

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 few
5 studies have been done on herbivores. We present a competition model that predicts
6 the outcome of competition between herbivore species competing for plants. Our
7 model imbeds well-known concepts of the resource-ratio theory, such as the minimum
8 level of resources, consumption vectors, and the quotas of resources required 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: the minimal
13 requirement of resource for herbivores (R^*), and spatial segregation of resources
14 embedded into different plants. The first process (minimal requirement) follows the
15 classical R^* rule and determines the competitive exclusion principle. On the other
16 hand, foraging strategy of herbivores can allow coexistence because resources are
17 spatially segregated. Put together, these two processes determine how herbivore
18 species can coexist, since resources are bounded. Hence, a plant community rich
19 in one resource should support an herbivore community rich in the same resource,
20 leading to a bottom-up effect.

21 Introduction

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

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

sources? 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 (Sternern and Elser, 2002), we argue here that nutrients and energy contained in plant biomass rather than the plants themselves are the resources which 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 (Sternern 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 (Sternern 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 could be applied to herbivores if one considers that just like plants, herbivores are ultimately limited by energy and nutrients (figure 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 the 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 using Runge-Kutta 4 approximation, from package deSolve (Soetaert et al., 2010).

The model includes p herbivore species competing for k resources embedded into

89 n plant species. For each resource u , each herbivore has its own specific requirement,
 90 and each plant has its own resource availability. These requirements and availabilities
 91 are represented by quotas (i.e., quantity of resource per biomass unit). Hence, for
 92 an herbivore i , the biomass dynamic writes:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{\sum_{j=1}^n g_{ij} V_j Q_{vjR1}}{Q_{hiR1}}, \dots, \frac{\sum_{j=1}^n g_{ij} V_j Q_{vjRk}}{Q_{hiRk}} \right\} H_i - m_i H_i \quad (1)$$

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

101 Plant biomass is:

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

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

105 Resource availability is described as the plant biomass multiplied by the plant

106 quota of the considered element.

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

107 Table 2 represents a review of the state variables and the parameters used in the
108 model.

109 Results

110 Resources are provided by several plants that may be consumed differently, which rep-
111 resents a spatial segregation of resources. But each plant provides several resources;
112 thus, the stoichiometric balance of resources also plays a role. Spatial segregation
113 and stoichiometric balance will first be studied separately, then together.

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

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

126 and

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

127 Clearly, the competition outcome is driven by the foraging strategies of the com-
128 petitors, more specifically, on the efficiencies of their consumption functions (g_{ij}).
129 If $g_{11} > g_{21}$ and $g_{12} > g_{22}$, herbivore 1 consumes both plants more efficiently than
130 its competitor. Thus, the competitive exclusion principle holds, and herbivore 2 is
131 excluded. The reverse situation ($g_{11} < g_{21}$ and $g_{12} < g_{22}$) leads to the exclusion of
132 herbivore 1. However, if the two herbivores are specialized on different plant species
133 ($g_{11} > g_{21}$ and $g_{12} < g_{22}$, or $g_{11} < g_{21}$ and $g_{12} > g_{22}$), coexistence is possible. In
134 other words, despite the fact that herbivores compete for a single resource, the com-
135 petitive exclusion principle does not necessarily hold. Hence, plants species create a
136 spatial segregation of the resource, and specialization of herbivores on different plant
137 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):

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

where $\overline{V}|_{Ru}$ 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 outcomes. 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 re-
sources (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 equilib-
rium 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 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 its consumption vector is determined by the ratios of re-
sources embedded in plant biomass. An important consequence is that all herbivores

175 have the same slope for their consumption vector when feeding on a single plant
 176 species. This constraint precludes coexistence, and the resource-ratio embedded in
 177 plant biomass determines which of the competitors will displace the other (figure 2).
 178 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 outcompete other herbivores. Plant re-
 190 source ratios determine the outcome of competition between herbivores, which is a
 191 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 re-
 195 sources 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 consumption of another plant. Due to spatial segregation among resources, herbi-
 198 vores may control their diet by allocating more time/energy to feed on specific plants
 199 rather than others. Therefore, each herbivore may find a specific pathway to collect
 200 resources (Simpson and Raubenheimer, 1995; Raubenheimer and Simpson, 1999).
 201 The foraging strategy of a given herbivore is graphically represented by the con-
 202 sumption vector, which is the combination of the consumption vectors for all plant
 203 species consumed. By consuming more efficiently a given species than others, an
 204 herbivore can control the slope of its consumption vector.

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

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

211

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

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

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

214

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

215 Note that the slopes depend on \bar{V}_1 and \bar{V}_2 , which themselves depend both on the
 216 herbivore and the plant parameters (including the supply parameters). Hence, ZNGIs
 217 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):

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

222

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

223 These isoclines \bar{R}_1 and \bar{R}_2 represent the ZNGIs in the case where herbivore i consumes
 224 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 depend only on 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 different
 229 ZNGIs. Thus, if boundary ZNGIs of two herbivores cross each other, coexistence
 230 might be possible. Determining existence of an equilibrium point is possible by

231 solving the following system (see appendix 3 for details):

$$\begin{cases} g_{11}\bar{V}_1Q_{V1R1} + g_{12}\bar{V}_2Q_{V2R1} = m_1Q_{H1R1} \\ g_{21}\bar{V}_1Q_{V1R2} + g_{22}\bar{V}_2Q_{V2R2} = m_2Q_{H2R2} \end{cases} \quad (17)$$

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
234 are all positive), then an equilibrium point exists.

