

**Multiple resource limitation of plants and its consequences for herbivores and their impacts**

Neha Mohanbabu<sup>1\*</sup> and Mark E. Ritchie<sup>1</sup>

<sup>1</sup>Department of Biology, Syracuse University, Syracuse, NY, USA 13244

\*Author of correspondence

Mailing Address: Life Sciences Complex, 107 College Place, Syracuse, NY 13210, USA

Phone: +1-315-876-7609; [nehamohanbabu@gmail.com](mailto:nehamohanbabu@gmail.com)

Co-author email: [meritchi@syr.edu](mailto:meritchi@syr.edu)

Running title: Plants, herbivores and multiple resources

Keywords: theoretical model, producer-consumer systems, resource ratio, response ratio, resource gradients, herbivory intensity

Type of article: Letters

Word count:

Abstract: 147 words

Main text: 4867 words

Text Box1: 605 words

Number of references: 87

Number of figures, tables and boxes: 6

Statement of Authorship: NM and MR developed the analytical model. NM performed all the statistical analyses and wrote the first draft of the manuscript and MR contributed substantially to revisions.

Data accessibility statement: All new data used in the study will be archived in a public repository and the data DOI will be included in the article. Data from other sources (publicly available databases and previously published work) were used in this manuscript and have been cited appropriately.

Conflict of interest statement: We declare that there is no conflict of interest

24    **Abstract**

25    Substantial evidence suggests plants and herbivores are limited by multiple resources but their role in  
26    driving plant-herbivore interactions is still poorly understood. Here we model multiple resource  
27    limitation of plants and herbivores and derive analytical solutions for steady-state plant biomass,  
28    herbivore biomass and herbivore impact. The model predicts “apparent” limitation of herbivore biomass  
29    by resources that otherwise do not limit herbivore growth. Consequently, higher supply of plant-growth  
30    limiting resources allows herbivores to persist at lower supplies of herbivore growth-limiting resources.  
31    Likewise, increased supply of these non-limiting resources to herbivores can dramatically increase  
32    herbivore impacts on plants. Additionally, the outcomes of herbivore exclusion experiments should  
33    differ along different resource gradients, depending on herbivore response to plant resource  
34    concentrations. Analysis of existing and new data from marine, freshwater and terrestrial systems  
35    supports several of these predictions. Our analysis expands ecologists’ understanding of plant-herbivore  
36    dynamics to accommodate multiple limiting resources.

## Introduction

Herbivory is a foundational trophic interaction central to the secondary production and stability of food webs. The magnitude of herbivory varies across ecosystems (Cyr & Face 1993) and understanding the factors that drive such variation is a long-standing objective in ecology (Hairston *et al.* 1960; Oksanen *et al.* 1981; Ritchie & Olff 1999; Olff *et al.* 2002; Cebrian & Lartigue 2004). An important question is whether herbivore abundance and herbivore impact on plants change in response to the type and magnitude of resources that limit plant growth. Most previous studies, motivated by Liebig's Law of the minimum, view plant growth as limited by a single resource in any given ecosystem. However, research over the past two decades has demonstrated that plant growth can be simultaneously limited by more than one resource (Elser *et al.* 2007; Harpole *et al.* 2011; Fay 2015). If so, such multiple resource-limitation may have significant impacts on how the suite of important plant resources influence herbivores.

The impact of multiple resource limitation on herbivores is still poorly understood. Classical studies on herbivore dynamics have transitioned from arguing that herbivore abundances are solely under top-down control of predators (i.e. independent from resource supply to plants)(Hairston *et al.* 1960), to the idea that variation in the supply of a single limiting resource to plants produces gradients of herbivore biomass or intensity (Oksanen *et al.* 1981; Oksanen 1992; Chase *et al.* 2000; Wilkinson & Sherratt 2016). In many of these modeling scenarios (Mazancourt *et al.* 1998; Chase *et al.* 2000; Loladze 2000; Thébault & Loreau 2003, 2005) consumers and producers are often assumed to be limited by the same resource directly or indirectly via plant biomass, e.g., P in freshwater aquatic and N in terrestrial systems (Elser & Urabe 1999; Holdo *et al.* 2007). While it is possible that herbivores are limited by the same set of resources as plants, the differences in cellular demand for different resources between autotrophs and heterotrophs (Elser *et al.* 2000; Sterner & Elser 2002; Lemoine *et al.* 2014) suggests that the resource(s) that limit herbivore growth may be a subset of or exclusive of the set of resources that limit plants.

Resources that only limit plant growth and thus drive plant resource concentration ratios and biomass might indirectly or “apparently” limit herbivore dynamics. Altering the supply of resources that might exclusively co-limit plants but not herbivores may also modify herbivore impacts on plant biomass across different resource gradients. Ultimately, relatively little is known about the impact of multiple resource limitation on higher trophic interactions.

Multiple resource limitation of plants may also impact herbivores by modifying plant quantity, quality (nutrient content or ratio of nutrients), and allocation to defensive compounds (Bryant *et al.* 1983; Coley *et al.* 1985; Herms & Mattson 1992). Additionally, some resources such as carbon are allocated to both metabolic and structural components, further affecting plant mortality and palatability to herbivores. Herbivores preferentially feed on tissue rich in certain resources such as P in aquatic systems (Sterner & Schulz 1998; Urabe *et al.* 2003) or N in terrestrial systems (Mattson 1980; Griffin *et al.* 1998) or alternatively feed on tissue with higher resource: carbon ratio such as P:C or N:C, respectively (Hessen 1992; Awmack & Leather 2002; Hessen *et al.* 2002; Welte *et al.* 2020). Plant biomass and tissue concentrations of different resources generally increase with resource addition (Bracken *et al.* 2015) in the absence of consumers. However, it is harder to predict biomass responses of plants under herbivory. Biomass reflects a balance between growth and consumption, and consumption may outstrip growth under certain plant resource concentrations, leading to a pattern of decreasing plant biomass at higher plant resource supplies. Therefore, different scenarios of herbivore response to plant biomass and resource concentrations (e.g. plant biomass, single resource concentration, or ratio of resource concentrations) need to be explored.

In this paper, we develop an analytical model to explore the impact of multiple resource limitation on plant-herbivore dynamics. We use the terms plants and herbivores to broadly refer to any primary producers and consumers, respectively, in the ecosystem even though they may not classically be considered “plants,” e.g., cyanobacteria, corals, or “herbivores,” e.g., heterotrophic bacteria, salps. We

derive analytical steady-state solutions for the responses of plant and herbivore biomass to resource limitation by four types of resources (Box 1, Fig. 1a) under three different scenarios of herbivore responses to resources in addition to plant biomass. Herbivores may respond a) only to plant biomass and not plant resource concentrations (Fig. 1b); b) to concentration of a single plant resource (Fig. 1c); and c) to ratios of resources in plant tissue (Fig. 1d). Our model predictions suggest potential for resources that do not directly limit herbivore growth to influence biomass and conditions for persistence of herbivores. The model also provides several new hypotheses for variation in herbivore biomass and impacts on plants along different resource gradients. Finally, we discuss examples from both aquatic and terrestrial ecosystems as evidence to highlight the utility of the modelling framework.

## **Methods**

### **Limitation by three essential resources**

We consider a system in which plants are limited by three interactively essential resources (Sperfeld *et al.* 2012; also called multiplicative colimitation in Saito *et al.* 2008). Examples include plants limited by water, N and P in terrestrial ecosystems (Elser *et al.* 2007; Harpole *et al.* 2007; Cleland & Harpole 2010), by light, P and N in freshwater systems (Elser *et al.* 2007; Karlsson *et al.* 2009; Harpole *et al.* 2011) or by light, iron (Fe) and P in marine pelagic systems (Sunda & Huntsman 1997; Downing *et al.* 1999; Elser *et al.* 2007). By considering three different resources including carbon which is ubiquitous to life, we will explore several different scenarios addressing the impact of resources on both plants and herbivores. The general set of eq 1.1-1.5 (Box1) will be used to explore plant-herbivore dynamics under specific paradigms of herbivore limitation.

### **Plant-resource dynamics**

Resources are taken up by plants as defined by eq. 1.1 (Box1). Eq. 1 provides the general form of resource dynamics for resource  $x$  as a function of plant biomass  $S$ .

$$\frac{dR_x}{dt} = I_x - f(R_x)S; \quad f(R_x^*) = \frac{I_x}{S} \quad (1)$$

Once resources are taken up by plants they are incorporated into metabolic activity and experience turnover (eq. 1.2, Box1). Although most resources are directly absorbed by plants, carbon assimilation occurs with an efficiency  $\varepsilon$ , that depends on the supply of “surrogate resources for acquiring carbon” or SRC resources ( $I_{SRC}$ ) like water or light. Further, we assume a proportion  $q$  of internal plant concentration of carbon ( $r_C$ ) is metabolically active, and  $1-q$  is “non-metabolic”, that is, allocated to structure or defense or other purposes. Eq. 2 tracks the rate of change of concentration of resource in the tissue.

$$\frac{dr_x}{dt} = f(R_x^*) - \gamma_x r_x; \quad r_x^* = \frac{I_x}{\gamma_x S^*} \quad (2)$$

Therefore, the steady-state internal concentrations ( $r_x^*$ ) of the four types of resources are-

$$qr_C^* = \frac{\varepsilon I_{SRC}}{\gamma_C S^*}; \quad r_{PAH}^* = \frac{I_{PAH}}{\gamma_{PAH} S^*}; \quad r_P^* = \frac{I_{OP}}{\gamma_{OP} S^*}; \quad r_H^* = \frac{I_{OH}}{\gamma_{OH} S^*} \quad (3)$$

