

1 **Title:** Bottom-up stoichiometry at the base of the food web: a resource-  
2 ratio approach applied to herbivore competition

### 3 **Abstract**

4 Interspecific competition plays an important role in structuring communities but  
5 few studies have been done on herbivores. We present a competition model that  
6 predicts the outcome of competition between herbivore species competing for plants.  
7 Our model imbeds well-known concepts of the resource-ratio theory, such as the  
8 minimum level of resources, consumption vectors, and the quotas of resources in the  
9 biomass. However, unlike traditional approaches that focused on plants as resources,  
10 we suggest that chemical elements and energy bounded in plant biomass represent the  
11 ultimate resources that herbivores compete for. Our model shows that the outcomes  
12 of competition between herbivores result from two main processes. First, plants  
13 create a spatial segregation of resources, which may promote coexistence between  
14 herbivores according to their foraging strategies. Second, packaging of resources  
15 within plants creates a bottom-up stoichiometric constraint, which strongly drives  
16 the way herbivores consume resources. This packaging of resources also bounds  
17 resource availability. Together, these two processes determine how herbivore species  
18 may coexist. Hence, a plant community rich in one resource should support an  
19 herbivore community rich in the same resource, leading to a bottom-up effect.

## 20 Introduction

21 Interspecific competition for resources is thought to play an important role in struc-  
22 turing communities (Gause, 1934; Tilman, 1987). Modelling approaches have proven  
23 helpful to predict competitive outcomes, when resources are well identified and the  
24 number of different resources is limited. Hence, the theory is particularly well suited  
25 for autotrophic organisms (e.g., algae or plants) competing for essential nutrients  
26 (Tilman, 1982). Nutrients (i.e., chemical elements constituting biomass) are well-  
27 identified non-substitutable resources, and competition is usually acute for only a  
28 few limiting nutrients, such as for instance, phosphorous (P), nitrogen (N), or potas-  
29 sium (K). In short, models predict that niche segregation along resource ratios should  
30 promote species coexistence. For example, plants with low N:P requirement are more  
31 likely to coexist with plants with high N:P requirement. Tilman (1980) provided a  
32 graphical representation of these competition-coexistence processes based on Zero-  
33 Net-Growth Isoclines and consumption vectors, usually referred to as the resource-  
34 ratio theory. In the last few decades, the resource-ratio theory has helped popularize  
35 the use of competition models to predict competitive outcomes in experimental set  
36 ups and in semi-natural conditions.

37 However, the transfer of such a theory to higher trophic levels is not obvious. The  
38 main reason is that for heterotrophic organisms, resources are not easy to charac-  
39 terize. Consider for instance the case of herbivores. If one considers that plants are  
40 the resources herbivores compete for, questions arises: to what extent does a given  
41 herbivore require more of a given plant species than another? Should plant species  
42 be considered essential non-substitutable resources, or substitutable resources? For

example, the diet of the red deer (*Cervus elaphus*) in Europe includes 145 different plant species (Gebert and Verheyden-Tixier, 2001). How many of these species are really essential for red deer, and how many of the essential resources are substitutable? This question is a research topic in itself. As a consequence, predicting competitive outcomes in heterotrophic communities with simple models remains extremely challenging and restricted to very specific cases (Murray and Baird, 2008). This limitation may prevent significant progress in our understanding of community structure at higher trophic levels.

In accordance with the theory of biological stoichiometry (Sternner and Elser, 2002), we argue here that nutrients and energy contained in plant biomass rather than the plants themselves are the resources that limit the growth rate of herbivores and for which herbivores compete for. In this case, most of the upper-cited challenges disappear. Hence, nutrients and energy clearly are essential non-substitutable resources for heterotrophs. For example, nitrogen is required in proteins and nucleic acids, and phosphorous is required in phospholipids, nucleic acids, or bones. The number of essential nutrients required for heterotrophic organism biomass of heterotrophs does not exceed 26 (Sternner and Elser, 2002). The fact that herbivore's growth rate may be limited by food quality (e.g., the level of nitrogen or phosphorus in plant biomass) rather than food quantity has been widely documented (Sternner et al., 1992; Hessen, 1992; Urabe and Watanabe, 1992). Moreover, it is possible to determine the requirements of a given herbivore for a given element, using metabolism studies (Mould and Robbins, 1981). In addition, it is clear that the ratios of nutrients required in the biomass vary across herbivore species. For example, the C:N:P

ratio markedly varies among zooplanktonic herbivores (Andersen and Hessen, 1991; Sterner et al., 1992). In table 1, we show that such a variation is observed as well in terrestrial herbivores. Based on these observations, a competition model based on niche segregation across herbivore species along energy and nutrient axes appears perfectly relevant. All these arguments support the idea that the resource ratio theory can be applied to herbivores if one considers that just like plants, herbivores are ultimately limited by energy and nutrients (fig. 1).

Yet, a major challenge remains: while plants take up energy and different nutrients separately, herbivores consume these resources already packaged within the plant biomass they ingest. This constraint precludes a straightforward use of the resource ratio theory. In this paper, we introduce a theoretical framework that adapts the classical resource-ratio theory to the specific case of herbivores consuming nutrients and energy that are bounded in fixed ratios in plant biomass. We show that it is possible to predict the competitive outcomes based on plant stoichiometry, and on herbivore feeding strategies.

## The model

Simulations and graphics were performed with R software (R Development Core Team, 2017). Equations for isoclines and consumption vector slopes were found analytically, as well as stability of equilibrium points. Results were also tested with simulations.

The model includes  $p$  herbivore species competing for  $k$  resources embedded into  $n$  plant species. For each resource  $u$ , each herbivore  $i$  has its own specific require-

ment, and each plant  $j$  has its own resource availability. These requirements and availabilities are represented by quotas (i.e., quantity of resource per unit of biomass). Hence, for an herbivore  $i$ , the biomass dynamics write:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{\sum_{j=1}^n g_{ij} V_j Q_{VjR1}}{Q_{HiR1}}, \dots, \frac{\sum_{j=1}^n g_{ij} V_j Q_{VjRk}}{Q_{HiRk}} \right\} H_i - m_i H_i \quad (1)$$

where  $H_i$  is herbivore  $i$  biomass,  $V_j$  is plant  $j$  biomass,  $g_{ij}$  is consumption rate of plant  $j$  by herbivore  $i$ ,  $m_i$  is mortality rate of herbivore  $i$ ,  $Q_{VjRk}$  is the quota of resource  $k$  into plant  $j$  biomass (for example: g  $R_k$ /kg of plant  $j$ ), and  $Q_{HiRk}$  is quota of resource  $k$  into herbivore  $i$  biomass (for example: g  $R_k$ /kg of herbivore  $i$ ). The ratio between herbivore and plant quotas for a given resource represents how this chemical element limits the growth of this herbivore. According to Liebig's law of the minimum, the least available resource relative to herbivore requirements (over the  $k$  resources) is assumed to be growth limiting.