235 Next, competition outcome will depend on the relative orientation of the con-
236 sumption vector of herbivores (Tilman, 1980). For a given herbivore, the consump-
237 tion vector slope writes:

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

238 It appears that this vector slope depends on \bar{V}_1 and \bar{V}_2 , which themselves varies with
239 plant supply points (S_1 and S_2). Hence, for a given herbivore in the case of packaged
240 resources, vectors do not have a constant slope valid for all supply conditions. This
241 is why instead of consumption vectors, the model allows the calculation of boundary
242 vectors that determine an area in the phase plan where each herbivore species could
243 coexist with the other one.

244 It is possible to determine a boundary relation between plant supply points (S_1
245 and S_2) that allows each herbivore i to consume both resources when one resource is
246 limiting, and leads to \bar{V}_1 and \bar{V}_2 at steady state. These boundary supply points are

247 \bar{S}_{1Hi} and \bar{S}_{2Hi} for plant 1 and 2 respectively consumed by herbivore i (see appendix
248 3 for details).

$$\bar{S}_{2Hi} = (\bar{S}_{1Hi} - a_1) \frac{g_{i2} \bar{V}_2}{g_{i1} \bar{V}_1} + a_2 \bar{V}_2 \quad (19)$$

249 Hence, boundary vector slopes are:

$$\vec{C}_{H1} = \begin{pmatrix} \bar{S}_{1H1} Q_{V1R1} + \bar{S}_{2H1} Q_{V2R1} \\ \bar{S}_{1H1} Q_{V1R2} + \bar{S}_{2H1} Q_{V2R2} \end{pmatrix} \quad (20)$$

250

$$\vec{C}_{H2} = \begin{pmatrix} \bar{S}_{1H2} Q_{V1R1} + \bar{S}_{2H2} Q_{V2R1} \\ \bar{S}_{1H2} Q_{V1R2} + \bar{S}_{2H2} Q_{V2R2} \end{pmatrix} \quad (21)$$

251 These two boundary vectors play a similar role as consumption vectors in Tilman's
252 model. However, as resources are packaged into plants, vector slopes depend on
253 the way herbivore species feed on plants containing resources (eq. 19). Hence,
254 assuming plant 1 is richer in resource 1 ($Q_{V1R1} > Q_{V2R1}$), and plant 2 is richer in
255 resource 2 ($Q_{V1R2} < Q_{V2R2}$), and assuming herbivore 1 is more limited by resource 1
256 ($Q_{H1R1} > Q_{H1R2}$), and herbivore 2 is more limited by resource 2 ($Q_{H2R1} < Q_{H2R2}$),
257 two general strategies can be considered. The first one occurs when each herbivore
258 species consumes preferentially the plant species which gives the greater quantity
259 of the most limiting resource for this herbivore species, and which is less limiting
260 for its competitor (i.e., $g_{11} > g_{12}$ and $g_{21} < g_{22}$). In that case, if we consider the
261 boundary vectors for herbivore 1 and for herbivore 2, we can define several zones on
262 the phase plan (see figure 3). The zone between the two boundary vectors represents
263 the supply conditions allowing stable coexistence of the two herbivore species. Thus,

each herbivore consumes the most profitable plant (i.e., quotas and consumption functions follow a similar trend), but each herbivore is specialized (more or less) on a different plant than its competitor, which promotes coexistence.

The second case represents the reverse situation, where each herbivore species consumes preferentially the plant species which 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 realistic solution (with both herbivore species persisting). Thus, competitive exclusion is the general outcome.

Spatial segregation of resources embedded in plants and herbivore response to bottom-up stoichiometry are the two key points. If resources are not spatially decoupled or if herbivores do not have a feeding strategy that can compensate for the bottom-up stoichiometry imbalance, coexistence is impossible between herbivore species. The following cases illustrate this argument. A first case occurs when herbivore species are not selective at all: they consume plant species according to their respective biomass. In that case, both herbivores consume resources in the same way (i.e., $g_{11} = g_{21}$ and $g_{12} = g_{22}$). Hence, there is no segregation in herbivore consumption: all herbivore species have the same consumption vector, which is similar to the case where only one plant species is present (see figure 2). Therefore, the trajectory will either cross herbivore 1 ZNGI first, and this herbivore will be excluded, or the trajectory will cross herbivore 2 ZNGI first, and this herbivore will be excluded. Coexistence will be unlikely because even if resources are spatially segregated, herbivores are constrained by plant stoichiometry.

287 A second case occurs when the previous assumptions on herbivore and plant
 288 quotas (i.e., inequality for herbivore requirements, and inequality for plant prof-
 289 itability) are released. Therefore, both herbivores can have the same quotas (i.e.,
 290 $Q_{h1R1} = Q_{h2R1}$ and $Q_{h1R2} = Q_{h2R2}$) but different consumption functions. In that
 291 case, one plant will be more interesting for both herbivores (i.e., the plant that is
 292 richer for the most limiting resource). Hence, the herbivore that can consume this
 293 plant the most efficiently will exclude its competitor. Again, bottom-up stoichiome-
 294 try constrained herbivore coexistence. Another case can occur when both plants have
 295 the same quotas (i.e., $Q_{v1R1} = Q_{v2R1}$ and $Q_{v1R2} = Q_{v2R2}$). In that case, the system
 296 is similar to the case where only one plant is present, which leads to competitive
 297 exclusion. Here, spatial segregation does not occur.

