biological interactions are affected by global change. Carbon-flow models of trophic interactions are a helpful tool to investigate these mechanisms. With these models, we can study populations and their feeding interactions using parameters from empirical studies. When simulating population interactions using these models, we can manipulate selected biotic (e.g., feeding rate or tissue stoichiometry) or abiotic (e.g., temperature or nutrient supply) variables to gain insight into the direction and intensity of their effect on population dynamics and biomass production.

2.1 The theoretical background

The development of theoretical models of population interactions started about a century ago with the models independently published by Alfred J. Lotka (1910) and Vito Volterra (1926). The Lotka-Volterra model of predator-prey interactions assumed exponential growth of the prey species and a linear functional response (type I, see Box 1) by the predator. The dynamics of this system are oscillating cycles of growth and decline. The predator population will grow until it decimates its resource so much that it cannot sustain such a high predator density. Then the predator population shrinks, allowing the prey population to recover, which will lead to an increase in the predator population, restarting the cycle.

Michael L. Rosenzweig and Robert H. MacArthur (1963) updated the Lotka-Volterra model by replacing the prey exponential growth with a more realistic logistic growth and changing the functional response of the predator to type II (Holling 1959, see Box 1). They introduced a maximum density for the prey – their carrying capacity. The introduction of a maximum feeding rate put a more realistic limit on predator feeding.

The Rosenzweig-MacArthur model still forms the basis for many studies modelling population dynamics. It was further extended by Peter Yodzis and Stuart Innes (1992) by making production, feeding, and metabolic rates dependent on body mass.

Based on these models, we can simulate population dynamics using ordinary differential equations, where each equation represents one of the species in the system. A two-species system would consist of one equation for the prey and one for the predator. The equations contain all the rates that define how the species biomass changes at each time step.

The resource (R) equation would at minimum resemble:

$$\frac{dR}{dt} = gR - fP \tag{1}$$

including a growth term with growth rate g and a loss term given by feeding rate f from the predator P.

The basic predator equation:

$$\frac{dP}{dt} = afP - lP \tag{2}$$

includes a growth term based on feeding rate f on the prey and assimilation efficiency a. and the predator biomass loss l due to metabolism and death.

From this starting point, we can build increasingly complex systems by including more interactions and species to form longer food chains or even large food webs. Besides scaling with biotic factors like body mass, this framework allows us to define the model rates dependent on abiotic factors like temperature or nutrient availability.

Following the metabolic theory of ecology (Brown et al. 2004), the biological rates of metabolism, respiration, consumption, and growth can scale with body mass and body temperature. This approach allows us to apply basic physical principles impacting physiological rates to whole populations (Hillebrand et al. 2009).

In addition to body mass and temperature, essential nutrients and their ratios also play a significant role in determining biological rates and processes (Elser et al. 2000b; Sterner et al. 2002; Frost et al. 2005; Hillebrand et al. 2009). Ecological stoichiometry focuses on the balance of nutrient demand and supply between an organism and its food, which impacts feeding rates, growth rates, and efficiency (Hillebrand et al. 2009).

The basal prey species in biological systems are often plants, but plants do not just grow without resources. Their growth is dependent on water and light, but also the availability of nutrients. Models that simulate plant growth based on nutrient availability have employed a concept from biochemistry (Seeling and Claassen 1990; Bonachela et al. 2011; McNickle and Brown 2014). Michaelis-Menten enzyme kinetics describes the rate at which enzymes are formed (reaction rate) based on the substrate concentration (Michaelis et al. 2011). The parameters used are V_{max}, the maximum reaction rate, and K, the half-saturation density, i.e., the substrate concentration at which the reaction rate reaches half of V_{max}.

Applied to plant nutrient uptake, V_{max} is the maximum nutrient uptake rate, and K is the nutrient density at which the nutrient uptake rate reaches half of V_{max}.

The achieved nutrient uptake rate V based on nutrient density N is then given by:

$$V = \frac{V_{max} * N}{K + N} \tag{3}$$

The result is a hyperbolic function of nutrient uptake rate dependent on nutrient density, equivalent to the type II functional response (Box 1) used for predator feeding in the Rosenzweig-MacArthur model (McNickle and Brown 2014).

Combining the carbon-flow models of trophic interactions introduced above with nutrient-explicit plant growth allows us to investigate the effect of global change on biomass production in a nutrient-plant-herbivore system.

Box 1: Functional Responses

Functional responses describe the relationship between predator feeding rate and prey density. The type I functional response used in the Lotka-Volterra model describes a linear increase of feeding rate with prey density (see Fig B1).

Crawford Stanley Holling (1959) introduced a mechanistic model, which explicitly includes the handling time and attack rate of the predator when foraging for prey. The result is a so-called type II functional response: A saturating hyperbolic curve meaning that even at unlimited prey supply, the predator cannot increase its feeding rate infinitely (Jeschke et al. 2002).

Another version of the functional response, type III, has a sigmoidal shape, with a low predation risk at low prey densities and a maximum feeding rate reached at high prey supply (Real 1977).

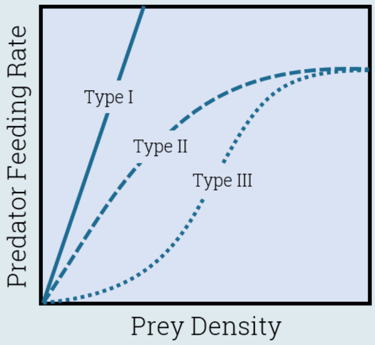

Figure B1: Functional response curves of type I (solid), II (dashed) & III (dotted)

2.2 The role of temperature

Temperature plays a significant role in shaping ecological interactions as many biological rates scale with temperature (Gillooly et al. 2001; Brown et al. 2004; Vasseur and McCann 2005; Dell et al. 2011; Rall et al. 2012; Gilbert et al. 2014; Amarasekare 2015). Model studies integrate this temperature dependency using activation energies, a concept introduced by Arrhenius (1889). The original concept describes the energy necessary to start a chemical reaction. Since biological rates result from chemical processes, we can use activation energy to describe the relationship between such rates and temperature (Brown et al. 2004; Rall et al. 2012). Positive activation energy means the rate increases with temperature; negative activation energy represents a decrease.

Metabolism, for example, has an average activation energy of 0.64 (Fussmann et al. 2014). Other rates typically assumed to scale with temperature are carrying capacity, with a negative activation energy of -0.77 on average, and feeding rates, with a mean activation energy of 0.47 (Carbone et al. 1999; Brown et al. 2004; Rall et al. 2012; Fussmann et al. 2014). Metabolism increases more strongly with temperature than feeding rates while carrying capacity decreases under warming.

Using population models like those described above, we can easily include this temperature-dependency in the equations and simulate the system under different temperature conditions. The temperature dependency of biological rate r is given by the exponential function:

$$r = i * e^{AkT} \tag{4}$$

Where i is the intercept of the rate. e is the exponential function, with A as activation energy, the Boltzmann constant k, and the absolute temperature in Kelvin T.

The resulting temperature-dependent models allow us to explore the pathways through which global warming affects trophic interactions.

2.3 Temperature dependency of plant growth

Most physiological functions of plants include temperature-dependent mechanisms (Klock 1995). It is therefore not surprising that plant growth, like other biological rates, scales with temperature. In some ecosystems, the temperature is even the most relevant factor for determining primary productivity (Bassirirad 2000).

Furthermore, plants need at least 17 different elements and a nutritional balance to grow (Rastetter et al. 1997; Mengel et al. 2007). Nitrogen (N) and phosphorus (N) are the most common elements in plant tissue aside from carbon. They are also the most relevant to vital processes, with P as a vital RNA component, while plants need N to produce proteins (Leal et al. 2017). Consequently, N and P are also the elements most frequently considered limiting to plant growth (Reich and Oleksyn 2004; Grover and

Chrzanowski 2004; Cross et al. 2015).

Temperature-dependent plant growth is included in population models, for example, by making carrying capacity dependent on temperature (Vasseur and McCann 2005; Binzer et al. 2015; O'Gorman et al. 2017; Bernhardt et al. 2018). However, details on the mechanisms causing this temperature-dependency are often lacking. Investigating the changes in the kinetic parameters of plant nutrient uptake (maximum uptake rate and half-saturation density) with temperature will help to understand the pathways through which plant growth is affected by warming (Bassirirad 2000). In chapter 1 of this thesis, I strive to open the black box of temperature-dependent plant growth by establishing how the uptake of the two essential nutrients N & P by the plants is affected by warming. Using this knowledge, I aim to develop a model that includes the flow of energy (C) and elements (N&P) between populations. Coupling the flow of energy and elements will help improve our understanding of how global change will alter trophic interactions, population dynamics and community biomass production.

3 | Plant stoichiometry

As described above, plants, just like any other living organism, need certain elements to grow (Rastetter et al. 1997; Mengel et al. 2007). The balance (ratio) of these elements in the tissue is the subject of ecological stoichiometry (Sterner et al. 2002). The C:N:P ratios (see Box 2) of organisms and ecosystems are relevant for all kinds of ecological processes, including litter decomposition, N fixation, population dynamics, ecosystem composition, and the resilience of organisms to stress (Sterner et al. 2002; Sardans et al. 2012).

To this day, studies of nutrient limitation in the marine environment often use the ratio established by Alfred C. Redfield (1934). The Redfield ratio (C:N:P) for marine phytoplankton is 106:16:1. However, phytoplankton and other autotrophic organisms show a wide range of variation in C:N:P ratios. Those variations can result from differences in abiotic factors like light, water, nutrient availability, CO_2-levels, and temperature. Biotic factors like size, growth rate, species, or functional group also affect C:N:P ratios (Sterner et al. 2002; Elser et al. 2010; Cross et al. 2015; Guiz et al. 2015).

Temperature is one of the abiotic factors having a substantial impact on plant stoichiometry (Reich and Oleksyn 2004; Domis et al. 2014; Yvon-Durocher et al. 2015). Both N & P content in plant tissue tend to decline with increasing temperature (Reich and Oleksyn 2004; Cross et al. 2015). Variations in nutrient ratios with latitude are also often discussed: the N:P ratio of plants decreases from tropics to poles, as P content doubles relative to N content (Sterner et al. 2002; Kerkhoff et al. 2005; Yvon-Durocher et al. 2015). Several hypotheses are trying to explain this gradient, all of which point to either the temperature or nutrient supply variations with latitudes as the cause for varying nutrient ratios (Yvon-Durocher et al. 2015). Both temperature and nutrient supply change as a result of global change. Therefore, we can expect variations in plant stoichiometry (Sardans et al. 2012). The effect of temperature on C:N:P ratios shows significant variation depending on nutrient supply, highlighting the importance of studying both in parallel (Yvon-Durocher et al. 2015).

Changes in C:N:P ratio are not necessarily just a passive reaction of the plants to the factors described above. By being flexible in their stoichiometric compositions, plants can actively react to pressures from their environment (Klausmeier et al. 2007; Bonachela et al. 2011; Zhou et al. 2020). Homeostasis describes the degree to which an organism is flexible in its elemental composition: Complete homeostasis means no flexibility in nutrient ratios; the less homeostatic an organism is, the more flexible its elemental composition (Sterner et al. 2002). By maintaining an ideal nutrient balance, homeostasis was often considered beneficial for the organism (Yu et al. 2015). However, a flexible stoichiometry may have other advantages by providing nutrient storage, which can buffer phases of nutrient limitation (Meunier et al. 2014; Leal et al. 2017).

Plants are more flexible in their tissue elemental ratios than animals, as they can store nutrients more easily (Sterner et al. 2002; Yu et al. 2011). Nonetheless, plants need their nutrient ratio to stay within certain limits to meet all demands; as vital plant parts like chloroplasts, mitochondria, and ribosomes are relatively stable in their stoichiometry (Elser et al. 2010). The plant growth rate also limits nutrient storage. If the growth rate is very high, all available nutrients are allocated to growth, and there are none left to be stored (Persson et al. 2010). Therefore, a realistic model should not allow for flexibility and impose limits for it to be applicable even at extreme nutrient supplies (Klausmeier et al. 2008). Yu et al. (2011) report the variation of N and P concentrations in vascular plants. Within one plant species, they report variation of up to 25% around the mean for N and up to 50% for P. The higher homeostasis of N may be explained by its overall higher abundance in plant tissue, meaning that there is less potential for variation (Yu et al. 2011).

Even though it is widely recognized that plants can vary their stoichiometry (Geider and La Roche 2002; Cross et al. 2015; Yvon-Durocher et al. 2017), we lack detailed information on how this flexibility affects plant growth and plant-herbivore interactions. Models that do not include this flexibility in plant stoichiometry may underestimate biomass production under global change (Kwiatkowski et al. 2018). It is vital to understand the effect of flexible stoichiometry on population dynamics, to validate previous models on ecosystem response to the global change drivers warming and nutrient supply. In chapter 2 of this thesis, I address this challenge by simulating population dynamics using carbon-flow models that include flexible plant stoichiometry within realistic limits.

4 | Herbivore compensatory behaviour

The variation in plant carbon to nutrient ratios associated with flexible stoichiometry impacts all the organisms interacting with the plant. According to ecological stoichiometry theory, an organism's growth rate is always partly determined by the similarity or difference between the stoichiometry of the organism and that of its resource (Sterner et al. 2002; Leal et al. 2017). As a result, herbivore performance, i.e., growth and reproduction, is directly affected by changes in the quality, defined by elemental composition, of their food plants (Loladze et al. 2000; Sardans et al. 2012; Bukovinszky et al. 2012; Leal et al. 2017).

There is considerable variation in elemental stoichiometry among species, populations, individuals, and life stages of herbivores. Nonetheless, herbivores are more homeostatic than plants (Sterner et al. 2002; Persson et al. 2010; Bukovinszky et al. 2012; Leal et al. 2017). Herbivores face the pressure of unpredictable variation in plant stoichiometry while maintaining homeostasis themselves (Logan et al. 2004). As a result, changes in plant N and P content due to global change could reduce biomass and nutrient transfer efficiency from the plant to the herbivore (Urabe et al. 2003; Elser et al. 2010; Leal et al. 2017). The lower transfer between plant and herbivore could create 'stoichiometric bottlenecks' adversely affecting higher trophic levels, by decreasing their nutrient supply from below (Van Donk et al. 2008; van de Waal et al. 2010; Schoo et al. 2013; Domis et al. 2014; Deutsch et al. 2015).

Additionally, herbivore tissue has much higher N and P content than their plant resource. This large mismatch means that they need to survive on food with low nutrient content relative to their demands (Sterner et al. 2002; Logan et al. 2004; Leal et al. 2017). This mismatch results in low C assimilation efficiency, as excess C is egested (Loladze et al. 2000; Atkinson et al. 2017). For example, an herbivorous insect with a C:N ratio of 6.5 may feed on a plant with a C:N ratio of 36. The insect needs to take up substantial amounts of plant food to satisfy their nutrient demand. For each unit of N, the herbivore takes up 5.5 times as much C as it needs, which results in the production of large amounts of C-rich detritus, potentially affecting nutrient recycling (Loladze et al. 2000; Sterner et al. 2002). Variations in the stoichiometric mismatch between plant and herbivore can affect whole ecosystems through bottom-up and top-down processes.

Herbivores may resort to various mechanisms to deal with the stoichiometric mismatch between themselves and their resource. They may increase their food intake, select for high-quality food, improve their assimilation, reduce the excretion of vital elements, or produce low nutrient biomass (Sterner et al. 2002; Logan et al. 2004; Hillebrand et al. 2009; Johnson and McNicol 2010; Persson et al. 2010; Sardans et al. 2012; Leal et al. 2017; Jochum et al. 2017). Possible long term consequences of low-quality food are a switch in metabolic type toward omnivory or cannibalism, or a shift in species composition favouring herbivore species adapted to high C:N, or species that are less homeostatic (Sterner et al. 2002; Anderson et al. 2005; Sardans et al. 2012; Leal et al. 2017; Atkinson et al. 2017).

Increasing their food intake by adjusting feeding rates is a short-term response mechanism that is potentially available to many consumers (Cruz-Rivera and Hay 2000; Jochum et al. 2017; Guo et al. 2019; Iannino et al. 2019). There is growing evidence that consumer species, including herbivores, detritivores, and carnivores indeed react to decreased food quality with increasing feeding rates (Cruz-Rivera and Hay 2000; Berner et al. 2005; Fink and Von Elert 2006; Hillebrand et al. 2009; Suzuki-Ohno et al. 2012; Ott et al. 2012; Jochum et al. 2017; Urabe et al. 2018). The stoichiometric mismatch between plant and herbivore is a relevant factor for determining the herbivore population feeding rate (Hillebrand et al. 2009). By increasing feeding rates to compensate for the relative lack of essential nutrients in their low-quality food, herbivores may be able to maintain higher population biomass (Urabe et al. 2018). However, compensatory feeding comes at the cost of decreased growth efficiency, meaning that they may not reach the abundance they would have under a high-quality food supply (Frost et al. 2005; Anderson et al. 2005; Hillebrand et al. 2009; Urabe et al. 2018).

By changing population interactions, compensatory feeding can influence the direction and magnitude of global change impacts on biological communities. Chapter 2 of this thesis investigates the importance of compensatory feeding by herbivores to evaluate biomass production and population dynamics under a range of temperature and nutrient supply conditions.

Box 2: A short note on ratios

In literature, elemental ratios are most commonly reported using the carbon to nutrient notation (e.g., C:N, C:P, C:N:P), rather than nutrient to carbon (e.g., N:C). I adhere to this convention in my general introduction and discussion, to avoid confusion. However, in research chapter 2, the quality of plant tissue as food for the herbivore is a focal topic. In this context, the N:C notation is more intuitive than C:N, as increasing plant N:C corresponds to improved food quality for the herbivore. Table B1 gives a simplified overview of the meaning of high or low C:N and N:C ratios in the context of research chapter 2.

Table B1: Meaning of plant C:N and N:C for plant and herbivore

Plant C:N	Plant N:C	Meaning for the plant	Meaning for the herbivore
High	Low	Higher C biomass per unit N	Lower food quality
Low	High	Lower C biomass per unit N	Higher food quality

5 | Research objectives and study outline

5.1 Research objectives

The impacts of global change on biological systems are manifold. Through human action, these impacts will intensify in the future. Therefore, we must understand how global change drivers influence the function of ecosystems and the provision of ecosystem services. Previously, warming has been found to either decrease or increase biomass production, or even have no effect at all (Vasseur and McCann 2005; Olsen et al. 2012; Domis et al. 2014; Binzer et al. 2015; Robinson et al. 2018). Changing biomass production has direct consequences for the functioning of ecosystems and human use of ecosystem services. To improve our understanding of these consequences, we must be aware of the mechanisms influencing the effect of warming on the processes underlying ecosystem functioning (Fox 2018). Studying the effect of global change on plant-herbivore interactions is of major importance as they mediate many of the bottom-up and top-down mechanisms shaping ecosystems (McQueen et al. 1989; Brett and Goldman 1996; Borer et al. 2006; Hillebrand et al. 2009). For example, the amount of plant material passing through the herbivore plays an essential role in determining where and how much C is stored in the ecosystem, and influences nutrient recycling (Cebrian 1999; Gruner et al. 2008; Schmitz 2008; Hillebrand et al. 2009).

There is a wealth of literature investigating the impact of global change on ecosystems. However, although evidence increases that the different global change drivers interact (Heger et al. 2019), many studies include only one: warming, nutrient cycles, increasing CO_2 supply or any of the others. Including several global change drivers often pushes the boundaries of what we can control and measure experimentally (Oliver and Morecroft 2014). In this case, models, informed by experimental data allow us to explore the bigger picture.