### Production proportional to the product of multiple plant resource concentrations

Previous research suggests that growth should be approximately proportional to the product of essential resource concentrations under multiple resource limitation (Saito *et al.* 2008; Sperfeld *et al.* 2012). Therefore, we assumed plant production is a function of internal resource concentrations  $[r_C][r_{PAH}][r_P]$ . We can easily justify the product approximation using a terrestrial plant example. Biomass production is driven by fixation of C-based biomolecules from internal leaf  $[CO_2]$ , catalyzed by N-rich enzymes such as RuBisCo (Spreitzer & Salvucci 2002) or PEP carboxylase (Izui *et al.* 2004), and can approximately be described as a second order reaction rate proportional to  $[Enzyme][CO_2]$ . The concentration of  $CO_2$  is proportional to evapotranspiration, which increases with supply of water to the leaf [Water] (SRC resource). Furthermore, enzyme concentration [Enzyme] is a function of the rate of conversion of N-based compounds (PAH resource) into amino acids and proteins, as “catalyzed” by P-

rich RNA (*OP* resource), which can be captured by a second order reaction proportional to the product  $[N][\text{RNA-P}]$  (Loladze & Elser 2011). Substituting  $[\text{Water}]$  for  $\text{CO}_2$  and  $[N][\text{RNA-P}]$  for  $[\text{Enzyme}]$  yields plant growth being proportional to the product of three concentrations  $[\text{Water}][N][\text{RNA-P}]$ . Similarly, producer production in aquatic systems will likely be a function of  $[\text{Light}][N][P]$  while for marine pelagic systems it might be  $[\text{Light}][\text{Fe}][P]$ .

#### **Optimal allocation of carbon to metabolic and non-metabolic components**

Plants acquire and allocate carbon either to metabolic components that participate in chemical reactions that support growth or to other compounds, such as structural tissue, cell walls, and consumer defenses, that presumably improve the ability of plant cells to persist (e.g., increase leaf longevity). Thus, we hypothesized that plant mortality would be inversely proportional to the allocation of carbon to non-metabolic purposes. Using equation 1.3 (Box1) we define the rate of change of plant biomass in the absence of herbivores as

$$\frac{1}{S_U} \frac{dS_U}{dt} = ur_{PAH}^* r_{OP}^* q r_C^* - \frac{d}{(1-q)r_C^*} \quad (4)$$

where  $u$  [ $\text{t}^{-1}\text{g}_{PAH}^{-1}\text{g}_{OP}^{-1}\text{g}_C^{-1}$ ] is the conversion efficiency of resources into plant tissue. We can find an optimal allocation of carbon to metabolic function,  $q^*$ , that maximizes plant growth rate.

$$q^* = 1 - \frac{1}{r_C^*} \sqrt{\frac{d}{ur_{PAH}^* r_{OP}^*}} \quad (5)$$

#### **Steady-state plant and herbivore biomass**

Substituting eq. 5 into 4 we get the steady state plant biomass in the absence of herbivores-

$$S_U^* = \left[ \frac{I_{SRC} \varepsilon}{\gamma_C} \right]^{\frac{1}{2}} \left[ \frac{u I_{PAH} I_{OP}}{\gamma_{PAH} \gamma_{OP} d} \right]^{\frac{1}{4}} \quad (6)$$

Using eq. 1.4 (Box1), we can obtain the steady state standing biomass for plants when herbivores are present. To describe herbivore biomass dynamics, we assume a Type 2 functional response of herbivores to plant biomass implying that herbivores are satiated at high plant biomass and further explore three different scenarios of herbivory by changing the herbivory function,  $h(a, r_C^*, r_{PAH}^*, r_{OP}^*, t)$ :

a) Herbivore growth responds to plant biomass

This is similar to the other classic models of plant-herbivore interactions where herbivores change proportionally in response to available plant biomass. Eq. 1.4 and 1.5 (Box1) can be modified to fit this scenario when  $h(.)$  is just a function of the attack rate,  $a$ .

$$\frac{1}{S_G} \frac{dS_G}{dt} = ur_{PAH}^* r_{OP}^* q^* r_C^* - \frac{aH}{1 + atS_G} - \frac{d}{(1 - q^*)r_C^*};$$

$$H^* = \frac{e}{D} \left[ \frac{ua^2(e - Dt)^2 \varepsilon I_{SRC} I_{PAH} I_{OP}}{\gamma_C \gamma_{PAH} \gamma_{OP} e D^2} - \sqrt{\frac{ud I_{PAH} I_{OP}}{\gamma_{PAH} \gamma_{OP}}} \right] \quad (7)$$

The herbivore dynamics can be represented as-

$$\frac{1}{H} \frac{dH}{dt} = \frac{eaS_G}{1 + atS_G} - D; \quad S_G^* = \frac{D}{a(e - Dt)} \quad (8)$$

Eq. 7 and 8 show steady-state herbivore ( $H^*$ ) and plant biomass ( $S_G^*$ ). Using steady-state plant biomasses from eq. 6 and 8, we estimate impact of herbivores as a response ratio ( $S_u^*/S_G^*$ ).

$$RR = \frac{a(e - Dt) \varepsilon^{\frac{1}{2}} u^{\frac{1}{4}}}{(\gamma_{PAH} \gamma_{OP} d)^{\frac{1}{4}} \gamma_C^{\frac{1}{2}}} I_{SRC}^{\frac{1}{2}} (I_{PAH} I_{OP})^{\frac{1}{4}} \quad (9)$$

b) Herbivore growth responds to a plant resource concentration and biomass

In addition to plant biomass, herbivore growth may also respond to plant concentrations of a single resource such as nitrogen or sodium (Mattson 1980; McNaughton 1988; Griffin *et al.* 1998; Kaspari



2020), causing herbivores to seek food rich in those elements. In order to incorporate this resource limitation of herbivore growth in the model, we assume that herbivory function,  $h(.)$ , is also a function of tissue concentration of the herbivore growth-limiting resource ( $r_{PAH}$ ). The resulting equations for plant and herbivore dynamics are

$$\frac{1}{S_G} \frac{dS_G}{dt} = ur_{PAH}^* r_{OP}^* q^* r_C^* - \frac{ar_{PAH}^* H}{1 + atS_G} - \frac{d}{(1 - q^*) r_C^*};$$

$$H^* = \frac{e}{D} \left[ \frac{u(Dat)^2 \gamma_{PAH} \varepsilon I_{SRC} I_{PAH} I_{OP}}{\gamma_C \gamma_{OP} (eaI_{PAH} - D\gamma_{PAH})^2} - \sqrt{\frac{udI_{PAH} I_{OP}}{\gamma_{PAH} \gamma_{OP}}} \right] \quad (10)$$

$$\frac{1}{H} \frac{dH}{dt} = \frac{ear_{PAH}^* S_G}{1 + atS_G} - D; \quad S_G^* = \frac{1}{Dat} \left[ \frac{eaI_{PAH}}{\gamma_{PAH}} - D \right] \quad (11)$$

Eq. 10 provides the steady-state herbivore biomass,  $H^*$ . We calculate herbivore impact,  $RR$ , by substituting steady-state plant biomasses from eq. 6 and 11 in eq. 1.5.

$$RR = \frac{Dt\gamma_{PAH}^{\frac{3}{4}} (I_{SRC} \varepsilon)^{\frac{1}{2}} (uI_{PAH} I_{OP})^{\frac{1}{4}}}{\left[ eI_{PAH} - \frac{D\gamma_{PAH}}{a} \right] \gamma_C^{\frac{1}{2}} (\gamma_{OP} d)^{\frac{1}{4}}} \quad (12)$$

c) Herbivore growth responds to plant resource to carbon ratio and biomass

Alternatively, herbivores may also respond to ratios of different resources in addition to plant biomass.

Herbivores often favor plants with higher  $r_{PAH} : r_C$  ratio (Awmack & Leather 2002; Hessen *et al.* 2002).

The herbivory function with a response to  $r_{PAH} : r_C$  changes the dynamics of plants and herbivores to resources.

$$\frac{1}{S_G} \frac{dS_G}{dt} = ur_{PAH}^* r_{OP}^* q^* r_C^* - \frac{ar_{PAH}^* H}{(1 - q^*) r_C^* (1 + atS_G)} - \frac{d}{(1 - q^*) r_C^*} \quad (13)$$

The optimal allocation of carbon to metabolism was re-derived for this scenario by maximizing the plant growth function in eq. 13.

$$q^* = 1 - \frac{1}{r_C^*} \sqrt{\frac{d}{ur_{PAH}^* r_{OP}^*} \left[ \frac{ar_{PAH}^* H}{(1 + atS^*)} + d \right]} \quad (14)$$

Lastly, the dynamics of herbivore biomass was mathematically defined as-

$$\frac{1}{H} \frac{dH}{dt} = \frac{ear_{PAH}^* S_G}{(1 - q^*) r_C^* (1 + atS_G)} - D; \quad S_G^* = \frac{1}{a \left[ \frac{eI_{PAH}\gamma_C}{D\gamma_{PAH}\epsilon I_{SRC}} - t \right]} \quad (15)$$

By plugging  $S_G^*$  in steady state solution for eq. 13, we get steady state herbivore biomass,  $H^*$  as a function of resource supplies.

$$H^* = \frac{e\gamma_C}{a^2 \epsilon I_{SRC}} \left[ \frac{ua^4 I_{OP} I_{PAH} (e\gamma_C I_{PAH} - tD\gamma_{PAH}\epsilon I_{SRC})^2}{D^2 \gamma_{OP} \gamma_{PAH}^3 \gamma_C^2} - \frac{d(D\gamma_{PAH}\epsilon I_{SRC})^2}{(e\gamma_C I_{PAH} - tD\gamma_{PAH}\epsilon I_{SRC})^2} \right] \quad (16)$$

Similar to the previous cases, we calculate impact of herbivory from the steady-state plant biomasses from eq. 6 and 15. The estimated impact of herbivory is-

$$RR = \frac{a(uI_{PAH}I_{OP})^{\frac{1}{4}} [eI_{PAH}\gamma_C - tD\gamma_{PAH}\epsilon I_{SRC}]}{(d\gamma_{OP}\gamma_{PAH}^5)^{\frac{1}{4}} (\gamma_C \epsilon I_{SRC})^{\frac{1}{2}}} \quad (17)$$

Since resource types  $PAH$  and  $OH$  are similar in their effect on herbivore biomass, we derive the equations for resources that only limit herbivore growth ( $OH$  resource) in the Supporting Information (Appendix S1 eq. S1-10) and discuss those results with those for  $PAH$  resource.

