

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 strong bottom-up stoichiometric constraint, which partially or
16 totally drives the way herbivores consume resources. This packaging of resources also
17 bounds resource availability. Together, these two processes determine how herbivore
18 species may coexist. Hence, a plant community rich in one resource should support
19 an 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). Indeed, nutrients (i.e., chemical elements constituting biomass) are
27 well-identified non-substitutable resources, and usually, competition is acute for only
28 a few limiting nutrients, such as, for instance, phosphorous (P), nitrogen (N), or
29 potassium (K). In short, models predict that niche segregation along resource ratios
30 should promote species coexistence. For example, plants with low N:P requirement
31 are more likely to coexist with plants with high N:P requirement. Tilman (1980)
32 provided a graphical representation of these competition-coexistence processes based
33 on Zero-Net-Growth Isoclines and consumption vectors, usually referred to as the
34 resource-ratio theory. In the last few decades, the resource-ratio theory has helped
35 popularize the use of competition models to predict competitive outcomes in exper-
36 imental set ups and in semi-natural conditions.

37 However, the transfer of such a theory to higher trophic levels is not obvious.
38 The main reason is that for heterotrophic organisms, resources are not easy to char-
39 acterize. Consider for instance the case of herbivores. If one considers that plant
40 species are the resources herbivores compete for, questions arises: to what extent
41 does a given herbivore require more of a given plant species than another? Should
42 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 2, 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 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 dynamic writes:

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

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 the plant biomass multiplied by the plant

104 quota of the considered element.

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

105 Table 1 represents a review of the state variables and the parameters used in the
106 model.

107 Results

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

112 Spatial segregation of resources

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

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

117 \overline{R}_{Hi} represents the level of resource remaining available for another herbivore, it also
118 represents the minimal threshold of resource availability for herbivore species i (i.e.,
119 if resource availability is below this threshold this herbivore species cannot maintain

120 a population at steady state). Hence, it can be assimilated to Tilman's R^* .

121 For simplicity, consider the case where two herbivore species (H_1 and H_2) compete
122 for one resource (R) embedded into two plants species (V_1 and V_2). Extending
123 equation 4, resource availabilities for each herbivore species at steady state write:

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

124 and

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

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

173 have the same slope for their consumption vector when feeding on a single plant
174 species. This constraint precludes coexistence, and the resource-ratio embedded in
175 plant biomass determines which of the competitors will displace the other (figure 2).
176 Since herbivore respective requirements are located along a gradient of resource ra-
177 tios (R_1/R_2), the one that shows a ratio closer to the plant ratio than any other one
178 will outcompete other herbivore species. Hence, despite differences in requirements,
179 two herbivores cannot coexist on several resources.

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

190 **Competition for several plant species and several resources**

191 In this section, we present the general case of the model, where herbivores compete
192 for multiple resources embedded into multiple plants (i.e., spatial segregation of re-
193 sources and bottom-up stoichiometry play a role). Assuming that nutrient quotas
194 differ among plant species, the consumption of a given plant is not equivalent to

195 consumption of another plant. Due to spatial segregation among resources, herbi-
 196 vores may control their diet by allocating more time/energy to feed on specific plants
 197 rather than others. Therefore, each herbivore may find a specific pathway to collect
 198 resources (Simpson and Raubenheimer, 1995; Raubenheimer and Simpson, 1999).
 199 The foraging strategy of a given herbivore is graphically represented by the con-
 200 sumption vector, which is the combination of the consumption vectors for all plant
 201 species consumed. By consuming more efficiently a given species than others, an
 202 herbivore can control the slope of its consumption vector.

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

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

209

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

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

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

212

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

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

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

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

220

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

221 These isoclines \bar{R}_1 and \bar{R}_2 represent the ZNGIs in the case where herbivore i consumes
 222 only plant j and is limited by R_1 (eq. 15) or R_2 (eq. 16). In case of two plants
 223 consumed, the real \bar{R}_1 and \bar{R}_2 will lie between two boundary ZNGIs, one for each
 224 plant (see fig. 3). It appears that ZNGI slopes depend only on herbivore constant
 225 parameters. Therefore, boundary ZNGIs are parallel to the axis. Moreover, two
 226 herbivores having similar quotas but different feeding strategies would have different
 227 ZNGIs. Thus, if boundary ZNGIs of two herbivores cross each other, coexistence
 228 might be possible. Determining existence of an equilibrium point is possible by

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

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

230 where \bar{V}_1 and \bar{V}_2 are biomass at equilibrium for plant 1 and 2 respectively. If system
231 17 leads to a realistic equilibrium point (plant biomasses and herbivores biomasses
232 are all positive), then an equilibrium point exists.