Plant biomass is:

$$\frac{dV_j}{dt} = S_j - a_j V_j - \sum_{i=1}^p g_{ij} V_j H_i \quad (2)$$

where  $S_j$  is a function representing the increase of plant biomass (gross supply),  $a_j$  is intrinsic loss per capita, such as senescence, the last term on the right represents consumption by herbivores.

Resource availability is described as plant biomass multiplied by the plant quota of the considered resource.

$$R_u = \sum_{j=1}^n V_j Q_{VjRu} \quad (3)$$

105 Table 2 presents a review of the state variables and parameters used in the model.

## 106 Results

107 Resources are provided by several plants that may be consumed differently, which  
108 represents a spatial segregation of resources. But each plant provides several re-  
109 sources, already packaged at a given species-specific ratio; thus, the stoichiometric  
110 balance of resources also plays a role. Spatial segregation and stoichimetric balance  
111 will first be studied separately, then together. For the sake of clarity, details on  
112 the calculations are provided in appendices, and only the main results are presented  
113 here.

### 114 Spatial segregation of resources

115 Let's consider a limiting resource ( $R$ ). Herbivores have access to this resource through  
116 the consumption of  $n$  species of plants, depending on their respective feeding strat-  
117 egy. Resource availability at steady state, for each herbivore, is (see appendix 1 for  
118 details):

$$\overline{R}_{Hi} = \sum_{j=1}^n \frac{S_j}{a_j + g_{ij}\overline{H}_i} Q_{VjR} \quad (4)$$

119  $\overline{R}_{Hi}$  represents the level of resource remaining available for another herbivore, it also  
120 represents the minimal threshold of resource availability for herbivore species  $i$  (i.e.,  
121 if resource availability is below this threshold this herbivore species cannot maintain  
122 a population at steady state). Hence, it can be assimilated to Tilman's  $R^*$ .

123 For simplicity, consider the case where two herbivore species ( $H_1$  and  $H_2$ ) compete

for one resource ( $R$ ) embedded into two plants species ( $V_1$  and  $V_2$ ). Extending equation (4), resource availabilities for each herbivore species at steady state write:

$$\overline{R}_{H1} = \frac{S_1}{a_1 + g_{11}\overline{H}_1}Q_{V1R} + \frac{S_2}{a_2 + g_{12}\overline{H}_1}Q_{V2R} \quad (5)$$

and

$$\overline{R}_{H2} = \frac{S_1}{a_1 + g_{21}\overline{H}_2}Q_{V1R} + \frac{S_2}{a_2 + g_{22}\overline{H}_2}Q_{V2R} \quad (6)$$

Clearly, the competition outcome is driven by the foraging strategies of the competitors, more specifically, on the relative efficiencies of their consumption functions ( $g_{ij}$ ). If  $g_{11} > g_{21}$  and  $g_{12} > g_{22}$ , herbivore 1 consumes both plants more efficiently than its competitor. Thus, the competitive exclusion principle holds, and herbivore 2 is excluded. The reverse situation ( $g_{11} < g_{21}$  and  $g_{12} < g_{22}$ ) leads to the exclusion of herbivore 1. However, if the two herbivores are specialized on different plant species ( $g_{11} > g_{21}$  and  $g_{12} < g_{22}$ , or  $g_{11} < g_{21}$  and  $g_{12} > g_{22}$ ), coexistence is possible. In other words, despite the fact that herbivores compete for a single resource, the competitive exclusion principle does not necessarily hold. Hence, plants species create a spatial segregation of the resource, and specialization of herbivores on different plant species, similar to niche segregation in space, makes coexistence possible.

## Bottom-up stoichiometry

Herbivores usually compete for several resources. According to the classical resource-ratio theory (Tilman, 1982), increasing the number of resources considered should promote coexistence between consumers. Consider  $p$  herbivores feeding on one plant

species embedding  $k$  resources. According to the Liebig's law of the minimum expressed by the minimum function in equation (1), for each herbivore  $i$  the interplay between resource requirement and resource availability will determine which resource is the most limiting for growth (Grover, 1997). Depending on herbivore requirements, and ratios of resources available in plant biomass, several herbivore species feeding on a single plant species may not be limited by the same resource.

For a single herbivore  $i$ , feeding on one plant ( $V$ ), the level of a limiting resource  $R_u$  in plant biomass at equilibrium writes (see appendix 2 for details):

$$\overline{R}_{uHi} = \overline{V}|_{R_u} Q_{VRu} = \frac{m_i}{g_i} Q_{HiRu} \quad (7)$$

where  $\overline{V}|_{R_u}$  is plant biomass at steady state when  $R_u$  is limiting. Similarly to the former case, this level represents the level of resource available to another herbivore and is therefore a key driver of competitive outcome. It can be graphically represented by a Zero Net Growth Isocline (ZNGI) on the phase space of the  $k$  resources in plant biomass. Resource consumption by an herbivore is represented by a consumption vector (Tilman, 1980). As for the classical resource-ratio theory (Tilman, 1982), this graphical representation is a valuable tool to address the competitive outcomes between herbivore species.

For simplicity, consider two herbivore species ( $H_1$  and  $H_2$ ) competing for two resources ( $R_1$  and  $R_2$ ) embedded into a single plant species ( $V$ ). According to equation (7), the slopes of the ZNGIs only depend on herbivore parameters, which are constant (for a given herbivore). Therefore, the ZNGIs are parallel to the axis on



the phase plan  $\{R_1, R_2\}$ . A first necessary condition for coexistence at equilibrium is that the ZNGIs of the two herbivores cross one another (Tilman, 1982), which implies that these herbivores are not limited by the same resource.

A second necessary condition relies on the slopes of the consumption vectors of the competitors (Tilman, 1982). The consumption vectors graphically illustrate how resource consumption drives the levels of resources from resource supply to equilibrium levels. In the phase plan, resource supply is represented by the supply point  $S$ , which is the total amount of resources at equilibrium in absence of consumption:

$$S_{R_1} = Q_{VR_1}(S - a\bar{V}) \quad (8)$$

$$S_{R_2} = Q_{VR_2}(S - a\bar{V}) \quad (9)$$

A given herbivore  $i$  consumes resource  $R_1$  at a rate  $g_i\bar{V}\bar{H}_iQ_{VR_1}$  and resource  $R_2$  at a rate  $g_i\bar{V}\bar{H}_iQ_{VR_2}$ . Thus, the consumption vector  $\vec{C}_i$  slope writes:

$$\vec{C}_i = \begin{pmatrix} g_i\bar{V}\bar{H}_iQ_{VR_1} \\ g_i\bar{V}\bar{H}_iQ_{VR_2} \end{pmatrix} = g_i\bar{V}\bar{H}_i \begin{pmatrix} Q_{VR_1} \\ Q_{VR_2} \end{pmatrix} \quad (10)$$

It appears that the slope of the consumption vector is determined by the ratios of resources embedded in plant biomass. An important consequence is that all herbivores have the same slope for their consumption vector when feeding on a single plant species. This constraint precludes coexistence, and the resource-ratio embedded in plant biomass determines which of the competitors will displace the other (fig. 2). Since herbivore respective requirements are located along a gradient of resource ra-

179 tios ( $R_1/R_2$ ), the one that shows a ratio closer to the plant ratio than any other one  
180 will outcompete other herbivore species. Hence, despite differences in requirements,  
181 two herbivores cannot coexist on several resources.