## Results

We find that the response of plant biomass, herbivore biomass and impact of herbivory,  $RR$ , to resource supplies varies considerably across scenarios of herbivore growth response to plant biomass and resource concentrations. As expected, the steady-state biomass of plants in the absence of herbivores increased in response to supply of plant-growth limiting resource (Fig. 2a, filled black circles are higher

than filled grey circles) with plant biomass being more sensitive to supply of *SRC* resource compared to *PAH* or *OP* resources.

### **Herbivore growth responds to plant biomass**

When herbivore growth responded only to plant biomass rather than a specific resource or resource ratio, we found that plant biomass under herbivory,  $S_G^*$ , was invariant with resource supply (Fig. 2a and Table 1a). In contrast, herbivore biomass  $H^*$  increased linearly with supply of plant growth-limiting resources ( $I_{SRC}$ ,  $I_{PAH}$ ,  $I_{OP}$ ) (Fig. 2a and Table 1b). The response ratio of excluding herbivores,  $RR$ , therefore, was also proportional to greater supply of plant growth-limiting resources. Response ratio is predicted to be more sensitive to  $I_{SRC}$  than to  $I_{OP}$  and  $I_{PAH}$  (Table 1c). Finally, increasing the supply of resources that only limits plant growth,  $I_{OP}$ , lowers the thresholds of other resource supplies required for herbivore persistence (Fig 3a). As  $I_{OH}$  does not limit plant growth, herbivore biomass and grazing intensity do not change with its supply (Table 1).

### **Herbivore growth responds to a plant resource concentration**

When herbivore growth responds to a concentration of resource that limits growth of both plants and herbivores,  $r_{PAH}$  (e.g. N, P), steady-state biomass of plants under herbivory ( $S_G^*$ ) increases with the supply of resource that limits growth of both plants and herbivores ( $I_{PAH}$ ), (Fig. 2b). In contrast,  $S_G^*$  does not change in response to supply of the resources that only limit plant growth,  $I_{SRC}$  or  $I_{OP}$  (Table 1a). Herbivore biomass increases linearly with supply of resources that only limit plant growth ( $I_{SRC}$  and  $I_P$ ), similar to the biomass limitation scenario. Counterintuitively, however, herbivores biomass declines with increasing  $I_{PAH}$  (Fig. 2b and Table 1b). The response ratio increases weakly with increasing  $I_{OP}$  and strongly with  $I_{SRC}$  but declines with increasing  $I_{PAH}$ . Finally, increasing  $I_{OP}$  allows herbivores to exist at high  $I_{PAH}$  without any associated increases in  $I_{SRC}$  supply (Fig 3b). These results hold qualitatively even for

supply of resources that limit only herbivore growth,  $I_{OH}$ , such as N limitation of mammalian herbivores (See Supporting Information Appendix S1 for details).

### **Herbivore growth responds to plant resource to carbon ratio**

Herbivores may convert more of the plant biomass consumed to growth when plants are higher in a ratio of certain resources, rather than their absolute concentration of a particular resource. We explored plant ratio of the *PAH* resource to carbon (Fig 2c). Any increase in supply of *PAH* resource, increases plant internal  $r_{PAH}$ :  $r_C$  content, leading to an increase in herbivore biomass at equilibrium. In contrast, increase in supply of *SRC* resource decreases plant  $r_{PAH}$ :  $r_C$ , thus reducing herbivore biomass. Patterns for resources that only limit herbivores, *OH*, are similar to those for *PAH* resources (Appendix S1 eq. S7-10). Consequently, the change in response ratio, *RR*, to excluding herbivores varies along different resource supply gradients. *RR* will increase with greater  $I_{PAH}$  and  $I_{OP}$  (ex. nitrogen or phosphorus) and decline with greater  $I_{SRC}$  (Table 1c). Finally, greater supply of only plant-limiting resource  $I_{OP}$  again allows herbivores to thrive in regions with lower supplies of herbivore growth-limiting resources (Fig 3c).

### **Discussion**

Changing climate and anthropogenic manipulations of global biogeochemical cycles are altering natural ecosystems at unprecedented rates (Peñuelas *et al.* 2013; IPCC 2014) and affect multiple potentially limiting resources to plants and herbivores. Our model analyzes how plant-herbivore dynamics change under varying supply of multiple resources. A key result is that resources that limit growth for only one trophic level can influence the dynamics of the other even though growth of the second trophic level is limited by a different resource. This outcome can occur in several ways. First, *OP* resources that only limit plant growth can “apparently” limit herbivore biomass, as inferred from predicted positive association between herbivore biomass and *OP* resources (Table 1b,  $I_{OP}$ ). Secondly, this apparent limitation allows herbivores to persist under low supply rates of herbivore growth-limiting *PAH* or *OH*

resources at higher supplies of *OP* resources (Fig. 3a-c). Secondly, increasing resources that only limit herbivore growth can also increase (single resource limitation) or decrease (resource ratio limitation) plant biomass, even though plants are not limited by that resource (Table 1b,  $I_{OH}$ ). Moreover, responses of plants and herbivores to a given resource depend on the type of resource that limits either plant or herbivore growth.

A second major result is that herbivore biomass and impact (*RR*) are contingent on herbivore growth response to plant concentration of a single resource or to plant resource ratio ( $r_{PAH}:r_C$  or  $r_{OH}:r_C$ ). Under the former scenario, increasing supply of herbivore growth-limiting resource reduces herbivore biomass (Table 1b, Fig. 2b). Although counterintuitive, this result occurs because plant biomass increases faster with increasing  $I_{PAH}$  than does the tissue concentration ( $r_{PAH}^*$ ) of *PAH* resource, and ultimately causes plant growth rate to decline with increasing  $I_{PAH}$  due to density (biomass) dependence. Slower plant growth supports lower herbivore consumption rate and thus herbivore biomass declines with increasing  $I_{PAH}$ . In contrast, herbivore growth response to a resource ratio leads to an increase in herbivore biomass and impact with the resource in the ratio numerator (Table 1b, Fig. 2c) but a decline in both measures with increasing *SRC* resource (which controls C acquisition and/or assimilation). These predictions provide alternative testable hypotheses about how herbivore biomass and impact on plant biomass change across different environmental resource gradients; however, few such tests have been made.

Although our modelling approach evaluated several alternative assumptions about the functional form for growth and loss for both plants and herbivores, we discuss here two other assumptions. They are 1) excluding herbivore feedbacks on resource turnover and supply rate and 2) treating all resources as essential. First, herbivores can impact turnover rate of the resource that limits their growth, e.g., *PAH* or *OH* resources, and thereby modify environmental and plant tissue concentrations of that resource (Frank & Groffman 1998; Ritchie *et al.* 1998; Piñeiro *et al.* 2010; Plum *et al.* 2020). Including such herbivore effects might result in altered sensitivity of herbivore biomass to environmental supply of *PAH*

or *OH* resources. For example, acceleration of N cycling by herbivores otherwise N-limited in their growth (McNaughton *et al.* 1997) in some terrestrial systems may make herbivore biomass less sensitive to soil N supply but increase the sensitivity of both plants and herbivores to supplies of other *OP* and *SRC* resources, such as phosphorus or water (Veldhuis *et al.* 2014). Alternatively, herbivores may slow down resource turnover by consuming tissue with higher  $r_{PAH}:r_C$ , thereby leaving litter with lower  $r_{PAH}:r_C$  and yielding slower decomposition rates and reducing the supply rate of *PAH* resource (Bardgett & Wardle 2010). Under such scenarios, herbivore biomass may become more sensitive to supply of  $I_{PAH}$  and other resources. Secondly, there are instances where environmental resources for plants might be substitutable rather than essential. For example, Fe, Zn, Cd and Co, have been shown to bind interchangeably to enzyme active sites (Morel *et al.* 1994; Sunda & Huntsman 1995), thus allowing organisms to compensate for low supply of one ligand by consumption of another. Likewise, herbivores may in some cases substitute energy-rich soluble carbohydrates for *PAH* or *OH* (Behmer & Joern 1994) resources. However, analysis of plant-herbivore dynamics in the context of multiple substitutable resources is more complex and, while beyond the scope of this paper, is a worthy open research topic.

## **Model evaluation**

As a preliminary evaluation of the model, we identified putative *SRC*, *PAH* and *OP* resources for different autotrophs and their consumers in aquatic and terrestrial systems and reviewed or explored in new data relationships of herbivore abundance or biomass with measured availability of different environmental resources. Consistent with scenarios of herbivore growth response to plant biomass only or to plant resource ratios, herbivore abundance has been shown to increase with N (putative  $I_{PAH}$ ) in terrestrial systems (McNaughton 1985; Fritz & Duncan 1994; Griffin *et al.* 1998; Griffith & Grinath 2018) and with phosphorus (putative  $I_{PAH}$ ) in aquatic systems (Sterner & Schulz 1998; Urabe *et al.* 2003). In contrast, we present new data consistent with the scenario that herbivore growth responds only to plant *PAH* resource concentration. Abundance of some putatively N-limited herbivores such as krill (*Euphausia*

*superba*) decreases with increasing nitrate and nitrite availability (Fig. 4a), even after controlling for dissolved P and Si. Similarly, in a terrestrial ecosystem, grasshoppers known to be limited by N (Strengbom *et al.* 2008) decreased in abundance with increasing soil N content (Fig. 4b) in a set of abandoned old fields at Cedar Creek (Knops & Tilman 2000).