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

$$\alpha_{vj} = \frac{Q_{vjR2}}{Q_{vjR1}} \quad (22)$$

300 In case of two plants, supply point will lie between the two extreme slopes (α_{v1} and
 301 α_{v2}) defining a feasibility cone. Therefore, the whole phase plan is not available. Re-
 302 source supply occurs only within this feasibility cone, which adds another constraint
 303 on herbivore persistence and competition.

Discussion

Unlike classical studies on herbivore competition we consider here that the resource limiting herbivores growth is not plant biomass but rather, the essential nutrients contained in plant biomass.

According to our results, the fundamental difference between herbivore competition and plant competition is that resources are not independent, which leads to specific constraints for herbivores. Thus, several differences exist between classical resource-ratio theory of competition usually applied to plants (Tilman, 1980) and our model for herbivores. First, if only one plant species is available, coexistence is almost impossible even if herbivore compete for several resources. Second, ZNGI can be represented with boundary ZNGI delimiting resource levels at steady state.

Third, consumption vectors are not informative because their slope varies with supply points. However, boundary vectors can be calculated, and they play a similar role as usual consumption vectors. Last, due to this packaging effect of resources and to plant quotas, resource availability itself is constrained. Hence, part of the phase plan might be unavailable. This is a major difference with models assuming a total independence between resources (such as N and P for plants) within which availabilities of resources can vary independently from one another. When resources are packaged, they are not independent. Thus, some supply couples (e.g., large quantity of R_1 and almost no R_2 available) is unlikely because plants will provide both resources (according to their own ratio). Hence, parameter space allowing herbivore persistence can be narrower than predicted by its ZNGI and vector.

More generally, existing theories about coexistence between herbivores are based

on niche segregation. This segregation may depend on space utilization or on relationship between body size and metabolism (Owen-Smith and Novellie, 1982). Our approach is different and allows us to disentangle the different mechanisms of niche segregation. We argue that coexistence between herbivores can occur by two ways, which are diversity between foraging strategies as well as stoichiometric diversity between niches. Diversity between foraging strategies is a spatially niche segregation within which each herbivore species consumes one plant species more than others, assuming that this plant species has the best profitability for this herbivore species. If this spatial segregation is total, with each herbivore species specialized on one plant species which is different from other competitors, coexistence occurs without other constraint than herbivore species-specific persistence. The second way is niche segregation based on resource ratios (i.e., a bottom-up stoichiometric component). Although the packaging effect creates a supplementary level of complexity, divergence with classic resource-ratio models should not impede the rising of a clear conclusion: coexistence is favoured by requirement segregation as well as consumption segregation; only one of them (i.e., different requirements and similar consumptions, or similar requirements and different consumptions) 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., ZNGI represent species requirements, and vectors represent species impact), these two components are merged for herbivore competition (boundary ZNGIs and boundary vectors involve both aspects).

350 Nonetheless, our model allows us to disentangle the relative effects of the bottom-
351 up stoichiometric component (i.e., plant and herbivore resource quotas) and the non-
352 stoichiometric component (i.e., spatial segregation) of the competitive interaction.
353 Indeed, the foraging strategy of the competing herbivores will mainly determine
354 the competitive outcome. Non-selective herbivores (representing case 2 and case
355 4 with non-selective behavior) will show a strong bottom-up stoichiometric effect.
356 Therefore, coexistence is unlikely. For example, non-selective zooplanktonic filters,
357 such as cladocerans (limited by P) and copepods (limited by N), usually do not
358 coexist: either one group or the other dominates according the N:P ratio of the
359 consumed algae (Andersen and Hessen, 1991; Hessen, 1992; Sterner et al., 1992;
360 Elser et al., 1996; Koski, 1999). A similar assumption can be made for non-selective
361 terrestrial grazer herbivores (Albon and Langvatn, 1992) for which coexistence would
362 be unlikely. On the other hand, selective herbivores, specialized on a few plants,
363 would show a strong spatial component and a weaker stoichiometric component of
364 the interaction (representing case 2 and case 4 with selective behavior). Therefore,
365 they should be more prone to coexist.

366 Concerning the stoichiometric component, our assumption is that a stoichiometric
367 diversity between niches exists among herbivore species, and field studies tend to
368 show it. For aquatic herbivores, such as zooplankton, it seems that grazers (especially
369 *Daphnia sp.*) are P-limited, while copepods seem to be N-limited (see above). This
370 stoichiometric diversity exists for terrestrial herbivores either (see table 1). Chemical
371 requirements for wild herbivores are mostly unknown, but for mammal herbivores,
372 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 big species should be more concerned by P-limitation (Grasman and Hellgren, 1993). More generally, it seems that nutrient requirement and absorption constraint depend on body size and digestive system (Janis, 1976).

Concerning the spatial component and the foraging strategy, several studies have been done, mainly on terrestrial herbivore species. It seems that most of migrated species adopt an extraction maximizing strategy: through seasons, they move from places to places that have a large amount of nutritive quality elements (Albon and Langvatn, 1992). There, they can find plant communities with a high proportion of nutritional plant species. They adopt this strategy rather than selecting nutritious species within communities (Ben-Shahar and Coe, 1992). On the other hand, resident species mostly adopt a demand minimizing strategy: sometimes, they have a low metabolic rate, and flexible breeding period, which allow them to decrease demand in energy during dry period (Murray, 1991). Moreover, for continental herbivore species, the diet quality decreases when body size increases, especially during dry season (Codron et al., 2007).

