Nutrient-limited food webs with up to three trophic levels: feasibility, stability, assembly rules, and effects of nutrient enrichment

Florence Hulot, Michel Loreau

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Florence D. Hulot* **and Michel Loreau**

Laboratoire d'Ecologie, UMR 7625

Ecole Normale Supérieure

46, rue d'Ulm

75230 Paris Cedex 05

France

* Corresponding author: florence.hulot@ens.fr

Tél: +33 1 44 32 39 97

Fax: +33 1 44 32 38 85

Abstract

Community structure is controlled, among multiple factors, by competition and predation. Using the R^* rule and graphical analysis, we analyse here the feasibility, stability and assembly rules of resource-based food webs with up to three trophic levels. In particular, we show that (1) the stability of a food web with two plants and two generalist herbivores does not require that plants' resource exploitation abilities trade-off with resistance to the two herbivores, and (2) food webs with two plants and either one generalist herbivore and a carnivore or two generalist herbivores and two generalist carnivores are not feasible because of cascade competition between top consumers. The relative strength of species interactions and the relative impacts of plants and herbivores on factors which control their growth also play a critical role. We discuss how community structure constrains assembly rules and yields cascades of extinctions in food webs.

Keywords: food-web structure; interaction strength; assembly rules; secondary extinction; graphical analysis; isoclines; isoplanes;

Introduction

Species diversity is a pivotal theme of ecology. Because this diversity is threatened, in particular by human activities, and because numerous human activities depend on services provided by ecosystems, studying this diversity is also a challenge for society. Understanding the links between species diversity and the functioning and sustainability of ecosystems has been during the last decade the subject matter of intensive theoretical and experimental research (see for a review Tilman, 1999; Loreau, 2000; Loreau et al., 2001; Kinzig et al., 2002; Loreau et al., 2002). The maintenance of species diversity, however, remains an intriguing question. How do species assemble to form communities? What are the assembly rules of food webs?

The ultimate driver of community assembly is introduction of new species by speciation or immigration (Drake et al., 1999). If we define assembly rules as the constraints acting on a common species pool to determine the actual composition of a community (Fraser et al., 1997), interspecific interactions are factors contributing to the success of invasion and the final composition of communities. Exploitative competition and predation have been analysed by several authors in the perspective of community assembly and lead to handy rules. These rules are primarily based on the R^* rule proposed by Tilman (1982, p. 44) and state that the better nutrient exploiter always excludes its competitor, whatever the order of invasion. Wolkowicz (1989) and Grover (1994, 1995, 1997, p. 147) extended this rule to food chains and showed that only a strict order of species invasions could lead to communities with specialist herbivores preying upon plants limited by the same nutrient. The successful order of invasions may be summarised as follows. The plants should invade by decreasing order of resource exploitation ability, and the invasion of the next plant should come after the invasion of the herbivore that preys upon the previous invading plant. For instance, the second plant in the resource exploitation hierarchy can invade a community only if the better resource exploiter is controlled by a herbivore. If the assembly order is not respected, either the invasion event fails and the initial community remains unchanged, or the invasion event succeeds but some species of the initial community are excluded. Holt et al. (1994) and Leibold (1996) analysed communities with a generalist herbivore preying upon plants exploiting the same resource. In such communities, plants interact through exploitative competition mediated by a common resource (Tilman, 1982, p. 72) and apparent competition mediated by a shared predator (Holt, 1977). Community stability is insured if plants have a trade-off between their abilities to exploit the resource and to defend against consumers (Holt et al., 1994; Leibold, 1996). The assembly sequence in such a food web is first invasion by the plant that best exploits the resource, followed by invasion of the herbivore, and finally invasion by the plant that is less efficient at exploiting the resource but more resistant to herbivore grazing. Later, Grover (1997, p. 160) studied food webs with specialist top predators preying upon specialist herbivores, which themselves prey upon plants that compete for a resource. He showed that a top predator could only invade communities in which plants are controlled by herbivores. If a plant is not controlled by a herbivore, the invading top predator and the plant interact through cascade competition, an indirect form of resource competition that propagates in food chains. Consequently, either the uncontrolled plant or the top predator is excluded from the community. Because of cascade competition, several specialist top predators cannot coexist in communities with multiple nutrient-limited food chains. Only the winner of the cascade competition persists.