Herbivore biomass association with putative surrogate carbon assimilation (*SRC*) resources appear equally varied. Some studies are consistent with the scenario of herbivore growth response to plant biomass only: mammalian herbivore biomass or abundance often increases with supply rates of water (Fritz & Duncan 1994; Griffin *et al.* 1998; Griffith & Grinath 2018). However, other herbivore biomass associations with putative *SRC* resources are consistent with the scenario of herbivore response to plant resource ratios. For example herbivore biomass or abundance decreases with increasing precipitation in terrestrial systems (Hempson *et al.* 2015; Wade *et al.* 2017; Walter 2018; Andrade *et al.* 2020) and light in freshwater systems (Urabe & Sterner 1996; Sterner & Schulz 1998; Scheuerell *et al.* 2002). Likewise, planktonic herbivores decrease with increasing light and silica in marine systems (Pondaven *et al.* 2007; Hessen *et al.* 2008; Pančić *et al.* 2019).

#### **Evidence for apparent resource limitation of herbivores**

All herbivore response scenarios predict “apparent limitation” of herbivore biomass by *OP* resources, i.e., those not involved in C assimilation or limiting to herbivore growth. This apparency takes the form of a positive association between herbivore biomass or abundance with an *OP* resource in the ecosystem. Putatively phosphorus-limited *Daphnia spp* abundance (Urabe *et al.* 2003), from Northern Temperate Lakes Long Term Ecological Research (LTER)(Carpenter *et al.* 2017a,b) were positively associated with dissolved N concentration after statistically accounting for dissolved P (Fig. 4c). Similarly, in the oceans, N and/or Fe are non-limiting to growth of certain herbivores but are limiting to primary production (Coale *et al.* 1996; Elser *et al.* 2007; Plum *et al.* 2020). Data from Palmer LTER site in the

Southern Ocean (Palmer Station Antarctica LTER *et al.* 2019, 2020) shows that abundance of putatively P-limited salps (*Salpa thomsonii*) (Alcaraz *et al.* 2014; Plum *et al.* 2020) increases with nitrate and nitrite content (Fig. 4d), implying an apparent limitation of salps by N. Apparent limitation of marine herbivores by Fe has also been reported in the Western Subarctic Pacific (Saito *et al.* 2005), where heterotrophic nanoflagellates numbers responded positively to and reduced algal abundance more strongly in response to Fe addition (Fig. 4e). In terrestrial systems, studies are scarcer, but a few field and experimental studies have also shown that putatively N-limited insect herbivores increase with soil P (Bishop *et al.* 2010; Joern *et al.* 2012; La Pierre & Smith 2016). In addition, we present new data that show higher densities of ostensibly N-limited grasshoppers (Orthoptera) in P-fertilized fenced grassland plots in Serengeti National Park in Tanzania (Fig. 4f). These examples suggest that “apparent limitation” of herbivores by non-growth-limiting resources may be common, but further work is needed to explore such patterns.

#### **Response to resources limiting only herbivore growth (resource OH)**

Our model allows for incorporating resources that do not affect plant growth but may limit herbivore per capita growth (*OH* resources). For example, studies increasingly note the importance of micronutrients such as sodium on plant-herbivore interactions (McNaughton 1988; Wallisdevries 1996; McNaughton *et al.* 1997; Kaspari *et al.* 2017; Kaspari 2020). Even though sodium has no direct impact on plant growth under a wide range of plant growth conditions, plants high in sodium are often more palatable to herbivores. As a result, increasing Na may lead to higher impact of herbivores or a reduction in plant biomass that is unrelated to any effect of Na on plant growth. Herbivore abundance and plant consumption has been reported to increase with increasing environmental Na (Kaspari *et al.* 2017; Prather *et al.* 2018). Although current hypotheses argue for limitation by Na alone, the positive association between Na and herbivory is actually only consistent with the hypothesis that herbivores respond to Na:C rather than just Na content. Limitations of herbivore growth by other micronutrients



such as Ca might produce similar effects. These possibilities represent opportunities for further exploration of cross-trophic level resource dependencies driven by herbivore growth-limiting resources.

### **Outcomes of herbivore exclusion experiments along resource gradients**

Impacts of herbivores on plant biomass may change considerably with the magnitude and type of different resource supplies (Table 1c, Appendix S3 Fig. S1) and the herbivore growth response scenarios we explored yield different expected patterns. The response ratio ( $RR$ ), typically reported as  $\ln(RR)$ , is defined as the ratio of biomass in a fenced plot to that of an unfenced plot. Our results suggest that  $RR$  - resource supply relationships are best described by power or exponential functions with fractional exponents (Table 1c); we find that generally  $RR$  is more sensitive to increasing resources at low supply and less so at high supply. In addition, predictions of herbivore exclusion experimental results differ drastically among our herbivore growth response scenarios for increasing  $SRC$  and  $PAH$  resources but not for  $OP$  resources. For all scenarios, herbivore impacts should increase moderately with supply of “apparently limiting”  $OP$  resources (Fig. S1a), and in the scenario when herbivores solely respond to plant biomass, herbivore impacts should be greater with increasing supplies of all resources except  $OH$  resource (Table 1, Fig. S1a-c, solid line). These patterns invite a general prediction that herbivore impacts increase in general with resource supply. In contrast, in the scenario of herbivore growth response only to plant  $PAH$  or  $OH$  concentration, enclosure experiments should have larger effects at higher  $SRC$  resource supply (e.g., light, precipitation) but weaker effects at increasing  $PAH$  resource (e.g., N, P) and  $OH$  resource (e.g., sodium) supply (Fig. S1b-d dotted line, Table 1c). Finally, in the scenario where herbivore growth response is to a resource ratio,  $r_{PAH}:r_C$  or  $r_{OH}:r_C$ , experimental results become exponentially and positively sensitive to the supply of  $PAH$  resource (Fig. S1b, dashed line), positively sensitive to  $OH$  resource (Fig. S1d, dashed line), but are weakened by increasing  $SRC$  resource (Fig. S1c, dashed line). These different outcomes suggest that herbivore enclosure experiments carried out across

multiple resource gradients might test which of these scenarios is most applicable to the ecosystem of interest, such as a mammalian-grazed grassland vs pelagic marine.

Another consequence of plant limitation by multiple resources is that sensitivity of herbivore impacts to a change in resource supply may also depend on the supply of other resources. Unfortunately, despite literally thousands of reported herbivore exclosure studies, almost none have measured supply rates or availabilities of candidate *OP* resources, such as P in terrestrial systems, N in freshwater aquatic systems and Fe in marine systems, that would allow these hypotheses to be tested. More field studies are needed that measure multiple resources for plants and herbivores in addition to plant biomass inside and outside exclosures.

### **Thresholds for herbivore persistence**

Our theoretical framework reimagines the emergence of herbivore control of productivity as resource availability increases (Exploitation Ecosystems Hypothesis (EEH) (Oksanen *et al.* 1981; Oksanen 1992) in a multiple resource supply context. Minimum thresholds for herbivore persistence based on supplies of different resources help identify conditions or habitats where herbivores can occur. Particularly, our model predicts that *OP* resources that limit plant but not herbivore growth also determine minimum thresholds of *PAH* or *OH* resources for herbivore persistence and by extension conditions for herbivore distributions. For example, in terrestrial systems, higher P associated with young volcanic soils otherwise low in N may allow for more herbivores to occur in such habitats. Alternatively, extensive addition of *OP* resources, such as might occur in agricultural ecosystems, may support larger populations of insect pests. Different species of herbivores may vary in their resource thresholds depending on their body size and metabolism (Olf *et al.* 2002), and modifications of supplies of multiple resources might affect which herbivores may co-occur and thus patterns in richness and diversity of herbivores. Our model suggests that multiple resource limitation of plants may be important for many of these patterns.

In conclusion, we developed a framework to understand the cross-trophic level influence of multiple resource limitation of plants. We explore the effect of different types of resources and herbivore resource response scenarios on herbivore biomass and impact. Our findings regarding “apparent” limitation of herbivores by resources that do not limit herbivore growth, and dependence of herbivore biomass on herbivore response to single resource concentration or resource ratios, provides explanations for some hitherto ignored patterns in herbivory. Additionally, multiple resource limitation framework also suggests that increasing supply of resources non-limiting to herbivore growth too can allow herbivores to persist even when herbivore growth-limiting resources are sparse. These wide variety of responses of herbivore biomass and impact to different resource supplies provide a lens to study different types of herbivores responding to changing climate and anthropogenic manipulation of resources.

**Acknowledgements:** We are grateful to NSF (DEB – 1557085) for funding. We also thank Hugh Ducklow, Barbara Prezelin, and Steve Carpenter for granting us permission to use their data available through Palmer and Northern Temperate Lakes LTER networks. This manuscript greatly benefitted from feedbacks provided by members of the Plant Ecology labs at SU.

#### **References:**

- Alcaraz, M., Almeda, R., Duarte, C.M., Horstkotte, B., Lasternas, S. & Agustí, S. (2014). Changes in the C, N, and P cycles by the predicted salps-krill shift in the southern ocean. *Front. Mar. Sci.*, 1.
- Andrade, J.F., Alvarado, F., Carlos Santos, J. & Santos, B.A. (2020). Rainfall reduction increases insect herbivory in tropical herb communities. *J. Veg. Sci.*, 31, 487–496.
- Awmack, C.S. & Leather, S.R. (2002). Host Plant Quality and Fecundity in Herbivorous Insects. *Annu. Rev. Entomol.*, 47, 817–844.
- Bardgett, R.D. & Wardle, D.A. (2010). *Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*. Oxford University Press.