However, there are some limits to this model. We pay only attention to the requirement for a given herbivore species. But we do not consider what happens in case of an overconsumption of a non-limiting nutrient. In fact, we can have a more

396 physiological approach. Considering the case where an herbivore species consuming
 397 a plant species that gives a small amount of a limiting nutrient and a large amount
 398 of a non-limiting nutrient, one can argue that an excretion cost might exist for this
 399 nutrient. This can limit the amount of plant consumed by this herbivore species.

400 Finally, this model gives an interesting conclusion. The stoichiometric constraints
 401 should go up through the trophic chain. It means that, on a soil that is poor in a
 402 given nutrient (e.g., nitrogen), we should find plant species that can survive with a
 403 poor availability for this nutrient. Then, they contain a small amount of this nutrient
 404 and they will sustain herbivore species that are poor in this nutrient, leading to a
 405 strong bottom-up effect.

406 **Appendix 1**

407 When p herbivores compete for a limiting resource R provided by n plants, equations
 408 1, 2 and 3 respectively write:

$$\frac{dH_i}{dt} = \frac{\sum_{j=1}^n g_{ij} V_j Q_{VjR}}{Q_{HiR}} H_i - m_i H_i \quad (23A)$$

409

$$\frac{dV_j}{dt} = S_j - a_j V_j - \sum_{i=1}^p g_{ij} V_j H_i \quad (24A)$$

410

$$R = \sum_{j=1}^n V_j Q_{VjR} \quad (25A)$$

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

$$\bar{V}_j = \frac{S_j}{a_j + g_{ij}\bar{H}_i} \quad (26A)$$

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

$$\bar{R}_{Hi} = \sum_{j=1}^n \bar{V}_j Q_{VjR} = \sum_{j=1}^n \frac{S_j}{a_j + g_{ij}\bar{H}_i} Q_{VjR} \quad (27A)$$

413 **Appendix 2**

414 When p herbivores compete for several resources embedded into 1 plant, equations
415 1 and 2 respectively become:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{Q_{VR1}}{Q_{HiR1}}, \dots, \frac{Q_{VRk}}{Q_{HiRk}} \right\} g_i V H_i - m_i H_i \quad (28A)$$

416

$$\frac{dV}{dt} = S - aV - \sum_{i=1}^p g_i V H_i \quad (29A)$$

417 and equation 3 for the limiting resource k writes:

$$R_k = V Q_{VRk} \quad (30A)$$

418 At steady state, it is possible to determine resource k availability for each herbivore

419 *i.* Equation 28A at steady state becomes:

$$\frac{Q_{VRk}}{Q_{HiRk}} g_i \bar{V}|_{Rk} \bar{H}_i - m_i \bar{H}_i = 0 \quad (31A)$$

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

$$\bar{V}|_{Rk} = \frac{m_i}{g_i} \frac{Q_{HiRk}}{Q_{VRk}} \quad (32A)$$

421 and

$$\bar{R}_k = \bar{V}|_{Rk} Q_{VRk} = \frac{m_i}{g_i} Q_{HiRk} \quad (33A)$$

422 **Appendix 3**

423 In a case of two herbivore species (H_1 and H_2) competing for two resources (R_1 and

424 R_2) embedded into two plant species (V_1 and V_2), the system considered becomes:

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{g_{i1} V_1 Q_{V1R1} + g_{i2} V_2 Q_{V2R1}}{Q_{HiR1}}, \frac{g_{i1} V_1 Q_{V1R2} + g_{i2} V_2 Q_{V2R2}}{Q_{HiR2}} \right\} H_i - m_i H_i \quad (34A)$$

425 with H_i being either H_1 or H_2

$$\frac{dV_j}{dt} = S_j - a_j V_j - g_{1j} V_j H_1 - g_{2j} V_j H_2 \quad (35A)$$

426 with V_j being either V_1 or V_2

$$R_k = V_1 Q_{V1Rk} + V_2 Q_{V2Rk} \quad (36A)$$

427 with R_k being either R_1 or R_2 .

428 Each herbivore has two zero net growth isoclines (ZNGI), but their calculation
 429 is not straightforward because of multiple sources for R_1 and R_2 . However, it is
 430 possible to define boundary ZNGIs. Considering that herbivore i can consume both
 431 plants, its foraging strategy will lie between exclusive consumption of plant 1, on
 432 one side, and exclusive consumption of plant 2, on the other side. Thus, for an
 433 herbivore i focusing on plant j exclusively and being limited by resource k , equation
 434 34A becomes

$$\frac{dH_i}{dt} = \frac{g_{ij} V_j Q_{VjRk}}{Q_{HiRk}} H_i - m_i H_i \quad (37A)$$

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

$$\frac{g_{ij} \bar{V}_j Q_{VjRk}}{Q_{HiRk}} - m_i = \frac{g_{ij} \bar{R}_k}{Q_{HiRk}} - m_i = 0 \quad (38A)$$