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

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

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

245 Hence, assuming plant 1 is richer in resource 1 ($Q_{V1R1} > Q_{V2R1}$), and plant 2
 246 is richer in resource 2 ($Q_{V1R2} < Q_{V2R2}$), and assuming herbivore 1 is more limited
 247 by resource 1 ($Q_{H1R1} > Q_{H1R2}$), and herbivore 2 is more limited by resource 2
 248 ($Q_{H2R1} < Q_{H2R2}$), two general strategies can be considered. The first one occurs
 249 when each herbivore species consumes preferentially the plant species which gives
 250 the greater quantity of the most limiting resource for this herbivore species, and
 251 which is less limiting for its competitor (i.e., $g_{11} > g_{12}$ and $g_{21} < g_{22}$). In that
 252 case, if we consider the boundary vectors for herbivore 1 and for herbivore 2, we
 253 can define several zones on the phase plan (see fig. 3). The zone between the two
 254 boundary vectors represents the supply conditions allowing stable coexistence of the
 255 two herbivore species. Thus, each herbivore consumes the most profitable plant
 256 according to its own needs (i.e., quotas and consumption functions follow a similar
 257 trend), which promotes coexistence.

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

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

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

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

270 Consumption functions allow herbivores to partially drive the way they consume
 271 resources. However, if herbivores are not selective at all, then they consume plants ac-
 272 cording to their respective biomass. In that case, both herbivores consume resources
 273 in the same way (i.e., $g_{11} = g_{21}$ and $g_{12} = g_{22}$). Hence, there is no segregation in
 274 herbivore consumption: all herbivores have the same consumption vector, which is
 275 similar to the case where only one plant species is present (see fig. 2). Therefore,
 276 the trajectory will either cross herbivore 1 ZNGI first, and this herbivore will be
 277 excluded, or the trajectory will cross herbivore 2 ZNGI first, and this herbivore will
 278 be excluded. Coexistence will be unlikely because even if resources are spatially
 279 segregated, herbivores are constrained by plant stoichiometry.

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

285 Discussion

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

288 contained in plant biomass. Since resources are not independent, several differences
289 exist between classical resource-ratio theory of competition usually applied to plants
290 (Tilman, 1980) and our model for herbivores.

291 First, plants represent a spatial segregation of resources. Thus, even if herbivores
292 compete for the same resources, a specialized consumption on different plants may
293 promote coexistence. Second, resource packaging into plants has a strong impact on
294 the way herbivores consume resources, which is a bottom-up stoichiometry. Thus,
295 if two herbivores consume the same plant, they will show the same consumption
296 vector, which means that the plant drives resource consumption by herbivores. Last,
297 the general case where herbivores compete for several resources provided by several
298 plants, consumption strategy of herbivores plays a role and allows herbivores to
299 partially drive competition outcome. However, bottom-up stoichiometry is still a key
300 driver for competition and constrains the realized parameter space. This is a major
301 difference with models assuming a total independence between resources (such as N
302 and P for plants) within which availabilities of resources can vary independently from
303 one another. When resources are packaged, they are not independent. Thus, some
304 supply couples (e.g., large quantity of R_1 and almost no R_2 available) is unlikely
305 because plants will provide both resources (according to their own ratio). Hence,
306 parameter space allowing herbivore persistence can be narrower than predicted by
307 its ZNGI and vector.