The analyses summarised above show that assembling a community with up to three trophic levels and several species at each trophic level is not a straightforward process. Nevertheless several assembly rules emerge from these analyses. These assembly rules take the form of “if-then-else” rules (Drake et al., 1999). If the life-history parameters of a species fulfil some conditions, then the invasion succeeds. Else, either the species settles while other species of the initial community are excluded, or the invasion event fails. These analyses have been fruitful to understand how successive invasions might lead to a community with a reticulated structure. They offer an alternative to the simple food-chain model in which nutrient enrichment is the sole factor that limits food-chain length (Oksanen et al., 1981; Kaunzinger et al., 1998). However, these analyses have so far focused on specific communities with either specialist consumers or a single generalist herbivore. In the present paper, we extend these assembly rules to nutrient-based food webs with (1) two plants and two generalist herbivores, and (2) two plants, two generalist herbivores and a specialist carnivore. We focus on nutrient-based food webs because ignoring resource competition between basal species amounts to ignoring the role of competition between basal species and keystone predation in community structure and assemblage (Berlow et al., 2004). We analyse the feasibility and stability of these food webs. We also examine the effects of nutrient enrichment on the equilibrium values of the populations, the effects of species extinction and the risks of secondary extinctions. This study extends current knowledge on the functioning of communities by analysing relative interactions strengths of species and their consequences on community assembly and dynamics. We show that (1) nutrient-based food webs with two plants and two generalist herbivores are feasible and stable under some conditions. In particular, such food webs do not require that plants trade off competitive ability and resistance to predation by the two herbivores. (2) Nutrient-based food webs with two plants and either one generalist herbivore and a carnivore or two generalist herbivores and two generalist carnivores are not feasible because of cascade competition. (3) Nutrient-based food webs with two plants, two generalist herbivores and a specialist carnivore preying upon one of the herbivores are feasible and stable under some conditions, but these conditions differ depending on which herbivore the carnivore preys upon. (4) The responses of these nutrient-based food webs to nutrient enrichment, their assembly rules and the effects of species extinctions depend on relative interaction strengths within the community. Extinction of a species can lead to cascading extinctions in other parts of the food web because of the strong constraints on the feasibility, stability and assembly of complex communities.

1. The model

In this section we present our general model of nutrient-based food webs with up to three trophic levels. Although our model does not address any particular ecosystem (terrestrial, pelagic or soil for instance), we interpret the trophic levels as plants, herbivores and carnivores for the sake of clarity. The origin of species immigrating in the community will not be considered explicitly.

The general model is:

$$\begin{aligned}
\frac{dC_z}{dt} &= C_z\left(\sum_j e_{jz} f_{jz} H_j - \mu_z\right) \\
\frac{dH_j}{dt} &= H_j\left(\sum_i a_{ij} b_{ij} P_i - d_j - \sum_z e_{jz} C_z\right) \\
\frac{dP_i}{dt} &= P_i\left(k_i l_i R - m_i - \sum_j a_{ij} H_j\right) \\
\frac{dR}{dt} &= I - \left(q + \sum_i k_i P_i\right) R
\end{aligned} \tag{1}$$

where $i, j, z = 1, 2$, R is the resource pool, P_i, H_j and C_z are population densities of plants, herbivores and carnivores respectively. I represents the external nutrient input and q the nutrient loss rate; k_i, a_{ij} and e_{jz} are the consumption rates of the nutrient by plant i, of plant i by herbivore j, and of herbivore j by carnivore z, respectively; l_i, b_{ij} and f_{jz} are their associated conversion coefficients of resource into newborn consumers. We will indicate equilibrium values with an asterisk (*) and the identity of the species present in the community in subscripts as follows: plant 1 and/or 2; herbivores 1 and/or 2; carnivores 1 and/or 2. For example $R^*_{(1,2;2)}$ represents the equilibrium value of the resource in the community containing plants P_1 and P_2 and herbivore H_2. A subscript S indicates a specialist consumer.

Species are linked only by trophic interactions and all functional responses are linear (Lotka-Volterra interactions). This allows us to consider generalist consumers. Indeed, with type II functional responses, the effect of multiple preys on predator growth rate is not simply the sum of the effect of each prey (Arditi et al., 1996), which complicates the analysis notably. Although nutrient cycling is important for ecosystem functioning, we do not take it into account explicitly because it does not influence species coexistence directly. However, the constant external nutrient input I may include recycled nutrient.