436 which leads to

$$\bar{R}_k = \frac{m_i}{g_{ij}} Q_{HiRk} \quad (39A)$$

437 \bar{R}_k represents the slope of the boundary ZNGI for herbivore i consuming plant j and
 438 being limited by resource k . In case of two plants and two resources, each herbivore
 439 will have two boundary ZNGIs for each resources. The real value of \bar{R}_k will lie
 440 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 respectively and are solutions of the following system:

$$\begin{cases} g_{11}\bar{V}_1Q_{V_1R_1} + g_{12}\bar{V}_2Q_{V_2R_1} = m_1Q_{H_1R_1} \\ g_{21}\bar{V}_1Q_{V_1R_2} + g_{22}\bar{V}_2Q_{V_2R_2} = m_2Q_{H_2R_2} \end{cases} \quad (40A)$$

If system (40A) has two realistic solutions (i.e., $\bar{V}_1 > 0$ and $\bar{V}_2 > 0$), and if these equilibrium plant biomasses allow both herbivores to persist (i.e., $\bar{H}_1 > 0$ and $\bar{H}_2 > 0$), then coexistence occurs at that equilibrium point.

Stability of this equilibrium point can usually be determined by consumption vectors. Knowing \bar{V}_1 and \bar{V}_2 at this equilibrium point, it is possible to determine a boundary relation between plant supply points (S_1 and S_2) that allows herbivore 1 to consume both resources when R_1 is limiting, and leads to \bar{V}_1 and \bar{V}_2 at steady state. Similarly, we can determine a relation that allows herbivore 2 to consume both resources when R_2 is limiting, and leads to \bar{V}_1 and \bar{V}_2 . The relations are:

$$\bar{S}_{2H1} = (\bar{S}_{1H1} - a_1)\frac{g_{12}\bar{V}_2}{g_{11}\bar{V}_1} + a_2\bar{V}_2 \quad (41A)$$

$$\bar{S}_{2H2} = (\bar{S}_{1H2} - a_1) \frac{g_{22} \bar{V}_2}{g_{21} \bar{V}_1} + a_2 \bar{V}_2 \quad (42A)$$

Where S_{1H1} and S_{2H1} are the boundary supply points for plant 1 and 2 respectively for herbivore 1. Similarly, S_{1H2} and S_{2H2} are boundary supply points for herbivore 2.

References

- Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513.
- Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnology and Oceanography* 36:807–814.
- ARC. 1980. The nutrient requirements of ruminant livestock. Agricultural Research Council. CBA, Slough, UK .
- Asleson, M. A., E. C. Hellgren, and L. W. Varner. 1996. Nitrogen requirements for antler growth and maintenance in white-tailed deer. *Journal of Wildlife Management* 60:744–752.
- Ben-Shahar, R., and M. J. Coe. 1992. The relationships between soil factors, grass nutrients and the foraging behavior of wildbeest and zebra. *Oecologia* 90:422–428.
- Chase, J., and M. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press.

476 Codron, D., J. A. Lee-Thorp, M. Sponheimer, J. Codron, D. De Ruiter, and J. S.
 477 Brink. 2007. Significance of diet type and diet quality for ecological diversity of
 478 african ungulates. *Journal of Animal Ecology* 76:526–537.

479 Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism
 480 size, life history, and n:p stoichiometry. *Bioscience* 46:674–684.

481 Elton, C. 1927. *Animal ecology*. University of Chicago Press.

482 Gause, G. 1934. *The Struggle for Existence*. Williams and Wilkins ed., Baltimore,
 483 Maryland. 163 pp.

484 Gebert, C., and H. Verheyden-Tixier. 2001. Variations of diet composition of red
 485 deer (*cervus elaphus* l.) in europe. *Mammal Review* 31:189–201.

486 Grasman, B. T., and E. C. Hellgren. 1993. Phosphorus nutrition in white-tailed deer:
 487 Nutrient balance, physiological responses, and antler growth. *Ecology* 74:2279–
 488 2296.

489 Grover, J. 1997. *Resource Competition*. Chapman & Hall ed., London. 332 pp.

490 Hessen, D. O. 1992. Nutrient element limitation of zooplankton production. *Ameri-*
 491 *can Naturalist* 140:799–814.

492 Holter, J. B., H. H. Hayes, and S. H. Smith. 1979. Protein requirement of yearling
 493 white-tailed deer. *Journal of Wildlife Management* 43:872–879.

494 Hutchinson, G. E. 1957. Population studies - animal ecology and demography - con-
 495 cluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–
 496 427.

- 497 Janis, C. 1976. The evolutionary strategy of equidae and origins of rumen and cecal
498 digestion. *Evolution* 30:757–774.
- 499 Koski, M. 1999. Carbon : Nitrogen ratios of baltic sea copepods - indication of
500 mineral limitation? *Journal of Plankton Research* 21:1565–1573.
- 501 Ludwig, F., T. E. Dawson, H. de Kroon, F. Berendse, and H. H. T. Prins. 2003.
502 Hydraulic lift in acacia tortilis trees on an east african savanna. *Oecologia* 134:293–
503 300.
- 504 Macarthur, R., and R. Levins. 1967. Limiting similarity convergence and divergence
505 of coexisting species. *American Naturalist* 101:377–385.
- 506 Menard, C., P. Duncan, G. Fleurance, J. Y. Georges, and M. Lila. 2002. Compara-
507 tive foraging and nutrition of horses and cattle in european wetlands. *Journal of*
508 *Applied Ecology* 39:120–133.
- 509 Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. *Journal of*
510 *Wildlife Management* 45:323–334.
- 511 Murray, M. G. 1991. Maximizing energy retention in grazing ruminants. *Journal of*
512 *Animal Ecology* 60:1029–1045.
- 513 Murray, M. G., and D. R. Baird. 2008. Resource-ratio theory applied to large herbi-
514 vores. *Ecology* 89:1445–1456.
- 515 Owen-Smith, N., and P. Novellie. 1982. What should a clever ungulate eat. *American*
516 *Naturalist* 119:151–178.