308 More generally, existing theories about coexistence between herbivores are based
309 on niche segregation. This segregation may depend on space utilization or on rela-
310 tionship between body size and metabolism (Owen-Smith and Novellie, 1982). Our

311 approach is different and allows us to disentangle the different mechanisms of niche
312 segregation. We argue that coexistence between herbivores can occur by two ways,
313 which are diversity between foraging strategies as well as stoichiometric diversity
314 between niches. Diversity between foraging strategies is a spatially niche segregation
315 within which each herbivore species consumes one plant species more than others,
316 assuming that this plant species has the best profitability for this herbivore species.
317 If this spatial segregation is total, with each herbivore species specialized on one
318 plant species which is different from other competitors, coexistence occurs without
319 other constraint than herbivore species-specific persistence.

320 The second way is niche segregation based on resource ratios (i.e., a bottom-
321 up stoichiometric component). Although the packaging of resources within plants
322 creates a supplementary level of complexity, divergence with classic resource-ratio
323 models should not impede the rising of a clear conclusion: coexistence is favoured
324 by segregation in requirements and consumption; only one of them (i.e., different
325 requirements and similar consumption, or similar requirements and different con-
326 sumption) is not enough. We retrieve here the two classical components of the
327 niche theory (Chase and Leibold, 2003): species requirement (Hutchinson, 1957)
328 and species impact (Elton, 1927; Macarthur and Levins, 1967). However, while
329 these two components are clearly separated for competition between plants (i.e.,
330 ZNGIs represent species requirements, and vectors represent species impact), these
331 two components are merged for herbivore competition (boundary vectors involve
332 both aspects). Moreover, in classical theory, both ZNGIs and vectors are only driven
333 by the consumer (the plant), while consumption by herbivore is partially driven by

334 the consumed plant (bottom-up stoichiometry).

335 Our model allows us to disentangle the relative effects of the bottom-up stoi-
336 chiometric constraint and the spatial segregation of resources. Hence, the foraging
337 strategy of competing herbivores will mainly determine the competitive outcome.
338 On the one hand, non-selective herbivores (feeding on a single plant species or show-
339 ing a non-selective feeding behavior) will show a strong bottom-up stoichiometric
340 effect. Therefore, coexistence is unlikely. For example, non-selective zooplanktonic
341 filters, such as cladocerans (limited by P) and copepods (limited by N), usually do
342 not coexist: either one group or the other dominates according the N:P ratio of the
343 consumed algae (Andersen and Hessen, 1991; Hessen, 1992; Sterner et al., 1992; Elser
344 et al., 1996; Koski, 1999). A similar assumption can be made for non-selective ter-
345 restrial grazer herbivores (Albon and Langvatn, 1992) for which coexistence would
346 be unlikely. On the other hand, selective herbivores, specialized on a few plants,
347 would show a strong spatial component and a weaker stoichiometric component of
348 competition. Therefore, they should be more prone to coexist.

349 Field studies tend to show that stoichiometric diversity between niches exists
350 among herbivore species. Among aquatic herbivores, such as herbivorous zooplank-
351 ton, it seems that grazers (especially *Daphnia sp.*) are P-limited, while copepods
352 seem to be N-limited (see above). This stoichiometric diversity exists for terrestrial
353 herbivores either (see table 2). Chemical requirements for wild herbivores are mostly
354 unknown, but for mammal herbivores, numerous studies have used data from cattle
355 as proxy for diet requirement for wild species (Voeten and Prins, 1999). Nevertheless,
356 data begins to be available. For example, N requirements have been estimated for

357 fawns (Smith et al., 1975), yearlings (Holter et al., 1979) and adults (Asleson et al.,
358 1996) of white-tailed deer (*Odocoileus virginianus*), as well as P requirement for
359 white-tailed deer (Grasman and Hellgren, 1993) and moose (Schwartz et al., 1987).
360 Moreover, males from large species should be more prone to P-limitation (Gras-
361 man and Hellgren, 1993). More generally, it seems that nutrient requirement and
362 constraints for absorption vary with body size and digestive system (Janis, 1976).

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

378 We pay only attention to the requirements for a given herbivore species, but
379 we do not consider what happens in case of an overconsumption of a non-limiting

380 nutrient. In fact, a more physiological approach can be proposed. If an herbivore
 381 species feeds on a plant species that gives a small amount of a limiting nutrient and a
 382 large amount of a non-limiting nutrient, one can argue that an excretion cost might
 383 exist for this nutrient. This can limit the amount of plant consumed by this herbivore
 384 species.