Many models have included temperature-dependent biological rates, like metabolism, plant growth rate, or animal feeding rate in models, using C (energy) as the main currency (Binzer et al. 2012; Rall et al. 2012; Fussmann et al. 2014). Other models have focused on the stoichiometry of organisms and the mismatch between them. In such models, the nutrients (elements) serve as the currency traded between populations and their environment (Elser and Urabe 1999; Elser et al. 2010). My thesis aims to improve our understanding of the coupling of the flow of elements and energy through biological systems and how this is influenced by the combined effect of two major global change drivers, warming and changing nutrient cycles. Therefore, one question I investigate in this thesis is: (1) How do the global change drivers of warming and changing nutrient supply interact to affect the flow of elements and energy between the environment, plant and herbivore populations?

To address the gaps in the study of biological systems under global change, I extend literature models with currently often lacking mechanisms. My first aim is to explore the temperature-dependence of plant nutrient uptake. Based on this knowledge, I develop nutrient-explicit models of the flow of elements and energy between populations. These models provide more realistic insights into the (interactive) effect of nutrient supply and warming on primary production, feeding interactions and overall biomass production. With these models, I aim to answer the following questions: (2) What role does temperature play in determining plant nutrient uptake rates? (3) What is the effect of temperature-driven plant nutrient uptake on community biomass production under warming and different nutrient supplies?

As established above, the plants are flexible in their carbon to nutrient ratio within certain bounds. The consequences of flexible stoichiometry for plant performance are still poorly understood (Leal et al. 2017). Therefore, the next logical step is to extend the nutrient-explicit model with flexible plant stoichiometry. This model will help explore the question: (4) How does flexible plant stoichiometry mediate the effect of warming and nutrient supply on plant and herbivore growth and interaction?

Herbivores possess their own response mechanisms when faced with food quality changes, resulting from flexible stoichiometry and varying nutrient supply. For example, they can resort to compensatory feeding. This mechanism has the potential to mediate the effect of global change on biological systems. Consequently, I further extend the model to include an adaptive herbivore feeding rate, which adjusts to the nutrient content of the food plant. With this model, I address the open question: (5) Is compensatory feeding a helpful strategy for herbivores to meet the challenge of low food quality?

Together, the model extensions described above will give us insight into the overarching question: (6) How relevant are the currently understudied mechanisms of temperature-dependent plant nutrient uptake, flexible stoichiometry and compensatory feeding for accurate prediction of population dynamics, biomass production and ecosystem service provision under global change?

5.2 Study outline

In research chapter 1, I contribute to opening the black box of the mechanisms determining the temperature-dependency of plant growth by establishing how plant nutrient uptake varies with temperature. This chapter starts with a literature review of studies that report the kinetic variables maximum uptake rate (V_{max}) and half-saturation density (K) for N or P uptake under different temperatures. Next, I use these variables to develop a nutrient-explicit population model where the growth of the plant pool depends directly on its nutrient uptake rate. With this model, I test the effect of global change on biomass production, by simulating nutrient-plant-herbivore interactions across a temperature gradient and under several nutrient supply scenarios.

Based on the results from chapter 1, I develop ‘stoichiometrically explicit’ (Sterner et al. 2002) models of the flow of elements and energy between the environment, plants and herbivores in research chapter 2. With these models, I explore the effect of flexible stoichiometry and compensatory feeding on population dynamics and survival. The assumptions for these models are that plants fit the conformer type (i.e., they conform to environmental conditions up to certain limits), while herbivores are regulators (i.e., they keep their stoichiometry constant) (Meunier et al. 2014). Unlike the model in chapter 1, the C uptake of the plant now depends on the amount of N available. At the same time, I assume that the herbivore strives for elemental homeostasis and can increase its feeding rate to meet its stoichiometric requirements (Logan et al. 2004).

To investigate the effect and relevance of the mechanisms of flexible stoichiometry and compensatory feeding for the response of biological systems to global change, I simulate three different models across a temperature and nutrient gradient. The first is the baseline model, similar to the model developed in chapter 1. In the second model, I add flexible plant stoichiometry. The third model includes both flexible stoichiometry and compensatory feeding mechanisms. The differences in the responses of these three model systems to temperature and nutrient supply show the relevance of flexible stoichiometry and compensatory feeding in determining ecosystem response to the combined effect of global warming and changing nutrient cycles on biological systems.

Together the research chapters contribute to our mechanistic understanding of the pathways through which the global change drivers of warming and changing nutrient supply affect population dynamics, survival, and biomass production. They also provide insight into the relevance of previously understudied mechanisms like plant-nutrient uptake, flexible stoichiometry and compensatory feeding for future studies informing policy on climate change mitigation.

II

Research Chapters

1 | Opening the black box of plant nutrient uptake

Opening the black box of plant nutrient uptake under warming predicts global patterns in community biomass and biological carbon storage

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Research

Opening the black box of plant nutrient uptake under warming predicts global patterns in community biomass and biological carbon storage

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The effect of climate change on the amount of carbon stored in the different biological compartments of complex natural communities is relevant for a range of ecosystem functions and services. Temperature-dependency of many physiological and ecological processes drives this storage capacity. As opposed to other physiological rates, the temperature-dependence of nutrient uptake by plants has, to date, not been thoroughly investigated and therefore was not explicitly included in food web models. In a meta-study, we extracted experimental data to establish the temperature-dependence of the parameters determining plant nutrient uptake. Overall, we found an increase in the maximum uptake rate, as well as the half-saturation density. As the respiration rates of plants (biomass loss) increase more strongly than the nutrient uptake rates (driving biomass gain under nutrient limitation), our results suggest that warming should decrease plant biomass. We applied these temperature-dependent nutrient uptake rates by plants to a model of a three-level food-chain composed of two nutrients, a plant pool, and an herbivore pool. Having established plant nutrient uptake rates based on real data to replace the previously used assumption of logistic growth, we were able to use realistic natural nutrient deposition rates as the input variables in this model. This mechanistic model approach allowed us to show the quantitative responses of natural communities to realistic fertilization rates for the first time. We ran the model under realistic nutrient supply scenarios based on deposition data from the literature, adding a scenario of anthropogenic fertilization. We found decreases in overall community biomass with increasing temperature, but the intensity of this decrease varied strongly depending on the nutrient supply scenario. Our findings highlight the importance of including other global change drivers besides warming, as they can mediate the temperature impact on changes in global carbon storage and thus biomass-related ecosystem services.

Keywords: biomass distribution, carbon storage, fertilization, global warming, nutrient deposition, plant nutrient uptake, temperature dependence

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Introduction

Despite increasing awareness that we are facing climatic change, many of the consequences of such change are still a matter of speculation (Scheffers et al. 2016). The effect of increasing temperatures on community biomass – the combined biomass of all plants and animals within a community – is of particular relevance. Biomass forms the basis of many, if not most, of the ecosystem functions and services we rely on (Brose 2008, Schneider et al. 2016, Dee et al. 2017). Obvious examples would be the production of food and timber resources, but biomass is also needed for services such as water retention, climate regulation or erosion control (de Groot et al. 2002, Kremen 2005, Verkerk et al. 2014, Caputo et al. 2016). Furthermore, biomass can act as a source or a sink of carbon and changes in biomass can therefore either help to mitigate or in the worst-case scenario aggravate climate change (Kirschbaum 2003, Hymus and Valentini 2007). Therefore it is crucial to understand how future global warming will affect community biomass.

Community biomass is the result of complex interactions between individuals and populations, which are in turn the result of complex physiological processes (Walther et al. 2002, Traill et al. 2010). Various studies have shown that some of these physiological processes such as respiration, growth or feeding, are affected by temperature, and thereby may lead to changes in biomass production with temperature (Savage et al. 2004, Poertner and Knust 2007, Ehnes et al. 2011, Rall et al. 2012, Deutsch et al. 2015). However, as a result of the complex nature of biological systems such as food webs, the direction and magnitude of the effect of temperature on biomass production are not yet entirely clear (Montoya and Raffaelli 2010, Englund et al. 2011, Brose et al. 2012, Uszko et al. 2017).

The temperature dependencies of respiration and feeding rates, as well as their variation between trophic levels, have by now been well established (Gillooly et al. 2001, Rall et al. 2010, Dell et al. 2011, Amarasekare and Savage 2012). Respiration rates and feeding rates have been found to increase with temperature, but feeding does so to a lesser extent than respiration (Rall et al. 2010, Vucic-Pestic et al. 2011, Rosenblatt and Schmitz 2016, Lang et al. 2017). This mismatch may stabilize population dynamics but could ultimately lead to starvation and extinction of higher trophic levels and result in an overall decline in biomass (Binzer et al. 2012 2015, Rall et al. 2012, Fussmann et al. 2014, Amarasekare 2015, Uszko et al. 2017).

In many models plants have been assumed to grow logistically with a temperature-dependence coming from their carrying capacity – the maximum biomass density of the primary producer (O'Connor et al. 2009, Binzer et al. 2012, Dell et al. 2014, Gilbert et al. 2014). The temperature dependence of carrying capacity for plants has rarely been directly measured (but see Bernhardt et al. 2018 for an example), instead field abundances are mostly used as an approximation (Savage et al. 2004). As a result there is no clear consensus on the temperature effect. Carrying capacity has frequently been suggested to decrease with warming (Savage et al. 2004, Dell et al. 2014, Fussmann et al. 2014), while others models assumed different dynamics including temperature independent carrying capacity, as well as an increase in carrying capacity with warming (Vasseur and McCann 2005, Amarasekare 2015, O'Gorman et al. 2017, Uszko et al. 2017). Assuming a direct temperature effect on carrying capacity is, however, a purely descriptive approach and leaves the question of the underlying processes unanswered (Gilbert et al. 2014, Uszko et al. 2017).

Plants are reliant not only on sunlight and water but also on nutrients in order to produce biomass. While there have been models that explicitly included nutrients, such models have not established a temperature dependency of nutrient uptake (Huisman and Weissing 1999, Brose 2008). Similar to feeding rates of animals, nutrient uptake by plants is the result of a range of biological processes, and as such, it is very likely to change with temperature. There have been experimental studies of the relation between temperature and nutrient uptake, which looked at one or two plant species at the most (Cruz et al. 1993, Lee and Dunton 1999, Smit 2002, Adam et al. 2003, Khandan-Mirkohi and Schenk 2009, Nishikawa et al. 2009). A synthesis of such experimental results, which would lead to a generalized temperature-dependency of nutrient uptake rates, is still lacking. Including these rates into models of population dynamics will allow us to gain insight into the direction of change in plant carrying capacity, and can improve our understanding of the mechanisms through which temperature influences plant growth.

In addition to temperature increases associated with climate change, there are also changes in nutrient supply resulting from anthropogenic factors (Sala et al. 2000, Galloway et al. 2008, Sentis et al. 2017). As nutrients present a potential limiting factor to plant growth, an increase or decrease in nutrient supply can further impact the amount of biomass produced by the plants, which in turn affects the higher trophic levels. Some studies found interactive effects of temperature and nutrient supply on food web dynamics (O'Connor et al. 2009, Binzer et al. 2012, 2015, Sentis et al. 2014, 2017). These models have generally assumed logistic growth for the basal species. A new model explicitly including nutrient uptake as the basis for plant growth can help us understand how variation in nutrient supply may affect the biomass of a system under warming conditions.

In this study, we aim to gain insight into the effect of temperature on 1) the nutrient uptake by plants and 2) consequently on community biomass under different nutrient supply scenarios. In the first part of our study, we carried out a meta-study investigating the effect of temperature on nitrogen and phosphorus uptake by plants. As carrying capacity has generally been assumed to decrease with rising temperature, we would expect 1) a decrease in the plants' maximum nutrient uptake rate with temperature, as well as 2) a decrease in nutrient uptake efficiency at low nutrient densities, indicated by an increase in half-saturation density, i.e. the nutrient density at which the uptake reaches half of its maximum. In the second part of our study, we used the results of the meta-study to simulate a three-level food chain under warming at different nutrient supplies. Our model food chain consists of a plant resource and an herbivore consumer (Gilbert et al. 2014). The basal level consists of nutrients in the form of nitrogen and phosphorus pools (Fig. 1). Based on the results of previous studies (Binzer et al. 2012, Fussmann et al. 2014), we would expect 3) the community biomass of this system to decline with warming. By investigating changes in plant nutrient uptake under warming and exploring the effects of these changes on population dynamics, we aim to fill this gap in our understanding of how warming will affect the total biomass of natural communities.

Material and methods

Meta-study

The first aim of our study was to establish quantitative relationships for the temperature dependency of nitrogen and phosphorus uptake by plants. We established density-dependent nutrient uptake rates using saturating hyperbolic Michaelis–Menten curves, similar to a type II functional response often used to describe predator feeding rates (Holling 1959, Rall et al. 2012). We determined the shape of these curves by two parameters: the maximum uptake rate (*V*) and the half-saturation density (*K*) (Fig. 2). To establish the temperature dependency of nutrient uptake, we investigated how *V* and *K* change with temperature based on literature data.

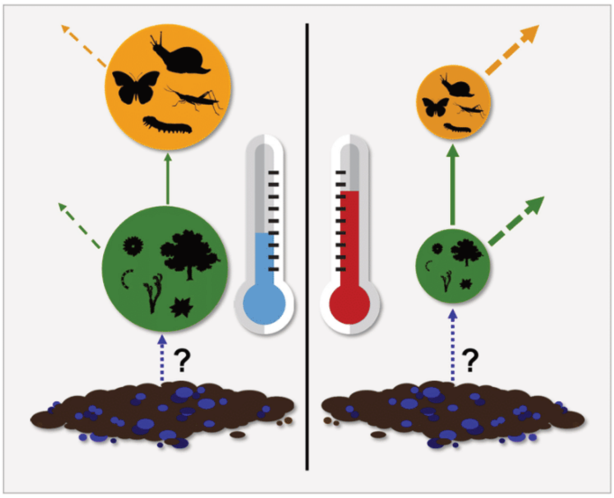

Figure 1. Conceptual visualization of the three-level food chain. The nutrients (blue) are taken up by the plants (green), which are in turn consumed by the herbivores (orange). Arrows indicate in- and outflow-rates. A change in arrow thickness and pool size between the left-hand (cold) side and the right-hand (warm) side indicates a temperature impact on the rates. The temperature impact on nutrient uptake is still unclear.

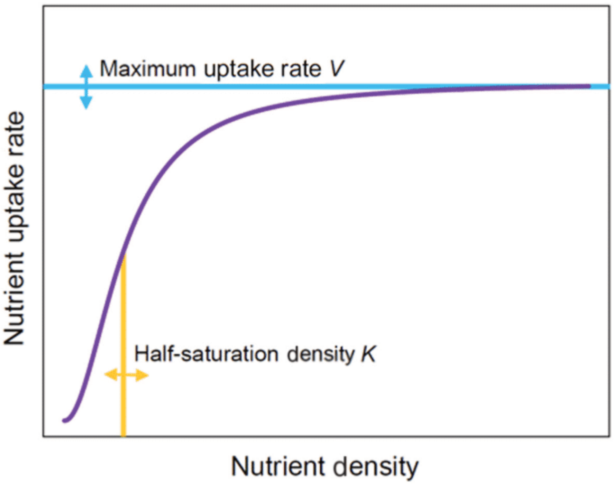

Figure 2. Conceptual illustration of temperature effects on nutrient uptake by plants. Maximum uptake rate *V* (blue) represents the saturation value of the curve, while half-saturation density *K* (yellow) determines its steepness, i.e. the efficiency of nutrient uptake at low densities. Both parameters may increase or decrease with temperature.

We conducted an extensive literature search using 'Web of Science' with a broad range of search terms: (plant OR autotroph OR phytoplankton OR pimary producer) AND (nitrogen OR phosphorus) AND (uptake OR kinetics OR Michaelis-Menten OR half-saturation) AND (temperature OR activation energy OR warming OR climate). Out of the 2636 studies found using these search terms, we selected those that reported maximum uptake rate and half-saturation density of nitrogen, phosphorus or both for at least two different temperatures. We found six studies matching these criteria, two of which reported parameters for two plant species, while the others each focused on one species (see Table 1 for an overview).

Using the parameter values reported in these studies we built a dataset for eight species, covering plant species from the largest to the smallest – including phytoplankton as well as tree species (Table 1). In one study *V* and *K* were investigated for both nutrients (Nishikawa et al. 2009), the others focused on either phosphorus or nitrogen. In total, the dataset includes six species with parameter values for nitrogen and parameters for four primary producer species for phosphorus. We thus have two parameters for ten species-nutrient pairs, resulting in 20 unique parameter–species combinations. Across studies, the temperatures ranged from 9°C to 40°C, with individual studies reporting between two to six different temperatures. The studies reported their parameters using various units (µM or µmol for half-saturation density and pmol $cell^{-1} h^{-1}$, nmol $m^{-2} s^{-1}$, µmol g^{-1} root fresh weight h^{-1}, µmol g^{-1} dry weight h^{-1} and pm $cm^{-2} s^{-1}$ for maximum uptake rate). Khandan-Mirkohi and Schenk (2009), did not explicitly report their parameter values. Hence, we extracted these values from the reported graphs using DataThief III (Tummers et al. 2005).

Table 1. Overview of studies reporting half-saturation densities and maximum nutrient uptake rates for nitrogen (N) and phosphorus (P) uptake. Additional variables used in some studies were the nutrient supply (N-limited, N-rich), the nutrient type (NO_3^-, NH_4^+) or the plant part measured (root or leaf).

Species	Plant type	Nutrient	Temperatures °C (no. measurements)	Additional variables	Source
Acer rubrum	tree	N	14–34 (3)		Adam et al. 2003
Ceratonia siliqua	tree	N	10–40 (6)	NO_3^- or NH_4^+; rich or limited	Cruz et al. 1993
Coscinodiscus wailesii	phytoplankton	N and P	9–20 (2)		Nishikawa et al. 2009
Eucampia zodiacus	phytoplankton	N and P	9–20 (2)		Nishikawa et al. 2009
Euphorbia pulcherrima	shrub	P	15–25 (3)		Khandan-Mirkohi and Schenk 2009
Gracilaria gracilis	algae	N	15–20 (2)	NO_3^- or NH_4^+; rich or limited	Smit 2002
Tagetes patula	herb	P	15–25 (3)		Khandan-Mirkohi and Schenk 2009
Thalassia testudinum	algae	N	16–30 (3)	NO_3^- or NH_4^+; root or leaf	Lee and Dunton 1999

In order to establish the temperature dependence of the parameters half-saturation density *K* and maximum uptake rate *V* we fitted

$$x = x_0 e^{E_x T_{Arr}} \tag{1}$$

to the data, where x_0 is a normalization constant for parameter *x* (here: *K* or *V*), *E* is the activation energy for the different parameters, and thus represents their temperature dependence. Negative activation energy means a decrease in the given process with temperature, positive activation energy stands for an increase. T_{Arr} is the Arrhenius temperature as described by:

$$T_{Arr} = \frac{T - T_0}{k \times T \times T_0} \tag{2}$$

where T is the experimental temperature in Kelvin. We set T_0 to 293.15 K, i.e. 20°C, to place the intercept of the relationship within the range of experimental temperatures. k is the Boltzmann constant with a value of $8.61 \times 10^{-5}\,\mathrm{eV\,K^{-1}}$ (Gillooly et al. 2001, Rall et al. 2012).

Due to the different units and the additional variables reported in three of the studies (Cruz et al. 1993, Lee and Dunton 1999, Smit 2002), regressions were performed separately for each of the 20 parameter–species combinations. For studies that only used temperature, we performed linear regressions of the ln-transformed parameters against Arrhenius temperature (Rall et al. 2012). For the studies including additional variables (nutrient supply, nutrient type or plant part measured, see Table 1), we performed linear-mixed-effect regression models where we included the additional variables as a random effect, allowing us to separate the effect of Arrhenius temperature from the effect of the other variables (R, nlme-package, lme-function, Pinheiro et al. 2017). The resulting slopes are equal to the activation energy for each parameter-species combination. We then averaged these activation energies over all species and used the average in our model. In addition, combinations of minimum and maximum activation energies were used for sensitivity analyses. We performed all statistical analyses in R ver. 3.4.2 (<www.r-project.org>).