411 Behmer, S.T. & Joern, A. (1994). The influence of proline on diet selection: sex-specific feeding  
 412 preferences by the grasshoppers *Ageneotettix deorum* and *Phoetaliotes nebrascensis*  
 413 (Orthoptera: Acrididae). *Oecologia*, 98, 76–82.

414 Bishop, J.G., O'Hara, N.B., Titus, J.H., Apple, J.L., Gill, R.A. & Wynn, L. (2010). N-P Co-Limitation of  
 415 Primary Production and Response of Arthropods to N and P in Early Primary Succession on  
 416 Mount St. Helens Volcano. *PLOS ONE*, 5, e13598.

417 Bracken, M.E.S., Hillebrand, H., Borer, E.T., Seabloom, E.W., Cebrian, J., Cleland, E.E., *et al.* (2015).  
 418 Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient  
 419 concentrations to nitrogen and phosphorus additions. *Oikos*, 124, 113–121.

420 Bryant, J.P., Chapin, F.S. & Klein, D.R. (1983). Carbon/Nutrient Balance of Boreal Plants in Relation to  
 421 Vertebrate Herbivory. *Oikos*, 40, 357–368.

422 Carpenter, S., Kitchell, J., Cole, J. & Pace, M. (2017a). Cascade Project at North Temperate Lakes LTER  
 423 Core Data Zooplankton 1984 - 2016. *Environ. Data Initiat.*, ver 4.

424 Carpenter, S., Kitchell, J., Cole, J. & Pace, M. (2017b). Cascade Project at North Temperate Lakes LTER  
 425 Core Data Nutrients 1991 - 2016. *Environ. Data Initiat.*, ver 3.

426 Cebrian, J. & Lartigue, J. (2004). Patterns of Herbivory and Decomposition in Aquatic and Terrestrial  
 427 Ecosystems. *Ecol. Monogr.*, 74, 237–259.

428 Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches : Linking Classical and Contemporary Approaches*.  
 429 Interspecific Interactions. University of Chicago Press.

430 Chase, J.M., Leibold, M.A., Downing, A.L. & Shurin, J.B. (2000). The Effects of Productivity, Herbivory,  
 431 and Plant Species Turnover in Grassland Food Webs. *Ecology*, 81, 2485–2497.

432 Cleland, E.E. & Harpole, W.S. (2010). Nitrogen enrichment and plant communities. *Ann. N. Y. Acad. Sci.*,  
 433 1195, 46–61.

434 Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., *et al.* (1996). A massive  
435 phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the  
436 equatorial Pacific Ocean. *Nature*, 383, 495–501.

437 Coley, P.D., Bryant, J.P. & F. Stuart Chapin, I. (1985). Resource availability and plant antiherbivore  
438 defense. *Science*, 230, 895–900.

439 Cyr, H. & Face, M.L. (1993). Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems.  
440 *Nature*, 361, 148–150.

441 Downing, J.A., Osenberg, C.W. & Sarnelle, O. (1999). Meta-Analysis of Marine Nutrient-Enrichment  
442 Experiments: Variation in the Magnitude of Nutrient Limitation. *Ecology*, 80, 1157–1167.

443 Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., *et al.* (2007). Global  
444 analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and  
445 terrestrial ecosystems. *Ecol. Lett.*, 10, 1135–1142.

446 Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., *et al.* (2000). Biological  
447 stoichiometry from genes to ecosystems. *Ecol. Lett.*, 3, 540–550.

448 Elser, J.J. & Urabe, J. (1999). The Stoichiometry of Consumer-Driven Nutrient Recycling: Theory,  
449 Observations, and Consequences. *Ecology*, 80, 735–751.

450 Fay, P.A. (2015). Grassland productivity limited by multiple nutrients. *Nat. Plants*, 1, 1–5.

451 Frank, D.A. & Groffman, P.M. (1998). Ungulate Vs. Landscape Control of Soil C and N Processes in  
452 Grasslands of Yellowstone National Park. *Ecology*, 79, 2229–2241.

453 Fritz, H. & Duncan, P. (1994). On the carrying capacity for large ungulates of African savanna  
454 ecosystems. *Proc. R. Soc. Lond. B Biol. Sci.*

455 Griffin, M.P.A., Cole, M.L., Kroeger, K.D. & Cebrian, J. (1998). Dependence of Herbivory on Autotrophic  
456 Nitrogen Content and on Net Primary Production Across Ecosystems. *Biol. Bull.*, 195, 233–234.

457 Griffith, K.A. & Grinath, J.B. (2018). Interactive effects of precipitation and nitrogen enrichment on multi-  
458 trophic dynamics in plant-arthropod communities. *PLOS ONE*, 13, e0201219.

459 Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community Structure, Population Control, and  
460 Competition. *Am. Nat.*, 94, 421–425.

461 Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., *et al.* (2011).  
462 Nutrient co-limitation of primary producer communities. *Ecol. Lett.*, 14, 852–862.

463 Harpole, W.S., Potts, D.L. & Suding, K.N. (2007). Ecosystem responses to water and nitrogen amendment  
464 in a California grassland. *Glob. Change Biol.*, 13, 2341–2348.

465 Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., *et al.* (2015). Ecology of  
466 grazing lawns in Africa. *Biol. Rev.*, 90, 979–994.

467 Herms, D.A. & Mattson, W.J. (1992). The Dilemma of Plants : To Grow or Defend. *Quarterly Rev. Biol.*, 67,  
468 283–335.

469 Hessen, D.O. (1992). Nutrient Element Limitation of Zooplankton Production. *Am. Nat.*, 140, 799–814.

470 Hessen, D.O., Færøvig, P.J. & Andersen, T. (2002). Light, Nutrients, and P:c Ratios in Algae: Grazer  
471 Performance Related to Food Quality and Quantity. *Ecology*, 83, 1886–1898.

472 Hessen, D.O., Leu, E., Færøvig, P.J. & Falk Petersen, S. (2008). Light and spectral properties as  
473 determinants of C:N:P-ratios in phytoplankton. *Deep Sea Res. Part II Top. Stud. Oceanogr.*,  
474 Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change, 55,  
475 2169–2175.

476 Holdo, R.M., Holt, R.D., Coughenour, M.B. & Ritchie, M.E. (2007). Plant productivity and soil nitrogen as  
477 a function of grazing, migration and fire in an African savanna. *J. Ecol.*, 95, 115–128.

478 IPCC. (2014). *IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II*  
479 *and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.*

480 Izui, K., Matsumura, H., Furumoto, T. & Kai, Y. (2004). PHOSPHOENOLPYRUVATE CARBOXYLASE: A New  
 481 Era of Structural Biology. *Annu. Rev. Plant Biol.*, 55, 69–84.

482 Joern, A., Provin, T. & Behmer, S.T. (2012). Not just the usual suspects: insect herbivore populations and  
 483 communities are associated with multiple plant nutrients. *Ecology*, 93, 1002–1015.

484 Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L. & Jansson, M. (2009). Light limitation of nutrient-  
 485 poor lake ecosystems. *Nature*, 460, 506–509.

486 Kaspari, M. (2020). The seventh macronutrient: how sodium shortfall ramifies through populations, food  
 487 webs and ecosystems. *Ecol. Lett.*, 23, 1153–1168.

488 Kaspari, M., Roeder, K.A., Benson, B., Weiser, M.D. & Sanders, N.J. (2017). Sodium co-limits and  
 489 catalyzes macronutrients in a prairie food web. *Ecology*, 98, 315–320.

490 Knops, J.M.H. & Tilman, D. (2000). Dynamics of Soil Nitrogen and Carbon Accumulation for 61 Years  
 491 After Agricultural Abandonment. *Ecology*, 81, 88–98.

492 La Pierre, K.J. & Smith, M.D. (2016). Soil nutrient additions increase invertebrate herbivore abundances,  
 493 but not herbivory, across three grassland systems. *Oecologia*, 485–497.

494 Lemoine, N.P., Giery, S.T. & Burkepile, D.E. (2014). Differing nutritional constraints of consumers across  
 495 ecosystems. *Oecologia*, 174, 1367–1376.

496 Loladze, I. (2000). Stoichiometry in Producer–Grazer Systems: Linking Energy Flow with Element Cycling.  
 497 *Bull. Math. Biol.*, 62, 1137–1162.

498 Loladze, I. & Elser, J.J. (2011). The origins of the Redfield nitrogen-to-phosphorus ratio are in a  
 499 homoeostatic protein-to-rRNA ratio. *Ecol. Lett.*, 14, 244–250.

500 Mattson, W.J. (1980). Herbivory in Relation to Plant Nitrogen Content. *Annu. Rev. Ecol. Syst.*, 11, 119–  
 501 161.

502 Mazancourt, C. de, Loreau, M. & Abbadie, L. (1998). Grazing Optimization and Nutrient Cycling: When  
 503 Do Herbivores Enhance Plant Production? *Ecology*, 79, 2242–2252.

504 McNaughton, S.J. (1985). Ecology of a Grazing Ecosystem : The Serengeti. *Ecol. Monogr.*, 55, 259–294.

505 McNaughton, S.J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature*, 334,

506 343–345.

507 McNaughton, S.J., Banyikwa, F.F. & McNaughton, M.M. (1997). Promotion of the Cycling of Diet-

508 Enhancing Nutrients by African Grazers. *Science*, 278, 1798–1800.

509 Morel, F.M.M., Reinfelder, J.R., Roberts, S.B., Chamberlain, C.P., Lee, J.G. & Yee, D. (1994). Zinc and

510 carbon co-limitation of marine phytoplankton. *Nature*, 369, 740–742.