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

391 **Appendix 1**

392 When p herbivores compete for a limiting resource R provided by n plants, equations
 393 1, 2 and 3 respectively write:

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

394

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

395

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

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

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

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

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

398 **Appendix 2**

399 When p herbivores compete for several resources embedded into 1 plant, equations
400 1 and 2 respectively become:

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

401

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

402 and equation 3 for the limiting resource k writes:

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

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

404 *i*. Equation 25A at steady state becomes:

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

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

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

406 and

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

407 **Appendix 3**

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

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

$$\frac{dH_i}{dt} = \text{Min} \left\{ \frac{g_{i1} V_1 Q_{V1R1} + g_{i2} V_2 Q_{V2R1}}{Q_{HiR1}}, \frac{g_{i1} V_1 Q_{V1R2} + g_{i2} V_2 Q_{V2R2}}{Q_{HiR2}} \right\} H_i - m_i H_i \quad (31A)$$

410 with H_i being either H_1 or H_2

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

411 with V_j being either V_1 or V_2

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

412 with R_k being either R_1 or R_2 .

413 Each herbivore has two zero net growth isoclines (ZNGI), but their calculation
 414 is not straightforward because of multiple sources for R_1 and R_2 . However, it is
 415 possible to define boundary ZNGIs. Considering that herbivore i can consume both
 416 plants, its foraging strategy will lie between exclusive consumption of plant 1, on
 417 one side, and exclusive consumption of plant 2, on the other side. Thus, for an
 418 herbivore i focusing on plant j exclusively and being limited by resource k , equation
 419 31A becomes

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

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

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

421 which leads to

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

422 \bar{R}_k represents the slope of the boundary ZNGI for herbivore i consuming plant j and
 423 being limited by resource k . In case of two plants and two resources, each herbivore
 424 will have two boundary ZNGIs for each resources. The real value of \bar{R}_k will lie
 425 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:

$$\begin{cases} g_{11}\bar{V}_1Q_{V_1R_1} + g_{12}\bar{V}_2Q_{V_2R_1} = m_1Q_{H_1R_1} \\ g_{21}\bar{V}_1Q_{V_1R_2} + g_{22}\bar{V}_2Q_{V_2R_2} = m_2Q_{H_2R_2} \end{cases} \quad (37A)$$

If system (37A) 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 consumption vector 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 boundary consumption vector that allows herbivore 2 to consume both resources when R_2 is limiting, and leads to \bar{V}_1 and \bar{V}_2 . The boundary vector slopes

443 write:

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

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

445 Vector slopes depend on both herbivore and plant parameters.

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Table 1: 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	$M.M^{-1}$