- 517 Raubenheimer, D., and S. J. Simpson. 1999. Integrating nutrition: a geometrical
518 approach. *Entomologia Experimentalis Et Applicata* 91:67–82.
- 519 Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1987. Protein digestion in
520 moose. *Journal of Wildlife Management* 51:352–357.
- 521 Simpson, S. J., and D. Raubenheimer. 1995. The geometric analysis of feeding and
522 nutrition: a user's guide. *Journal of Insect Physiology* 41:545–553.
- 523 Smith, S. H., J. B. Holter, H. H. Hayes, and H. Silver. 1975. Protein requirement of
524 white-tailed deer fawns. *Journal of Wildlife Management* 39:582–589.
- 525 Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Solving differential equations in
526 R: Package *deSolve*. *Journal of Statistical Software* 33:1–25.
- 527 Sterner, R., and J. Elser. 2002. *Ecological stoichiometry: the biology of elements
528 from molecules to the biosphere*. Princeton Univ Press, New Jersey, USA. 584 pp.
- 529 Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships
530 among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeo-
531 chemistry* 17:49–67.
- 532 Tilman, D. 1980. Resources - a graphical-mechanistic approach to competition and
533 predation. *American Naturalist* 116:362–393.
- 534 ———. 1982. *Resource Competition and Community Structure*, vol. 17. Princeton
535 Univ Press, New Jersey, USA. 296 pp.
- 536 ———. 1987. The importance of the mechanisms of interspecific competition. *Amer-
537 ican Naturalist* 129:769–774.

- 538 Treydte, A. C., I. M. A. Heitkonig, and F. Ludwig. 2009. Modelling ungulate depen-
539 dence on higher quality forage under large trees in african savannahs. Basic and
540 Applied Ecology 10:161–169.
- 541 Urabe, J., and Y. Watanabe. 1992. Possibility of n or p limitation for planktonic
542 cladocerans: an experimental test. Limnology and Oceanography 37:244–251.
- 543 Voeten, M., and H. Prins. 1999. Resource partitioning between sympatric wild and
544 domestic herbivores in the tarangire region of tanzania. Oecologia 120:287–294.

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
State Variables		
H_i	Herbivore i biomass	M
V_j	Plant j biomass	M
R_k	Resource k mass	M
Parameters		
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	$M.M^{-1}$

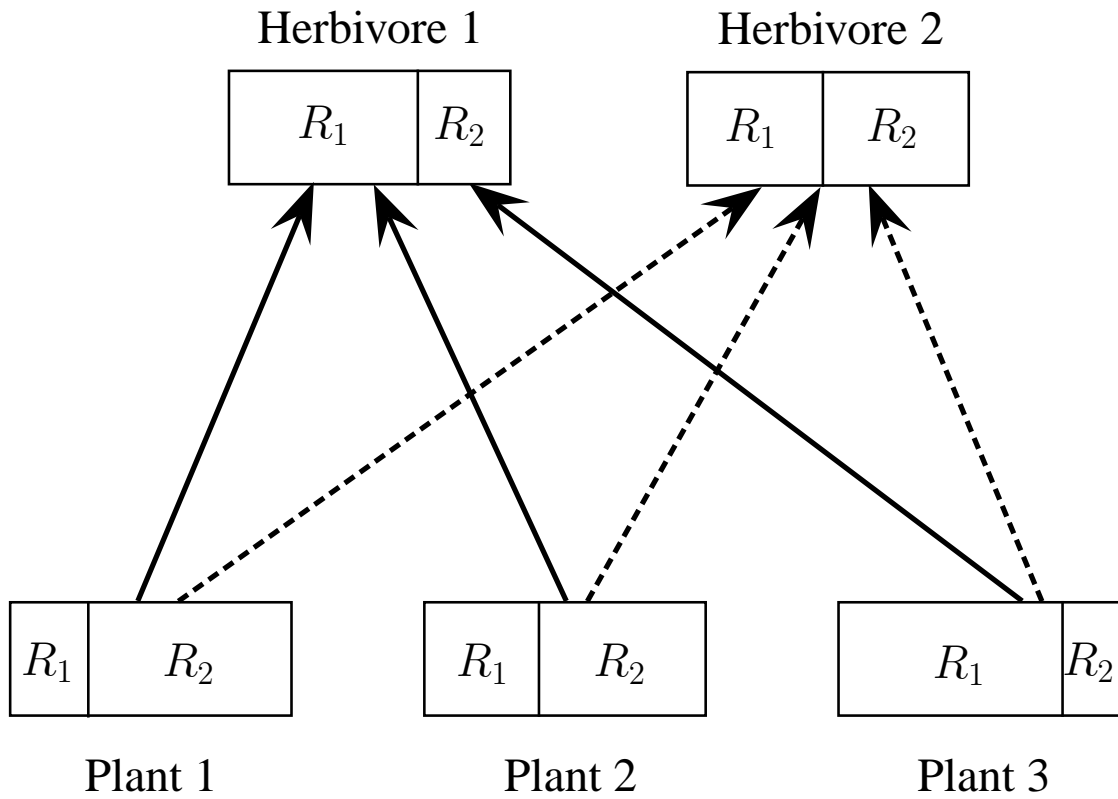


Figure 1: Each herbivore species has its own resource ratio between resource 1 (R_1) and resource 2 (R_2). This species feeds on different plant species with different resource ratios. Herbivore requirements as well as their resource consumptions are key factors for their persistence.