Population models

Using a simplified carbon flow model we investigated the role a temperature-dependent plant nutrient uptake plays in determining population dynamics. The system consists of a plant pool as primary producers (*R*) and an herbivore pool as consumers (*C*), both expressed in carbon units, as well as two nutrient pools: nitrogen (*N*) and phosphorus (*P*), forming the energetic basis for the plant pool (Fig. 1). The dynamics of the system are described by:

$$\begin{aligned}\frac{dN}{dt} = D\left(S_N - N\right) - \frac{1}{r_{N,R}} \times \min\Bigg(\left(\frac{r_{N,R} \times V_N \times N}{K_{N,R} + N}\right) \\ \left(\frac{r_{P,R} \times V_P \times P}{K_{P,R} + P}\right)\Bigg) \times R + m_C \times C \times \frac{1}{r_{N,C}}\end{aligned} \tag{3}$$

$$\begin{aligned}\frac{dP}{dt} = D\left(S_P - P\right) - \frac{1}{r_{P,R}} \times \min\Bigg(\left(\frac{r_{N,R} \times V_N \times N}{K_{N,R} + N}\right) \\ \left(\frac{r_{P,R} \times V_P \times P}{K_{P,R} + P}\right)\Bigg) \times R + m_C \times C \times \frac{1}{r_{P,C}}\end{aligned} \tag{4}$$

$$\begin{aligned}\frac{dR}{dt} = \min\Bigg(\left(\frac{r_{N,R} \times V_N \times N}{K_{N,R} + N}\right), \left(\frac{r_{P,R} \times V_P \times P}{K_{P,R} + P}\right)\Bigg) \\ \times R - \frac{f \times R^b}{K_C^b + R^b} \times C - m_R \times R\end{aligned} \tag{5}$$

$$\frac{dC}{dt} = e \times \frac{f \times R^b}{K_C^b + R^b} \times C - m_C \times C \tag{6}$$

where D is the turnover rate; S_i refers to the supply rate of nutrient i. $r_{i,j}$ stands for the ratio of carbon to nutrient i in the biomass of j (either R or C), which converts the nutrients taken up into carbon. V_i symbolizes the maximum uptake rate and K_i the half-saturation density for nutrient i for the plant. K_C is the half-saturation density of the plant resource for the herbivore consumer. m_j is the metabolic rate. e stands for the assimilation efficiency of the consumer, f is the maximum feeding rate of the herbivore consumer and h is the Hill-exponent shaping the functional response of the consumer. The last terms of the nutrient equations (Eq. 3, 4) describe a nutrient recycling feedback loop. Nutrient i is freed by the herbivore through excretion, which is determined by the metabolic loss m_C of the herbivore and the inverse of the carbon to nutrient ratio $r_{i,C}$ of herbivore biomass.

Parameter definition

Our model includes the following temperature-dependent parameters: maximum nutrient uptake rate, V_i, herbivore maximum feeding rate, f, half-saturation densities, K_i, herbivore assimilation efficiency, e, and metabolism, m_j, of plants and herbivores. Other parameters are either independent of temperature, or temperature dependence has not yet been established (Uszko et al. 2017): turnover rate D, nutrient supply S_i, and carbon to nutrient ratios $r_{i,C}$ and $r_{i,R}$ of the herbivore and the plant, respectively.

We ran the model using different nitrogen and phosphorus supplies in order to simulate oligotrophic, average and eutrophic systems. We based the scenarios on measurements of nitrogen and phosphorus deposition acquired from literature (Dentener et al. 2006, Mahowald et al. 2008, Tipping et al. 2014). In addition to the average nutrient supply we used the minimum value that was reported to represent an oligotrophic system and the maximum for an eutrophic scenario (Table 2). We added an additional fertilization scenario to these literature-based scenarios in which we multiplied the nutrient supply from the eutrophic scenario by a factor of ten (Table 2). A factor of ten was chosen to reflect the high increases in nutrient input from anthropogenic sources we are already seeing (Galloway et al. 2008). We set the turnover rate of the system to 0.1 [1/day], meaning that it takes 10 days to renew the nutrients in the system (Cebrian 1999). We obtained the typical nutrient contents in plant tissue from a meta-study by Kerkhoff et al. (2005). Based on the data they compiled, we used a mean content of nutrients in plant tissue of 1.93% (SD = 1) and 0.15% (SD = 0.1) for nitrogen and phosphorus, respectively. As our model focusses only on nitrogen and phosphorus as nutrients, we pooled the remainder of the biomass (i.e. 97.92%) under the label of carbon, as the primary element. The resulting ratios of carbon to nitrogen in the tissue of the plant resource (r_N) of 50.7, and 662.7 for carbon to phosphorus (r_P) are similar to ratios reported in the literature (Elser et al. 2010). For the herbivore, we used constants for $r_{N,C}$ (6.5) and $r_{P,C}$ (171.6).

We used the mean estimates from our meta-study as activation energies for maximum uptake rate V_i, and half-saturation density K_i in our model. The parameter value at T_0, i.e. 20°C, was used as reference value and converted to realistic units (day^{-1} for V_i and g m^{-2} for K_i). We obtained the normalization constants and temperature dependencies for all other parameters from previous studies (Table 3). We set the Hill exponent, h, of the consumer to 1.2, i.e. a type III functional response (Vucic-Pestic et al. 2011, Kalinkat et al. 2013). The starting densities of nutrients, plants, and herbivores were all set to unity at 1 g m^{-2}. Simulations were run over a temperature-gradient from 10 to 25°C under four different nutrient supply scenarios (oligotrophic, average, eutrophic and fertilized, Table 2) for 100 000 timesteps (days). In addition we investigated a warming scenario, by comparing biomasses for each nutrient supply scenario at the initial temperature with the biomasses for the same nutrient supply at a 4°C higher temperature.

Global patterns of biomass

We wanted to show how a uniform increase in temperature by 4°C would shape global patterns of biomass. Two models were constructed that predicted the change in biomass in response to nutrient enrichment, in a system with average nutrient supply and a fertilized system (see above, parameters in Table 2). Both models assumed that temperature increased by four degrees. The change in biomass was then predicted across the globe using a linear model. Predictions were based on the current (1979–2013) annual temperature at a resolution of 30 arc-seconds (Biol 1, CHELSA Bioclim, Karger et al. 2017), and the slopes and intercepts derived from the two models based on 1) average and 2) fertilized systems.

Data deposition

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3sr11g3> (Marx et al. 2019).

Results

Temperature dependence of nutrient uptake

Our literature-derived database provided us with values for the half-saturation density and the maximum uptake rate for several plant species across a range of temperatures (see Supplementary material Appendix 1 Fig. A1–A8 for individual fits). The average activation energies for both

Table 2. Global nitrogen and phosphorus deposition rates (g m^{-2} day^{-1}).

	Oligotrophic	Average	Eutrophic	Fertilized	Source
Nitrogen	7.5×10^{-5}	1.4×10^{-3}	0.3×10^{-2}	0.03	Dentener et al. 2006
Phosphorus	8.5×10^{-6}	1.2×10^{-4}	0.1×10^{-2}	0.01	Mahowald et al. 2008, Tipping et al. 2014

Table 3. Temperature dependent parameters.

Parameter	Definition	Normalization constant	Activation energy	Source
m_C	herbivore metabolism	0.03	0.67	Brown et al. 2004, Lang et al. 2017
f	herbivore feeding rate	0.58	0.47	Yodzis and Innes 1992, Fussmann et al. 2014
K_C	herbivore half-saturation density	1	−0.11	Mulder and Hendriks 2014, Fussmann et al. 2014
e	herbivore assimilation efficiency	0.544	0.541	Lang et al. 2017
m_R	plant metabolism	0.01	0.69	Ryan 1995, Cannell 2000 Brown et al. 2004
V_N	maximum nitrogen uptake rate	0.17	0.22	this study
V_P	maximum phosphorus uptake rate	4.98	0.3	this study
$K_{N,R}$	half-saturation density of nitrogen	0.32	0.08	this study
$K_{P,R}$	half-saturation density of phosphorus	0.21	0.22	this study

Note that the parameters herbivore metabolism, plant metabolism, herbivore feeding rate and herbivore half saturation density include the effects of herbivore and plant body mass.

half-saturation density and maximum uptake rate were positive for nitrogen as well as for phosphorus (Fig. 3a). An increase of half-saturation densities with increasing temperature means that uptake of nutrients at low concentrations is reduced, eventually counteracted by an increase of maximum-uptake rates that increases the uptake rates across the whole range of nutrient concentrations.

While the average activation energy was positive for all parameters, the half-saturation density of nitrogen uptake (K_N), showed a negative activation energy in some studies (Fig. 3a). The activation energy for K_N ranged from −0.15 and 0.32, with a mean of 0.08. As the half-saturation density expresses the inefficiency of nutrient uptake, this suggests that the effect of warming on the efficiency of nitrogen uptake can, therefore, be positive as well as negative, but on average warming decreases efficiency (i.e. a positive activation energy of the half-saturation density). The activation energy of the half-saturation density of phosphorus uptake (K_P) ranged from 0.03 and 0.63, with a mean of 0.22. The average activation energy of K_P was higher than that of K_N and showed a wide range (Fig. 3a). The efficiency of phosphorus uptake, therefore, decreases with warming, but the magnitude of this decrease varies.

At the same time, the maximum nutrient uptake rate (V_i) showed a consistent increase with temperature, with positive activation energies for both nitrogen and phosphorus in all studies. In the case of nitrogen, the six species showed a range of activation energies of V_N from 0.11 to 0.39, with a mean of 0.22. For phosphorus, the activation energy of V_P ranged from 0.15 to 0.58, with a mean of 0.3. With increasing temperatures plants, therefore, increase the maximum amount of nutrients, they can take up per unit of time if infinite nutrients would be available. The trends are similar for nitrogen and phosphorus with maximum phosphorus uptake rates having a broader range and higher average temperature effect on maximum uptake.

Our results suggest that the half-saturation density and the maximum nutrient uptake rate both increase with warming. As the half-saturation density expresses the inefficiency of nutrient uptake, these two consequences of warming have contrary effects on the nutrient uptake by plants. As the activation energies for the maximum nutrient uptake, V_i, were found on average to be higher (0.22) than those for the half-saturation density, K_i (0.08), we see a positive net effect of warming on nutrient uptake (Fig. 3b–c).

In order to test the robustness of our results and justify the use of the average activation energy in our analysis, we additionally carried out a sensitivity analysis by comparing the most extreme scenarios (Supplementary material Appendix 1 Fig. A11). One extreme scenario would be the one in which temperature would have a negative, or somewhat less positive effect on plant growth, using the minimum activation energy for the maximum uptake rate and the maximum activation energy for the half-saturation density (the uptake inefficiency). The opposite extreme is the one where temperature has the most positive effect on plant nutrient uptake with the highest possible activation energy for maximum uptake rate and the lowest possible activation energy for half-saturation density. We found that our overall conclusion that nutrient uptake increases with warming is generally robust against variation in parameters between these extremes (Supplementary material Appendix 1 Fig. A11).

Simulations of biomass densities

We integrated the activation energies derived from our meta-study into the nutrient–plant–herbivore food-chain model described by Eq. 3–6. From the resulting time series, we can gain insight into the impacts of temperature and nutrient supply on plant and herbivore biomass. In all scenarios, the system enters a stable equilibrium after around 2500 time steps (days). We performed our analyses with the total biomass (i.e. the combined biomass of plant and herbivore) at the last time step (after 100 000 days) of each simulation. In all scenarios, increased temperature resulted in lower total biomass, while higher nutrient supply increased total biomass (Fig. 4a). For instance, an oligotrophic system at 25°C had 34% less total biomass than a system with the same nutrient supply at 10°C. A fertilized system had 51% less total biomass at 25°C, compared to 10°C. In a system at a temperature

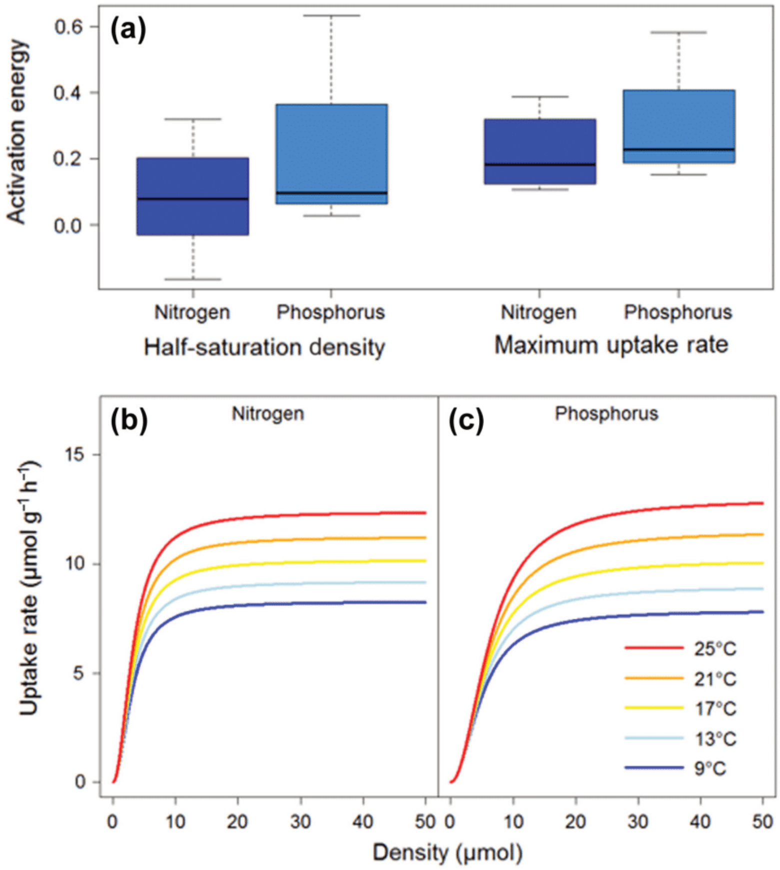

Figure 3. Temperature dependency of nutrient uptake by plants. (a) Activation energies for the half-saturation density (K_i) and the maximum uptake rate (V_i) for the nitrogen and phosphorus uptake by plants. (b–c) Nutrient uptake curves at different temperatures for nitrogen and phosphorus respectively.

of 25°C the eutrophic scenario produced a 3% higher total biomass than the oligotrophic scenario. At 10°C, the total biomass increase from oligotrophic to eutrophic was 14%. When comparing the oligotrophic to the fertilized scenario, a system at 25°C gained 17% total biomass, while at 10°C we found a 58% increase in total biomass in the fertilized scenario.

We calculated community respiration by summing up the respiration of the plant and herbivore populations. We calculated population respiration by multiplying plant or herbivore biomass with the respective temperature-dependent respiration rate (Schneider et al. 2016). Community respiration is directly affected by temperature through its positive activation energy but is also indirectly affected by temperature and nutrient supply as a result of their effects on biomass. We found community respiration to increase with increasing temperature. Increasing nutrient supply also resulted in higher respiration, as a consequence of the increase in total biomass (Fig. 4c).

In order to assess the potential effect of global warming, we looked at the changes in biomass that would result from warming the system by 4°C. An increase in temperature by 4°C resulted in a decline in biomass by 7.9% (oligotrophic cold system) to 18.3% (fertilized cold system). In all but the fertilized scenario, total biomass declined more strongly in a system with a warmer initial state (Fig. 4b). In the fertilized scenario this relationship was inverted, with the initially colder system showing a larger loss of biomass (18.3%) than the system with a warmer baseline temperature (16.7%).

Community respiration increased under a 4°C warming regime in all scenarios (Fig. 4d). Oligotrophic systems increased most, where the increase ranged from 24.2% in the warmer system to 34.7% in the colder system. The fertilized systems, by contrast, experienced community respiration increases between 18.3% and 19.4% (10°C and 21°C initial temperature, respectively). Systems that had higher initial temperatures experienced a lower increase of community respiration with 4°C warming than systems with initial cold temperatures.

Our results are based on a model with two nutrients that co-limit the growth of one plant. We have carried out sensitivity analyses addressing the consequences of scenarios in which only nitrogen (Supplementary material Appendix 1 Fig. A9) or phosphorous (Supplementary material Appendix 1

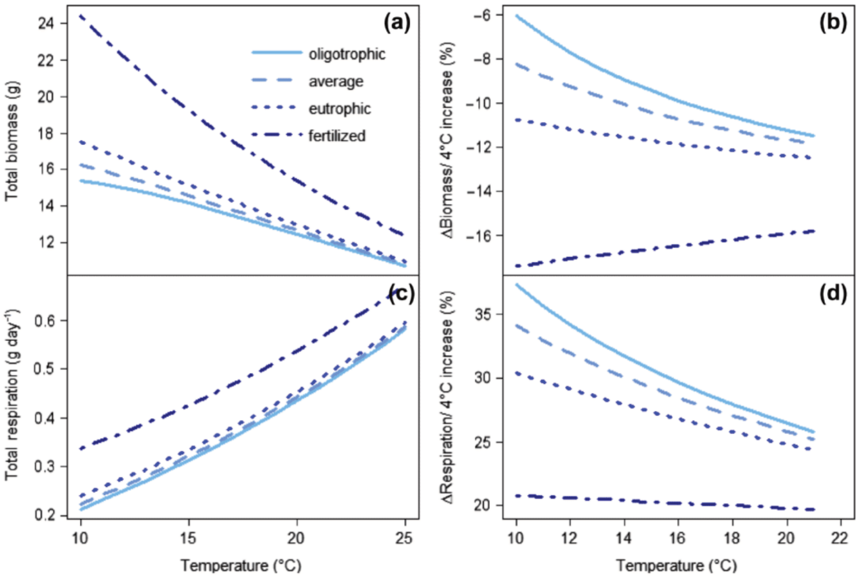

Figure 4. The impact of temperature on total biomass and total respiration under different nutrient supply scenarios. (a) Total community biomass at different temperatures; (c) the corresponding total respiration. (b–d) Show the %-change (Δ) in biomass and respiration, respectively, that would occur if the system would be warmed by 4°C, the x-axis here represents the baseline temperature.

Fig. A10) limit plant growth. The results show steep declines in biomass with temperature leading to plant extinction, which also causes crashes in total respiration.

Discussion

We addressed the temperature-dependence of nutrient uptake by plants and its consequence for the carbon storage across the biomass compartments of plants and herbivores using a model of a nutrient–plant–herbivore food chain. In our meta-study, we found positive activation energies for both half-saturation density and maximum uptake rate for the uptake of nitrogen (N) and phosphorus (P) by plants, meaning that these parameters all increase with warming. While an increase of half saturation densities implies a decrease of the nutrient-uptake efficiency with warming – especially at low nutrient concentrations – increased maximum uptake rates allow for better nutrient uptake in plants across the full range of nutrient concentrations. This finding, however, does not conflict with the decreasing plant carrying capacities of prior studies, which was also supported in our study. The decline of carrying capacity can be explained by the stronger increase of plant respiration (i.e. the biomass loss rate) compared to the nutrient uptake rate (constraining the biomass production rate). Consistent with our hypotheses and in agreement with prior studies, our simulations of a three-level food chain show a decrease in community biomass (i.e. the sum of the plant and herbivore biomasses) with warming, despite the increases in maximum uptake rates. These results on the plant nutrient uptake under warming and knock-on effects on the carbon distribution across the biomass pools provide a mechanistic understanding of climate change impacts on the total biomass of natural communities, which has implications for ecosystem functions and services.

