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

Abstract

Interspecific competition plays an important role in structuring communities but few studies have been done on herbivores. We present a competition model that predicts the outcome of competition between herbivore species competing for plants. Our model imbeds well-known concepts of the resource-ratio theory, such as the minimum level of resources, consumption vectors, and the quotas of resources required in the biomass. However, unlike traditional approaches that focused on plants as resources, we suggest that chemical elements and energy bounded in plant biomass represent the ultimate resources that herbivores compete for. Our model shows that the outcomes of competition between herbivores result from two main processes: the minimal requirement of resource for herbivores (R^*), and spatial segregation of resources embedded into different plants. The first process (minimal requirement) follows the classical R^* rule and determines the competitive exclusion principle. On the other hand, foraging strategy of herbivores can allow coexistence because resources are spatially segregated. Put together, these two processes determine how herbivore species can coexist, since resources are bounded. Hence, a plant community rich in one resource should support an herbivore community rich in the same resource, leading to a bottom-up effect.

Introduction

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

However, the transfer of such a theory to higher trophic levels is not obvious. The main reason is that for heterotrophic organisms, resources are not easy to characterize. Consider for instance the case of herbivores. If one considers that plant species are the resources herbivores compete for, questions arises: to what extent does a given herbivore require more of a given plant species than another? Should 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 (Sterner 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 (Sterner 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 (Sterner 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

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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, 2013). 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

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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:

$$\frac{\mathrm{d}H_i}{\mathrm{d}t} = \left(\mathrm{Min} \left\{ \frac{\sum_{j=1}^{n} g_{ij} V_j Q_{vjR1}}{Q_{hiR1}}, \ldots, \frac{\sum_{j=1}^{n} g_{ij} V_j Q_{vjRk}}{Q_{hiRk}} \right\} - m_i \right) H_i \tag{1}$$

93 where H_i is herbivore i biomass, V_j is plant j biomass, g_{ij} is consumption rate

94 of 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 quota

96 of resource k into herbivore i biomass (for example: g R_k/kg of herbivore i). The

97 ratio between herbivore and plant quotas sets influence of this chemical element on

98 growth limitation for this herbivore. According to Liebig's law of the minimum, the

99 least available resource relative to herbivore requirements is assumed to be growth

100 limiting.

101 Plant biomass is:

$$\frac{\mathrm{d}V_j}{\mathrm{d}t} = S_j - a_j V_j - \sum_{i=1}^{p} g_{ij} V_j H_i \tag{2}$$

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

quota of the considered element.

$$R_u = \sum_{j=1}^{n} V_j Q_{vjRu} \tag{3}$$

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

Results

Resources are provided by several plants, which is a spatial segregation of resources. But each plant provides several resources, which represents a stoichiometric balance issue between plant and herbivore. Spatial segregation and stoichimetric balance will first be studied separately then together.

Spatial segregation of resources

Consider a limiting resource (R). Herbivores have access to this resource through the consumption of n species of plants, depending on their feeding strategy. Resource availability at steady state, for each herbivore, is (see appendix 2 for details):

$$\overline{R}_{Hi} = \sum_{j=1}^{n} \frac{S_j}{a_j + g_{ij}\overline{H}_i} Q_{v1R} \tag{4}$$

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

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

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

123 for one resource (R) embedded into two plants species (V_1 and V_2). Extending

124 equation 4, resource availabilities for each herbivore species at steady state write:

$$\overline{R}_{H1} = \frac{S_1}{a_1 + g_{11}\overline{H}_1}Q_{v1R} + \frac{S_2}{a_2 + g_{12}\overline{H}_1}Q_{v2R} \tag{5}$$

125 and

$$\overline{R}_{H2} = \frac{S_1}{a_1 + g_{21}\overline{H}_2}Q_{v1R} + \frac{S_2}{a_2 + g_{22}\overline{H}_2}Q_{v2R} \tag{6}$$

126 Clearly, the competition outcome is driven by the foraging strategies of the com-

127 petitors, more specifically, on the efficiencies of their consumption functions (g_{ij}).