In our analysis, we study food-web feasibility and stability. A feasible food web means that all variables have positive equilibrium values. To study feasibility, we calculate equilibrium values and conditions leading to positive values. To analyse local stability, we conduct graphical isocline analyses, which take into account both species requirements and impacts. We define species resistance to herbivory as any way to reduce or eliminate herbivory through chemical, structural, and/or other traits such as crypticity and mimicry (Chase et al., 2000). This defence implies a decrease in the attack rate of herbivores on their prey (Chase et al., 2000). Species interaction strength, which is widely discussed in our analysis, is defined as the partial derivative of a species' growth rate with respect to small changes in another species' abundance; this metric defines the community matrix (for its advantages and disadvantages, see (Berlow et al., 2004)).

2. Isocline analysis

The food-web models we analyse in this paper are too complex to allow complete mathematical analysis. However, some constraints on food-web assembly and conditions for local stability can be derived from an isocline analysis. We present in this section the principles of isocline analysis for prey-predator interactions. The Zero Net Growth Isocline (ZNGI, Tilman, 1982, p. 61) of a species is a function of the factors that constrain its growth. For instance, in a two-trophic-level food chain, the ZNGI of a plant P_i is defined by resource availability (x-axis) and herbivore density (y-axis) (Eq. 1, Fig. 1). The ZNGI is the set of points for which the birth and death rates are equal. The ZNGI of plant P_i intersects the x-axis (resource availability) at the value $R^*_{P_i}$, the resource equilibrium value in the absence of herbivores. The lower $R^*_{P_i}$, the more competitive is plant P_i (Tilman, 1982, p. 44). The plant ZNGI increases monotonically with resource availability and herbivore density. The slope of the ZNGI is inversely proportional to the herbivore consumption rate: the higher the consumption rate, the shallower the slope (Leibold, 1996; Chase et al., 2003, p. 27). The consumption rate changes with the resistance of the prey to predation: it is low when the prey is resistant against predators and high when the prey is poorly defended against predators. Thus, the more resistant the plant against herbivory, the steeper the slope of the plant ZNGI (Leibold, 1996; Chase et al., 2003, p. 27).

Food webs with two plants P_i exploiting a limiting resource R and sharing a herbivore H_1 were analysed graphically by Leibold (1996) and Chase and Leibold (2003, p. 36). The plant ZNGIs intersect if one plant is a better resource exploiter (low $R^*_{P_i}$ value) and the other plant is more resistant to predation (high ZNGI slope). We define here plant P_1 as the better resource exploiter and plant P_2 as the more resistant plant to H_1 grazing. The plant ZNGIs define three equilibria: a coexistence equilibrium at the intersection point, a food chain with plant P_1 and herbivore H_1, and a food chain with plant P_2 and herbivore H_1 (Fig. 1). Depending on the supply point and the impact vectors, one of these equilibria will be reached. The impact vector of plant P_i has a negative horizontal component characterising the depletion of resource (per capita rate of resource consumption) and a positive vertical component characterising the net effect of plant on the herbivore (per capita birth rate of predator). The ZNGIs and the projection of the impact vectors define five regions in the resource-herbivore (R, H_1) plane. If the supply point lies in region 0, neither species can persist. If the supply point lies in region I or I' with a high resource availability and a high herbivore density, plant P_2, which is more resistant to herbivory, excludes plant P_1. If the supply point lies in region II or II' with a low resource availability and a low herbivore density, plant P_1, which is the better resource exploiter, excludes plant P_2. If the supply point lies in region III, a coexistence equilibrium is possible. If each species has a greater relative impact on the factor that most limits its relative growth, then the coexistence equilibrium is stable (Fig. 1A), otherwise it is unstable (Fig. 1B).

In summary, the conditions leading to the stable community R-P_1-P_2-H_1 may be formalised as follows:

- P_1 is a better competitor for the resource R than is P_2. Thus, $R^*_{(1)} < R^*_{(2)}$, with $R^*_{(i)} = m_i / k_i l_i$ (Condition 1, Table 1).
- P_2 is more resistant to H_1 herbivory than is P_1. Thus $k_1 l_1 / a_{11} < k_2 l_2 / a_{21}$, where $k_i l_i / a_{i1}$ is the ZNGI slope of plant i in the (R-H_1) plane (Condition 2, Table 1).
- The impact vector of P_1 is steeper than the impact vector of P_2 in the (R, H_1) plane (Fig. 1A). Thus $C_{P_1(H_1)} > C_{P_2(H_1)}$, with $C_{P_i(H_1)} = a_{i1} b_{i1} / k_i$ (Condition 3, Table 1).
- The supply point lies in region III, i.e. the external nutrient input I is bounded between the two values $I_{(1,2;1)}$ and $I_{(2;1)}$ (Appendix A).