Table 2: 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

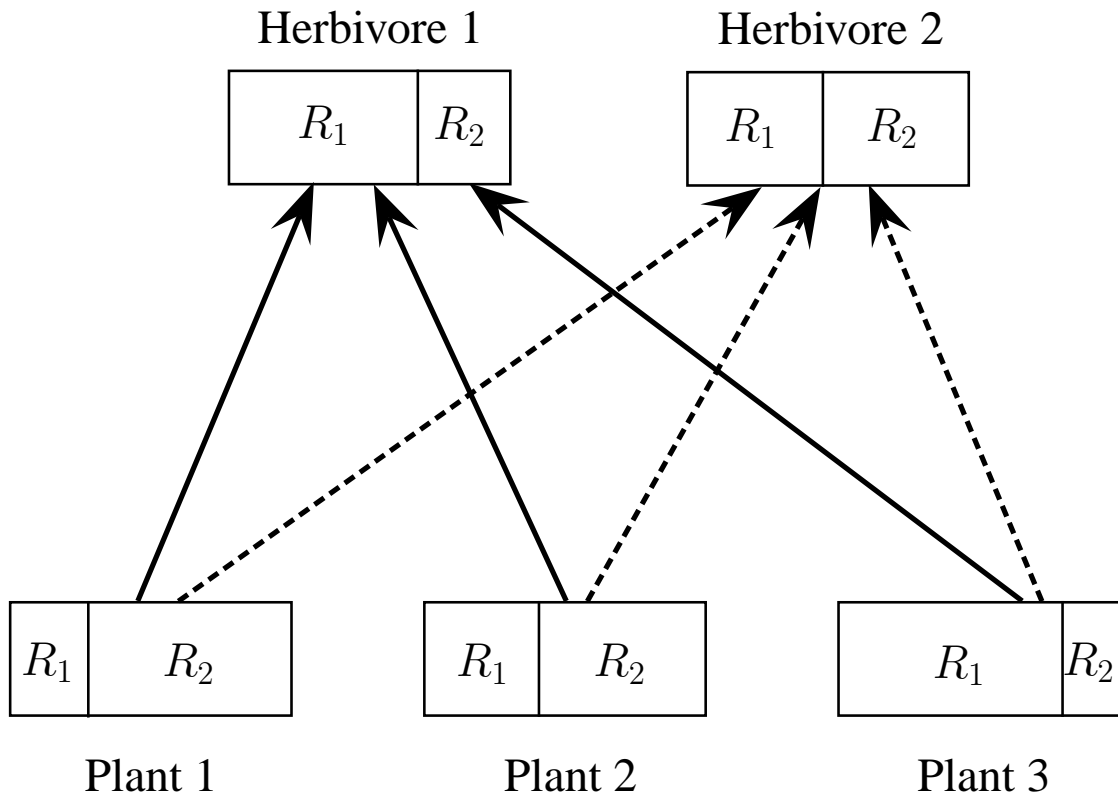


Figure 1: Each herbivore species has its own resource ratio between resource 1 (R_1) and resource 2 (R_2). This species feeds on different plant species with different resource ratios. Herbivore requirements as well as their resource consumptions are key factors for their persistence.