128 If $g_{11} > g_{21}$ and $g_{12} > g_{22}$, herbivore 1 consumes both plants more efficiently than

129 its competitor. Thus, the competitive exclusion principle holds, and herbivore 2 is

130 excluded. The reverse situation ($g_{11} < g_{21}$ and $g_{12} < g_{22}$) leads to the exclusion of

131 herbivore 1. However, if the two herbivores are specialized on different plant species

132 ($g_{11} > g_{21}$ and $g_{12} < g_{22}$, or $g_{11} < g_{21}$ and $g_{12} > g_{22}$), coexistence is possible. In

133 other words, despite the fact that herbivores compete for a single resource, the com-

134 petitive exclusion principle does not necessarily hold. Hence, plants species create a

135 spatial segregation of the resource, and specialization of herbivores on different plant

136 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 their requirements, and on the 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 (with $u \in [1, k]$) in plant biomass at equilibrium writes (see appendix 3 for details):

$$\overline{R}_{uHi} = \overline{V}|_{Ru} \, Q_{vRu} = \frac{m_i}{g_i} Q_{HiRu} \tag{7}$$

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 resources (R_1 and R_2) embedded into a single plant species (V). According to equation 7, the slopes of the ZNGIs only depend on herbivore parameters, which are constant. 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 difference between the slopes of the consumption vectors of the competitors (Tilman, 1982). The consumption vectors graphically illustrate how resource consumption drives the levels of resources from resource supply to equilibrium levels. In the phase plan, resource supply is represented by the supply point S, which is the total amount of resources at equilibrium in absence of consumption:

$$S_{R_1} = Q_{vR_1}(S - a\overline{V}) \tag{8}$$

$$S_{R_2} = Q_{vR_2}(S - a\overline{V}) \tag{9}$$

For a given herbivore i, the consumption vector $\vec{C}_i$ writes:

$$\vec{C}_i = \begin{pmatrix} g_i\overline{VH}_iQ_{vR_1} \\ g_i\overline{VH}_iQ_{vR_2} \end{pmatrix} = g_i\overline{VH}_i \begin{pmatrix} Q_{vR_1} \\ Q_{vR_2} \end{pmatrix} \tag{10}$$

The vectors slope is determined by the ratios of resources embedded in plant biomass. An important consequence is that all herbivores have the same slope of consumption

vector when feeding on a single plant. This constraint precludes coexistence, and the resource-ratio embedded in plant biomass determines which of the competitor will displace the other (figure 2). Hence, despite differences in requirement, two herbivores cannot coexist on several resources. This result is in contrast with the classical resource-ratio theory, which stipulates that two consumer may coexist on two resources under certain conditions. The reason is that classically, consumers are assumed to control the slope of their consumption vector (Tilman, 1982). This assumption is valid for primary producers, which take up essential nutrients independently in their environment, in the form of dissolved chemical molecules, but not for herbivores, which take up essential nutrients already bounded in plant biomass. Therefore, only the herbivore that can match plant stoichiometry the best can persist and outcompete other herbivores. This leads to a strong bottom-up stoichiometric constraint.

Competition for several plant species and several resources

In this section, we present the general case of the model, where herbivores compete for multiple resources embedded into multiple plants. Assuming that nutrient quotas differ among plant species, the consumption of a given plant is not equivalent to consumption of another plant. Due to spatial segregation among resources, herbivores may control their diet by allocating more time/energy to feed on specific plants rather than others. Therefore, each herbivore may find a specific pathway to collect resources (Simpson and Raubenheimer, 1995; Raubenheimer and Simpson, 1999). The foraging strategy of a given herbivore is graphically represented by the

consumption vector, which is the combination of the consumption vectors for all the plant species consumed. As a consequence, the slope of the consumption vector depends on the foraging strategy of the herbivore, which can adjust the slope by consuming more efficiently a given species versus the others. Thus, niche segregation among herbivore species is a combination of spatial segregation and segregation on the requirements. As we shall see, this niche segregation allows for coexistence of multiple herbivores on multiple resources.

To simplify, we consider here the case of two herbivores competing for two plants embedding two resources (see appendix 4 for details). The resource supply is represented in the phase plan by the supply point S, which is the total amount of resources at equilibrium in plants 1 and 2, in absence of consumption:

$$S_{R1} = Q_{v1R1}(S_{v1} - a\overline{V}_1) + Q_{v2R1}(S_{v2} - a\overline{V}_2) \tag{11}$$

$$S_{R2} = Q_{v1R2}(S_{v1} - a\overline{V}_1) + Q_{v2R2}(S_{v2} - a\overline{V}_2) \tag{12}$$

For a given herbivore i, the ZNGI slope $(\alpha|_{Ru})$ for each resource (R_u) is:

$$\alpha|_{Ru} = \frac{\overline{V}_1|_{Ru}Q_{v1R2} + \overline{V}_2|_{Ru}Q_{v2R2}}{\overline{V}_1|_{Ru}Q_{v1R1} + \overline{V}_2|_{Ru}Q_{v2R1}} \tag{13}$$

Note that the slope depends on $\{\overline{V}_1, \overline{V}_2\}$, which themselves depend both on the herbivore and the plant parameters (including the supply parameters). Hence, the ZNGI slope is not parallel to the axis.