The response of each population to nutrient enrichment is given by the partial derivative of the population with respect to nutrient input. The results show that the nutrient pool and the herbivore density are not affected by nutrient enrichment whereas the two plants have opposite responses: P_1 responds negatively and P_2 responds positively to nutrient enrichment (Leibold, 1996).

3. Feasibility and stability of a community with two plants and two generalist herbivores

In the previous section, we recalled the necessary and sufficient conditions allowing the feasibility and the stability of a food web R-P_1-P_2-H_1 with two plants P_i competing for the same resource R and sharing a consumer H_1. What happens if a herbivore H_2 preying upon the two plants invades this food web? If H_2 invades and settles, the food web R-P_1-P_2-H_1-H_2 (Fig. 2) will be significantly more complex than the initial one: in addition to indirect mutualism mediated by the two plants and the resource, the two herbivores will compete for two resources, P_1 and P_2, and the two plant species will face exploitative competition and apparent competition mediated by both H_1 and H_2. In this section we study (1) the feasibility and the stability of the R-P_1-P_2-H_1-H_2 food web and (2) how the food web can be assembled and the effects of a species' extinction.

In the following analysis, we assume as before that plant P_1 is the better resource exploiter and plant P_2 is more resistant to H_1 grazing. In the R-P_1-P_2-H_1-H_2 food web, the two generalist herbivores compete for two limiting resources. According to resource competition theory and assuming that the two resources are linearly substitutable, the herbivores can coexist only if they are not limited by the same resource (Tilman, 1982, p. 74). We assume in the following that H_1 is a better exploiter of plant P_1 than is H_2 and that H_2 is a better exploiter of plant P_2 than is H_1. In other words, H_1 decreases more than H_2 the equilibrium level of P_1 and H_2 decreases more than H_1 the equilibrium level of P_2. This condition translates mathematically as follows:

- H_1 is a better competitor for its resource P_1 than is H_2 ($P^*_{1(1;1)} < P^*_{1(1;2)}$) and H_2 is a better competitor for its resource P_2 than is H_1 ($P^*_{2(2;2)} < P^*_{2(2;1)}$) where $P^*_{i(i;j)} = d_j / a_{ij} b_{ij}$ is the equilibrium value of P_i in presence of herbivore H_j (Condition 4, Table 1).

(The alternative hypothesis where H_1 is a better exploiter of P_2 than H_2 and H_2 is a better exploiter of P_1 than H_1 simply leads to reverse the results of the following analysis.) Condition 4 is a necessary and sufficient condition to ensure positive equilibrium values for the resource R and the plants P_1 and P_2 (Appendix B). We show in the following paragraph that the feasibility of the R-P_1-P_2-H_1 food web is a necessary conditions for positive equilibrium values for the herbivores and, as a consequence, the feasibility of the R-P_1-P_2-H_1-H_2 food web.

Feasibility and stability conditions of the R-P_1-P_2-H_1 food web are given by the ZNGI analysis of the two plants in the (R-H_1) plane. The addition of herbivore H_2 leads to consider the Zero Net Growth Plane (ZNGP) of the plants in the (R, H_1, H_2) space (Fig. 3). The equations of the plant P_i's ZNGP in the (R, H_1, H_2) space is:

$$k_i l_i R^*_{(1,2;1,2)} - \sum_j a_{ij} H^*_{j(1,2;1,2)} - m_i = 0 \tag{2}$$

The intersection of the two ZNGPs is a line whose equation is:

$$H^*_{2(1,2;1,2)} = \frac{(m_1 k_2 l_2 - m_2 k_1 l_1) + H^*_{1(1,2;1,2)}(a_{11} k_2 l_2 - a_{21} k_1 l_1)}{(a_{22} k_1 l_1 - a_{12} k_2 l_2)} \tag{3}$$

We made the hypothesis that the R-P_1-P_2-H_1 food web is stable. Therefore, the P_1 ZNGP intersects the R-axis for a lower value than the P_2 ZNGP, and the plant ZNGPs cross in the (R, H_1) plane (conditions 1-3, Table 1). As a consequence, the two ZNGPs cross in the (R, H_1, H_2) positive orthant (Fig. 3), ensuring positive equilibrium values for H_1 and H_2. Thus the feasibility of the R-P_1-P_2-H_1 food web is a necessary condition for the feasibility of the R-P_1-P_2-H_1-H_2 food web.