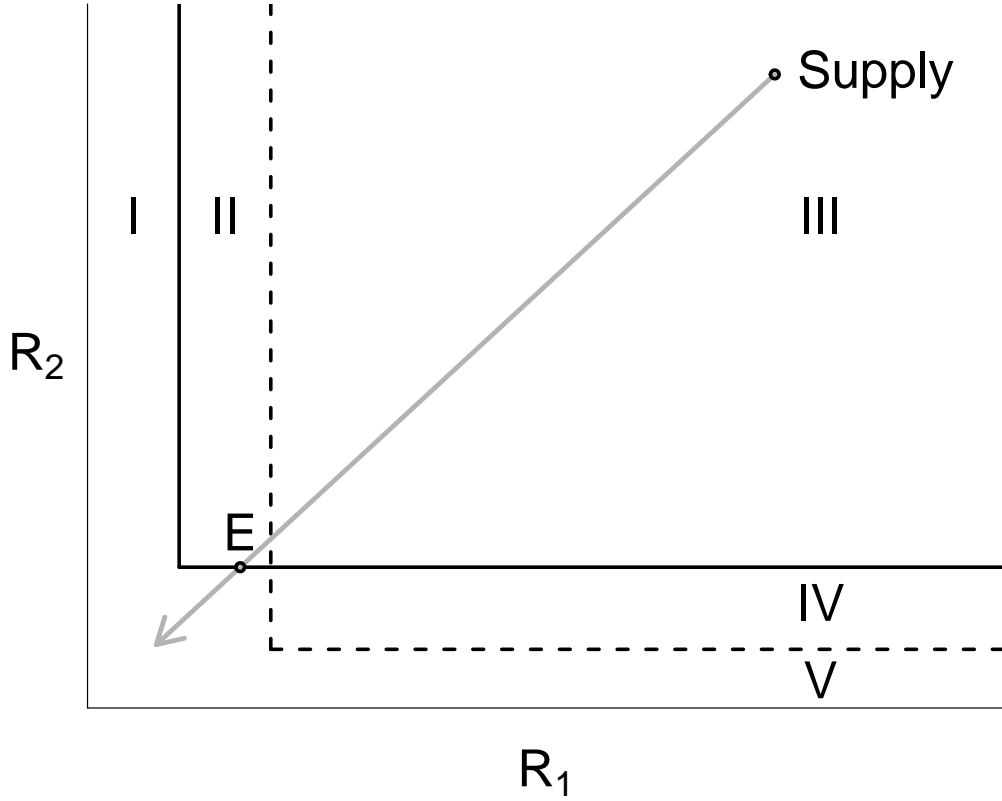


Figure 2: Phase plan with two herbivore species feeding on one plant species. Black solid lines are herbivore 1 ZNGI, dotted lines are herbivore 2 ZNGI, and grey arrow is the common consumption vector. Interpretations are quite similar with those from Tilman's model (Tilman, 1982). Roman numbers represent 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 quantities of 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 total amount of resources due to plant biomass rebuilding. Both herbivore species sample resources through the same consumption vector. In this example, the trajectory cross herbivore 2 ZNGY 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.