However, it is possible to define boundary ZNGI. Considering that herbivore i can

²¹⁴ consume both plants, its foraging strategy will lie between exclusive consumption of

²¹⁵ plant 1, on one side, and exclusive consumption of plant 2, on the other side. Thus,

²¹⁶ boundary ZNGI slope writes (see appendix 4 for details):

$$\overline{R}_u = \frac{Q_{hiRu}m_i}{g_{ij}} \tag{14}$$

²¹⁷ This isocline $\overline{R}_u$ represents the ZNGI in the case where herbivore i consumes only

²¹⁸ plant j and is limited by nutrient u. In case of two plants consumed, the real $\overline{R}_u$ will

²¹⁹ lie between two boundary ZNGI (one for each plant).

²²⁰ By looking at boundary ZNGI equation (14), it appears that ZNGI slopes depend

²²¹ only on herbivore constant parameters. Therefore, it is parallel to the axis. Moreover,

²²² two herbivores having similar quotas but different feeding strategies would have dif-

²²³ ferent ZNGI. Thus, if boundary ZNGI of two herbivores cross each other, coexistence

²²⁴ might be possible.

²²⁵ Next, competition outcome will depend on the relative orientation of the con-

²²⁶ sumption vector of herbivores (Tilman, 1980). However, vector slope calculation is

²²⁷ uneasy in the case of packaged resources because vector slope depends on plant sup-

²²⁸ ply points. Hence, for a given herbivore, vectors do not have a constant slope valid

²²⁹ for all supply conditions. This is why instead of consumption vectors, the model

²³⁰ allows the calculation of boundary vectors that determine an area in the phase plan

²³¹ where each herbivore species could coexist with an other one. It is possible to deter-

²³² mine a boundary relation between plant supply points (S_1 and S_2) that allows each

²³³ herbivore to consume both resources when one resource is limiting, and leads to $\overline{V}_1$

234 and $\overline{V}_2$ at steady state. These boundary supply points are S_{1hi} and S_{2hi} for plant 1

235 and 2 respectively (see appendix 4). Hence, boundary vector slopes are:

$$\vec{C}_{h1} = \begin{pmatrix} \overline{S}_{1h1}\ Q_{v1R1} + \overline{S}_{2h1}\ Q_{v2R1} \\ \overline{S}_{1h1}\ Q_{v1R2} + \overline{S}_{2h1}\ Q_{v2R2} \end{pmatrix} \tag{15}$$

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$$\vec{C}_{h2} = \begin{pmatrix} \overline{S}_{1h2}\ Q_{v1R1} + \overline{S}_{2h2}\ Q_{v2R1} \\ \overline{S}_{1h2}\ Q_{v1R2} + \overline{S}_{2h2}\ Q_{v2R2} \end{pmatrix} \tag{16}$$

237 These two boundary vectors play a similar role as consumption vectors in Tilman's

238 model. However, as resources are packaged into plants, vector slopes depend on the

239 way herbivore species feed on plants containing resources. Hence, assuming plant 1

240 is richer in resource 1 ($Q_{v1R1} > Q_{v2R1}$), and plant 2 is richer in resource 2 ($Q_{v1R2} <$

241 Q_{v2R2}), and assuming herbivore 1 is more limited by resource 1 ($Q_{h1R1} > Q_{h1R2}$), and

242 herbivore 2 is more limited by resource 2 ($Q_{h2R1} < Q_{h2R2}$), two general strategies can

243 be considered. The first one occurs when each herbivore species consumes preferen-

244 tially the plant species which gives the greater quantity of the most limiting resource

245 for this herbivore species, and which is less limiting for its competitor (i.e., $g_{11} > g_{12}$

246 and $g_{21} < g_{22}$). In that case, if we consider the boundary vectors for herbivore 1 and

247 for herbivore 2, we can define several zones on the phase plan (see figure 3). The zone

248 between the two boundary vectors represents the supply conditions allowing stable

249 coexistence of the two herbivore species. Thus, each herbivore consumes the most

250 profitable plant (i.e., quotas and consumption functions follow a similar trend), but

251 each herbivore is specialized (more or less) on a different plant than its competitor,

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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 figure 4), and in many cases equation 30A 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.