Meta-study

In our meta-study, we have only been able to find six studies reporting values for maximum nitrogen or phosphorus uptake rate and half-saturation densities at different temperatures. The small sample size limits our ability to make precise predictions of changes in plant nutrient uptake with increasing temperature. This uncertainty is captured in the relatively broad 95% confidence intervals of our estimated activation energies (Fig. 3a). In addition, measurements are often not replicated across many temperatures, which may create additional sources of error by inaccurate estimates of activation energies in the individual studies (see Pawar et al. 2016 for a detailed discussion on estimates of activation energies with small sample size). If there is no systematic source of error, however, averaging the activation energies across studies as in our metastudy should lead to more reliable mean estimates. Nonetheless, we can conclude that three of the four parameters (half saturation density of phosphorous uptake, and maximum uptake rates of phosphorous and nitrogen) do not include zero in these large confidence intervals, which suggests that they increase with warming. Only for the half-saturation density of nitrogen, we found negative activation energies for half of the studied species including the two marine species and one terrestrial species. The separation of responses in different ecosystems poses the questions whether there is a systematic difference between marine and terrestrial species or whether marine species are more variable in general. As soon as more data become available, it would be interesting to separate marine from terrestrial species. Our sensitivity analysis indicates that despite the low sample size and the resulting uncertainty in the parameter estimates, we can conclude that warming increases the nutrient uptake by plants. These overall positive activation energies allow us to make predictions as to the direction of such changes with global warming (Fig. 3a).

Overall, we found a higher variation in activation energies for phosphorus (P) uptake than for nitrogen (N). In other studies, the effects of global change drivers on plant P content have also been found to be more variable than for N (Gifford et al. 2000, Sardans et al. 2012). There might be an overall pattern that plants differ more strongly in their handling of P than they do for N, which could be the result of plants having developed more varying strategies to access P, due to its often limiting nature (Elser et al. 2007, Richardson et al. 2011).

While the average activation energies were all positive, they differed in their magnitude. These differences in activation energies between N and P uptake could indicate a shift in nutrient limitation with increasing temperatures. While we found higher uptake rates for N than for P at low temperatures, the higher average activation energy of the maximum nutrient uptake rate of P means that P uptake could match or even surpass N uptake at higher temperatures. A reason for these different temperature effects may be found in the increases in nutrient uptake efficiency in organisms associated with plants such as fungi (Bárcenas-Moreno et al. 2009). However, as plants need more N than P (Elser et al. 2000), they may not be able to use this potential for increased P uptake fully and could become increasingly N limited under warming conditions. Changing uptake rates might therefore lead to N being the limiting element for plant growth, rather than P. This effect might, however, be counteracted by the severe N fertilization from human sources, which is not matched by P input, as well as increasing N mobilization by bacteria under warming (Howarth 2004, Sardans et al. 2012).

Simulations

In prior model studies, carrying capacity (the plant biomass that is supported) has often been assumed to be constant or decrease with temperature (Uszko et al. 2017). To enable comparisons between these studies and our model in which plant densities depend on temperature-dependent nutrient uptake, we added a simulation with only plants and nutrients (Supplementary material Appendix 1 Fig. A14). The resulting final plant densities represent the carrying capacities and show a systematic decrease with warming. This pattern is the result of the interplay between multiple temperature-dependent processes. While the increase in maximum uptake rate with temperature might have led to higher plant biomasses, this is overcompensated by the increase in half-saturation density with temperature (indicating a decrease in nutrient-uptake efficiency) and a much stronger increase in metabolism leading to a strong biomass loss to respiration. Together, the results of our metastudy and model simulations thus support prior assumptions that carrying capacities should decrease with warming (see Uszko et al. 2017 for discussion) and a prior laboratory study (Bernhardt et al. 2018).

Previous studies of ecosystems under warming conditions have predicted a higher impact of increasing temperature in warmer systems like the tropics than in temperate zones (Deutsch et al. 2008, Dillon et al. 2010, Sunday et al. 2011). Our results confirm this expectation as we find warming by 4°C to result in an increased loss of biomass in systems with warmer baseline temperatures than in initially colder systems. This is a result of the exponential nature of the temperature dependencies of the physiological rates, where the rate of increase is higher at higher baseline temperature. This gradient can be illustrated at the global scale using mean annual temperature as the baseline (Fig. 5a) (CHELSA, Karger et al. 2017). Dillon et al. (2010) showed that the expected changes in metabolic rates due to increasing temperature are equivalent in magnitude in the tropics and temperate zones, despite the smaller increase in temperature expected in the tropical regions. Our results, however, show a more substantial loss of biomass and an increase in metabolism under tropical temperatures (Fig. 5a). This is the result of the 4°C temperature increase being applied to the whole global map, without including the lower projected temperature increase in the tropics (Deutsch et al. 2008). Future studies should thus tackle simulations of population densities at the level of grid cells with specific predictions of expected warming for different regions. In addition, this would allow using more highly resolved temperature time series of monthly or daily averages, which would decrease inaccuracies by averaging over non-linear relationships as described by Jensen's inequality (Bernhardt et al. 2018).

At all baseline temperatures, the loss of biomass is strongly amplified by fertilization. However, different from the other scenarios, the biomass loss due to 4°C warming in the fertilized scenarios is most substantial in the regions with a low baseline temperature (Fig. 5b). It appears that after a certain threshold of nutrient availability is crossed, the effect of warming is inverted. The difference in the effect of temperature in the fertilized scenario highlights the importance of investigating the interactions between temperature and nutrient supply (Cross et al. 2014).

Future directions

Warming affects all parts of biological systems in parallel. While our model includes many temperature-dependent rates (metabolism, feeding rate, nutrient uptake rate and assimilation efficiency), there are other rates, not considered in our model, that might be temperature-dependent. For example, abiotic and biotic processes relevant to the availability of nutrients in the system, like water availability or microbial activity, are likely affected by temperature and would imply a temperature impact on nutrient supply rate (Gilbert et al. 2014).

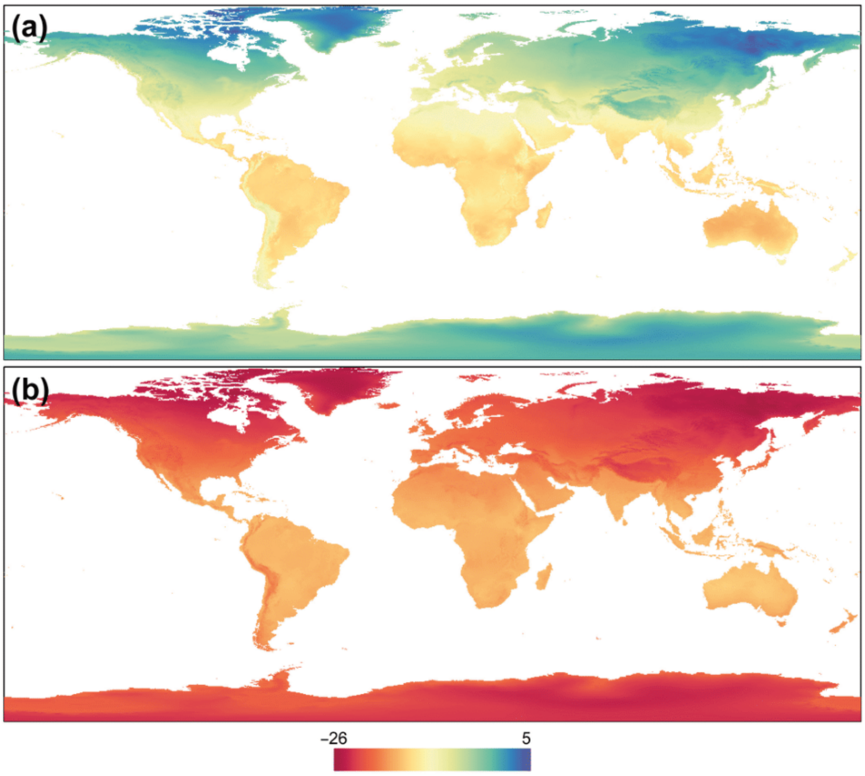

Figure 5. Change in biomass with 4°C warming compared to the current mean annual temperature (CHELSA, Karger et al. 2017). The map in (a) shows the change in biomass if a system with average nutrient supply is warmed by 4°C. (b) shows the change in biomass with 4°C warming in a fertilized system.

It is also important to mention that our method of establishing temperature dependencies assumes a monotonic increase or decrease rather than a hump-shaped temperature relation (Gilbert et al. 2014, Amarasekare 2015). It has been argued that models looking at only the increase are valid only for the 'biologically relevant temperature range' – temperatures that are below the optimum but high enough to yield positive growth rates (Savage et al. 2004). However, there are also arguments that under climate change temperatures that go beyond this range become relevant (Englund et al. 2011). While hump-shaped temperature relations are generally found for single species, the scaling of physiological rates at the community level across species might be well approximated by an Arrhenius relation with temperature (Yvon-Durocher and Allen 2012, Barneche et al. 2014). Future studies should use our temperature-dependent nutrient uptake rates at the species level and scale the results up to the community level across species.

As our study showed interactive effects of temperature and nutrient supply, another interesting expansion would be to allow plants to adapt to environmental conditions using a flexible stoichiometry. The resulting changes in plant nutrient content are likely to have effects on the higher trophic levels by changing feeding rates, as well as assimilation efficiency and, as a result, the growth rates of the herbivores (Rosenblatt and Schmitz 2016, Jochum et al. 2017, Skau et al. 2017). Along with temperature change and changes in nutrient supply CO_2 increases as a result of anthropogenic activities. This increase in carbon availability might further influence plant growth, especially when combined with temperature and nutrient supply (Rosenblatt and Schmitz 2016). In particular, CO_2 supply will likely play a role in the stoichiometry of plants, by changing the C:N ratios. It would, therefore, be useful to integrate CO_2 into the model.

Conclusions

Using explicit temperature dependencies of nutrient uptake as well as realistic nutrient supply scenarios, our model provides more realistic projections of carbon storage in biomass in the biological compartments of ecosystems than previous models. We found biomass to decline in all scenarios considered in this study. The more severe biomass decline with warming found in regions with warmer initial temperatures, implies a stronger decrease in biomass-based ecosystem functions and services in tropical areas than in temperate zones. When looking at the low-nutrient and warm scenario which is most likely to represent a tropical system, we see a biomass loss similar to that of a eutrophic system with colder temperatures best mimicking temperate ecosystems.

Our results show a different effect of warming on biomass in highly fertilized areas, where the effect is stronger in systems with colder initial temperatures. Agricultural areas in the temperate zones might, therefore, face particularly severe declines in biomass. Associated issues could be decreases in agricultural yields and declines in biological pest control. Overall, our study thus suggests warming to cause declines in the biological carbon storage across trophic levels and biomass declines in tropical as well as eutrophic temperate ecosystems, which will severely undermine the provisioning of ecosystem services.

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Supplementary material (available online as Appendix oik-06141 at <www.oikosjournal.org/appendix/oik-06141>). Appendix 1.

2 | Flexible Stoichiometry and compensatory feeding

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

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. 2015; 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 across different levels of nutrient availability. Together, these studies indicate considerable variation in the tissue stoichiometry of plants across sites and species.

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

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

In this study, we use a population-dynamics model integrating nutrient-plant and plant-herbivore interactions to address (1) how flexible stoichiometry and compensatory feeding affect population dynamics, stoichiometric mismatch, and carbon (C) storage in a tri-trophic nutrient-plant-herbivore system and (2) how these strategies affect the survival and biomass of plants and herbivores in a world faced with warming and changes in nutrient availability. We simulate the nutrient-plant-herbivore system (N represents the nutrients) using three models (Figure 1). We start from a baseline model, including the temperature dependencies of (1) plant nutrient uptake, (2) the herbivore feeding rate, and (3) the plant and herbivore metabolic rates. In the second model, we allow plants to adjust their N:C ratio by changing their C uptake as a function of N uptake, depending on nutrient availability (flexible stoichiometry model). In the third model, in addition to flexible stoichiometry, we give our herbivores the ability to adapt their feeding rate to the N:C ratio of their plant resource (compensatory feeding model). As compensatory feeding is a direct reaction to the varying plant N:C ratios, we refrained from running a model with compensatory feeding but without flexible stoichiometry, which would yield the same dynamics as the baseline model. We hypothesize that flexible plant stoichiometry should allow for higher biomass production even at low nutrient supply, along with a decrease in the plant N:C, as plants consume more C relative to N (compared to the baseline model).

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

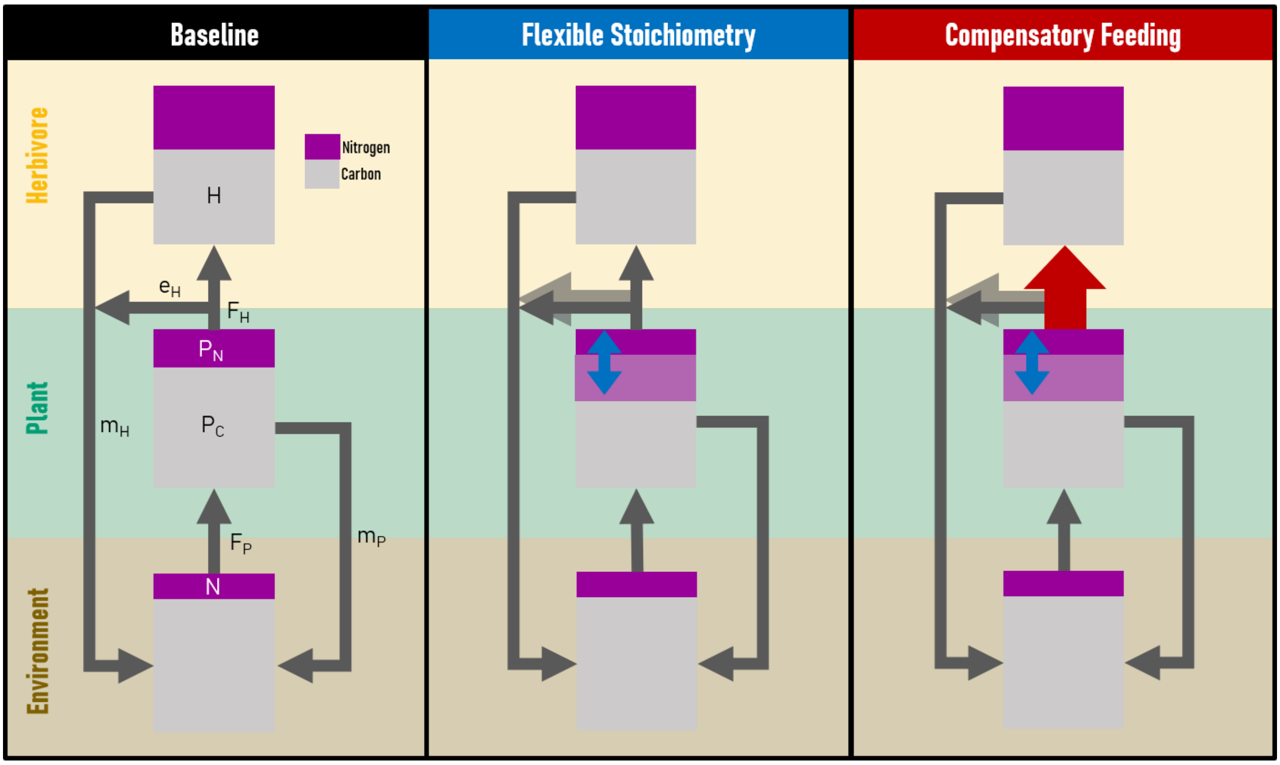

Figure 1: Conceptual figure showing the structure of our three models: baseline (left), flexible stoichiometry (middle) and compensatory feeding (right). The model terms are shown in the baseline panel with N as the environmental nitrogen pool, P_C and P_N as plant nitrogen and carbon respectively, and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

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 an 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:

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

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

$$F_P = \frac{V_N N}{K_N + N} P_C \tag{2}$$

where V_N refers to the maximum N uptake rate, and K_N is the half-saturation density. Here, the N uptake directly relates to plant biomass (P_C). This equation is equivalent to a type II functional response.

The herbivore feeding follows a type III functional response and is given by:

$$F_H = \frac{f_H P_C^h}{K_H^h + P_C^h} H \tag{3}$$

The plant C uptake is given by multiplying plant C:N with the N uptake.

The equations for the plant N and C compartments write:

$$\frac{dP_N}{dt} = F_P - \frac{P_N}{P_C} F_H - \frac{P_N}{P_C} m_P P_C \tag{4}$$

$$\frac{dP_C}{dt} = \frac{P_C}{P_N} F_P - F_H - m_P * P_C \tag{5}$$

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

$$\frac{dH}{dt} = e_H F_H - m_H H \tag{6}$$

Where e_H stands for the assimilation efficiency of the herbivore. f_H is their feeding rate, and K_H the half-saturation density. h is the Hill-exponent, which shapes the functional response of the consumer. The loss from the plant N pool to the herbivore is given by multiplying herbivore feeding with the plant N:C ratio. We assume the proportion of N and C transferred from the plant to the herbivore to be equivalent to the plant N:C ratio.

In the flexible stoichiometry model, the plant N:C ratio is related to N availability. Higher environmental N availability will increase N:C ratio, following a saturating hyperbolic curve up to the maximum N:C ratio (Figure 2a). The result is a decrease in the C uptake relative to the N uptake, as expressed by:

$$\frac{dP_C}{dt} = \frac{1}{((maxNC - minNC) * \frac{F}{K_N + \mathrm{F}}) + minNC} * F_P - F_H - m_P * P_C \tag{7}$$

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

In this model, the herbivore assimilation efficiency is dependent on their plant N content (Jochum et al. 2017) and given by:

$$logit(e_H) = a\,(\frac{P_N}{P_C + P_N} * 100) + b \tag{8}$$

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

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

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

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

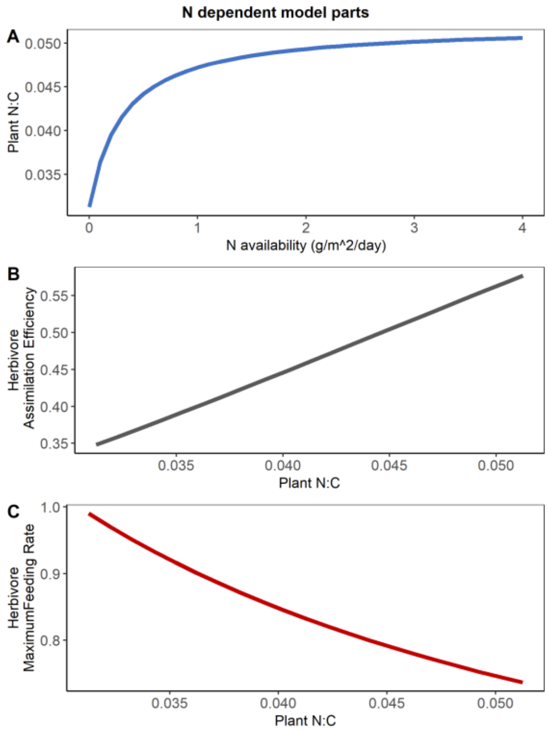

Figure 2: N-dependent model parameters. A) Plant N:C dependence on N availability; B) Herbivore assimilation efficiency based on plant N:C; C) Herbivore maximum feeding related to plant N:C ratio.

Parameters

We parameterized the models using literature data for both temperature-dependent and temperature-independent parameters. We set the temperature-independent parameters to the following values: We use a value of 0.1 [1/day] for the turnover rate D, meaning that the system's nutrients are renewed every ten days (Cebrian 1999). The Hill exponent, h, we set to 1.2, giving the herbivore a type III functional response (Vucic-Pestic et al. 2011; Kalinkat et al. 2013). 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 the values reported by Yu et al. (2011), who found a variation of about 25% for plant N:C, meaning that in the flexible stoichiometry model, min_{NC} is 0.037 and max_{NC} 0.022. The herbivores have a much higher N:C, which we set to 0.154, based on Elser et al. (2000b).

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

Model runs

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

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

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

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.