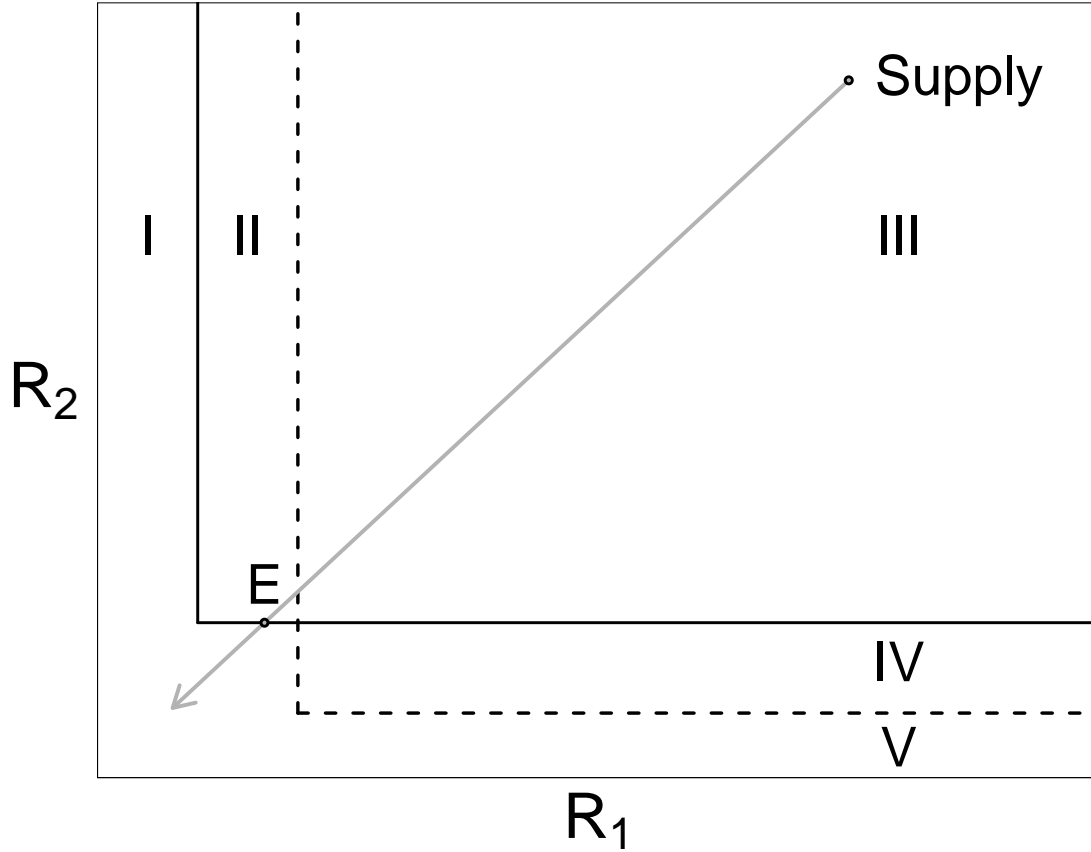


Figure 2: Phase plan with two herbivore species feeding on one plant species. Black solid lines are herbivore 1 ZNGIs, dotted lines are herbivore 2 ZNGIs, and grey arrow is the common consumption vector. Interpretations are quite similar with those from Tilman's model (Tilman, 1982). Roman numbers represent 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.

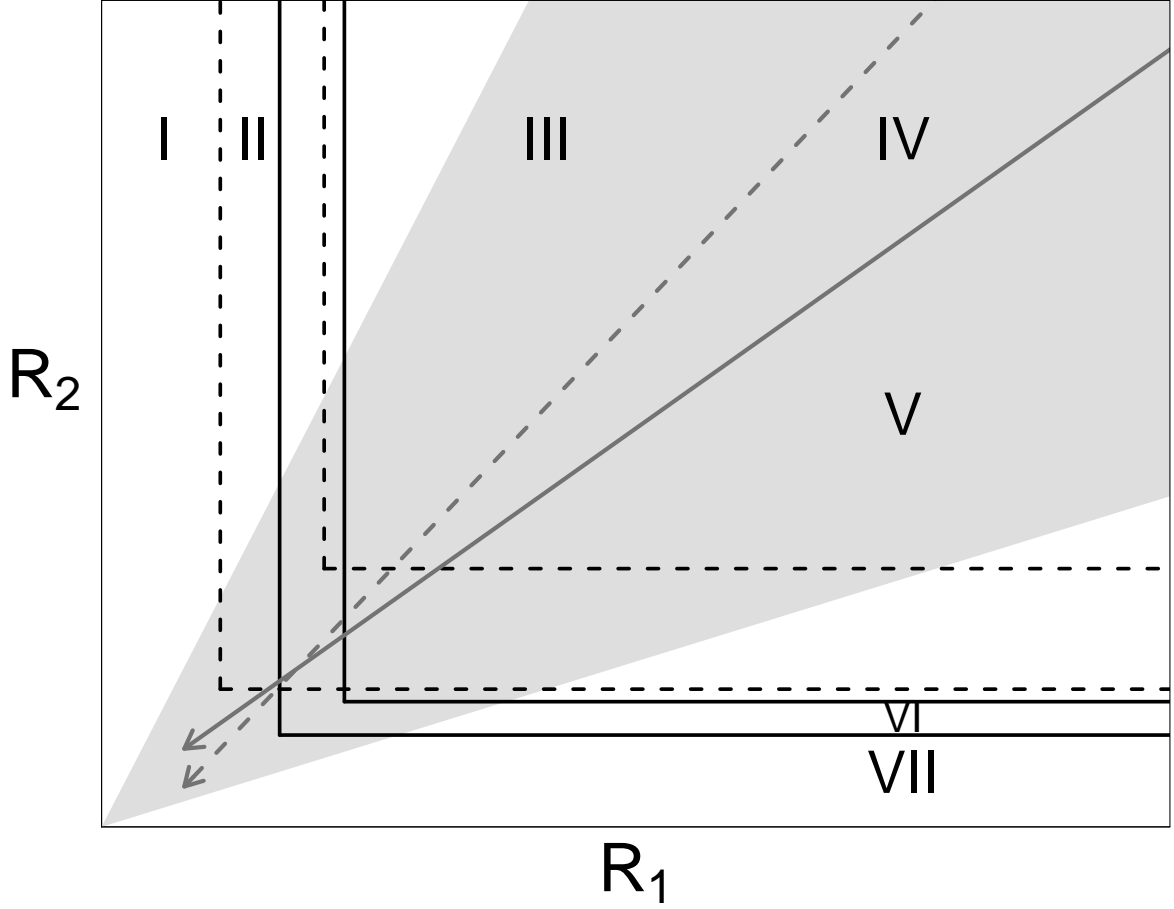


Figure 3: Phase plan for two coexisting herbivores. Lines represent boundary ZNGIs, and arrows are boundary vectors. Solid ZNGIs and solid vector belong to herbivore 1, while dotted ZNGIs and dotted vector belong to herbivore 2. Zone I and zone VII do not provide enough R_1 and R_2 respectively (i.e., 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.