A second case occurs when the previous assumptions on herbivore and plant quotas (i.e., inequality for herbivore requirements, and inequality for plant prof-

14

₂₇₅ itability) are released. Therefore, both herbivores can have the same quotas (i.e.,

₂₇₆ $Q_{h1R1} = Q_{h2R1}$ and $Q_{h1R2} = Q_{h2R2}$) but different consumption functions. In that

₂₇₇ case, one plant will be more interesting for both herbivores (i.e., the plant that is

₂₇₈ richer for the most limiting resource). Hence, the herbivore that can consume this

₂₇₉ plant the most efficiently will exclude its competitor. Again, bottom-up stoichiome-

₂₈₀ try constrained herbivore coexistence. Another case can occur when both plants have

₂₈₁ the same quotas (i.e., $Q_{v1R1} = Q_{v2R1}$ and $Q_{v1R2} = Q_{v2R2}$). In that case, the system

₂₈₂ is similar to the case where only one plant is present, which leads to competitive

₂₈₃ exclusion. Here, spatial segregation does not occur.

₂₈₄ Last, one can notice that plant stoichiometry constrains the supply point because

₂₈₅ of resource packaging into plants. Resource ratio within each plant will define a slope:

$$\alpha_{vj} = \frac{Q_{vjR2}}{Q_{vjR1}} \tag{17}$$

₂₈₆ In case of two plants, supply point will lie between the two extreme slopes (α_{v1} and

₂₈₇ α_{v2}) defining a feasibility cone. Therefore, the whole phase plan is not available. Re-

₂₈₈ source supply occurs only within this feasibility cone, which adds another constraint

₂₈₉ on herbivore persistence and competition.

₂₉₀ Discussion

₂₉₁ Unlike classical studies on herbivore competition we consider here that the resource

₂₉₂ limiting herbivores growth is not plant biomass but rather, the essential nutrients

₂₉₃ contained in plant biomass.

According to our results, the fundamental difference between herbivore compe-
tition 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 rela-
tionship 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).

Nonetheless, our model allows us to disentangle the relative effects of the bottom-up stoichiometric component (i.e., plant and herbivore resource quotas) and the non-stoichiometric component (i.e., spatial segregation) of the competitive interaction. Indeed, the foraging strategy of the competing herbivores will mainly determine

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the competitive outcome. Non-selective herbivores (representing case 2 and case 4 with non-selective behavior) will show a strong bottom-up stoichiometric effect. Therefore, coexistence is unlikely. For example, non-selective zooplanktonic filters, such as cladocerans (limited by P) and copepods (limited by N), usually do not coexist: either one group or the other dominates according the N:P ratio of the consumed algae (Andersen and Hessen, 1991; Hessen, 1992; Sterner et al., 1992; Elser et al., 1996; Koski, 1999). A similar assumption can be made for non-selective terrestrial grazer herbivores (Albon and Langvatn, 1992) for which coexistence would be unlikely. On the other hand, selective herbivores, specialized on a few plants, would show a strong spatial component and a weaker stoichiometric component of the interaction (representing case 2 and case 4 with selective behavior). Therefore, they should be more prone to coexist.

Concerning the stoichiometric component, our assumption is that a stoichiometric diversity between niches exists among herbivore species, and field studies tend to show it. For aquatic herbivores, such as zooplankton, it seems that grazers (especially *Daphnia sp.*) are P-limited, while copepods seem to be N-limited (see above). This stoichiometric diversity exists for terrestrial herbivores either (see table 1). Chemical requirements for wild herbivores are mostly unknown, but for mammal herbivores, numerous studies have used data from cattle as proxy for diet requirement for wild species (Voeten and Prins, 1999). Nevertheless, data begins to be available. For example, N requirements have been estimated for fawns (Smith et al., 1975), yearlings (Holter et al., 1979) and adults (Asleson et al., 1996) of white-tailed deer (*Odocoileus virginianus*), as well as P requirement for white-tailed deer (Grasman and Hellgren,

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

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

Appendix 3

When p herbivores compete for k resources embedded into 1 plant, equations 1, 2 and 3 respectively become:

$$\frac{\mathrm{d}H_i}{\mathrm{d}t} = \left(\mathrm{Min}\left\{\frac{Q_{vR1}}{Q_{hiR1}}, \dots, \frac{Q_{vRk}}{Q_{hiRk}}\right\} g_i V - m_i\right) H_i \tag{18A}$$

$$\frac{\mathrm{d}V}{\mathrm{d}t} = S - aV - \sum_{i=1}^{p} g_i V H_i \tag{19A}$$

$$R_k = V Q_{vRk} \tag{20A}$$

At steady state, it is possible to determine resource availability for each herbivore i. Assuming that R_u is a limiting resource, with $u \in [1, k]$.