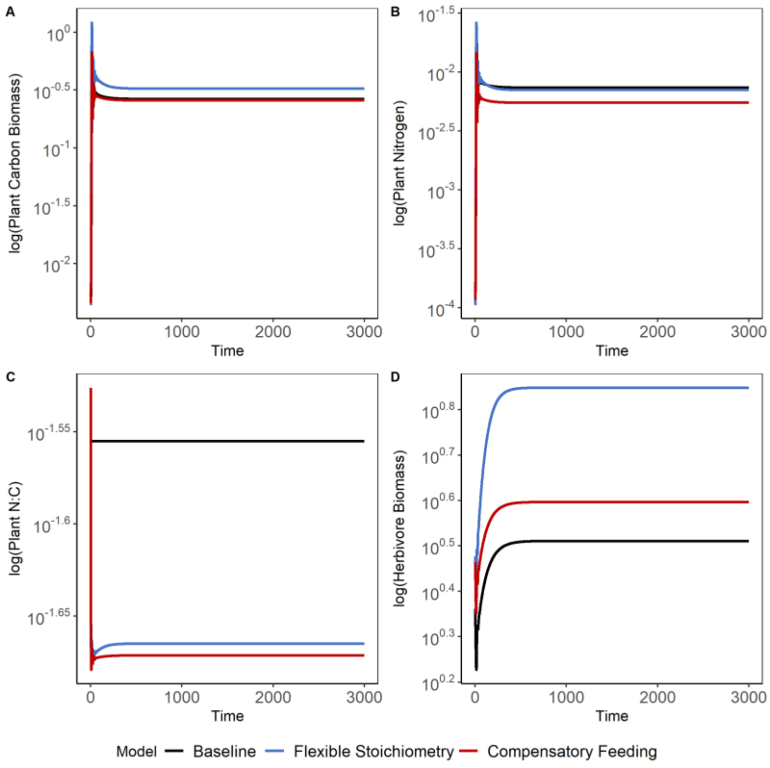

Figure 3: Time-series of the baseline, flexible stoichiometry and compensatory feeding models under mesotrophic conditions at 20°C. A) shows plant carbon biomass, B) plant nitrogen, C) plant N:C ratio, and D) herbivore biomass.

Temperature

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

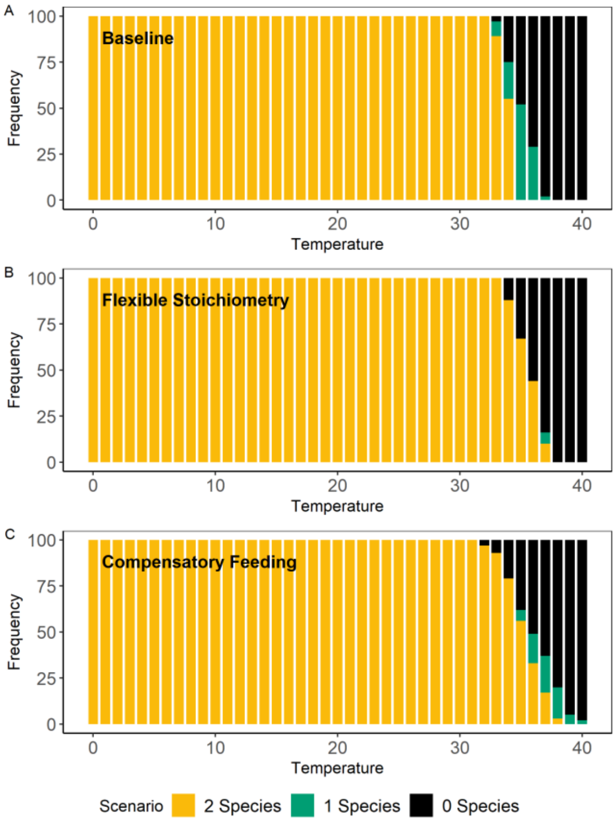

Figure 4: Frequency of survival scenarios across temperature. In yellow are the runs where both plants and herbivore survive, green are the runs where the plant survives, but the herbivore goes extinct and black shows the runs in which both species go extinct. Plot A shows the baseline model, B is the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

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

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

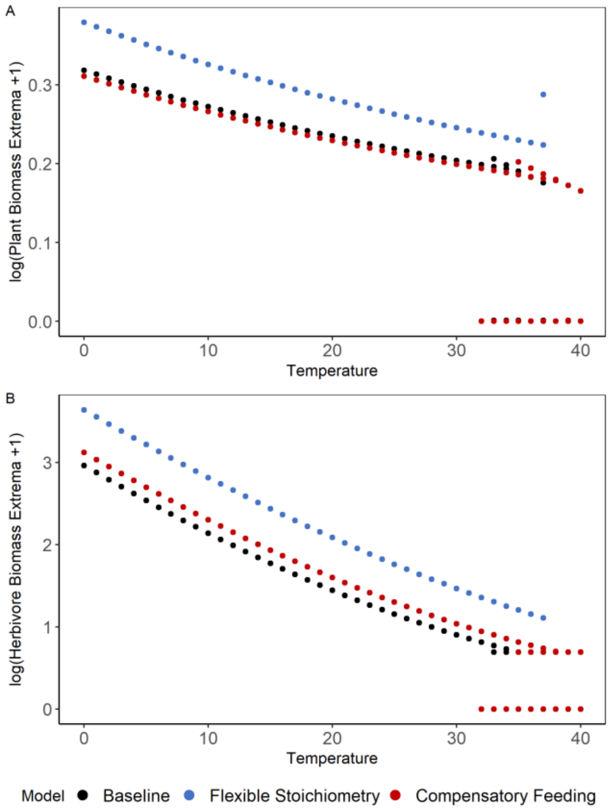

Figure 5: Bifurcation diagrams of equilibrium biomasses of plants (A) and herbivores (B) under mesotrophic conditions (0.00197 mg N/m²/day) across a temperature gradient.

Nutrient availability and temperature

In addition 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.

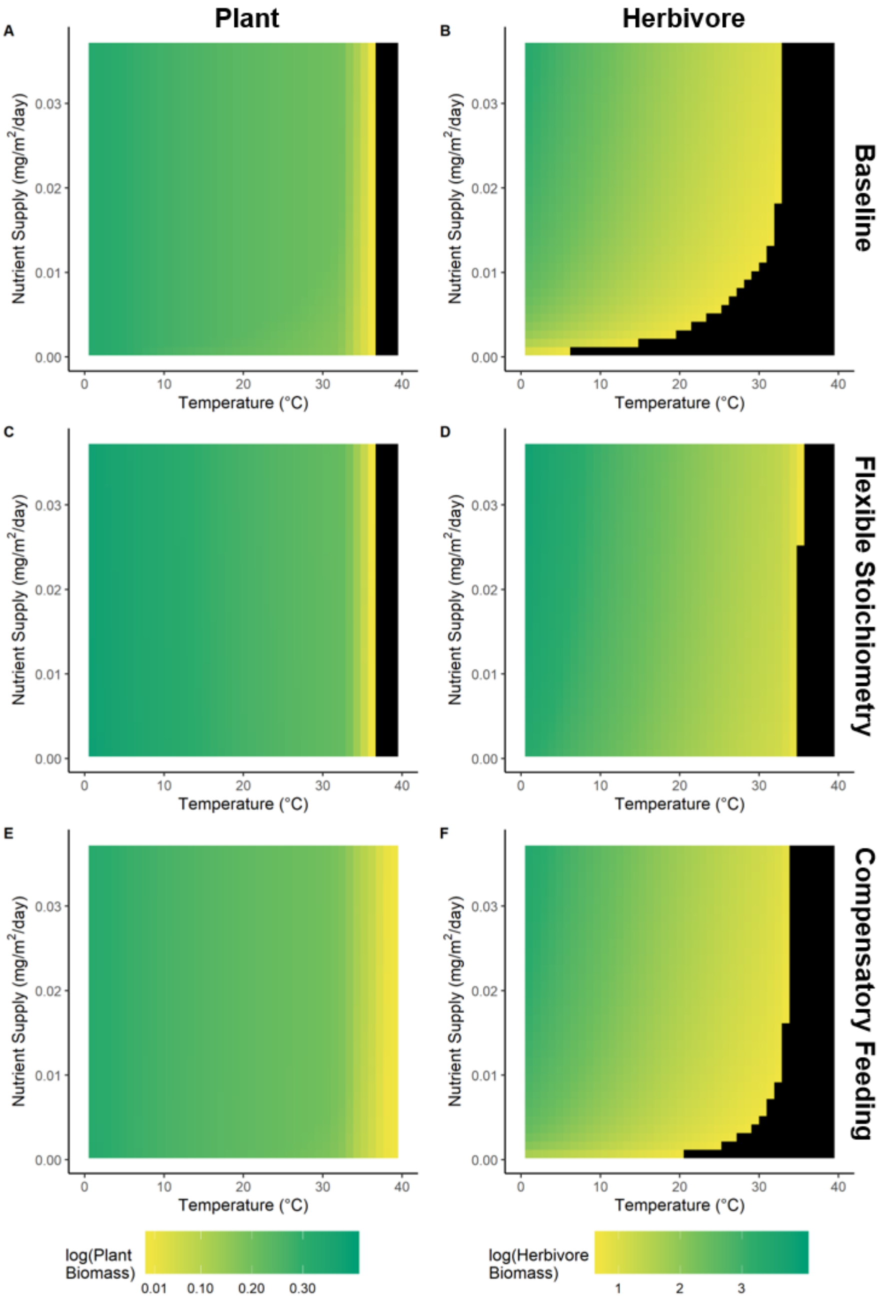

Figure 6: Heatmaps of the plant (left) and herbivore (right) biomass for the baseline model (A & B), the flexible stoichiometry model (C & D), and the compensatory feeding model (E & F). Black areas mean extinction.

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

Future directions

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

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

Rising levels of atmospheric CO_2 levels could have a further impact on plant N:C ratios. Zvereva et al. (2006) reviewed studies on plant quality as food for herbivores under elevated temperature, elevated CO_2, and a combination of both. They found that N concentration in plant tissue decreased under elevated CO_2 (see Rosenblatt & Schmitz (2016). However, rising temperatures can mitigate this effect, which is also highly species and context-specific (Robinson et al. 2012). Herbivore performance is negatively affected by increases in temperature, but positively if CO_2 rises simultaneously, possibly due to the rise in C demand from higher metabolic rates (Zvereva and Kozlov 2006; Malzahn and Doerfler 2016). The CO_2 level could impact plant chemistry, especially at intermediate N supplies, by influencing the steepness of the curve between the minimum and maximum plant N:C ratios. This finding shows how important it is to look at several global change factors in parallel instead of studying them in an isolated way. It would therefore be an interesting addition to run the three models under a range of CO_2 concentrations.

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

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

Conclusion

We investigated if flexible stoichiometry in plants and compensatory feeding in herbivores are beneficial strategies, especially when faced with warming or changes in nutrient availability. We found that flexible stoichiometry led to higher biomasses and increased survival under most conditions, thereby counteracting some of the negative impacts of moderate warming or low nutrient supply. As a result, we would expect a shift in communities towards plant species that display flexible stoichiometry under warming conditions. However, under very high temperatures, flexible stoichiometry might become too costly and is not necessarily beneficial anymore. Surprisingly, compensatory feeding does not appear to be a good strategy for herbivores under most conditions. Hence, we would expect this strategy to occur at a low frequency in warmer climates. Our findings highlight the importance of integrating adaptive and behavioural plasticity in population-dynamic models that address the consequences of global warming and eutrophication.

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III

General Discussion

1 | Synopsis

The world's ecosystems face the combined pressure of many anthropogenic global change drivers, including warming and changing nutrient cycles. As outlined in the introduction, these pressures take effect in biological systems through all kinds of pathways. To predict how global change will affect biomass production and the provision of ecosystem services, we must understand the effect of warming and nutrient supply on the processes underlying ecosystem functioning. Countless studies have investigated different aspects of ecosystem response to global change (e.g. Petchey et al. 1999; Brose et al. 2012; Domis et al. 2014; Cross et al. 2015; Binzer et al. 2015). Despite this wealth of literature, we still lack understanding of some of the pathways through which global change drivers influence ecosystem functioning. For example, the mechanisms behind the effect of warming on plant growth remain poorly understood.

Many of the rates and ratios determining biological interactions vary with temperature or body mass (Petchey et al. 1999; Savage et al. 2004; Vucic-Pestic et al. 2010; Ehnes et al. 2011; Englund et al. 2011; Rall et al. 2012). In addition to these sources of variation, organisms have an inherent ability to adapt to changing situations, e.g., by varying their elemental ratios or changing biological rates (Cruz-Rivera and Hay 2000; Klausmeier et al. 2007; Hillebrand et al. 2009; Bonachela et al. 2011; Jochum et al. 2017). The temperature-dependence of biological rates and organism responses to environmental pressures have the potential to severely affect model outcomes with respect to the direction or magnitude of the effect of global change (Vasseur and McCann 2005; Sistla and Schimel 2012; Moorthi et al. 2016; Kwiatkowski et al. 2018). Furthermore, interactive effects of several global change drivers come into focus more and more often, but there are still gaps in our knowledge of how these interactions might aggravate or mitigate any adverse effects of global change (Oliver and Morecroft 2014; Rillig et al. 2019).

In this thesis, I addressed some of these gaps in our understanding of the mechanisms and pathways through which global change affects biological systems by investigating the following questions:
(1) How do the global change drivers of warming and changing nutrient supply interact to affect the flow of elements and energy between the environment, plant and herbivore populations? (2) What role does temperature play in determining plant nutrient uptake rates? (3) What is the effect of temperature-driven plant nutrient uptake on community biomass production under warming and different nutrient supplies? (4) How does flexible plant stoichiometry mediate the effect of warming and nutrient supply on plant and herbivore growth and interaction? (5) Is compensatory feeding a helpful strategy for herbivores to meet the challenge of low food quality? (6) How relevant are the currently understudied mechanisms of temperature-dependent plant nutrient uptake, flexible stoichiometry and compensatory feeding for accurate prediction of population dynamics, biomass production and ecosystem service provision under global change?

I approach these questions by extending current models with temperature-dependent plant nutrient uptake and developing models in which the plants and herbivores can respond to environmental conditions, respectively, by adapting their stoichiometry and feeding rate. These models allow me to contribute to the discussion of how population dynamics, biomass production and the provision of ecosystem services are affected by global change (see, e.g., Yvon-Durocher et al. 2010; Traill et al. 2010; Domis et al. 2014; Cross et al. 2015; Dee et al. 2017).

2 | Findings & Implications

To begin answering the questions above and learn about the mechanisms causing the temperature-dependency of plant growth, I established temperature-dependent plant uptake rates of two essential nutrients: nitrogen (N) and phosphorus (P).

Using literature reports of experimental measurements, I found positive activation energies for the kinetic parameters of half-saturation density and maximum nutrient uptake rate for both nutrients. Positive activation energy means the parameter increases with temperature. Finding positive activation energy for maximum nutrient uptake rate tells us that the nutrient uptake curve's saturation point shifts upwards with increasing temperature. Therefore, if the environmental nutrient supply is high enough for plants to approach their maximum uptake rate, their nutrient uptake rate increases with warming. In contrast, the positive activation energy of the half-saturation density (nutrient supply at which half of the maximum uptake rate is reached) causes a decrease in nutrient uptake efficiency at low environmental nutrient density with warming.

The variation in activation energies is higher for P than N, consistent with the observation that plants appear to be more variable in their handling of P than of N (Gifford et al. 2000; Elser et al. 2007; Yu et al. 2011; Richardson et al. 2011; Sardans et al. 2012). The comparatively higher activation energy of the maximum uptake rate of P than of N could indicate a shift from P- to N-limitation as plants optimize their P uptake, but cannot keep up with their comparatively higher N demand (Elser et al. 2000a). On the other hand, the increasing N supply from anthropogenic sources may allow plants to operate close to their maximum uptake rate for N, while the comparatively lower P supply means that plants cannot fully use the increase in uptake potential under warming (Howarth 2004; Sardans et al. 2012).

Using this temperature-dependent nutrient uptake as a basis for plant growth, I simulated a nutrient-plant-herbivore community across a temperature gradient under different nutrient supply scenarios. Community biomass production decreased with warming and increased with nutrient supply. The plant carrying capacity is often expected to be independent of, or decrease with, warming (Uszko et al. 2017). Combining the findings from the meta-study in chapter 1 on activation energies of maximum nutrient uptake rates (0.22 for N, 0.3 for P uptake) with literature data on the activation energy of plant metabolism (0.64) indicates a decline in plant carrying capacity with warming, as metabolism increases more strongly than maximum nutrient uptake.

The initial climatic conditions of a system are likely to mediate the effect of a temperature rise, with a more substantial impact expected in already warm systems (Deutsch et al. 2008; Dillon et al. 2010; Sunday et al. 2011). Simulating a temperature increase of 4°C above the annual temperature average, I found a more substantial reduction in biomass production in regions with a higher baseline temperature than in initially cooler areas. In an already warm system, the temperature increase is more likely to tip the community over the edge of the ecologically feasible temperature range. In general, fertilization amplified the negative effect of warming on biomass production. Interestingly, under fertilization, the effect of warming by 4°C was more pronounced in regions with colder initial temperatures. Consequently, increasing nutrient supply can invert the relation between initial climatic conditions and vulnerability to warming, highlighting the importance of combining global change drivers in our models (Kratina et al. 2012; Domis et al. 2014; Cross et al. 2015; Binzer et al. 2015).

Making realistic predictions of changes in the flow of elements and energy through a nutrient-plant-herbivore system also means including flexibility in plant stoichiometry. Allowing plants to vary their carbon (C) uptake depending on N availability caused an increase in both plant and herbivore biomass. Evidently, the increase in primary production is sufficient to fully compensate for the decline in food quality for the herbivore. In other words, high quantity made up for low quality. Flexible stoichiometry in the plants also improved the herbivore's chances of survival when faced with adverse conditions like low nutrient supply or high temperature.

When herbivores face variable nutrient supply in their resource, it is only logical for them to develop a response mechanism like compensatory feeding (Cruz-Rivera and Hay 2000; Berner et al. 2005; Fink and Von Elert 2006; Suzuki-Ohno et al. 2012; Iannino et al. 2019). Interestingly, increasing feeding rates to compensate for low-quality food did not increase herbivore biomass. Instead, both plant and herbivore biomasses were lower in the compensatory feeding model than in the model with flexible stoichiometry only. The substantial decline in food quality causes such a large increase in herbivore feeding rate that they deplete their resource by 'overfeeding'. Under particularly adverse conditions, this increased top-down pressure can decrease plant biomass sufficiently to drive the herbivore into extinction. The extinction threshold depends on a combination of temperature and nutrient supply. Under oligotrophic conditions, we see extinctions at lower temperatures than under eutrophic conditions. The parallel increase of temperature and nutrient supply could decrease extinction pressure for herbivores, once more highlighting the importance of combining several global change drivers to make accurate predictions.

Accurately predicting biomass production and ecosystem service provision requires knowledge of whether and how the model extensions of temperature-dependent nutrient uptake, flexible stoichiometry, and compensatory feeding mediate the effects of warming and nutrient supply (Kremen 2005). In both of my research chapters, I found decreasing community biomass with warming. In chapter 2, I showed that flexible plant stoichiometry leads to an increase in biomass production, while at the same time decreasing the quality due to higher C:N ratios. Compensatory feeding decreased overall biomass production. Both biomass quantity and quality play a role in ecosystem service provision (de Groot et al. 2002; Finney et al. 2016). Whether biomass production or C to nutrient ratio is most important depends on the ecosystem service in focus (Finney et al. 2016). I will now discuss the implications of my findings for a few exemplary ecosystem services.

Carbon storage in plant and animal biomass is an important ecosystem service, especially in the face of climate change. Increased carbon storage may help mitigate global warming while decreasing storage could accelerate the rate of change (Kirschbaum 2003; Hymus and Valentini 2007; Verkerk et al. 2014). More biomass production means higher carbon storage by the ecosystem. My finding of decreased biomass production in chapter 1, points to a decrease in carbon storage provision with warming. However, the increase in biomass produced under the flexible stoichiometry model in chapter 2, indicates that models with a fixed plant stoichiometry may underestimate biomass production. Compensatory feeding by the herbivore caused a decline in biomass production, almost back to baseline level, proving how important it is to consider the different adaptive strategies of organisms when predicting ecosystem responses to global change.