The isoplane analysis of the R-P_1-P_2-H_1-H_2 food web leads to distinguish two cases depending on the relative resistance of the two plants to H_2 herbivory. Plant P_1 may be either less or more resistant to H_2 grazing than is P_2. In the first case, the plant ZNGPs cross in the (R, H_2) positive quadrant and the projection in the (H_1, H_2) plane of the intersection between these ZNGPs (Eq. 3) is a line whose slope is negative (Fig. 3a and b). In this case, the plants trade off abilities for resource exploitation and for resistance to both herbivores. Accordingly, we refer to this case as "food webs with two trade-offs". In the second case, the plant ZNGPs do not cross in the (R, H_2) positive quadrant and the projection in the (H_1, H_2) plane of the intersection between these ZNGPs (Eq. 3) is a line whose slope is positive (Fig. 3c and d). This implies that the plants trade off abilities for resource exploitation and for grazing resistance to herbivore H_1 but not to herbivore H_2. We refer to this case as "food webs with one trade-off". We analyse these two alternative food webs in the following sections.

3.1. Food webs with two trade-offs: P_2 is more resistant than P_1 to H_1 and H_2 herbivory

We analyse now the conditions insuring the feasibility and the stability of the R-P_1-P_2-H_1-H_2 food web in which plant P_2 is more resistant than P_1 to both H_1 and H_2 herbivory. This translates mathematically as follows:

- P_2 is more resistant to H_2 herbivory than P_1. Thus $k_1 l_1 / a_{12} < k_2 l_2 / a_{22}$, where $k_i l_i / a_{i2}$ is the slope of plant P_i's ZNGI in the (R, H_2) plane (Condition 5, Table 1).

As we show in Appendix B, necessary and sufficient conditions for the R-P_1-P_2-H_1-H_2 food web feasibility include, in addition to condition 4 and the feasibility of the R-P_1-P_2-H_1 system, that the external nutrient input is bounded ($I_{(1,2;1,2)} < I < I_{(1,2;2)}$) and that $a_{11}/a_{21} > a_{12}/a_{22}$ (Condition 6, Table 1). (We analyse below the alternative solution where $I_{(1,2;2)} < I < I_{(1,2;1,2)}$ and $a_{11}/a_{21} < a_{12}/a_{22}$ and show that it insures feasibility of the food web but precludes its stability.) If $I < I_{(1,2;1,2)}$, the system is not enough productive to support herbivore H_2. If $I \geq I_{(1,2;2)}$, herbivore H_1 is competitively excluded by herbivore H_2 because the most profitable resource for herbivore H_2, i.e. plant P_2, is favoured by high nutrient inputs to the detriment of the most profitable resource for herbivore H_1, i.e. plant P_1 (see below the effects of nutrient enrichment). Therefore, the two herbivores may coexist in the community only if the external nutrient input is bounded. The consumption rate a_{ij} is the denominator of the slope of plant P_i's ZNGI in the (R, H_j) plane. In the graphical analysis, condition 6 ($a_{11}/a_{21} > a_{12}/a_{22}$) means that the ZNGI of plant P_1 should be steeper in the (R, H_2) plane than in the (R, H_1) plane and the ZNGI of plant P_2 should be shallower in the (R, H_2) plane than in the (R, H_1) plane (Fig. 4a). As a consequence, the projection of the intersection between the plant ZNGPs in the positive quadrant of the (R, H_2) plane has a positive slope (Fig. 4a). This implies that (1) $R^*_{(1,2;1)}$, the equilibrium value of the resource in the R-P_1-P_2-H_1 community, is lower than $R^*_{(1,2;2)}$, the equilibrium value of the resource in the R-P_1-P_2-H_2 community, and (2) $R^*_{(1,2;1,2)}$, the equilibrium value of the resource in the R-P_1-P_2-H_1-H_2 community is intermediate between $R^*_{(1,2;1)}$ and $R^*_{(1,2;2)}$ (Fig. 4a). (In the case where $a_{11}/a_{21} < a_{12}/a_{22}$, the direction of the intersection between the plant ZNGPs is opposite, i.e., its projection in the positive quadrant of the (R, H_2) plane has a negative slope [Fig. 4c]. The condition $a_{11}/a_{21} < a_{12}/a_{22}$ implies that $R^*_{(1,2;2)} < R^*_{(1,2;1,2)} < R^*_{(1,2;1)}$.) We show below the consequences of condition 6 for food-web stability.