$$\overline{V}|_{Ru} = \frac{m_i}{g_i} \frac{Q_{hiRu}}{Q_{vRu}} \tag{21A}$$

Where $\overline{V}|_{Ru}$ is the steady state plant biomass when R_u is limiting. $\overline{R}_u$ is:

$$\overline{R}_u = \overline{V}|_{Ru} \, Q_{vRu} = \frac{m_i}{g_i} Q_{hiRu} \tag{22A}$$

Appendix 4

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

$$\frac{\mathrm{d}H_i}{\mathrm{d}t} = \left(\mathrm{Min} \left\{ \frac{g_{i1}V_1 Q_{v1R1} + g_{i2}V_2 Q_{v2R1}}{Q_{hiR1}}, \frac{g_{i1}V_1 Q_{v1R2} + g_{i2}V_2 Q_{v2R2}}{Q_{hiR2}} \right\} - m_i \right) H_i \tag{23A}$$

$$\frac{\mathrm{d}V_j}{\mathrm{d}t} = S_j - a_j V_j - g_{1j}V_j H_1 - g_{2j}V_j H_2 \tag{24A}$$

$$R_1 = q_{v1R1}V_1 + q_{v2R1}V_2 \tag{25A}$$

$$R_2 = q_{v1r2}V_1 + q_{v2r2}V_2 \tag{26A}$$

Each herbivore has two zero net growth isoclines (ZNGI), but their calculation is more complicate because of multiple sources for R_1 and R_2. However, it is possible to define boundary ZNGI. Considering that herbivore i can consume both plants, its foraging strategy will lie between exclusive consumption of plant 1, on one side, and exclusive consumption of plant 2, on the other side. Thus, for an herbivore

$_{411}$ i consuming each plant j (with $j \in [1,2]$) and limited by each resource u (with

$_{412}$ $u \in [1,2]$), equation 23A becomes

$$\frac{dH_i}{dt} = \left(\frac{g_{ij}V_j Q_{vjRu}}{Q_{hiRu}} - m_i \right) H_i \qquad (27A)$$

$_{413}$ At steady state, $\overline{R}_u = \overline{V}_j * Q_{vjRu}$. Thus,

$$\frac{g_{ij}\overline{V}_j Q_{vjRu}}{Q_{hiRu}} - m_i = \frac{g_{ij}\overline{R}_u}{Q_{hiRu}} - m_i = 0 \qquad (28A)$$

$_{414}$ which leads to

$$\overline{R}_u = \frac{Q_{hiRu}m_i}{g_{ij}} \qquad (29A)$$

$_{415}$ $\overline{R}_u$ represents the slope of the boundary ZNGI for herbivore i consuming plant j and

$_{416}$ limited by resource u. In case of two plants and two resources, each herbivore will

$_{417}$ have two boundary ZNGI for each resources. The real value of $\overline{R}_u$ will lie between

$_{418}$ the two boundary ZNGI.

$_{419}$ It is possible to calculate $\overline{V}_1$ and $\overline{V}_2$ that are the equilibrium biomass of plant 1

$_{420}$ and 2 respectively and are solutions of the following system:

$$\begin{cases} g_{11}\overline{V}_1 Q_{v1r1} + g_{12}\overline{V}_2 Q_{v2r1} = m_1 Q_{h1r1} \\ \\ g_{21}\overline{V}_1 Q_{v1r2} + g_{22}\overline{V}_2 Q_{v2r2} = m_2 Q_{h2r2} \end{cases} \qquad (30A)$$

$_{421}$ If system (30A) has two realistic solutions (i.e., $\overline{V}_1 > 0$ and $\overline{V}_2 > 0$), and if $\overline{H}_1 > 0$

$_{422}$ and $\overline{H}_2 > 0$, which means that coexistence occurs at that point, then this point is

$_{423}$ an equilibrium point. Knowing $\overline{V}_1$ and $\overline{V}_2$ at this equilibrium point, it is possible to

22

determine a boundary relation between plant supply points (S_1 and S_2) that allows

herbivore species 1 to consume both resources when R_1 is limiting, and leads to $\overline{V}_1$

and $\overline{V}_2$ 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 $\overline{V}_1$ and $\overline{V}_2$. The

relations are:

$$\overline{S}_{2h1} = (\overline{S}_{1h1} - a_1)\frac{g_{12}\overline{V}_2}{g_{11}\overline{V}_1} + a_2\overline{V}_2 \tag{31A}$$

$$\overline{S}_{2h2} = (\overline{S}_{1h2} - a_1)\frac{g_{22}\overline{V}_2}{g_{21}\overline{V}_1} + a_2\overline{V}_2 \tag{32A}$$

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.