182 This result is in contrast with the classical resource-ratio theory, which stipulates  
183 that two consumers may coexist on two resources under certain conditions. The  
184 reason is that classically, consumers are assumed to control the slope of their con-  
185 sumption vector (Tilman, 1982). This assumption is valid for primary producers,  
186 which take up essential nutrients independently in their environment, in the form of  
187 dissolved chemical molecules, but not for herbivores, which take up essential nutri-  
188 ents already bounded in plant biomass. Therefore, only the herbivore that can match  
189 plant stoichiometry the best can persist and outcompetes other herbivores. Plant  
190 resource ratios determine the outcome of competition between herbivores, which is  
191 a strong bottom-up stoichiometric constraint.

## 192 **Competition for several plant species and several resources**

193 In this section, we present the general case of the model, where herbivores compete  
194 for multiple resources embedded into multiple plants (i.e., spatial segregation of  
195 resources and bottom-up stoichiometry play a role). Assuming that nutrient quotas  
196 differ among plant species, the consumption of a given plant is not equivalent to  
197 the consumption of another plant. Due to spatial segregation among resources,  
198 herbivores may control their diet by allocating more time/energy to feed on specific  
199 plants rather than others. Therefore, each herbivore may find a specific pathway to  
200 collect resources (Simpson and Raubenheimer, 1995; Raubenheimer and Simpson,

1999). The foraging strategy of a given herbivore is graphically represented by the consumption vector, which is the combination of the consumption vectors for all plant species consumed. By consuming more efficiently a given species than others, an herbivore can control the slope of its consumption vector.

To simplify, we consider here the case of two competing herbivores feeding on two plants embedding two resources. These two herbivores will coexist only if they are not limited by the same resource. Let's consider the case where herbivore 1 is mostly limited by resource 1, and herbivore 2 is mostly limited by resource 2. The resource supply is represented in the phase plan by the supply point  $S$ , which is the total amount of resources at equilibrium in plants 1 and 2, in the absence of consumption:

$$S_{R1} = Q_{V1R1}(S_{V1} - a\bar{V}_1) + Q_{V2R1}(S_{V2} - a\bar{V}_2) \quad (11)$$

$$S_{R2} = Q_{V1R2}(S_{V1} - a\bar{V}_1) + Q_{V2R2}(S_{V2} - a\bar{V}_2) \quad (12)$$

For a given herbivore  $i$ , the ZNGI slopes ( $\alpha|_{R1}$  and  $\alpha|_{R2}$ ) for each resource (when  $R_1$  and  $R_2$  are limiting respectively) write:

$$\alpha|_{R1} = \frac{\bar{V}_1|_{R1}Q_{V1R2} + \bar{V}_2|_{R1}Q_{V2R2}}{\bar{V}_1|_{R1}Q_{V1R1} + \bar{V}_2|_{R1}Q_{V2R1}} \quad (13)$$

$$\alpha|_{R2} = \frac{\bar{V}_1|_{R2}Q_{V1R2} + \bar{V}_2|_{R2}Q_{V2R2}}{\bar{V}_1|_{R2}Q_{V1R1} + \bar{V}_2|_{R2}Q_{V2R1}} \quad (14)$$

Note that the slopes depend on  $\bar{V}_1$  and  $\bar{V}_2$ , which themselves vary with herbivore and plant parameters (including the supply parameters). Hence, ZNGIs are not parallel to the axis.

218 However, it is possible to define boundary ZNGIs. Considering that herbivore  $i$   
 219 can consume both plants, its foraging strategy will lie between exclusive consumption  
 220 of plant 1, on one side, and exclusive consumption of plant 2, on the other side. Thus,  
 221 boundary ZNGI slopes write (see appendix 3 for details):

$$\bar{R}_1|_j = \frac{m_i}{g_{ij}} Q_{HiR1} \quad (15)$$

$$\bar{R}_2|_j = \frac{m_i}{g_{ij}} Q_{HiR2} \quad (16)$$

222  
 223 These isoclines  $\bar{R}_1|_j$  and  $\bar{R}_2|_j$  represent the ZNGIs in the case where herbivore  $i$  con-  
 224 sumes only plant  $j$  and is limited by  $R_1$  (eq. 15) or  $R_2$  (eq. 16). In case of two plants  
 225 consumed, the real  $\bar{R}_1$  and  $\bar{R}_2$  will lie between two boundary ZNGIs, one for each  
 226 plant (see fig. 3). It appears that ZNGI slopes vary only with herbivore constant  
 227 parameters. Therefore, boundary ZNGIs are parallel to the axis. Moreover, two  
 228 herbivores having similar quotas but different feeding strategies would have differ-  
 229 ent ZNGIs. Thus, if boundary ZNGIs of two herbivores overlap, coexistence might  
 230 be possible. Existence of an equilibrium point can be determined by solving the  
 231 following system for  $\bar{V}_1$  and  $\bar{V}_2$  (see appendix 3 for details):

$$\begin{cases} g_{11}\bar{V}_1 Q_{V1R1} + g_{12}\bar{V}_2 Q_{V2R1} = m_1 Q_{H1R1} \\ g_{21}\bar{V}_1 Q_{V1R2} + g_{22}\bar{V}_2 Q_{V2R2} = m_2 Q_{H2R2} \end{cases} \quad (17)$$

232 where  $\bar{V}_1$  and  $\bar{V}_2$  are biomass at equilibrium for plant 1 and 2 respectively. If system  
 233 (17) leads to a realistic equilibrium point (plant biomasses and herbivores biomasses

are all positive), then an equilibrium point exists where both herbivore coexist.

Next, competition outcome will depend on the relative orientation of the consumption vector of herbivores (Tilman, 1980). For a given herbivore, it is possible to determine a consumption vector that allows this herbivore to consume both resources when one is limiting, and leads to  $\bar{V}_1$  and  $\bar{V}_2$  at steady state. This boundary consumption vector slope writes (see appendix 3 for details):

$$\vec{C}_{Hi} = \bar{H}_i \begin{pmatrix} g_{i1}\bar{V}_1Q_{V1R1} + g_{i2}\bar{V}_2Q_{V2R1} \\ g_{i1}\bar{V}_1Q_{V1R2} + g_{i2}\bar{V}_2Q_{V2R2} \end{pmatrix} \quad (18)$$

These boundary vectors play a similar role as consumption vectors in Tilman's model. The slope varies with herbivore requirements, since they drive  $\bar{V}_1$  and  $\bar{V}_2$  (eq. 17). It also appears that this vector slope varies with herbivore consumption functions ( $g_{ij}$ ) but also with plant traits ( $Q_{VjRk}$ ). Therefore, herbivores can partially control the slope of their consumption vector, but the bottom-up stoichiometry due to plant packaging of resources still plays a role. These two aspects (i.e., consumption and resource packaging) are key points to determine competition outcome.