511 Oksanen, L. (1992). Evolution of exploitation ecosystems I. Predation, foraging ecology and population

512 dynamics in herbivores. *Evol. Ecol.*, 6, 15–33.

513 Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of

514 primary productivity. *Am. Nat.*, 118, 240–261.

515 Olff, H., Ritchie, M.E. & Prins, H.H.T. (2002). Global environmental controls of diversity in large

516 herbivores. *Nature*, 415, 901–904.

517 Onoda, Y., Wright, I.J., Evans, J., Hikosaka, K., Kitajima, K., Niinemets, Ü., *et al.* (n.d.). Physiological and

518 structural tradeoffs underlying the leaf economics spectrum - Onoda - 2017 - New Phytologist -

519 Wiley Online Library. *New Phytol.*, 214, 1447–1463.

520 Palmer Station Antarctica LTER, Ducklow, H.W., Vernet, M. & Prezelin, B. (2019). Dissolved inorganic

521 nutrients including 5 macro nutrients: silicate, phosphate, nitrate, nitrite, and ammonium from

522 water column bottle samples collected between October and April at Palmer Station, 1991 -

523 2019. *Environ. Data Initiat.*, ver 9.

524 Palmer Station Antarctica LTER, Steinberg, D., Ross, R. & Quetin, L. (2020). Zooplankton collected aboard

525 Palmer Station LTER annual cruises off the western antarctic peninsula, 1993 - 2008. *Environ.*

526 *Data Initiat.*, ver 4.



527 Pančić, M., Torres, R.R., Almeda, R. & Kiørboe, T. (2019). Silicified cell walls as a defensive trait in  
528 diatoms. *Proc. R. Soc. B Biol. Sci.*, 286, 20190184.

529 Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., *et al.* (2013). Human-induced  
530 nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat.*  
531 *Commun.*, 4, 2934.

532 Piñeiro, G., Paruelo, J.M., Oesterheld, M. & Jobbágy, E.G. (2010). Pathways of Grazing Effects on Soil  
533 Organic Carbon and Nitrogen. *Rangel. Ecol. Manag.*, 63, 109–119.

534 Plum, C., Hillebrand, H. & Moorthi, S. (2020). Krill vs salps: dominance shift from krill to salps is  
535 associated with higher dissolved N:P ratios. *Sci. Rep.*, 10, 5911.

536 Pondaven, P., Gallinari, M., Chollet, S., Bucciarelli, E., Sarthou, G., Schultes, S., *et al.* (2007). Grazing-  
537 induced Changes in Cell Wall Silicification in a Marine Diatom. *Protist*, 158, 21–28.

538 Prather, C.M., Laws, A.N., Cuellar, J.F., Reihart, R.W., Gawkins, K.M. & Pennings, S.C. (2018). Seeking salt:  
539 herbivorous prairie insects can be co-limited by macronutrients and sodium. *Ecol. Lett.*, 21,  
540 1467–1476.

541 Ritchie, M.E. & Olff, H. (1999). Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, 400,  
542 557–560.

543 Ritchie, M.E., Tilman, D. & Knops, J.M.H. (1998). Herbivore Effects on Plant and Nitrogen Dynamics in  
544 Oak Savanna. *Ecology*, 79, 165–177.

545 Saito, H., Suzuki, K., Hinuma, A., Ota, T., Fukami, K., Kiyosawa, H., *et al.* (2005). Responses of  
546 microzooplankton to in situ iron fertilization in the western subarctic Pacific (SEEDS). *Prog.*  
547 *Oceanogr.*, Results from the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study  
548 (SEEDS), 64, 223–236.

549 Saito, M.A., Goepfert, T.J. & Ritt, J.T. (2008). Some thoughts on the concept of colimitation: Three  
550 definitions and the importance of bioavailability. *Limnol. Oceanogr.*, 53, 276–290.

551 Scheuerell, M.D., Schindler, D.E., Litt, A.H. & Edmondson, W.T. (2002). Environmental and algal forcing  
 552 of Daphnia production dynamics. *Limnol. Oceanogr.*, 47, 1477–1485.

553 Sperfeld, E., Martin-Creuzburg, D. & Wacker, A. (2012). Multiple resource limitation theory applied to  
 554 herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. *Ecol. Lett.*, 15, 142–  
 555 150.

556 Spreitzer, R.J. & Salvucci, M.E. (2002). RUBISCO: Structure, Regulatory Interactions, and Possibilities for a  
 557 Better Enzyme. *Annu. Rev. Plant Biol.*, 53, 449–475.

558 Sterner, R.W. & Elser, J.J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to*  
 559 *the Biosphere*. Princeton University Press.

560 Sterner, R.W. & Schulz, K.L. (1998). Zooplankton nutrition: recent progress and a reality check. *Aquat.*  
 561 *Ecol.*, 32, 261–279.

562 Strengbom, J., Reich, P.B. & Ritchie, M.E. (2008). High plant species diversity indirectly mitigates CO<sub>2</sub>-  
 563 and N-induced effects on grasshopper growth. *Acta Oecologica*, 34, 194–201.

564 Sunda, W.G. & Huntsman, S.A. (1995). Cobalt and zinc interreplacement in marine phytoplankton:  
 565 Biological and geochemical implications. *Limnol. Oceanogr.*, 40, 1404–1417.

566 Sunda, W.G. & Huntsman, S.A. (1997). Interrelated influence of iron, light and cell size on marine  
 567 phytoplankton growth. *Nature*, 390, 389–392.

568 Thébault, E. & Loreau, M. (2003). Food-web constraints on biodiversity–ecosystem functioning  
 569 relationships. *Proc. Natl. Acad. Sci.*, 100, 14949–14954.

570 Thébault, E. & Loreau, M. (2005). Trophic Interactions and the Relationship between Species Diversity  
 571 and Ecosystem Stability. *Am. Nat.*, 166, E95–E114.

572 Urabe, J., Clasen, J. & Sterner, R.W. (2003). Phosphorus limitation of Daphnia growth: Is it real? *Limnol.*  
 573 *Oceanogr.*, 42, 1436–1443.

574 Urabe, J. & Sterner, R.W. (1996). Regulation of herbivore growth by the balance of light and nutrients.  
575 *Proc. Natl. Acad. Sci.*, 93, 8465–8469.

576 Veldhuis, M.P., Howison, R.A., Fokkema, R.W., Tielens, E. & Olff, H. (2014). A novel mechanism for  
577 grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *J.*  
578 *Ecol.*, 102, 1506–1517.

579 Wade, R.N., Karley, A.J., Johnson, S.N. & Hartley, S.E. (2017). Impact of predicted precipitation scenarios  
580 on multitrophic interactions. *Funct. Ecol.*, 31, 1647–1658.

581 Wallisdevries, M.F. (1996). Nutritional Limitations of Free-Ranging Cattle: The Importance of Habitat  
582 Quality. *J. Appl. Ecol.*, 33, 688–702.

583 Walter, J. (2018). Effects of changes in soil moisture and precipitation patterns on plant-mediated biotic  
584 interactions in terrestrial ecosystems. *Plant Ecol.*, 219, 1449–1462.

585 Welte, E.A.R., Roeder, K.A., Beurs, K.M. de, Joern, A. & Kaspari, M. (2020). Nutrient dilution and climate  
586 cycles underlie declines in a dominant insect herbivore. *Proc. Natl. Acad. Sci.*

587 Wilkinson, D.M. & Sherratt, T.N. (2016). Why is the world green? The interactions of top–down and  
588 bottom–up processes in terrestrial vegetation ecology. *Plant Ecol. Divers.*, 9, 127–140.

589 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004). The worldwide  
590 leaf economics spectrum. *Nature*, 428, 821–827.

591

## Tables

Table 1: Summary of the approximate predicted relationships from different model assumptions for steady-state plant biomass, herbivore biomass and response ratio of herbivory based on a model with supply of resources  $I_{SRC}$  (surrogate resource for assimilating carbon),  $I_{PAH}$  (limiting to Producers And Herbivores), and  $I_{OP}$  (limiting to Only Plants). Relationship with  $I_{OH}$  (resource limiting to Only Herbivores) is based on a model with  $I_{OH}$ ,  $I_{SRC}$ , and  $I_{OP}$ . The overall trends from the  $OH$  resource model are congruent with the trends from  $PAH$  model but exponents associated with  $SRC$  and  $OP$  resources may differ between the two models (See Supporting Information Appendix S1).