Stability conditions are determined by the impact vectors of the plants in the (R, H_1, H_2) space and the supply point. Impact vectors should show a larger effect of the plants on the factor that most limits their growth and the supply points should lie in the appropriate region delimited by the projection of the impact vectors. However, comparing vectors in a 3-dimensional space is tricky. For that reason, we decompose the analysis by comparing the components of the impact vectors in planes that cross the intersection between the plant ZNGPs and are parallel to the reference planes (R, H_1), (R, H_2) and (H_1, H_2). The stability of the R-P_1-P_2-H_1-H_2 food web is then insured if the stability conditions are met in the three planes.

The intersection of the planes parallel to the (R, H_1) and (R, H_2) planes with the plant ZNGPs appears as in Fig. 1. In the plane parallel to the (R, H_1) plane, the impact vector of P_1 is steeper than the impact vector of P_2 (Condition 3, Table 1). Thus the necessary condition to insure stability is fulfilled in the plane parallel to the (R, H_1) plane. In the plane parallel to the (R, H_2) plane, the impact vector of P_1 should be steeper than the impact vector of P_2 to insure stability. This condition translates as follows:

- The impact vector of P_1 is steeper than the impact vector of P_2 in the (R, H_2) plane. Thus $C_{P_1(H_2)} > C_{P_2(H_2)}$, with $C_{P_i(H_2)} = a_{i2}b_{i2}/k_i$ (Condition 7, Table 1).

Condition 7 implies that the R-P_1-P_2-H_2 food web should be stable to insure the stability of the R-P_1-P_2-H_1-H_2 food web.

In the plane parallel to the (H_1, H_2) plane (Fig. 4b, d), the impact vector C_{P_i} of plant P_i is the ratio of the effect of P_i on H_1 to the effect of P_i on H_2 ($C_{P_i} = a_{i1}b_{i1}/a_{i2}b_{i2}$). However, condition 4 ($a_{11}b_{11}/a_{12}b_{12} > a_{21}b_{21}/a_{22}b_{22}$, Table 1) implies that $C_{P_1} > C_{P_2}$. In the isoplane analysis, the condition $C_{P_1} > C_{P_2}$ insures food-web stability in the plane parallel to the (H_1, H_2) plane only if $a_{11}/a_{21} > a_{12}/a_{22}$ (Fig. 4a), and not if $a_{11}/a_{21} < a_{12}/a_{22}$ (Fig. 4d). In conclusion, the R-P_1-P_2-H_1-H_2 food web in which the plants trade off competitive ability and resistance to the two herbivores has a stable equilibrium if conditions 1 to 7 (Table 1) are met and if the nutrient input is bounded ($I_{(1,2;1,2)} < I < I_{(1,2;2)}$). This implies that $R^*_{(1,2;1)} < R^*_{(1,2;1,2)} < R^*_{(1,2;2)}$.

In the R-P_1-P_2-H_1-H_2 food web with two trade-offs, nutrient enrichment has no effect on the plants' equilibrium values and has a positive effect on the resource pool equilibrium value (Fig. 5a, Appendix B). The effects of nutrient enrichment on the equilibrium values of the two herbivores are opposite: $H^*_{2(1,2;1,2)}$ increases and $H^*_{1(1,2;1,2)}$ decreases. The response of the herbivore level, i.e. ($H^*_{1(1,2;1,2)} + H^*_{2(1,2;1,2)}$) is undetermined (Appendix B). For $I \geq I_{(1,2;2)}$,

H_1 is excluded and the response of the food web R-P_1-P_2-H_2 to nutrient enrichment is similar to the response of the food web R-P_1-P_2-H_1: $P^*_{1(1,2;2)}$ decreases, $P^*_{2(1,2;2)}$ increases and $R^*_{(1,2;2)}$ and $H^*_{2(1,2;2)}$ do not respond to nutrient enrichment. For $I \geq I_{(2;2)}$, ($I_{(2;2)} = R^*_{(1,2;2)}\left[(\beta + a_{22}b_{22}q + k_2 d_2)/(a_{22}b_{22})\right]$ with $R^*_{(1,2;2)} = (a_{12}m_2 - a_{22}m_1)/\gamma$, β and γ values in Table 1), plant P_1 is excluded and the response of the remaining system R-P_2-H_2 to nutrient enrichment is the classical food chain response.