Another very relevant ecosystem service is food production. Here the balance of biomass quantity and quality is very relevant (Finney et al. 2016). Warming caused a decrease in biomass production that could be at least partly compensated by plant flexible stoichiometry. Simultaneously, flexible stoichiometry leads to a decrease in C:N ratios, decreasing the quality of crops for human consumption. To make predictions and suggestions for the future of our food supply, it is therefore very relevant to consider how temperature influences plant growth and investigate how flexible our food plants are and how they will react to the combination of changing nutrient supply, temperature and CO_2-concentrations.

An ecosystem service closely related food production is pest control. When faced with decreasing food quality, herbivores may react with increasing feeding rates. In chapter 2, I show that compensatory feeding is not beneficial for the herbivore biomass production under the circumstances modelled there, as by increasing their feeding rate, they deplete their resource. Consequently, we might not see increasing feeding rates long term. However, herbivores might still resort to compensatory feeding in the short term, if it is the only way they can maintain their elemental balance. Sudden feeding rate increases could potentially cause severe damage to crops. Therefore, we should combine more in-depth knowledge on crop quality responses to global change with information on plant pest reactions to changes in the quality of their plant prey, to predict changes in yield.

This short excursion into the potential implications of my findings for ecosystem service provision once more highlights the importance of considering the interactive effects of global change drivers and the inherent ability of organisms to adapt to changes in their environment. The models I developed in this thesis help complete our picture of future ecosystems, but there are still many more parts to uncover.

3 | Challenges & Extensions

3.1 Model challenges

Just like all models of population dynamics, the models in this thesis face certain challenges. For one, there is the so-called "curse of dimensionality" (Yodzis and Innes 1992). Natural populations interact with so many others, that if we were aiming to include all possible interactions, the result would be an immensely complex model. The results of such a model would be nearly impossible to read and interpret, aside from needing vast amounts of computational power. In addition, there is the "plague of parameters" (Yodzis and Innes 1992). Including all the parameters that play a role in population dynamics, makes it increasingly difficult to discern the effect of a single one.

When designing model studies to produce meaningful results that are also legible and computable, we forcibly need to make choices about what to include, to make them as complex as necessary, but as simple as possible. Following the example from Yodzis & Innes (1992), I aimed to make my models plausible by basing them on experimental data on rates and the scaling of rates to ensure the exclusion of biologically impossible parameter combinations. Using averages from several literature studies, my models stay within a biologically realistic range and are generally applicable, as they are not tailored to a single species. Nonetheless, this approach comes with a range of caveats. For example, we may be able to discern some general trends, but we cannot directly read off the effect of global change on a specific system. However, it is certainly possible to apply the models to a specific system, provided that we know the relevant parameter values. For example, we could use the model to explore the effect of flexible plant stoichiometry under warming of 4°C on the interaction of the herbivorous insect and its food plant described in the introduction. We could allow the C:N ratio of the plant to vary between 27 and 45, while the herbivore has to maintain homeostasis at its C:N ratio of 6.5, and determine how this affects plant and herbivore performance under various environmental conditions.

Even though my models include nutrients, they still use C as the main currency. The nutrients serve as a factor mediating the flow of C between the populations. This approach comes with its own caveats. Focusing on C as a proxy for biomass and using it to draw conclusions on population performance, may obscure certain aspects important for fitness and function related to elemental balance rather than biomass (Leal et al. 2017). For example, in the flexible stoichiometry model, the high biomass production may look like high performance, but there are likely to be costs associated with changing C:N ratios in the biomass. By increasing their C:N ratio plants give up their nutrient buffer and may struggle if the nutrient supply decreases (Meunier et al. 2014; Leal et al. 2017).

Studies combining data from different literature sources always face the danger of using incompatible data (Isles 2020). The model in chapter 1 uses data from several studies on plant nutrient uptake across at various temperatures. I accounted for differing units and any additional reported treatment or measurement differences. Nonetheless, there could be systematic variation between the methodology used in the studies. For example, there might be issues in using the measured data to assume whole plant nutrient uptake. For example, if one study measured nutrient uptake only in young roots, this could bias the results, nutrient uptake behaviour changes with root age (Le Deunff et al. 2019). Furthermore, the literature data covered marine and terrestrial species and various plant groups. There could be a systematic difference between habitats and variations with the plant size or amount of woody tissue (Rastetter et al. 1997). If more experimental data on plant nutrient uptake under different temperatures becomes available, it would be exciting and relevant to investigate these potential systematic variations.

For many temperature-dependent species traits, the performance increases with temperature up to a certain threshold, after which there is a fast decline. This relation is known as thermal response curves (Sinclair et al. 2016; Van Dievel et al. 2019). The relation of nutrient uptake and temperature may also not be linear, as we assumed here, but rather hump-shaped. More studies of nutrient uptake kinetics at different temperatures are needed to establish the shape of the relation.

Even though some of the limitations of model studies will always remain, there are numerous extensions to the models in this thesis that are worth exploring. I will outline some of these in the following section.

3.2 Possible extensions

Carbon dioxide concentration

Both of my chapters include the two global change drivers warming and changing nutrient supply. However, another driver is particularly relevant to plant growth: carbon dioxide (CO_2) concentration (Verspagen et al. 2014a; Boretti and Florentine 2019). In my research chapters, I assumed C always to be sufficiently available, so that the plant can allocate as much as it needs to maximize its growth, dependent on the limiting nutrient (Bassirirad 2000). The increase in CO_2-concentration associated with anthropogenic activities has an effect on plant N assimilation, growth and morphology, itself (Sardans et al. 2012). Increased CO_2 stimulates plant growth, improves their nutrient use efficiency and significantly increases C:N in most plants (Gifford et al. 2000; Bassirirad 2000; Elser et al. 2010; Sardans et al. 2012; Wei et al. 2018; Wang et al. 2019), which could change some of the dynamics described in this thesis.

Increasing plant C:N affects resource quality for the herbivores (and humans, in the case of crop plants). I have shown that, if plants are flexible in their stoichiometry, increasing N supply will decrease plant C:N. The response of plants to rising CO_2 in terms of growth and stoichiometry can be very different depending on the nutrient supply of the system (Rastetter et al. 1997; Elser et al. 2010; Verspagen et al. 2014a, b). At high N supply, the C:N ratio of plants remains low, even if CO_2 rises. At low N supply, CO_2-concentration drives C:N ratio (Verspagen et al. 2014a).

The combination of rising CO_2-levels and warming will likely also interactively affect plant growth and population interactions (Zvereva and Kozlov 2006). For example, even though nutrient uptake increases with warming, plant nutrient concentrations were reported to be lower under high CO_2-concentrations even at high temperature (Bassirirad 2000; Elser et al. 2010). An extension of this thesis could investigate the interactive effect of rising CO_2-levels with temperature and nutrient supply on biomass production and population interactions

There is also a difference in the effect of rising CO_2 depending on the photosynthetic type. While C3 plants show a significant increase in C:N ratio and increased photosynthetic efficiency under rising CO_2-levels, C4 plants do not (Elser et al. 2010; Sardans et al. 2012; Boretti and Florentine 2019). It would certainly be worth exploring these differences in more detail, as it would help us make predictions about the direction of the combined effects of warming and rising CO_2 for systems dominated by either photosynthetic type.

Phosphorus

N deposition increases more strongly through human action than P deposition (Sardans et al. 2012). This difference creates a potential mismatch between the N and P cycles. Increases in N supply parallel with rising CO_2-levels and warming would likely stimulate plant growth, but this may be hampered by P limitation (Elser et al. 2007; Persson et al. 2011; Sardans et al. 2012; Agren et al. 2012). There are far fewer studies of the effect of rising CO_2 on plant C:P ratios than on C:N (Sardans et al. 2012). The existing studies found more variable effects of rising CO_2 on plant C:P than plant C:N, showing the plant N is much more closely associated with C levels than plant P is (Penuelas and Matamala 1993; Luomala et al. 2005; Milla et al. 2006; Sardans et al. 2012; Wang et al. 2019).

In chapter 1, I established the temperature dependency of both N and P uptake. However, the models in chapter 2 only included N as a representative for the nutrients. Knowing the plant's potential flexibility in their C:P ratio to be up to 50% variation around the mean (Yu et al. 2011), I tested the applicability of the models to a system with P as the only nutrient and found results similar to the N-only model. Realistically, plant P and N content and demand will vary simultaneously. A valuable extension of chapter 2 would include P in the models explicitly and allow the plants flexibility in their C:N:P ratio. With information on the degree of flexibility of plant N:P ratios, we could then explore how uneven changes in N and P supply would affect plant growth and food quality for the herbivore.

Under experimental conditions, the optimal N:P ratio increased with warming, showing that warming is likely to interact with N and P supply in its impact on plant growth (Thrane et al. 2017; Yvon-Durocher et al. 2017; Puche et al. 2018). Extending the model to include the effect of CO_2-concentration on growth and C to nutrient ratios in addition to warming and changing nutrient supply, while also adding P as an additional nutrient can give us a more complete picture of the conditions that plants, and the populations they interact with, are likely to face under global change.

Food Webs

A system including only nutrients, plants and herbivores is of course very far from the real world. As described above, legibility and computational power limit the number of species we can model in detail. Furthermore, plant-herbivore interactions are quite relevant, as they often determine a large portion of ecosystem functioning by mediating both bottom-up and top-down interactions (McQueen et al. 1989; Brett and Goldman 1996; Borer et al. 2006; Hillebrand et al. 2009). Nonetheless, to test the applicability of our results to real ecosystems, it would be helpful to apply the models to more complex systems, by adding additional trophic levels or even simulating a small food web. Often, simulating a predator on top of a food chain destabilizes the system by creating oscillating dynamics (Otto et al. 2007; Binzer et al. 2012). Integrating a larger number of species in a food web brings back stability (Emmerson and Raffaelli 2004; Brose 2008; Rall et al. 2010). For this reason, it is likely advisable to move directly from the nutrient-plant-herbivore chain to a (small) food web, rather than a longer food chain.

Realistically, most herbivores will feed on several food plants, rather than have just one plant resource. This mixture of diet changes the effect food quality has on the herbivore. If a mixed plant diet is available, herbivore growth and assimilation efficiency are less affected by low average food quality (Urabe et al. 2018). In a food web context, we could also include omnivorous species, that can adjust whether they feed more on plant or animal resources depending on their requirements. Under warming, omnivores may tend more towards plant food, which is higher in C and can fuel the rising demands for metabolism (Carreira et al. 2016; Rho and Lee 2017).

Top-down and bottom-up control and the effect of mixed diets and omnivory are the kinds of mechanisms that we can explore by integrating the models from this thesis into a food web framework.

Nutrient recycling

In our current model definition, nutrients are directly recycled back to the environmental pool through plant and herbivore metabolism. Changes in herbivore nutrient demand can influence nutrient recycling and change the environmental nutrient supply (Logan et al. 2004; Persson et al. 2010; Leal et al. 2017). Modelling the recycling loop in more detail is especially relevant if we add P into the picture. In animals, N is excreted in a more considerable amount, while P is mostly retained. The higher loss of N relative to P could mean that food with higher N-content quality is needed to maintain the required C:N:P ratio (Logan et al. 2004).

Food with high C:N ratios compared to the herbivore demands will lead to the excretion of detritus with very high C content. Detritus with low nutrient content breaks down much more slowly (0.01% loss per day, compared to 1% loss/day for high N & P litter (Sterner et al. 2002)). The breakdown speed will affect how fast nutrients become available again for the plants to take up. A more detailed recycling loop would be a valuable extension of the model, which should also explicitly include detritivores, as they mediate how fast the excreted nutrients become accessible to the plant.

These are just some of the infinite options to extend the models developed in this thesis. In their current state, the models provide us with valuable insight into some of the effects of global change and the relevance of previously understudied mechanisms, thereby forming a valuable basis for future research.

4 | Conclusion

Adapting and responding to a rapidly changing world requires knowledge of how global change affects biological systems and ecosystem services provision. To contribute to our understanding of the processes and mechanisms behind the effect of warming and changing nutrient supply on population dynamics and biomass production, I developed a model that explicitly includes the temperature-dependency of plant nutrient uptake. I furthermore studied the importance of coping mechanisms like flexible stoichiometry in plants and compensatory feeding in herbivores for biological systems facing global change pressures. I found that it is necessary to take these mechanisms into account, as ignoring them might lead to an under-or overestimation of the effect of global change. My results also confirm the importance of combining several global change drivers in our studies. The findings in chapter 1 show that increased nutrient supply could change the role that initial climatic conditions play in the impact of warming on biomass production. Both chapters suggest that increasing nutrient supply could mediate the negative effect of warming on biomass production, while a system facing oligotrophic conditions may be more adversely affected under warming.

Together, these findings show that global change drivers interact in their effect on biological systems and that the coping mechanisms available to organisms can mediate these effects. These interactions highlight the importance of developing further model studies including several global change drivers and as many empirically informed mechanisms and processes as possible, to avoid under-or overestimation when informing policy on global change mitigation and adaption or ecosystem service provision.

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B

Supplementary Information Research Chapter 1

Oikos

OIK-06141

Marx, J. M., Rall, B. C., Phillips, H. R. P. and Brose, U. 2019. Opening the black box of plant nutrient uptake under warming predicts global patterns in community biomass and biological carbon storage. – Oikos doi: 10.1111/oik.06141

Appendix 1: Additional figures of Original data and model simulations

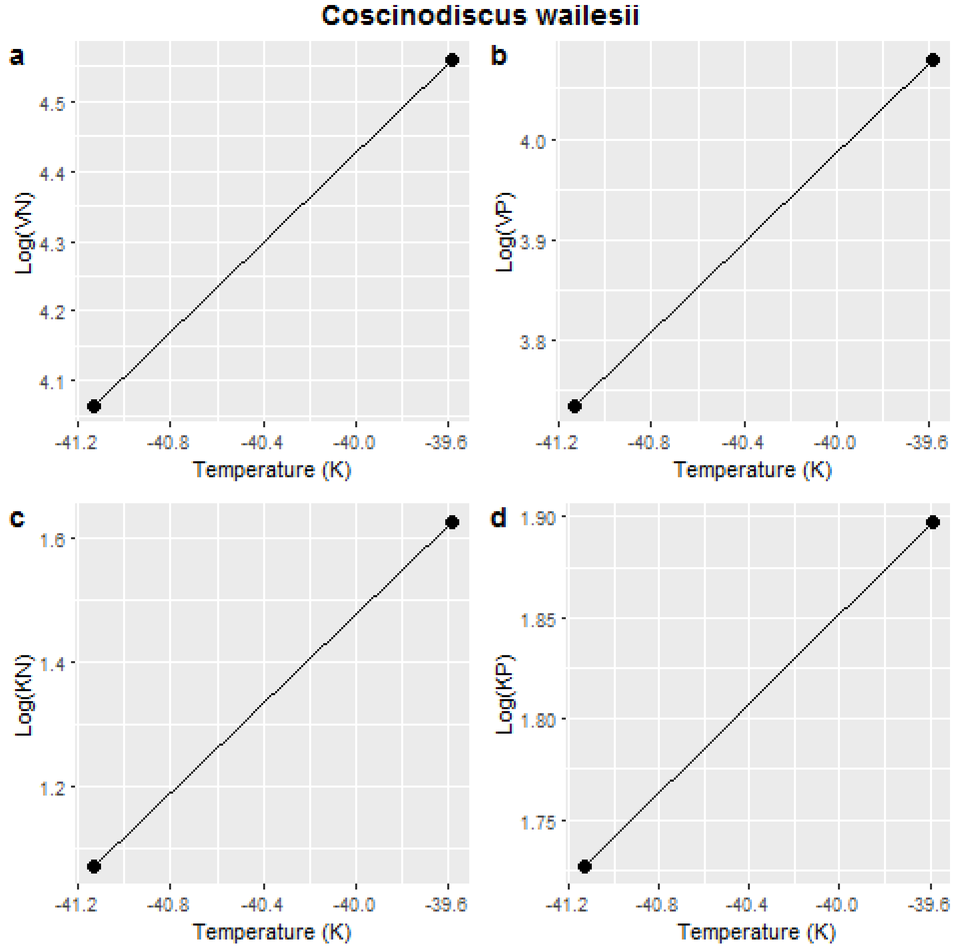

Figure A1: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen and phosphorus against temperature for phytoplankton species Coscinodiscus wailesii.

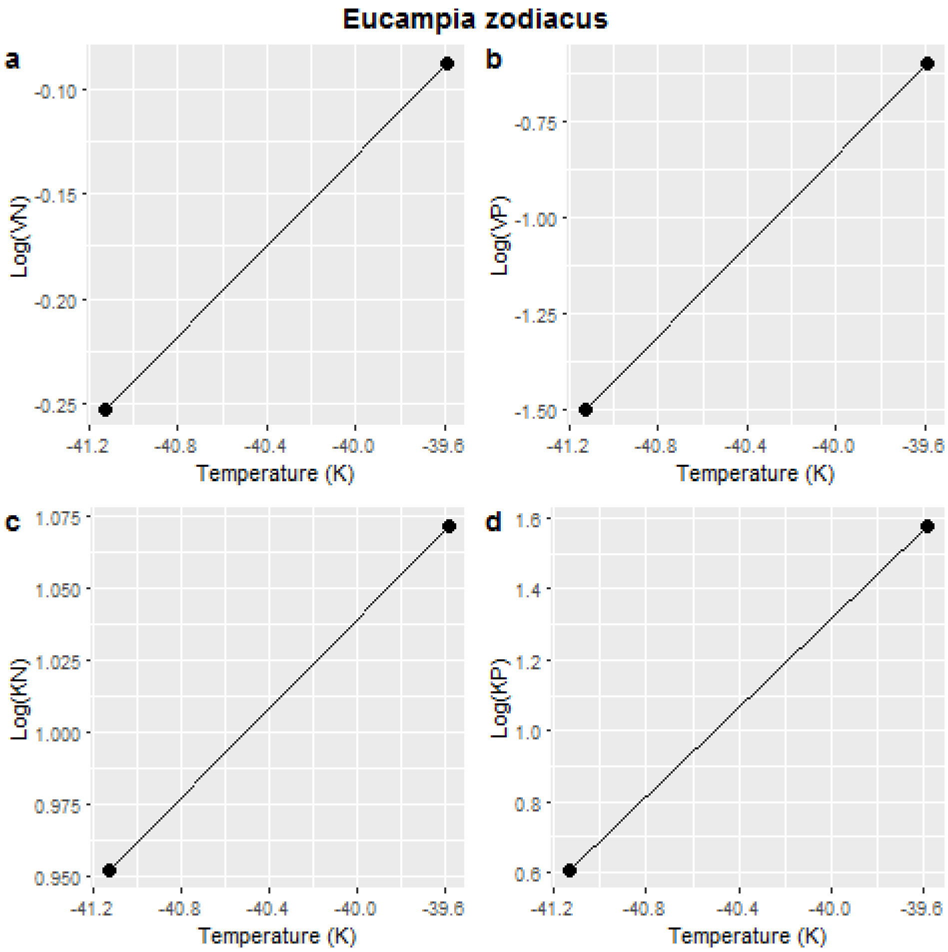

Figure A2: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen and phosphorus against temperature for phytoplankton species Eucampia zodiacus.