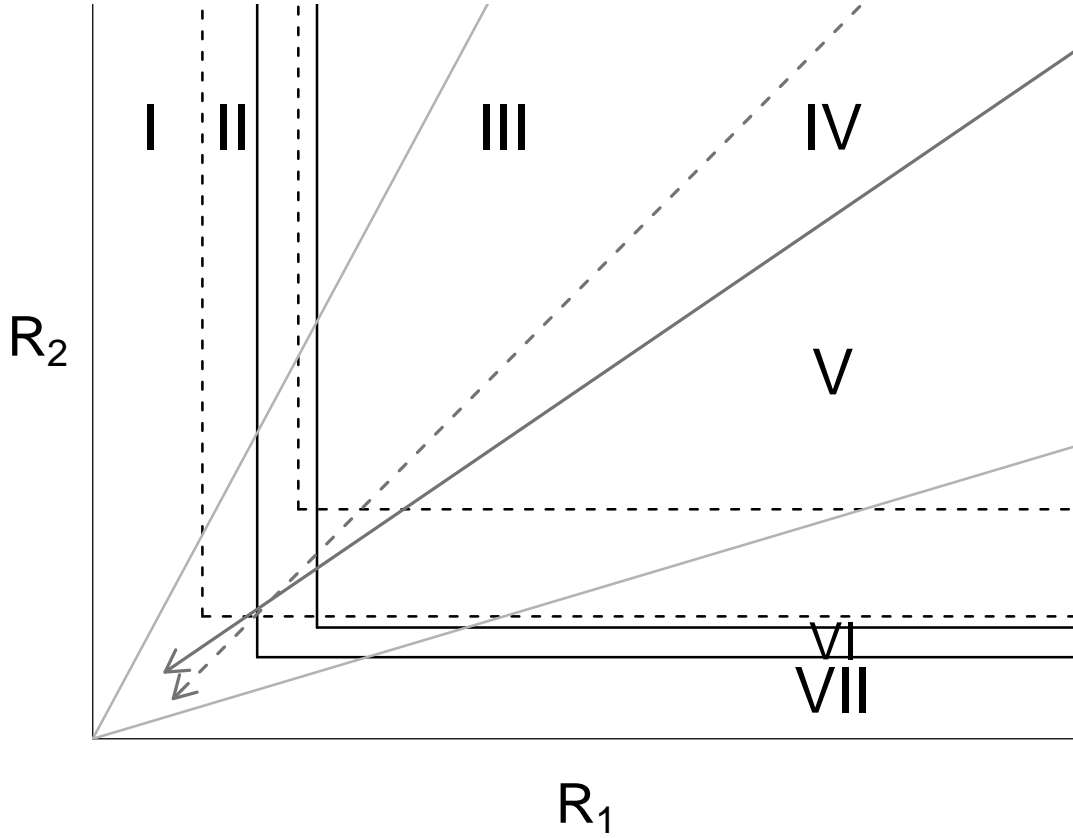


Figure 3: Phase plan for two coexisting herbivores. Lines represent boundary ZNGI, arrows are boundary vectors, and grey lines bound feasible supply conditions according to plants considered (i.e., feasibility cone). Continuous ZNGI and vector belong to herbivore 1, and dotted ZNGI and vector belong to herbivore 2. Zone I and zone VII contain not enough R_1 and R_2 respectively. Neither herbivore 1 nor herbivore 2 can survive. Zone II contains not enough R_1 for herbivore 2. Zone III does not allow herbivore 2 to survive if herbivore 1 is present. Zone V does not allow herbivore 1 to survive if herbivore 2 is present. Zone VI contains not enough R_2 for herbivore 1. If the supply point is within zone IV both herbivore can survive together: it is coexistence. Then, the cross zone of the two ZNGIs is a stable equilibrium point (SE).

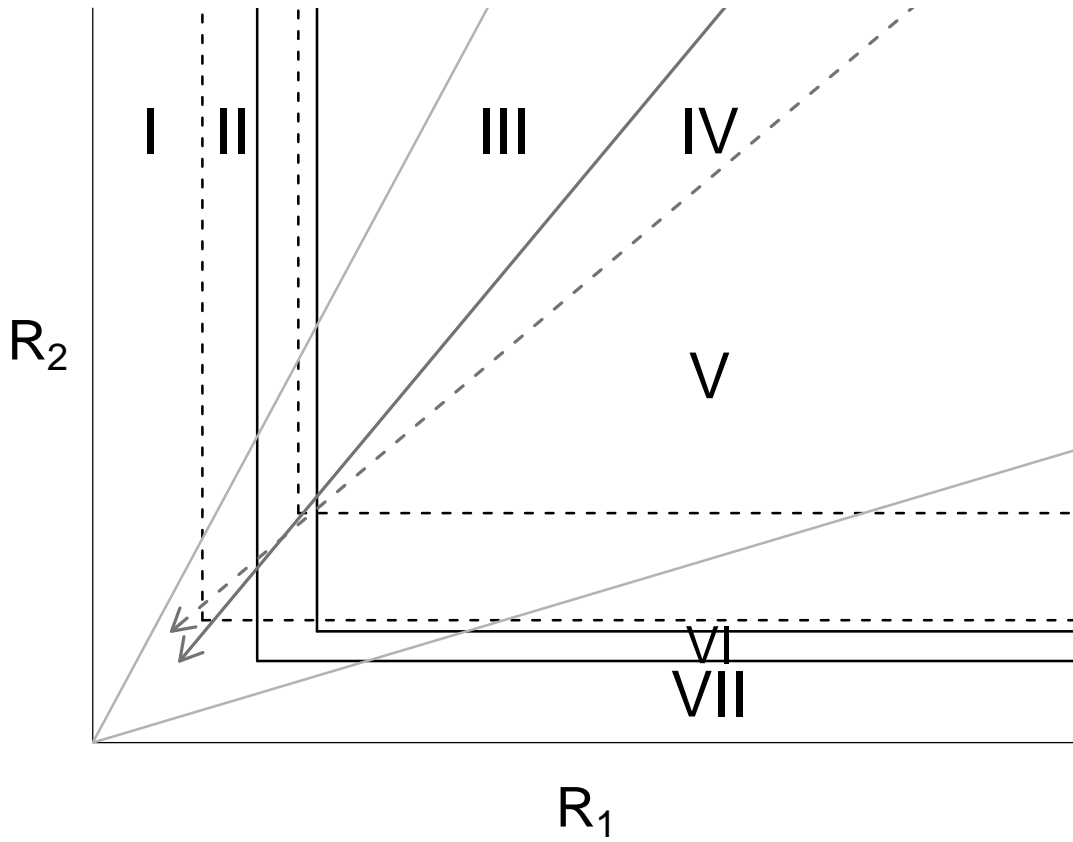


Figure 4: Phase plan for competitive exclusion. Representation of ZNGI and vectors is similar to figure 3, except for zone IV. This zone generally leads to exclusion of herbivore 1 or 2. The crossing zone of ZNGIs either can be a non stable equilibrium (NSE) or does not allow coexistence of the two herbivore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