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

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

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

| Symbols	Definitions	Dimensions
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 *per capita*	T^{-1}
S_j	plant j biomass supply	$M.T^{-1}$
a_j	plant j biomass natural loss rate *per capita*	T^{-1}
Q_{hiRu}	resource u quota for herbivore i	dimensionless
Q_{vjRu}	resource u quota for plant j	dimensionless
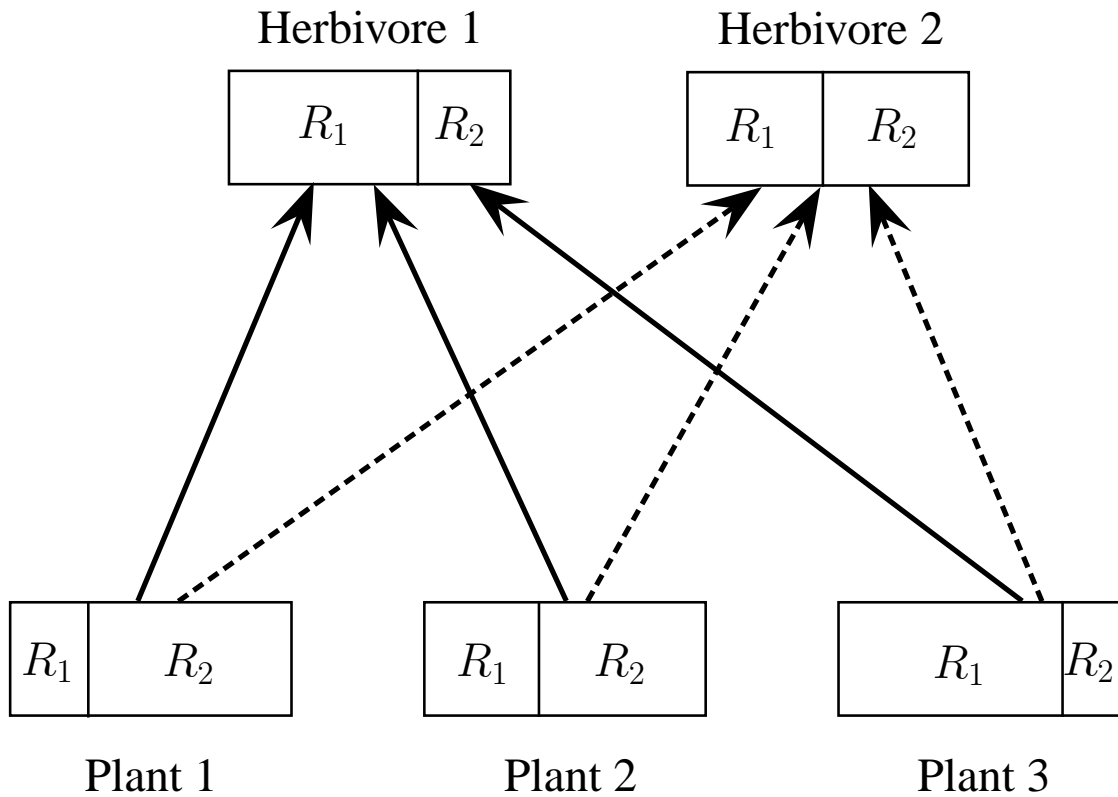
Figure 1: Each herbivore species has its own resource ratio between resource 1 (R_1) and resource 2 (R_2). This species feeds on different plant species with