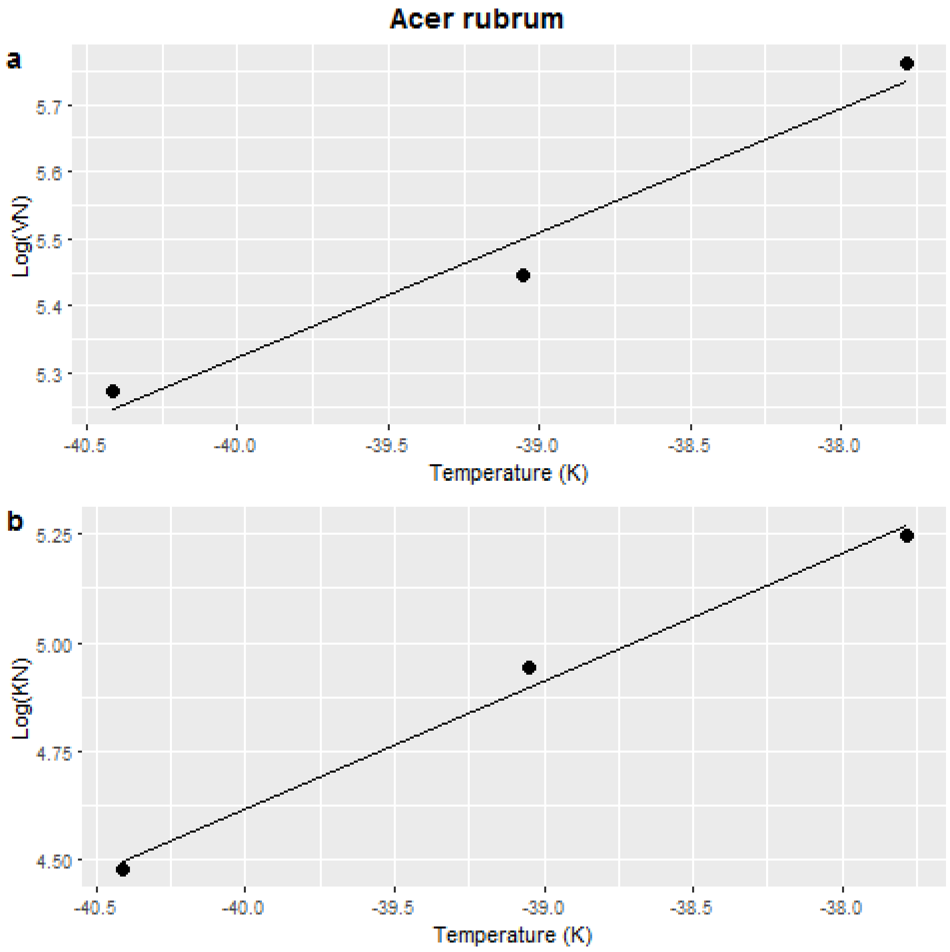

Figure A3: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen against temperature for tree species *Acer rubrum.*

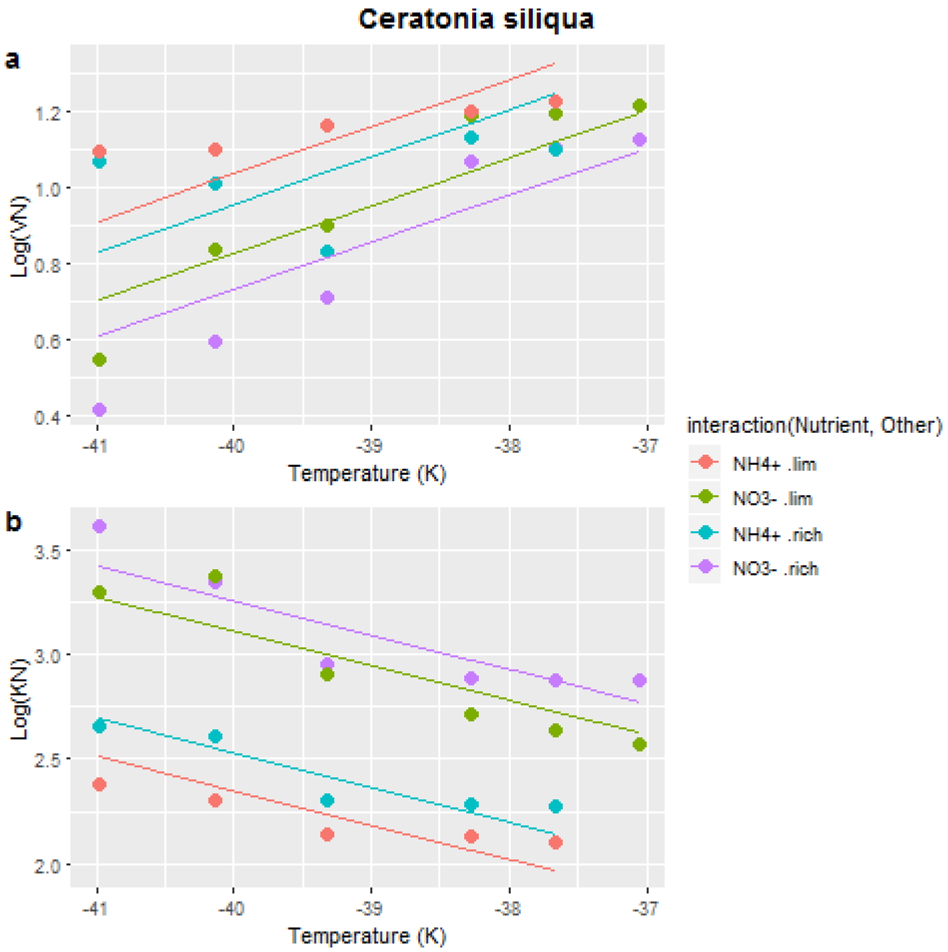

Figure A4: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen against temperature for tree species Ceratonia siliqua. *The colours represent the additional variables (nutrient type and nutrient density) used in the original study.*

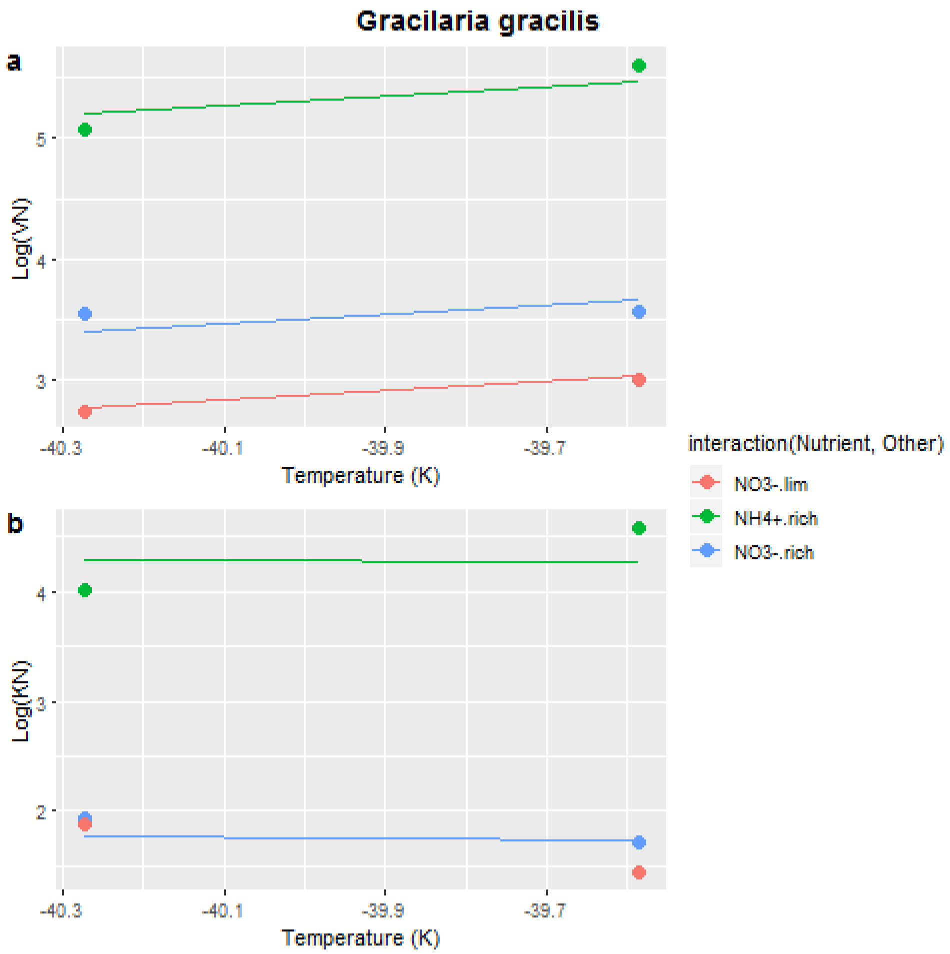

Figure A5: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen against temperature for algae species Gracilaria gracilis. *The colours represent the additional variables (nutrient type and nutrient density) used in the original study.*

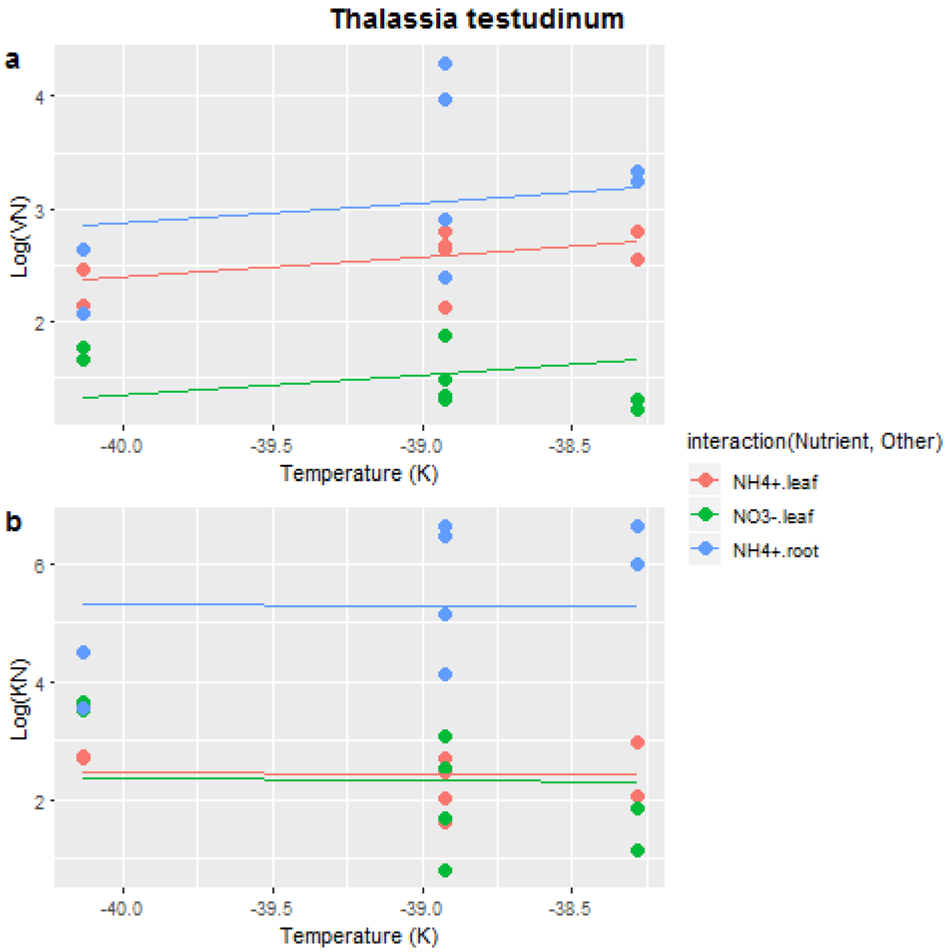

Figure A6: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of nitrogen against temperature for algae species Thalassia testudinum*. The colours represent the additional variables (nutrient type and plant part measured) used in the original study.*

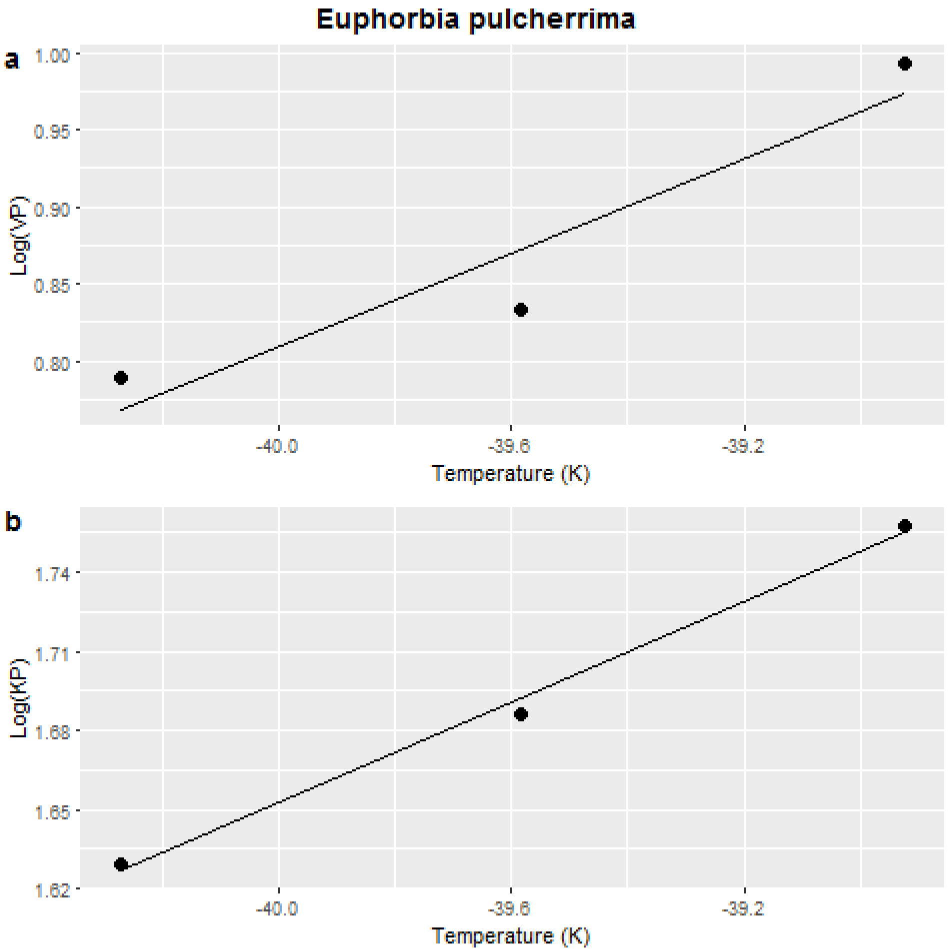

Figure A7: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of phosphorus against temperature for shrub species Euphorbia pulcherrima.

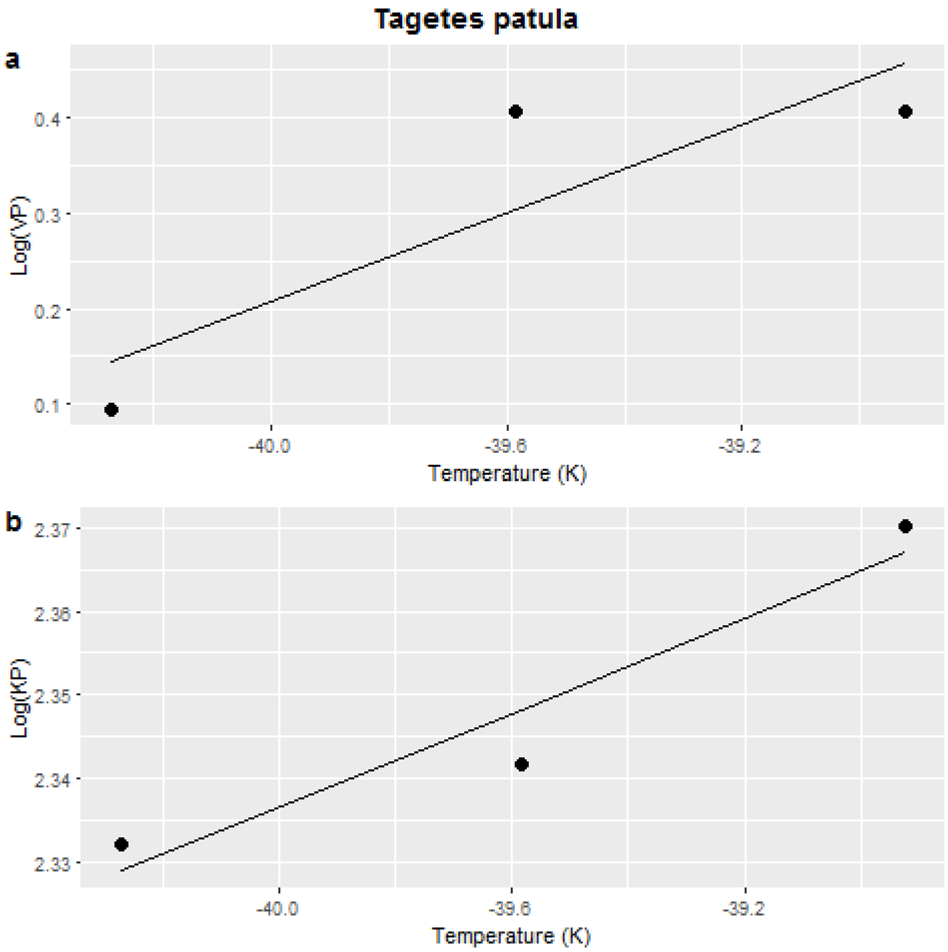

Figure A8: Original data & regression line of the log transformed maximum uptake rate (a & b) and half-saturation density (b & c) of phosphorus against temperature for herb species Tagetes patula.

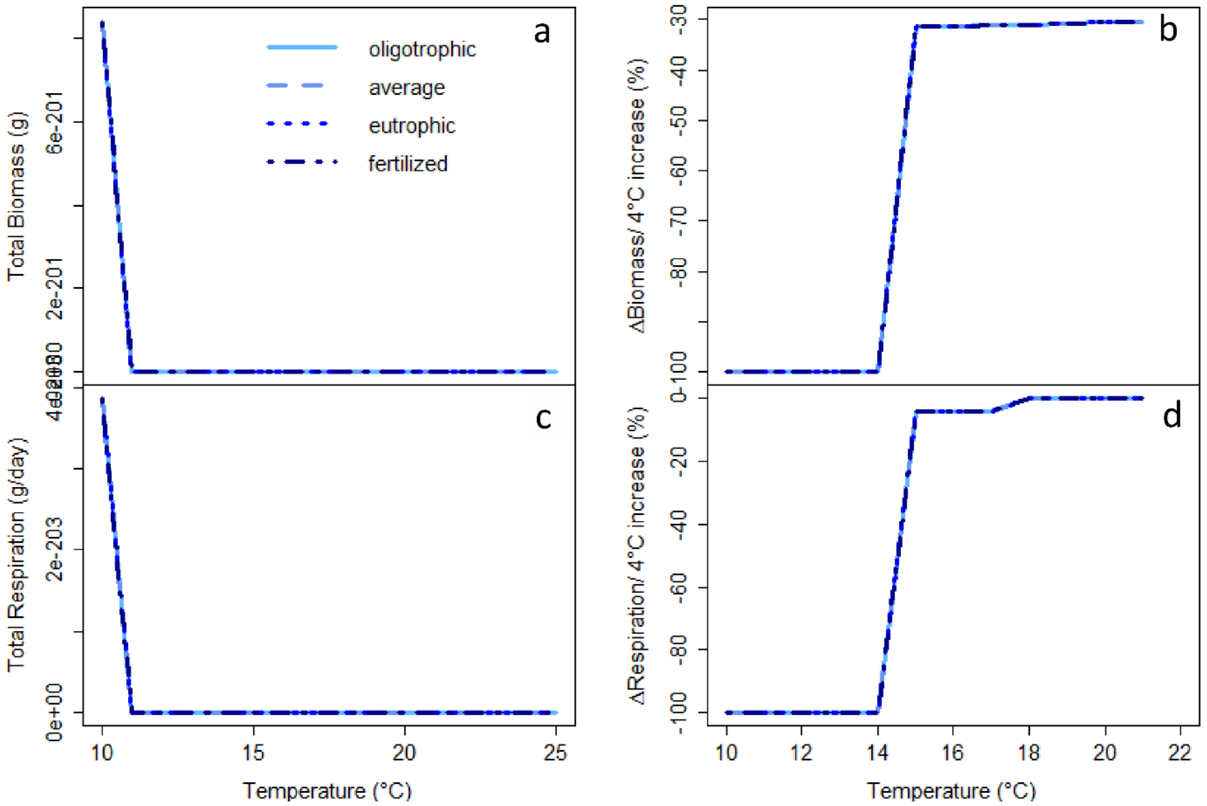

Figure A9: Results of simulations run with only nitrogen as nutrient. a total community biomass at different temperatures; c the corresponding total respiration. b and d show the %-change (Δ) in biomass and respiration, respectively, that would occur if the system would be warmed by 4°C, the x-axis here represents the baseline temperature.