Hence, assuming plant 1 is richer in resource 1 ( $Q_{V1R1} > Q_{V2R1}$ ), and plant 2 is richer in resource 2 ( $Q_{V1R2} < Q_{V2R2}$ ), and assuming herbivore 1 is more limited by resource 1 ( $Q_{H1R1} > Q_{H1R2}$ ), and herbivore 2 is more limited by resource 2 ( $Q_{H2R1} < Q_{H2R2}$ ), two general strategies can be considered. The first one occurs when each herbivore species consumes preferentially the plant species which gives the greater quantity of the most limiting resource for this herbivore species, and which is less limiting for its competitor (i.e.,  $g_{11} > g_{12}$  and  $g_{21} < g_{22}$ ). In that

case, if we consider the boundary vectors for herbivore 1 and for herbivore 2, we can define several zones on the phase plan (see fig. 3). The zone between the two boundary vectors represents the supply conditions allowing stable coexistence of the two herbivore species. Thus, each herbivore consumes the most profitable plant according to its own needs (i.e., quotas and consumption functions follow a similar trend), which promotes coexistence.

The second case represents the reverse situation, where each herbivore species consumes preferentially the plant species that provides greater quantity of the most limiting resource for its competitor (i.e.,  $g_{11} < g_{12}$  and  $g_{21} > g_{22}$ ). Hence, the zone between the boundary vectors does not allow coexistence (see fig. 4), and in many cases system (17) does not have any solution where both herbivore species can persist together. Thus, competitive exclusion is the general outcome.

One can notice that plant stoichiometry constrains the supply point because of resource packaging into plants. Resource ratio within each plant will define a slope:

$$\alpha_{Vj} = \frac{Q_{VjR2}}{Q_{VjR1}} \quad (19)$$

In case of two plants, supply point will lie between the two extreme slopes ( $\alpha_{V1}$  and  $\alpha_{V2}$ ) defining a feasibility cone (see fig. 3 and 4). Resource supply occurs only within this feasibility cone instead of the whole phase plan, which adds another constraint on herbivore persistence and competition.

Consumption functions allow herbivores to partially drive the way they consume resources. However, if herbivores are not selective at all, then they consume plants ac-

274 cording to their respective biomass. In that case, both herbivores consume resources  
 275 in the same way (i.e.,  $g_{11} = g_{21}$  and  $g_{12} = g_{22}$ ). Hence, there is no segregation in  
 276 herbivore consumption: all herbivores have the same consumption vector, which is  
 277 similar to the case where only one plant species is present (see fig. 2). Therefore,  
 278 the trajectory will either cross herbivore 1 ZNGI first, and this herbivore will be  
 279 excluded, or the trajectory will cross herbivore 2 ZNGI first, and this herbivore will  
 280 be excluded. Coexistence will be unlikely because even if resources are spatially  
 281 segregated, herbivores are constrained by plant stoichiometry.

282 Resource packaging is a strong driver for competition. Let's consider a last case  
 283 where both herbivores have the same quotas (i.e.,  $Q_{H1R1} = Q_{H2R1}$  and  $Q_{H1R2} =$   
 284  $Q_{H2R2}$ ) but different consumption functions. In that case, one plant is richer for  
 285 the most limiting resource, and the herbivore that can consume this plant the most  
 286 efficiently will exclude its competitor.

## 287 Discussion

288 Unlike classical studies on herbivore competition we consider here that resources  
 289 limiting herbivores growth are not plant biomasses but rather, the essential nutrients  
 290 contained in plant biomass. Since these essential resources are not independent,  
 291 several differences exist between classical resource-ratio theory of competition usually  
 292 applied to plants (Tilman, 1980) and our model for herbivores.

293 First, plants represent a spatial segregation of resources. Thus, even if herbivores  
 294 compete for the same resources, a specialized consumption on different plants may  
 295 promote coexistence. Second, resource packaging into plants has a strong impact on

296 resource acquisition by herbivores, which is a bottom-up stoichiometric constraint.  
 297 Thus, if two herbivores consume the same plant, they will show the same consump-  
 298 tion vector, which means that the plant drives resource consumption by herbivores.  
 299 Last, the general case where herbivores compete for several resources provided by  
 300 several plants, consumption strategies of herbivores play a role and allow herbivores  
 301 to partially drive competition outcome. However, bottom-up stoichiometry is still  
 302 a key driver for competition and constrains the realized parameter space. This is  
 303 a major difference with models assuming a total independence between resources  
 304 (such as N and P for plants) within which availabilities of resources can vary inde-  
 305 pendently from one another. Since resources are packaged within plants, they cannot  
 306 be consumed independently anymore. Thus, some supply couples (e.g., large quan-  
 307 tity of  $R_1$  and almost no  $R_2$  available) is unlikely because plants will provide both  
 308 resources (according to their own ratio). Hence, parameter space allowing herbivore  
 309 persistence can be narrower than predicted by ZNGIs and vectors.

310 More generally, existing theories about coexistence between herbivores are based  
 311 on niche segregation. This segregation may depend on space utilization or on rela-  
 312 tionship between body size and metabolism (Owen-Smith and Novellie, 1982). Our  
 313 approach is different and allows us to disentangle the different mechanisms of niche  
 314 segregation. We argue that coexistence between herbivores can occur by two ways,  
 315 which are diversity between foraging strategies as well as stoichiometric diversity  
 316 between niches.

317 The first way, diversity between foraging strategies, allows herbivores to take  
 318 advantage of the spatial segregation of resources. Hence, the foraging strategy of



319 competing herbivores will mainly determine the competitive outcome. On the one  
320 hand, non-selective herbivores (feeding on a single plant species or showing a non-  
321 selective feeding behavior) will show a strong bottom-up stoichiometric effect. There-  
322 fore, coexistence is unlikely. For example, non-selective zooplanktonic filters, such as  
323 cladocerans (limited by P) and copepods (limited by N), usually do not coexist: ei-  
324 ther one group or the other dominates according the N:P ratio of the consumed algae  
325 (Andersen and Hessen, 1991; Hessen, 1992; Sterner et al., 1992; Elser et al., 1996;  
326 Koski, 1999). A similar assumption can be made for non-selective terrestrial grazer  
327 herbivores (Albon and Langvatn, 1992) for which coexistence would be unlikely. On  
328 the other hand, selective herbivores, specialized on a few plants, would show a strong  
329 spatial component and a weaker stoichiometric component of competition. It is a  
330 spatially niche segregation within which each herbivore species consumes one plant  
331 species more than others, assuming that this plant species has the best profitabil-  
332 ity for this herbivore species. Therefore, they should be more prone to coexist. If  
333 this spatial segregation is total, with each herbivore species specialized on one plant  
334 species that is different from other competitors, coexistence occurs without other  
335 constraint than herbivore species-specific persistence.