	Herbivore growth responds to		
	Plant biomass only	Plant resource conc. and biomass	Plant resource: C and biomass
a) Steady state plant biomass ( $S_G^*$ )			
$I_{SRC}$	No change	No change	↑ approx. exponentially <sup>†</sup>
$I_{PAH}$	No change	↑ linearly	↓ as $1/I_{PAH}$
$I_{OP}$	No change	No change	No change
$I_{OH}$	No change	↑ linearly	↓ as $1/I_{OH}$
b) Steady state herbivore biomass ( $H^*$ )			
$I_{SRC}$	↑ linearly	↑ linearly	↓ approx. exponentially <sup>†</sup>
$I_{PAH}$	↑ linearly above a min $I_{PAH}$	↓ approx. as $1/I_{PAH}$	↑ approx. exponentially <sup>†</sup>
$I_{OP}$	↑ linearly above a min $I_{OP}$	↑ linearly above a min $I_{OP}$	↑ linearly
$I_{OH}$	No change	↓ approx. as $1/I_{OH}$	↑ approx. linearly
c) Response ratio of herbivory ( $S_U^*/S_G^*$ )			
$I_{SRC}$	↑ as $I_{SRC}^{1/2}$	↑ as $I_{SRC}^{1/2}$	↓ as $I_{SRC}^{-1/2}$ to max $\alpha I_{PAH}$
$I_{PAH}$	↑ as $I_{PAH}^{1/4}$	↓ as $I_{PAH}^{-3/4}$ above min $I_{PAH}$	↑ as $I_{PAH}^{5/4}$
$I_{OP}$	↑ as $I_{OP}^{1/4}$	↑ as $I_{OP}^{1/4}$	↑ as $I_{OP}^{1/4}$
$I_{OH}$	No change	↓ as $1/I_{OH}$	↑ linearly

\* Steady-state condition

† Shape of the function is sensitive to values of some of the parameters

Figures

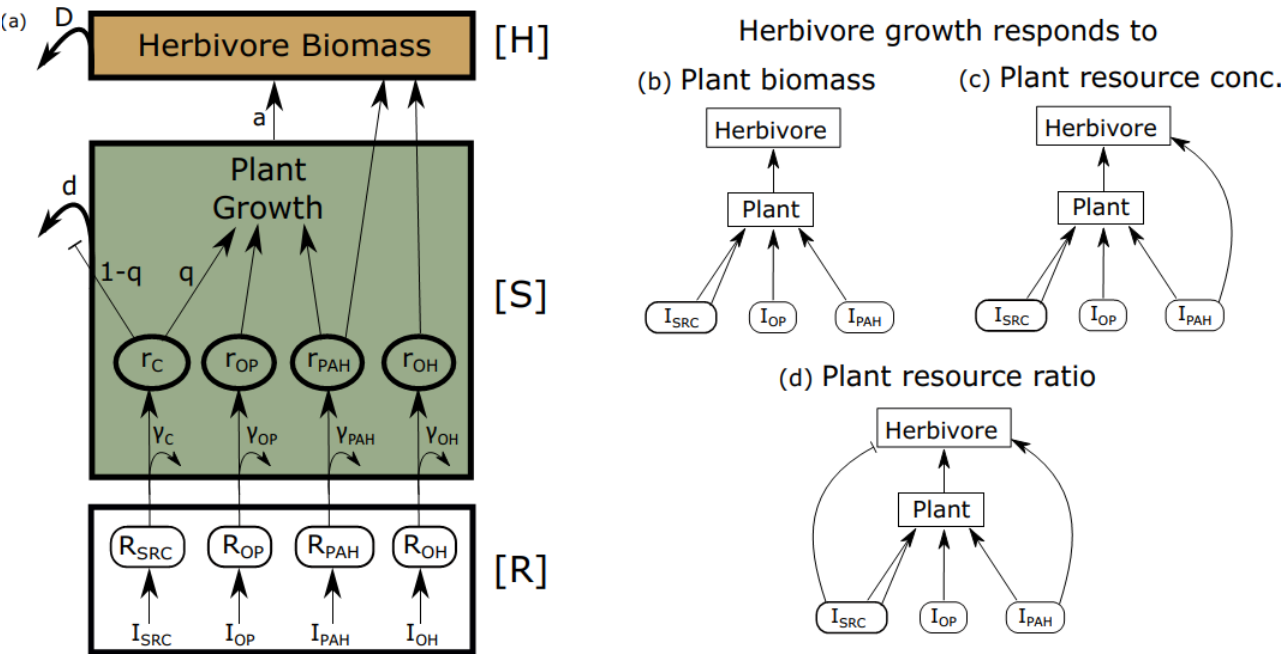


Figure 1:

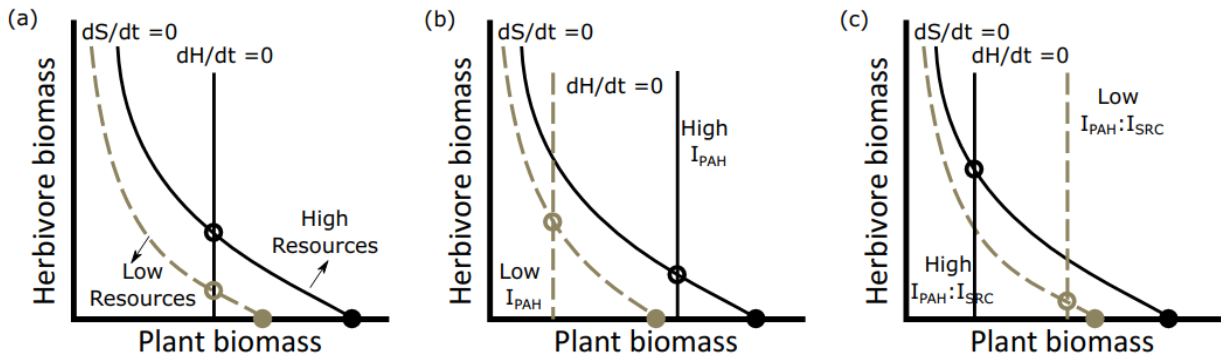


Figure 2:

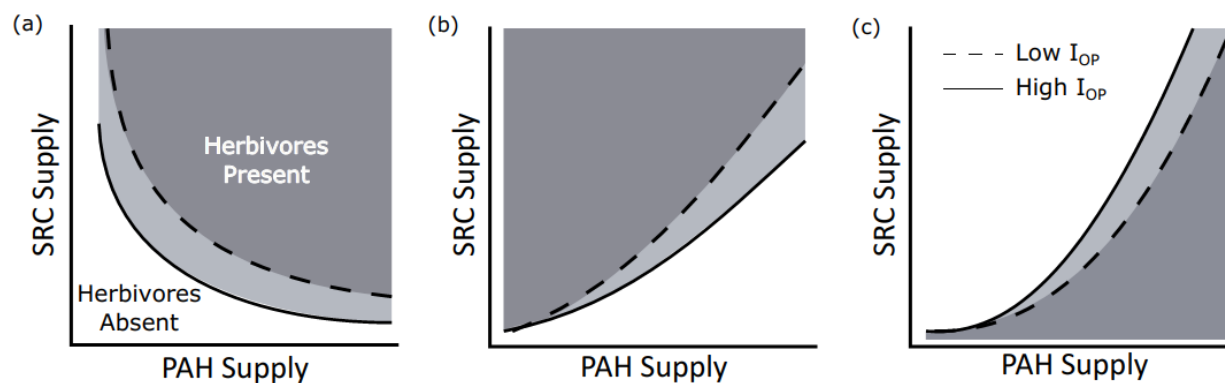
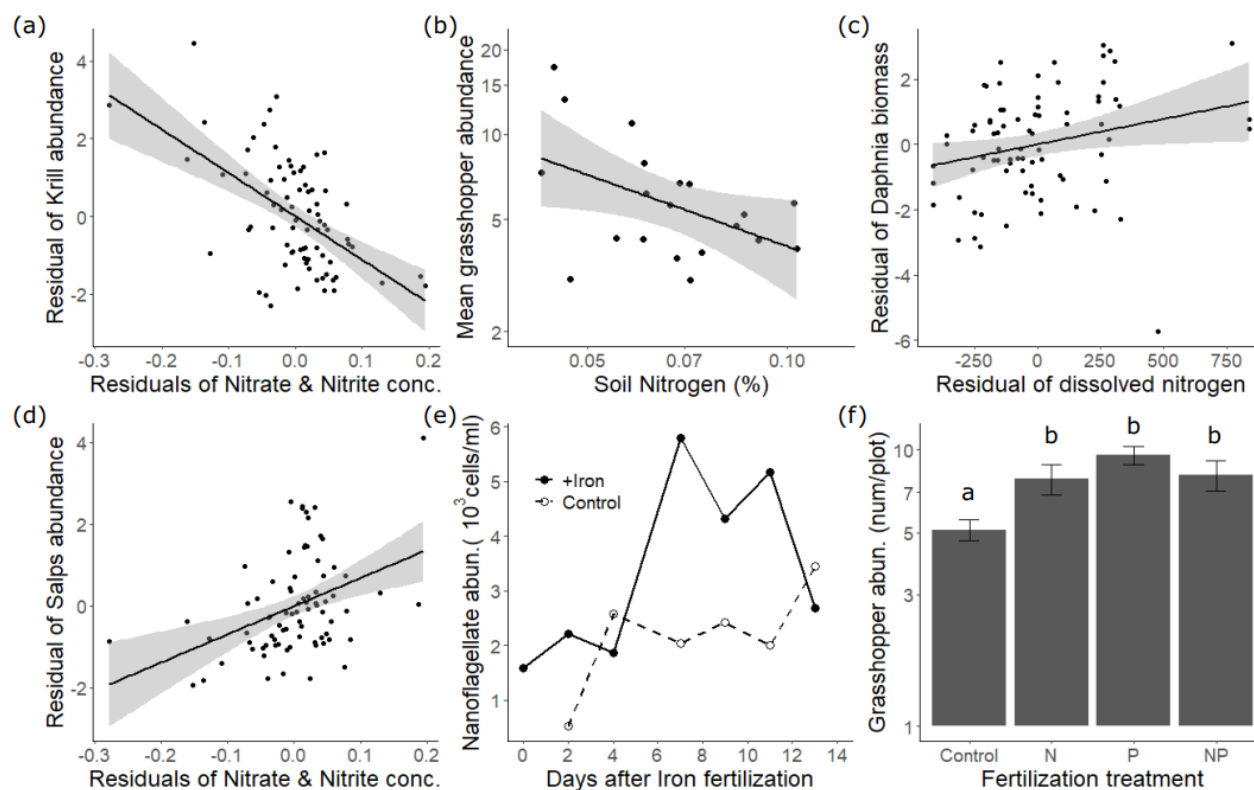


Figure 3:



## Figure legends

Figure 1: Graphical representation of the modelling framework. (a) A three-level food chain with four types of resources- *SRC*= Surrogate Resource for acquiring Carbon, *C*= Carbon, *OP*= limiting Only to Plants, *PAH*= limiting to Plants and Herbivores and *OH*= limiting Only to Herbivores. Other model abbreviations include, *I* for resource supply [units in  $\text{g}_{\text{resource}}\text{t}^{-1}\text{area}^{-1}$ ], *R* for resource concentration in the environment [ $\text{g}_{\text{resource}}\text{area}^{-1}$ ],  $\gamma$  for resource turnover in plant tissue [ $\text{t}^{-1}$ ], *r* for resource concentration in plant tissue [ $\text{g}_{\text{resource}}$ ], *S* for plant biomass [ $\text{g}_{\text{Plant}} \cdot \text{area}^{-1}$ ], *q* for proportion of carbon allocated towards metabolic processes,  $1-q$  for proportion allocated to structural compounds which reduce plant mortality, *d* for plant mortality in the absence of herbivory [ $\text{g}_{\text{resource}} \cdot \text{t}^{-1}$ ], *H* for herbivore biomass [ $\text{g}_{\text{Herbivore}} \cdot \text{area}^{-1}$ ], *a* is per capita attack rate by herbivores [ $\text{area} \cdot \text{g}_{\text{Herbivore}}^{-1}\text{t}^{-1}$ ] and *D* for herbivore mortality [ $\text{t}^{-1}$ ]. Different scenarios where herbivore growth responds to: (b) Plant biomass only, (c) Plant resource concentration and biomass, (d) Plant resource ratio and biomass. In c and d, *I<sub>PAH</sub>* can be replaced with *I<sub>OH</sub>*.