different resource ratios. Herbivore requirements as well as their resource consumptions are key factors for their persistence.
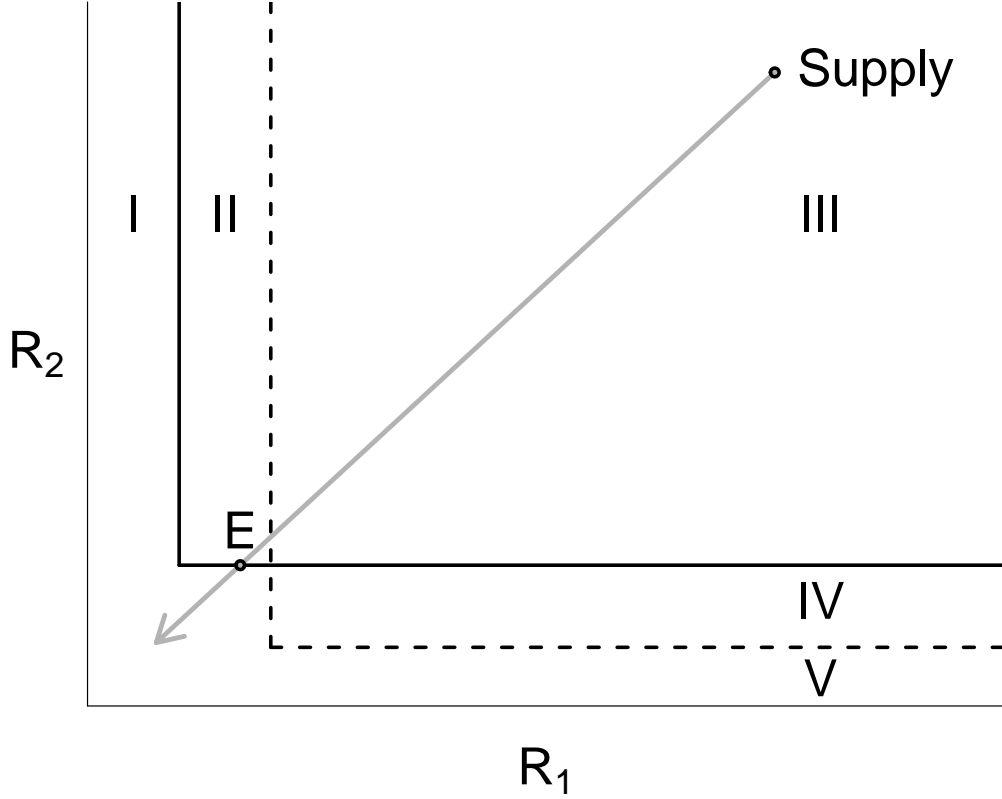
Figure 2: Phase plan with two herbivore species feeding on one plant species. Black lines are herbivore 1 ZNGI, dotted lines are herbivore 2 ZNGI, and grey arrow is the common consumption vector. Interpretations are quite similar with those from Tilman's model (Tilman, 1982). Roman numbers represent 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 exemple, 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.
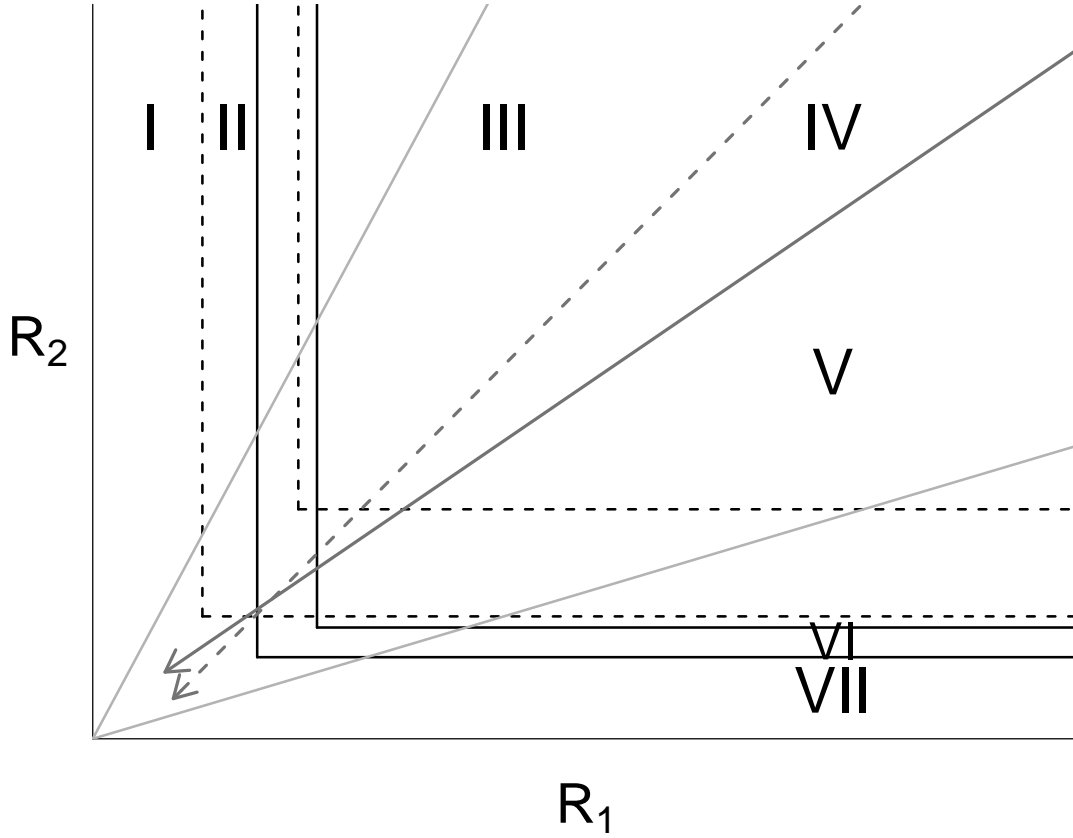