336 The second way is niche segregation based on resource ratios (i.e., a bottom-  
337 up stoichiometric component). Although the packaging of resources within plants  
338 creates a supplementary level of complexity, divergence with classic resource-ratio  
339 models should not impede the rising of a clear conclusion: coexistence is favoured  
340 by segregation in requirements and consumption; only one of them (i.e., different  
341 requirements and similar consumption, or similar requirements and different con-

sumption) is not enough. We retrieve here the two classical components of the niche theory (Chase and Leibold, 2003): species requirement (Hutchinson, 1957) and species impact (Elton, 1927; Macarthur and Levins, 1967). However, while these two components are clearly separated for competition between plants (i.e., ZNGIs represent species requirements, and vectors represent species impact), these two components are merged for herbivore competition (boundary vectors involve both aspects). Moreover, in classical theory, both ZNGIs and vectors are only driven by the consumer (the plant absorbing mineral nutrients), while consumption by an herbivore is partially driven by the consumed plant (bottom-up stoichiometry).

Field studies tend to show that stoichiometric diversity between niches exists among herbivore species. Among aquatic herbivores, such as herbivorous zooplankton, it seems that grazers (especially *Daphnia sp.*) are P-limited, while copepods seem to be N-limited (see above). This stoichiometric diversity also exists for terrestrial herbivores (see table 1). Chemical requirements for wild herbivores are mostly unknown, but for mammal herbivores, numerous studies have used data from cattle as proxy for diet requirement for wild species (Voeten and Prins, 1999). Nevertheless, data begins to be available. For example, N requirements have been estimated for fawns (Smith et al., 1975), yearlings (Holter et al., 1979) and adults (Asleson et al., 1996) of white-tailed deer (*Odocoileus virginianus*), as well as P requirement for white-tailed deer (Grasman and Hellgren, 1993) and moose (Schwartz et al., 1987). Moreover, males from large species should be more prone to P-limitation (Grasman and Hellgren, 1993). More generally, it seems that nutrient requirement and constraints for absorption vary with body size and digestive system (Janis, 1976).

365 Several studies have been done on foraging strategy and spatial segregation of  
366 resources, mainly on terrestrial herbivore species. On the one hand, it seems that  
367 most of migratory species adopt an extraction maximizing strategy: through sea-  
368 sons, they move from places to places that have a large amount of nutritive quality  
369 elements (Albon and Langvatn, 1992). There, they can find plant communities with  
370 a high proportion of nutritional plant species. They adopt this strategy rather than  
371 selecting nutritious species within communities (Ben-Shahar and Coe, 1992). Ac-  
372 cording to our model, this feeding strategy is likely to lead to competitive exclusion.  
373 However, migration allows these species to switch from nutrient sources to others,  
374 which decreases likelihood of exclusion. On the other hand, resident species mostly  
375 adopt a demand minimizing strategy: some species have a low metabolic rate, and  
376 flexible breeding period, which allow them to decrease demand in energy during dry  
377 period (Murray, 1991). Moreover, for continental herbivore species, the diet qual-  
378 ity decreases when body size increases, especially during dry season (Codron et al.,  
379 2007).

380 The present model provides a novel insight on competition between herbivores.  
381 However, improvements may be proposed. Among other things, we pay only atten-  
382 tion to the requirements for a given herbivore species, but we do not consider what  
383 happens in case of an overconsumption of a non-limiting nutrient. In fact, a more  
384 physiological approach can be proposed. If an herbivore species feeds on a plant  
385 species that gives a small amount of a limiting nutrient and a large amount of a non-  
386 limiting nutrient, one can argue that an excretion cost might exist for this nutrient.  
387 This can limit the amount of plant consumed by this herbivore species.

388 Finally, this model leads to an interesting implication. The stoichiometric con-  
 389 straints should go up through the trophic chain. It means that, on a soil that is poor  
 390 in a given nutrient (e.g., nitrogen), we should find plant species that can survive  
 391 with a poor availability for this nutrient. Then, they will provide a small amount  
 392 of this nutrient to consumer, thus sustaining herbivore species that are poor in this  
 393 nutrient, leading to a strong bottom-up effect throughout the whole food chain.

## 394 Appendix 1

395 When  $p$  herbivores compete for a limiting resource  $R$  provided by  $n$  plants, equations  
 396 (1), (2) and (3) respectively write:

$$\frac{dH_i}{dt} = \frac{\sum_{j=1}^n g_{ij} V_j Q_{V_j R}}{Q_{H_i R}} H_i - m_i H_i \quad (20A)$$

397

$$\frac{dV_j}{dt} = S_j - a_j V_j - \sum_{i=1}^p g_{ij} V_j H_i \quad (21A)$$

398

$$R = \sum_{j=1}^n V_j Q_{V_j R} \quad (22A)$$

399 Hence, for a given herbivore  $i$ , steady state biomass of a given plant  $j$  writes:

$$\bar{V}_j = \frac{S_j}{a_j + g_{ij} \bar{H}_i} \quad (23A)$$

400 Thus, for this herbivore  $i$ , resource availability at steady state writes:

$$\bar{R}_{Hi} = \sum_{j=1}^n \bar{V}_j Q_{VjR} = \sum_{j=1}^n \frac{S_j}{a_j + g_{ij} \bar{H}_i} Q_{VjR} \quad (24A)$$

## 401 Appendix 2

402 When  $p$  herbivores compete for several resources embedded into 1 plant, equations  
403 (1) and (2) respectively become:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{Q_{VR1}}{Q_{HiR1}}, \dots, \frac{Q_{VRk}}{Q_{HiRk}} \right\} g_i V H_i - m_i H_i \quad (25A)$$

404

$$\frac{dV}{dt} = S - aV - \sum_{i=1}^p g_i V H_i \quad (26A)$$

405 and equation (3) for the limiting resource  $k$  writes:

$$R_k = V Q_{VRk} \quad (27A)$$

406 At steady state, it is possible to determine resource  $k$  availability for each herbivore  
407  $i$ . Equation (25A) at steady state becomes:

$$\frac{Q_{VRk}}{Q_{HiRk}} g_i \bar{V}|_{Rk} \bar{H}_i - m_i \bar{H}_i = 0 \quad (28A)$$

408 where  $\bar{V}|_{Rk}$  is the steady state plant biomass when  $R_k$  is limiting. Thus,

$$\bar{V}|_{Rk} = \frac{m_i}{g_i} \frac{Q_{HiRk}}{Q_{VRk}} \quad (29A)$$

409 and

$$\bar{R}_k = \bar{V}|_{Rk} Q_{VRk} = \frac{m_i}{g_i} Q_{HiRk} \quad (30A)$$

### 410 Appendix 3

411 In a case of two herbivore species ( $H_1$  and  $H_2$ ) competing for two resources ( $R_1$  and  
412  $R_2$ ) embedded into two plant species ( $V_1$  and  $V_2$ ), the system considered becomes:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{g_{i1}V_1Q_{V1R1} + g_{i2}V_2Q_{V2R1}}{Q_{HiR1}}, \frac{g_{i1}V_1Q_{V1R2} + g_{i2}V_2Q_{V2R2}}{Q_{HiR2}} \right\} H_i - m_i H_i \quad (31A)$$

413 with  $H_i$  being either  $H_1$  or  $H_2$

$$\frac{dV_j}{dt} = S_j - a_j V_j - g_{1j} V_j H_1 - g_{2j} V_j H_2 \quad (32A)$$

414 with  $V_j$  being either  $V_1$  or  $V_2$

$$R_k = V_1 Q_{V1Rk} + V_2 Q_{V2Rk} \quad (33A)$$

415 with  $R_k$  being either  $R_1$  or  $R_2$ .