Figure 2: Isoclines and predicted changes in steady state biomass of plants and herbivores for different scenarios where herbivore growth responds to) Plant biomass only, b) Concentration of the resource limiting both plant and herbivore growth (*PAH*) and plant biomass, and c) Ratio of *PAH* resource to carbon concentration and biomass. Combinations of plant and herbivore biomass (isoclines) leading to steady-state plant biomass ( $dS/dt = 0$ ) are curves, while isoclines for steady-state herbivore growth are vertical lines. Closed circles denote steady-state plant biomass in the absence of herbivores ( $S_U^*$ ) while open circles denote steady state equilibria under herbivory. Gray curves and circles denote low resource supply while black denotes high resource supply. “*I*” denotes the supply rate of resources. *PAH*= limiting to Plants and Herbivores, *SRC*= Surrogate Resource to acquiring Carbon, *OP*= limiting Only to Plants.

Figure 3: Thresholds of different resource supplies required to support herbivore biomass when herbivore growth responds to) Plant biomass only, b) Concentration of the resource limiting both plant

and herbivore growth (*PAH*) and plant biomass, and c) Ratio of *PAH* resource to carbon concentration and biomass. The shaded parts define regions in the *SRC-PAH* resource supply plane in which herbivores can survive. Increase in supply of *OP* expands the thresholds for herbivores to survive. In the figures, “*I*” denotes the supply rate of resources. *PAH*= limiting to Plants and Herbivores, *SRC*= Surrogate Resource to acquiring Carbon, *OP*= limiting Only to Plants.

Figure 4: Data from different systems lending support to model predictions. a) A potentially N-limited marine grazer, krill, decreases with nitrate and nitrite concentrations ( $R^2 = 0.30$  for the residual-residual model) when phosphates and silicates are accounted for in a mixed model (Original data from Palmer LTER); b) Grasshopper abundance decreases with soil N at Cedar Creek ( $R^2 = 0.31$ ) (Original data from Cedar Creek LTER); c) *Daphnia* biomass increases with N content of water. While the trend is always significant in the mixed model, the  $R^2$  of the residual-residual model increases from 0.04 to 0.14 when a single outlier point is dropped from the analysis; d) Abundance of a potentially P-limited marine grazer, salps, increases with nitrate and nitrite concentration in water ( $R^2 = 0.15$  for the residual-residual model) when variation due to phosphates and silicates are accounted for (Palmer LTER dataset); e) Heterotrophic nanoflagellates that graze on micro-phytoplankton and phytoplankton increase with iron enrichment in the open seas (Figure reprinted from Saito et al. 2005 (Responses of microzooplankton to in situ iron fertilization in the western subarctic Pacific (SEEDS), Progress in Oceanography, Vol 64) with permission from Elsevier); and f) Grasshopper abundance is higher on P addition plots compared to controls in ungrazed plots at Serengeti National Park. Different letters on the bar graph represent significant differences based on Tukey’s post-hoc test. When present, grey regions around the regression line represent 95% confidence intervals. See Supporting Information Appendix S2 and S3 for more details on methods and statistical results.



### BOX1: General framework for multiple resource limitation in plant-herbivore interactions

Consider a trophic system with three interacting levels: resources, plant biomass and herbivore biomass. The dynamics at the different levels are linked via two consumer-resource interactions (Chase & Leibold 2003), plant-resource dynamics and herbivore-plant dynamics.

#### Plant-resource dynamics

Resources are supplied at a rate  $I_x$  [in units:  $\text{g}_{\text{resource}}\text{t}^{-1}\text{area}^{-1}$ ]. Resources of type  $x$  are then taken up by plants at some rate dependent on environmental resource concentration  $R_x$ , plant biomass  $S$  [ $\text{g}_{\text{plant}} \cdot \text{area}^{-1}$ ] and a mass-specific uptake function,  $f_x(R_x)$ . Resources in the environment change as the difference between supply rate and uptake rate-

$$\frac{dR_x}{dt} = I_x - f(R_x)S \quad (1.1)$$

The steady-state uptake rate is therefore  $f^*(R_x^*) = I_x/S$ . Once the resources are integrated into plant tissues, they experience turnover at a per unit resource rate proportional to steady-state internal resource concentration,  $\gamma_x[\text{t}^{-1}] r_x^*$ . Thus,

$$\frac{dr_x}{dt} = f(R_x^*) - \gamma_x r_x \quad (1.2)$$

By solving both equation 1.1 and 1.2 at equilibrium, we can obtain steady-state internal concentrations of resources,  $r_x^* = I_x/\gamma_x S$ .

#### Herbivore-Plant dynamics

The per capita rate of change of plant biomass is the difference between mass-specific plant growth and loss. Such loss is due to tissue mortality,  $m$  [ $\text{g}_{\text{plant}}\text{t}^{-1}$ ] and to herbivore consumption, which depends on herbivore biomass  $H$  [ $\text{g}_{\text{Herbivore}} \cdot \text{area}^{-1}$ ], attack rate  $a$  [ $\text{area} \cdot \text{g}_{\text{Herbivore}}^{-1}\text{t}^{-1}$ ], and resource concentrations of the plant,  $r_x^*$ . The plant growth function,  $z(r_x^*)$  converts resources to plant biomass with some efficiency

687  $u$  whereas the plant mortality function  $m(r_x^*)$  provides the rate of plant loss with  $d$  representing a basal  
 688 mortality rate that is independent of resources. Both plant growth function and mortality function may  
 689 be affected by resource concentrations. For example, in terrestrial systems, plants in high resource sites  
 690 have high growth rates but have short-lived leaves (Leaf Economic Spectrum (Wright *et al.* 2004; Onada  
 691 *et al.* 2017). Therefore, the mass-specific change in plant biomass is -

$$692 \quad \frac{1}{S_G} \frac{dS_G}{dt} = z(u, r_x^*, \dots) - h(a, r_x^*, \dots)H - m(d, r_x^*, \dots);$$

$$693 \quad H^* = \frac{[z(u, r_x^*, \dots) - m(d, r_x^*, \dots)]}{h(a, r_x^*, \dots)} \quad (1.3)$$

694 At steady-state, we obtain steady-state herbivore biomass ( $H^*$ ).

695 Mass-specific change in herbivore biomass depends on the amount and, under some scenarios, the  
 696 resource concentrations of plant biomass consumed, expressed as an herbivory function  $h(a, r_x^*)$ ,  
 697 conversion efficiency,  $e$  [ $\text{g}_{\text{herbivore}} \text{g}_{\text{plant}}^{-1}$ ], and a herbivore mortality,  $D$  [ $\text{t}^{-1}$ ].

$$698 \quad \frac{1}{H} \frac{dH}{dt} = eh(a, r_x^*, \dots)S - D \quad (1.4)$$

699 At steady-state, we acquire plant biomass in the presence of herbivores,  $S_G^*$ , and, plant biomass in the  
 700 absence of herbivores,  $S_U^*$ , when  $h(.)=0$  in eq 1.3 and solving it at equilibrium. Herbivore impact is  
 701 defined as a response ratio ( $RR$ ) of plant biomass in the absence of herbivory to plant biomass under  
 702 herbivory.

$$703 \quad RR = \left[ \frac{Biomass_{Ungrazed}}{Biomass_{Grazed}} \right] = \left[ \frac{S_U^*}{S_G^*} \right] \rightarrow (1.5)$$

#### 704 **Types of resources**

705 We define four categories of resources based on their hypothesized impact on plants and herbivores.

- a) **Surrogate Resource for acquiring Carbon (SRC)**- a resource that limits carbon assimilation such as CO<sub>2</sub>, light, or water. Inside the plant, C is present in both a labile form that directly affects growth and a stable or structural form that increases life span in the absence of herbivores.
- b) **Limiting to Plants And Herbivores (PAH)**- a resource limiting to both plants and herbivores, likely because it is involved in processes fundamental to all life, such as biochemical synthesis or DNA replication
- c) **Limiting Only to Plants only (OP)**- a resource that limits only plants but not herbivores, likely a resource that influences access to CO<sub>2</sub> or critical to synthesis of a photosynthetic enzyme
- d) **Limiting Only to Herbivores only (OH)**- a resource that is limiting to herbivores only but not plants, likely due to its importance in unique herbivore structure (e.g., bones) or function (e.g., lactation)

We show in the text that a range of plant-herbivore scenarios can be studied by assigning potential limiting resources to one these categories and using them in equation 1.1-1.5.