3.2. Food webs with one trade-off: P_2 is more resistant than P_1 to H_1 herbivory only

In the alternative case where P_2 is less resistant than P_1 to H_2 predation, the slope of the P_2 ZNGI is shallower than the slope of the P_1 ZNGI in the (R, H_2) plane ($k_2 l_2/a_{22} < k_1 l_1/a_{12}$, condition 5', Table 1). Condition 5' is opposite to condition 5 defined above. Consequently, the intersection between the plant ZNGPs (Eq. 3) has a positive slope (Conditions 2 and 5'; Fig. 3c). The feasibility of this R-P_1-P_2-H_1-H_2 food web is insured if conditions 1-5'-6-7 are satisfied and if the external nutrient input exceeds a threshold level $I_{(1,2;1,2)}$ (Appendix B).

The stability analysis of the system with one trade-off follows that of the food web with two trade-offs: the impact vectors of the plants should show a larger effect on the factor that most limits their growth in planes parallel to the (R, H_1), (R, H_2) and (H_1, H_2) planes and crossing the intersection between the plant ZNGPs. Therefore, the conditions that insure stability are (1) plant P_1 has a stronger effect on herbivore H_j than on the resource pool and plant P_2 has a stronger impact on the resource pool R than on herbivore H_j, and (2) the plants should have a greater relative impact on the herbivore that most limits their growth (Fig. 4f). The first criterion satisfies stability conditions in the planes parallel to the (R, H_1) and (R, H_2) planes and corresponds to conditions 3 and 7 (Table 1). Condition 7 in the food web with one trade-off means that plant P_1 is more resistant to H_2 but has a greater impact on H_2 growth rate than does its competitor P_2. Only this asymmetry in interactions insures food-web stability. The second criterion implies that condition 4 (Table 1) is met, as in the food web with two trade-offs. In conclusion, the necessary and sufficient conditions for the stability of the R-P_1-P_2-H_1-H_2 food web are met in the planes parallel to the (R, H_1), (R, H_2) and (H_1, H_2) planes if conditions 3, 7 and 4 (Table 1) are met.

Nutrient enrichment has no effects on plant equilibrium values and a positive effect on the resource pool. In contrast with the food web with two trade-offs, nutrient enrichment has a positive effect on the two herbivore equilibrium values and on the herbivore level ($H^*_{1(1,2;1,2)}$ + $H^*_{2(1,2;1,2)}$) (Appendix B, Fig. 5b).

3.3. Assembly rules for the R-P_1-P_2-H_1-H_2 food webs and cascades of extinctions

We have defined the conditions for the feasibility and stability of the two alternative R-P_1-P_2-H_1-H_2 food webs. But how can such food webs be assembled? What are the sequences of species invasions that lead to these food webs? We first analyse the order of species invasions in the food web where the plants trade off nutrient exploitation and grazing resistance to herbivore H_1 only. In this case, the food web R-P_1-P_2-H_1 is invaded by herbivore H_2, leading to the stable R-P_1-P_2-H_1-H_2 food web, if conditions 1-5'-6-7 defined above are met. Because the plants do not trade off nutrient exploitation and grazing resistance to herbivore H_2, the food web R-P_1-P_2-H_2 does not exist and the herbivore H_1 cannot invade it. Therefore the order of assemblage is P_1, H_1, P_2 and H_2. In the alternative food web where the plants trade off nutrient exploitation and grazing resistance with the two herbivores, herbivore H_2 can invade the food web R-P_1-P_2-H_1 because this is stable. Herbivore H_1 can also invade the food web R-P_1-P_2-H_2: because the plants trade off nutrient exploitation and grazing resistance to herbivore H_2, the food web R-P_1-P_2-H_2 is stable and may be invaded. For values of external nutrient input close to $I_{(1,2;1,2)}$, herbivore H_1 almost displaces herbivore H_2 but the two herbivores coexist in the R-P_1-P_2-H_1-H_2 food web (Fig. 5a). In conclusion, the order of species invasion to assemble the two alternative R-P_1-P_2-H_1-H_2 food webs depends on the relative strength of species interactions within the food webs.