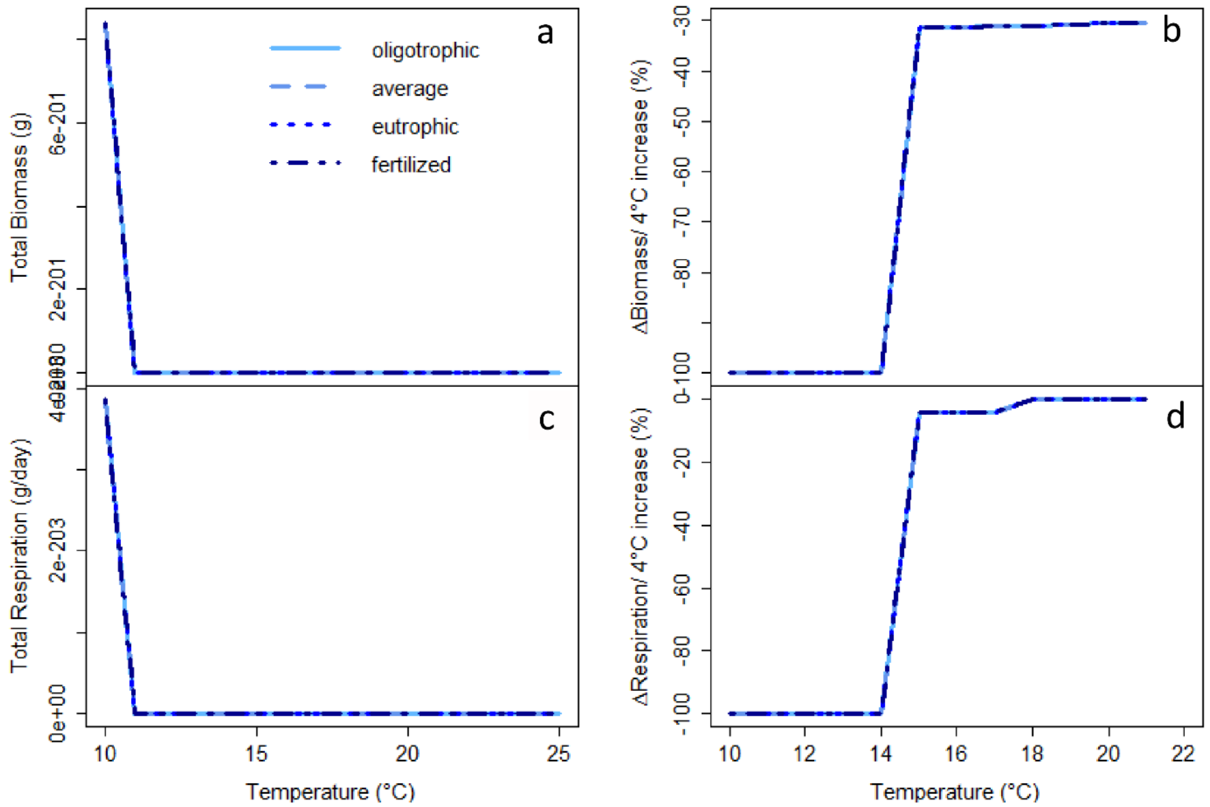

Figure A10: Results of simulations run with only phosphorus as nutrient. a total community biomass at different temperatures; c the corresponding total respiration. b and d show the %-change (Δ) in biomass and respiration, respectively, that would occur if the system would be warmed by 4°C, the x-axis here represents the baseline temperature.

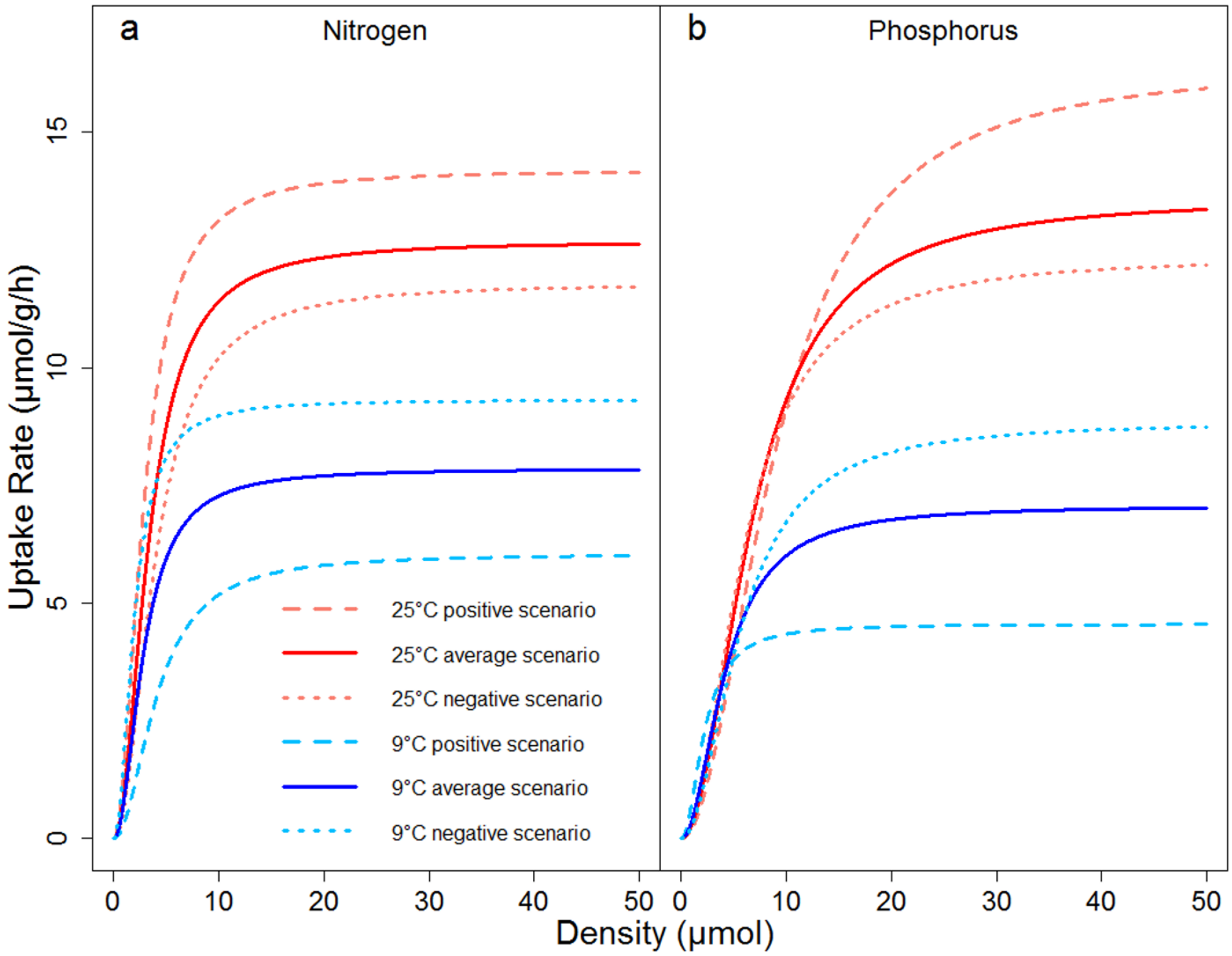

Figure A11: Sensitivity plot showing plant nutrient uptake curves at 9 and 25°C using the most positive, average and most negative scenario for plant nutrient uptake based on the activation energies of half-saturation density and maximum uptake rate. This figure shows plant nutrient uptake at 9°C in blue and 25°C in red. The solid lines represents the average activation energy as used in the model. The dashed lines shows plant nutrient uptake being most positively affected by temperature using the maximum activation energy for maximum uptake rate and the minimum activation energy for half-saturation density. The dotted lines show the most negative scenario for plant nutrient uptake using the minimum activation energy for maximum uptake rate and the maximum activation energy for half-saturation density.

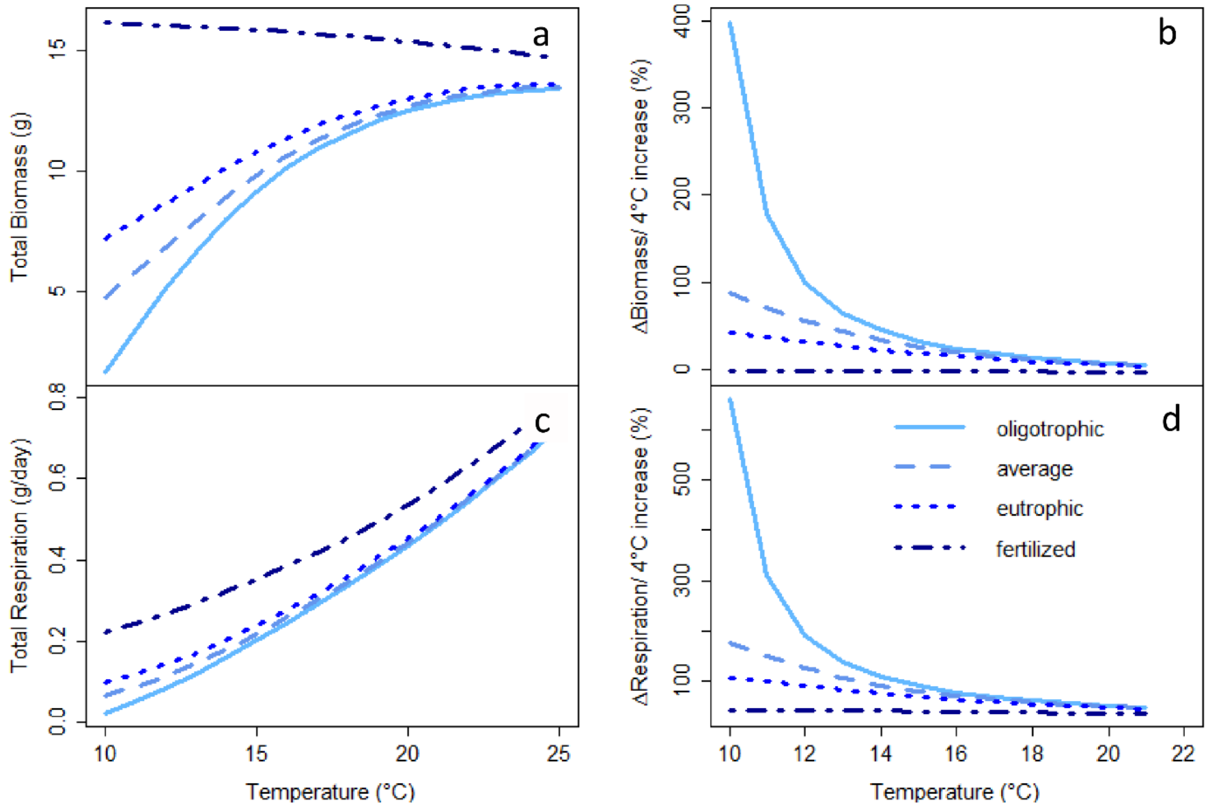

Figure A12: Results of simulations run under the most positive scenario using the maximum activation energy for maximum uptake rate and the minimum activation energy for half-saturation density. a total community biomass at different temperatures; c the corresponding total respiration. b and d show the %-change (Δ) in biomass and respiration, respectively, that would occur if the system would be warmed by 4°C, the x-axis here represents the baseline temperature.

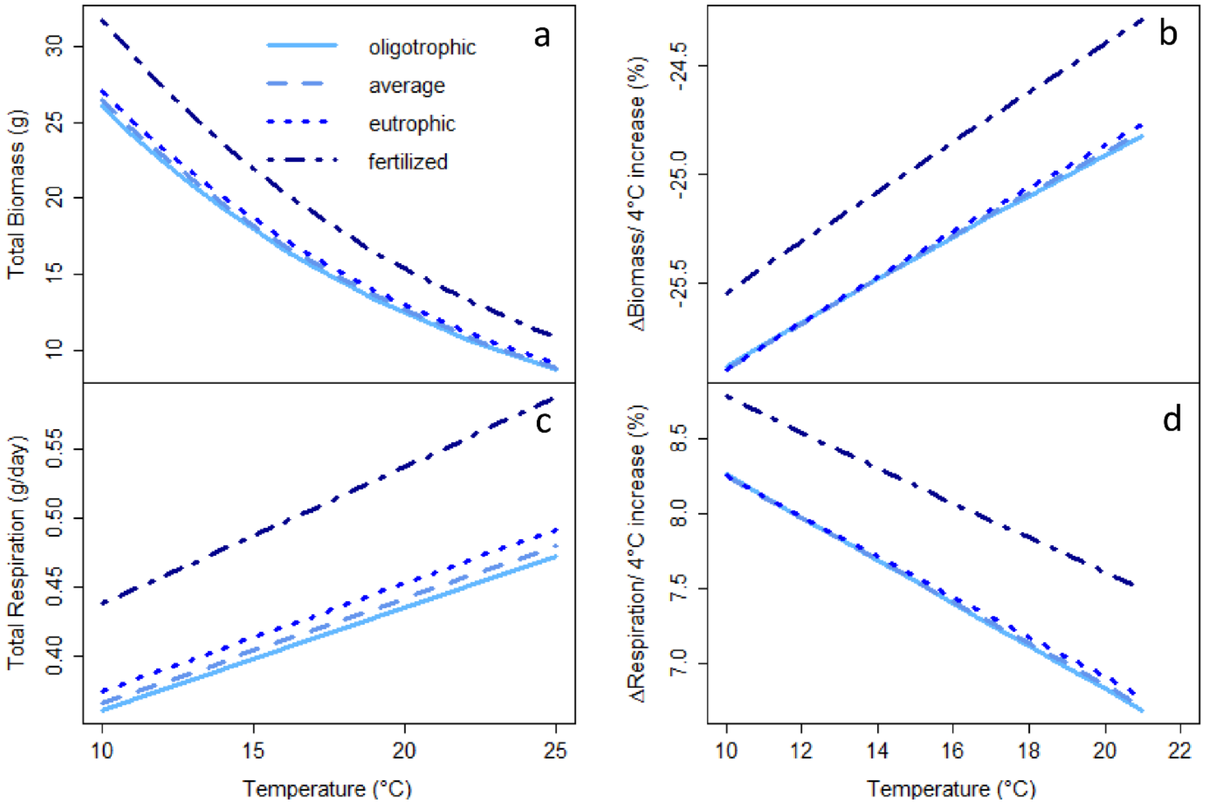

Figure A13: Results of simulations run under the most negative scenario using the minimum activation energy for maximum uptake rate and the maximum activation energy for half-saturation density. a total community biomass at different temperatures; c the corresponding total respiration. b and d show the %-change (Δ) in biomass and respiration, respectively, that would occur if the system would be warmed by 4°C, the x-axis here represents the baseline temperature.

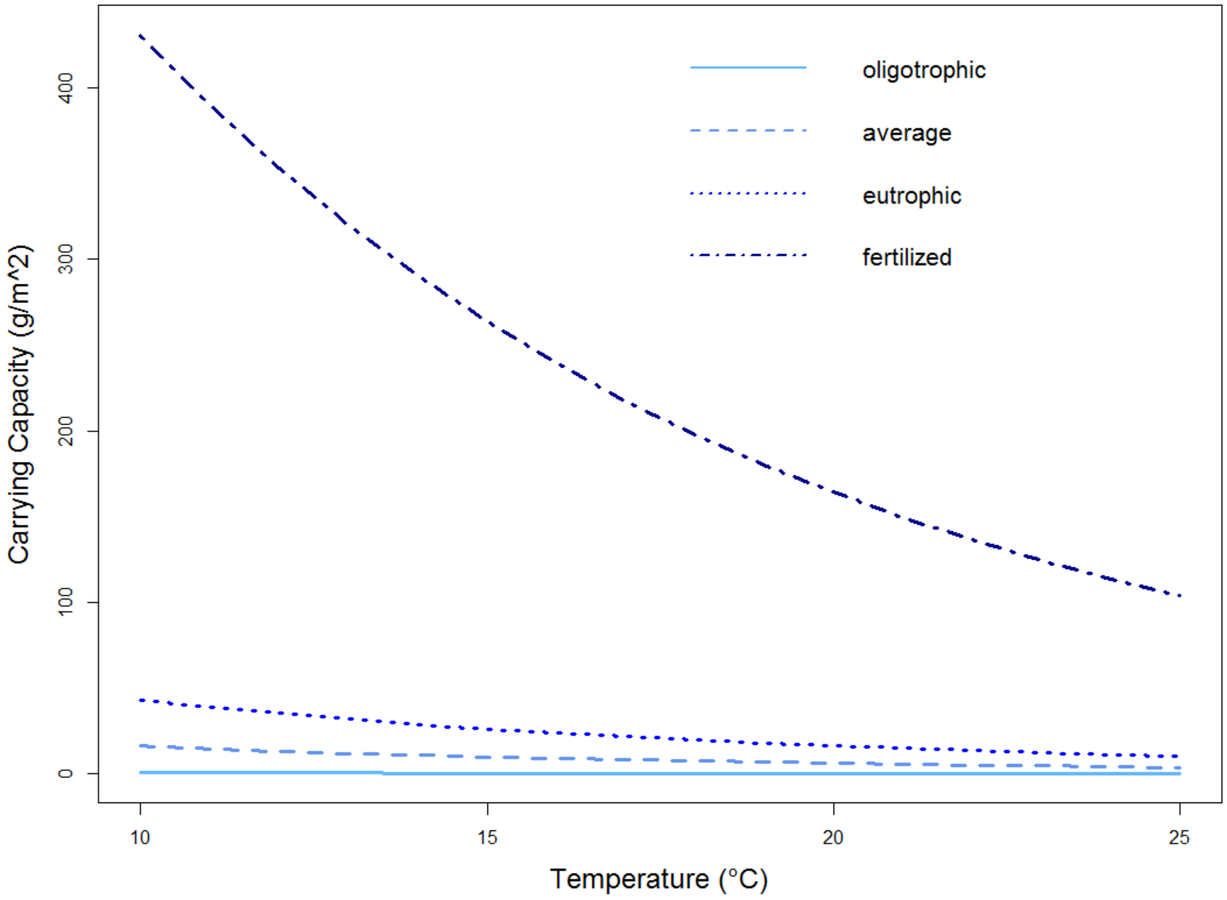

Figure A14: Carrying capacity against temperature. The four lines represent different nutrient density scenarios.

C

Ehrenwörtliche Erklärung

Ehrenwörtliche Erklärung

Ich versichere, dass mir die geltende Promotionsordnung bekannt ist (Promotionsordnung der Fakultät für Biowissenschaften der Friedrich-Schiller-Universität Jena vom 23.09.2019), ich die Dissertation selbstständig und ohne unerlaubte Hilfe Dritter angefertigt habe, keine Textabschnitte Dritter oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe und alle benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen in der Arbeit angegeben habe. Alle Stellen, die inhaltlich oder wörtlich aus Veröffentlichungen stammen sind kenntlich gemacht. Ich habe keine Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Folgende Personen haben mich bei der Auswahl und Auswertung des Materials sowie bei der Herstellung der einzelnen Manuskripte unterstützt: Benoit Gauzens, Björn C. Rall, Angélica L. González, Helen R. P. Philips und Ulrich Brose. Nähere Angaben sind den *Author Contributions* und Forschungskapiteln zu entnehmen.

Diese Dissertation lag noch nicht als staatliche oder andere wissenschaftliche Prüfungsarbeit einer Prüfungsbehörde vor und wurde bisher noch nicht veröffentlicht. Ich habe die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei keiner anderen Hochschule oder anderen Fakultät als Dissertation eingereicht.

Leipzig, den

Jori Maylin Marx