416 Each herbivore has two zero net growth isoclines (ZNGI), but their calculation  
417 is not straightforward because of multiple sources for  $R_1$  and  $R_2$ . However, it is

possible to define boundary ZNGIs. Considering that herbivore  $i$  can consume both plants, its foraging strategy will lie between exclusive consumption of plant 1, on one side, and exclusive consumption of plant 2, on the other side. Thus, for an herbivore  $i$  focusing on plant  $j$  exclusively and being limited by resource  $k$ , equation (31A) becomes

$$\frac{dH_i}{dt} = \frac{g_{ij}V_jQ_{VjRk}}{Q_{HiRk}}H_i - m_iH_i \quad (34A)$$

At steady state,  $\bar{R}_k = \bar{V}_j * Q_{VjRk}$ . Thus,

$$\frac{g_{ij}\bar{V}_jQ_{VjRk}}{Q_{HiRk}} - m_i = \frac{g_{ij}\bar{R}_k}{Q_{HiRk}} - m_i = 0 \quad (35A)$$

which leads to

$$\bar{R}_k = \frac{m_i}{g_{ij}}Q_{HiRk} \quad (36A)$$

$\bar{R}_k$  represents the slope of the boundary ZNGI for herbivore  $i$  consuming plant  $j$  and being limited by resource  $k$ . In case of two plants and two resources, each herbivore will have two boundary ZNGIs for each resources. The real value of  $\bar{R}_k$  will lie between the two boundary ZNGIs. As for classical resource-competition theory, coexistence is only possible if each herbivore is limited by a different resource than the other one. Hence, the boundary ZNGIs for  $H_1$  and  $H_2$  should partially overlap.

Let's consider the case where  $H_1$  is mostly limited by  $R_1$  and  $H_2$  is mostly limited by  $R_2$ . The first requirement for coexistence between these herbivores is that  $\bar{R}_1$  and  $\bar{R}_2$  together allow persistence of both herbivores. In other words, consumption of  $V_1$  and  $V_2$  should provide enough  $R_1$  to herbivore 1 and enough  $R_2$  to herbivore 2. It is possible to calculate  $\bar{V}_1$  and  $\bar{V}_2$  that are the equilibrium biomass of plant 1 and 2

436 respectively and are solutions of the following system:

$$\begin{cases} g_{11}\bar{V}_1Q_{V1R1} + g_{12}\bar{V}_2Q_{V2R1} = m_1Q_{H1R1} \\ g_{21}\bar{V}_1Q_{V1R2} + g_{22}\bar{V}_2Q_{V2R2} = m_2Q_{H2R2} \end{cases} \quad (37A)$$

437 If system (37A) has two realistic solutions (i.e.,  $\bar{V}_1 > 0$  and  $\bar{V}_2 > 0$ ), and if these  
 438 equilibrium plant biomasses allow both herbivores to persist (i.e.,  $\bar{H}_1 > 0$  and  $\bar{H}_2 >$   
 439  $0$ ), then coexistence occurs at that equilibrium point.

440 Stability of this equilibrium point can usually be determined by consumption  
 441 vectors. Knowing  $\bar{V}_1$  and  $\bar{V}_2$  at this equilibrium point, it is possible to determine  
 442 a boundary consumption vector that allows herbivore 1 to consume both resources  
 443 when  $R_1$  is limiting, and leads to  $\bar{V}_1$  and  $\bar{V}_2$  at steady state. Similarly, we can  
 444 determine a boundary consumption vector that allows herbivore 2 to consume both  
 445 resources when  $R_2$  is limiting, and leads to  $\bar{V}_1$  and  $\bar{V}_2$ . The boundary vector slopes  
 446 write:

$$\vec{C}_{H1} = \begin{pmatrix} g_{11}\bar{H}_1\bar{V}_1Q_{V1R1} + g_{12}\bar{H}_1\bar{V}_2Q_{V2R1} \\ g_{11}\bar{H}_1\bar{V}_1Q_{V1R2} + g_{12}\bar{H}_1\bar{V}_2Q_{V2R2} \end{pmatrix} = \bar{H}_1 \begin{pmatrix} g_{11}\bar{V}_1Q_{V1R1} + g_{12}\bar{V}_2Q_{V2R1} \\ g_{11}\bar{V}_1Q_{V1R2} + g_{12}\bar{V}_2Q_{V2R2} \end{pmatrix} \quad (38)$$

$$\vec{C}_{H2} = \bar{H}_2 \begin{pmatrix} g_{21}\bar{V}_1Q_{V1R1} + g_{22}\bar{V}_2Q_{V2R1} \\ g_{21}\bar{V}_1Q_{V1R2} + g_{22}\bar{V}_2Q_{V2R2} \end{pmatrix} \quad (39)$$

448 Vector slopes depend on both herbivore and plant parameters.



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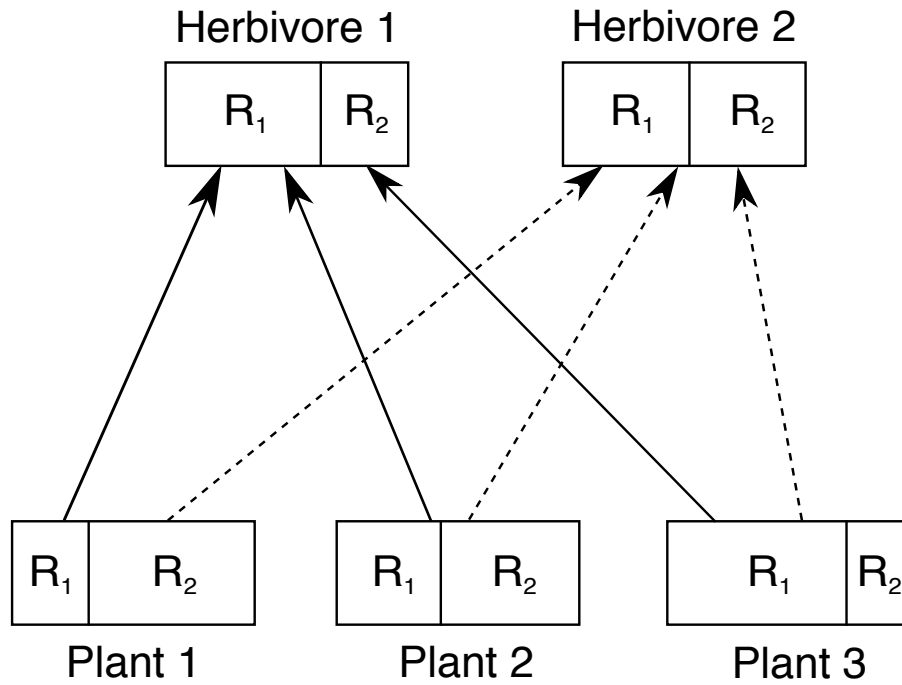
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**Table 1:** Minimum daily intake requirements of digestible protein (DP) and phosphorus (P) for four grazer species of different body weight (BW in kg). Modified from Treydte et al. (2009).