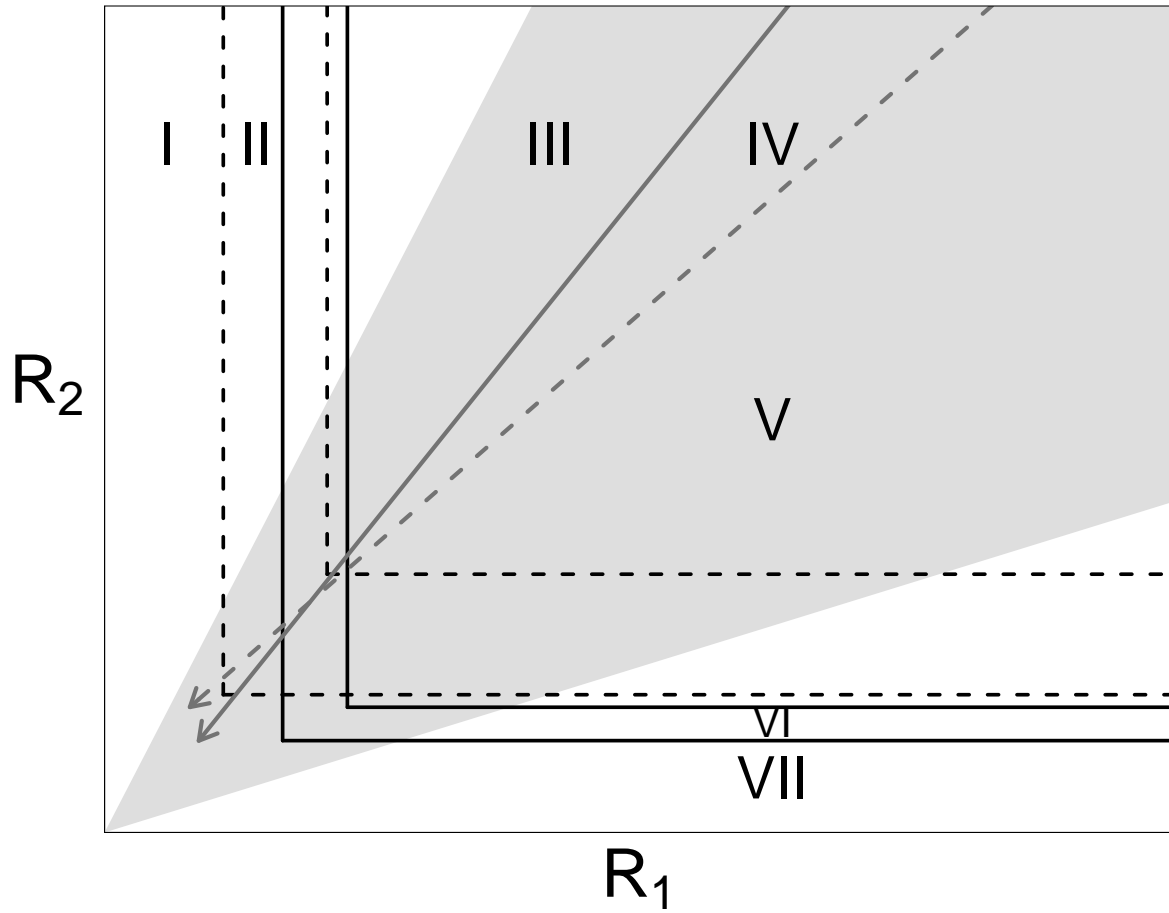


Figure 4: Phase plan for competitive exclusion between two herbivores. Representation of ZNGIs and vectors is similar to figure 3, except for zone IV. This zone generally leads to exclusion of herbivore 1 or 2. The crossing zone of ZNGIs either can be a non stable equilibrium or does not allow coexistence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