Figure 3: Phase plan for two coexisting herbivores. Lines represent boundary ZNGI, arrows are boundary vectors, and grey lines bound feasible supply conditions according to plants considered (i.e., feasibility cone). Continuous ZNGI and vector belong to herbivore 1, and dotted ZNGI and vector belong 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).
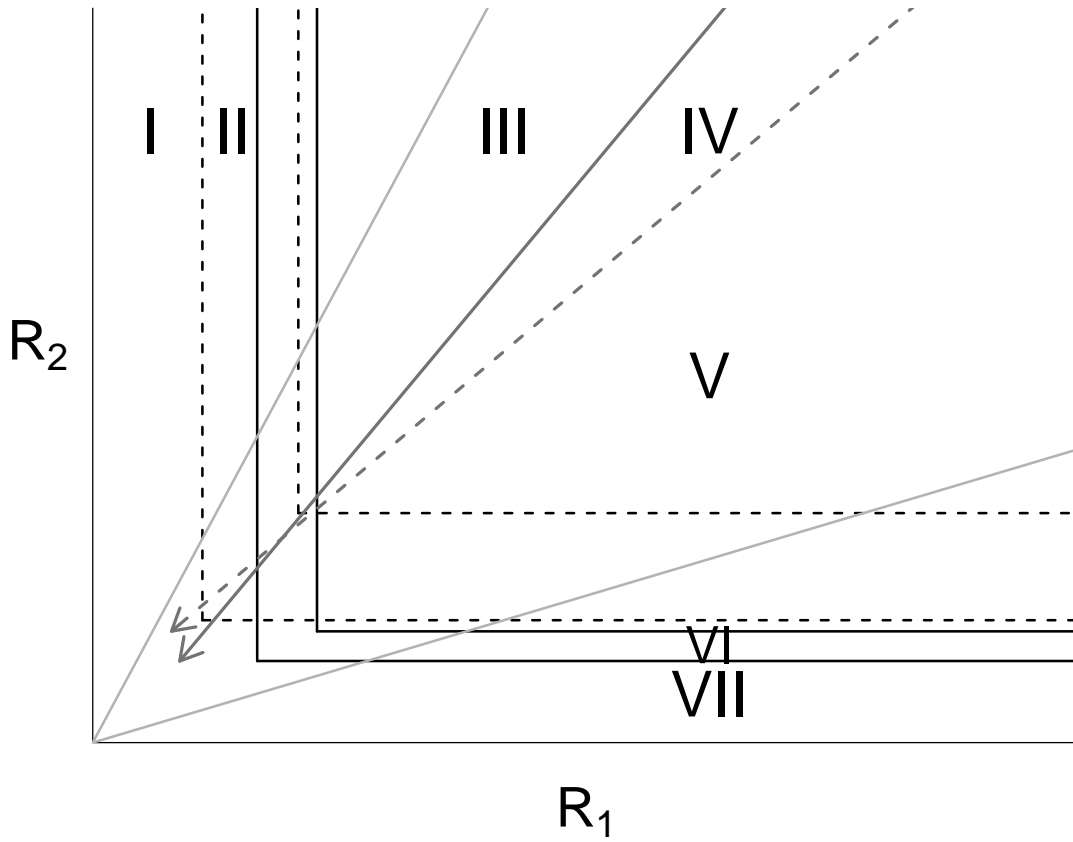
Figure 4: Phase plan for competitive exclusion. Representation of ZNGI and vectors is similar to figure 3, except for zone IV. This zone generally leads to exclusion of herbivore 1 or 2. The crossing zone of ZNGIs either can be a non stable equilibrium (NSE) or does not allow coexistence of the two herbivore species.