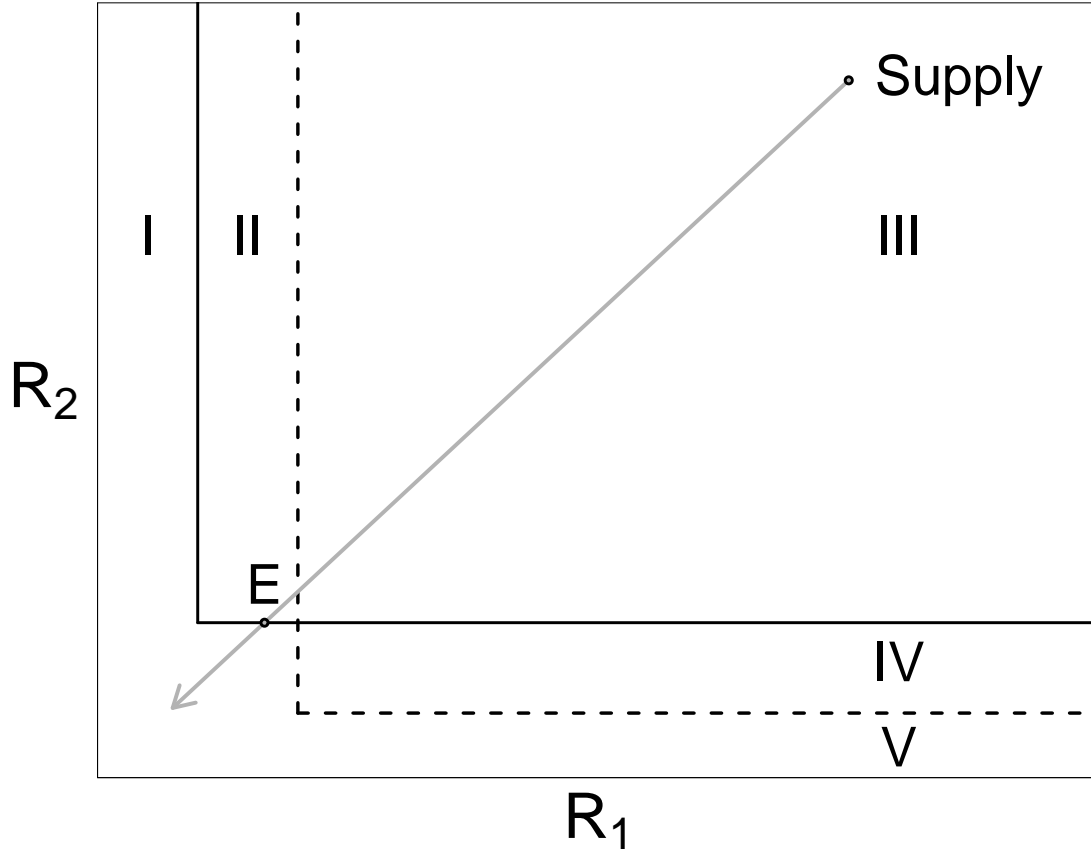
Intake (mg/kg BW/day)	Model scenario source	Warthog 83 kg BW	Wildebeest 143 kg BW	Zebra 271 kg BW	Buffalo 481 kg BW
DProtein	ARC (1980)	730	550	430	380
	Menard et al. (2002)	970	850	720	630
	Ludwig et al. (2003)	1040	910	770	680
P	ARC (1980)	9	14	18	20
	Menard et al. (2002)	13	27	37	42
DProtein:P ratio		83	38	23	18

**Table 2:** State variables and parameters used in the model. Dimensions for each variable and parameter are based on mass (M) and time (T).

Symbols	Definitions	Dimensions
<b>State Variables</b>		
$H_i$	Herbivore $i$ biomass	M
$V_j$	Plant $j$ biomass	M
$R_k$	Resource $k$ mass	M
<b>Parameters</b>		
$g_{ij}$	plant $j$ consumption rate by herbivore $i$	$T^{-1}.M^{-1}$
$m_i$	herbivore $i$ biomass mortality rate <i>per capita</i>	$T^{-1}$
$S_j$	plant $j$ biomass supply	$M.T^{-1}$
$a_j$	plant $j$ biomass natural loss rate <i>per capita</i>	$T^{-1}$
$Q_{HiRu}$	resource $u$ quota for herbivore $i$	$M.M^{-1}$
$Q_{VjRu}$	resource $u$ quota for plant $j$	$M.M^{-1}$

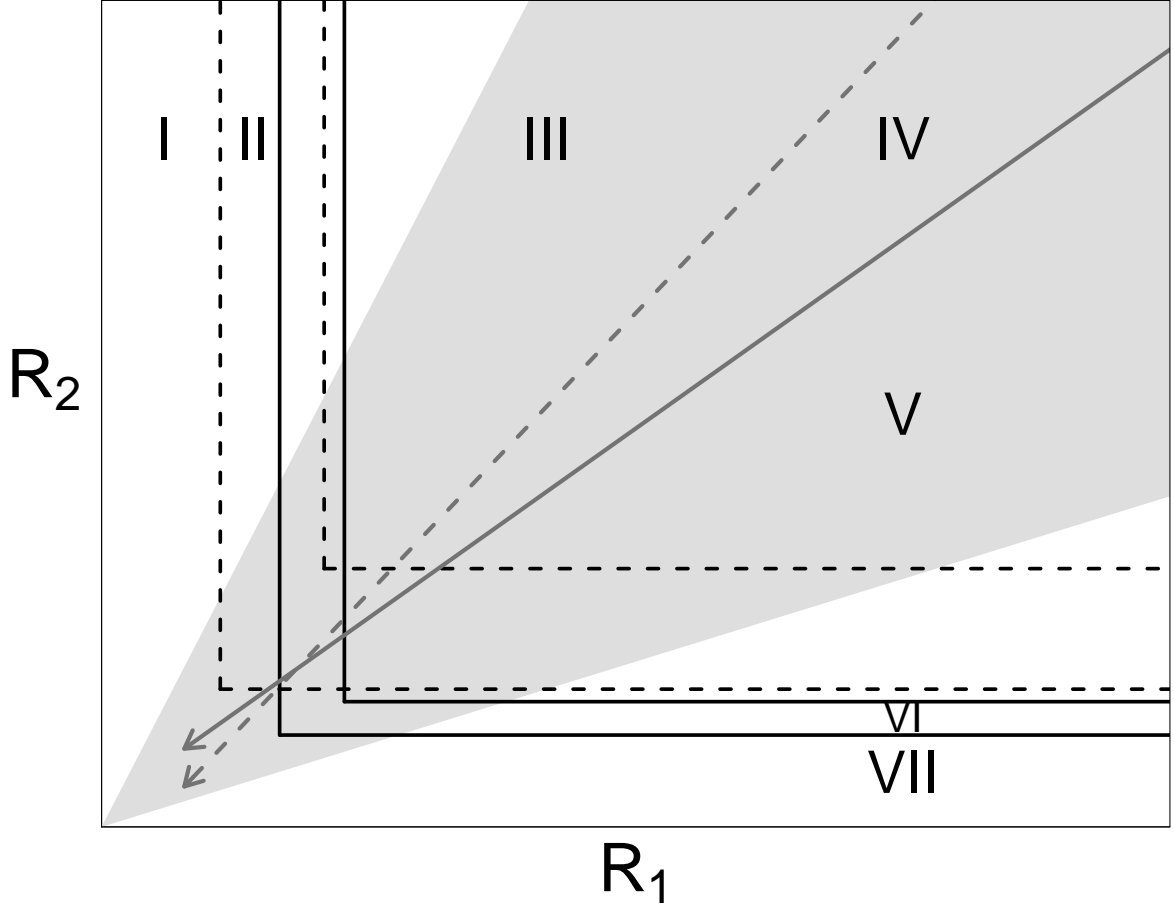


**Figure 1:** Conceptual diagram of resource competition between herbivore. Each herbivore species has its own resource ratio between resource 1 ( $R_1$ ) and resource 2 ( $R_2$ ). This species feeds on different plant species with different resource ratios. Herbivore requirements as well as their resource consumptions are key factors for their persistence.

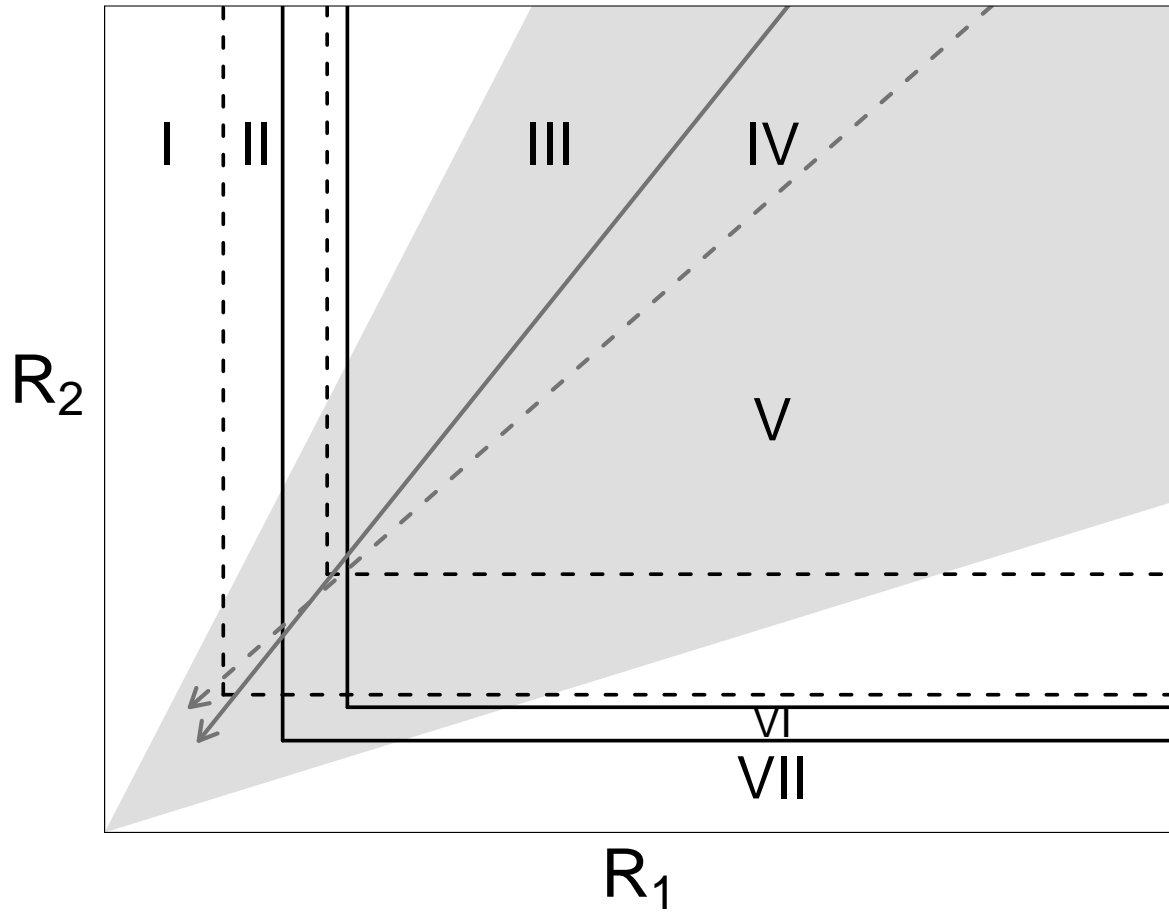


**Figure 2:** Phase plan with two herbivore species feeding on one plant species. Black solid lines are herbivore 1 ZNGIs, dotted lines are herbivore 2 ZNGIs, and grey arrow is the common consumption vector. Interpretations are quite similar with those from Tilman's model (Tilman, 1982). Roman numbers represent different zones for supply point position. Zone I and zone V do not provide sufficient amounts in  $R_1$  and  $R_2$  respectively. None herbivore species can live in these conditions. Zone II contains enough  $R_1$  for herbivore 1, but not for herbivore 2. Zone III potentially has enough quantities of both resources for both herbivore species. In zone IV, only herbivore 2 can survive because there is not enough  $R_2$  for herbivore 1. Supply point represents the total amount of resources due to plant biomass rebuilding. Both herbivore species sample resources through the same consumption vector since resource ratio between  $R_1$  and  $R_2$  is driven by the plant. In this example, the trajectory crosses herbivore 2 ZNGI first and then herbivore 1 ZNGI. The crossing point with herbivore 1 ZNGI becomes an equilibrium point (E). Herbivore 1 is limited by  $R_2$ . Herbivore 2 is excluded.





**Figure 3:** Phase plan for two coexisting herbivores. Lines represent boundary ZNGIs, and arrows are boundary vectors. Solid ZNGIs and solid vector belong to herbivore 1, while dotted ZNGIs and dotted vector belong to herbivore 2. Zone I and zone VII do not provide enough  $R_1$  and  $R_2$  respectively (i.e., neither herbivore 1 nor herbivore 2 can survive). Zone II does not provide enough  $R_1$  for herbivore 1. Zone III does not allow herbivore 1 to survive if herbivore 2 is present. Zone V does not allow herbivore 2 to survive if herbivore 1 is present. Zone VI contains not enough  $R_2$  for herbivore 2. If the supply point lies within zone IV both herbivores can coexist. However, resource packaging within plants constrains resource supply. This resource supply lies within a feasible cone (grey area): any points outside of this cone cannot occur due to resource ratios within plants.



**Figure 4:** Phase plan for competitive exclusion between two herbivores. Representation of ZNGIs and vectors is similar to fig. 3, except for zone IV. This zone generally leads to exclusion of herbivore 1 or 2. The crossing zone of ZNGIs either can be a non stable equilibrium or does not allow coexistence of the two herbivore species.