What happens if one of the species belonging to the R-P_1-P_2-H_1-H_2 food webs gets extinct? If one of the plants gets extinct, it will be followed by the extinction of the worse consumer of the remaining plant. If herbivore H_1 gets extinct and the plants trade off competitive ability and resistance to H_2 grazing, we predict no further extinction. But if the plants do not trade off competitive ability and resistance to H_2 grazing, the extinction of H_1 will be followed by the extinction of P_2: P_2 is excluded by P_1, which is the better nutrient exploiter and is more resistant to H_2 grazing. If H_2 gets extinct, the R-P_1-P_2-H_1 food web will suffer no secondary extinction.

In summary, we show that two generalist herbivores preying upon two plants competing for a limiting nutrient may form two qualitatively different food webs. The plants may trade off nutrient exploitation and grazing resistance either with the two herbivores (two trade-offs) or with only one herbivore (one trade-off). These two alternative food webs are feasible and stable if (1) each herbivore is a better exploiter of one of the two plants, (2) the external nutrient input is bounded for the food web with two trade-offs or higher than a threshold for the food web with one trade-off, and (3) the plants have a greater relative impact on the factor that most limits their growth. These two food webs differ qualitatively in their assembly rules, response to nutrient enrichment and susceptibility to secondary extinction.

4. Addition of a third trophic level

In this section we consider nutrient-based food webs with three trophic levels. We analyse the feasibility and stability of food webs with two plants and (1) one generalist herbivore and one carnivore, (2) two generalist herbivores and one specialist carnivore, or (3) two generalist herbivores and two generalist carnivores. We briefly mention food webs with two plants, two generalist herbivores and one generalist carnivore. Whenever these food webs are stable, we study their assembly rules, the effects of species extinction and of nutrient enrichment.

4.1. Communities with one generalist herbivore and one carnivore C_1

We consider now the food web R-P_1-P_2-H_1-C_{1S} where H_1 is a generalist herbivore and the carnivore C_{1S} preys upon H_1 (Fig. 6). Grover (1997, p. 160) showed that the community R-P_1-P_2-H_{1S}-C_{1S}, where the herbivore is a specialist, is not feasible. Either C_{1S} or P_2 is excluded. The reason is that the carnivore C_{1S} releases the plant P_1 from control by herbivore H_{1S}. Consequently plants $P_1$and P_2 are in competition for the resource and one or the other top-consumer of a food chain (C_{1S} or P_2) is excluded. This indirect interaction between the top-consumers of food chains limited by the same resource was called cascade competition by Grover (1997, p. 160). The question we ask here is whether this result is qualitatively changed if the herbivore H_1 is a generalist preying upon the plants P_1 and P_2.

The calculation of the equilibrium values in the food web where H_1 is a generalist herbivore shows that the community is not feasible: the resource equilibrium value $R^*_{(1,2;1;1)}$ should be equal to both $R^*_{(1;1;1)}$ and $R^*_{(2;1;1)}$. In other words, at the equilibrium, the two trophic chains R-P_1-H_1-C_{1S} and R-P_2-H_1-C_{1S} should equally depress the resource level, which is infinitely unlikely. Therefore a food web with two plants competing for a limiting resource, a herbivore and a carnivore, whatever the diet of the herbivore, is not feasible. In terms of assembly rules, this result means that the invasion of a three-trophic-level food chain R-P_1-H_1-C_{1S} by a plant P_2, or the invasion by a carnivore C_{1S} of a R-P_1-P_2-H_1 food web with P_1 and P_2 competing for a limiting resource and sharing a herbivore will lead either to the failure of the invasion or to the extinction of a species belonging to the community.

4.2. Communities with two generalist herbivores and a specialist carnivore C_{ZS}

We now consider the communities with two generalist herbivores and a specialist carnivore that preys either upon H_1 or H_2. Grover (1997, p. 160) showed that a community with R-P_1-P_2-H_{1S}-H_{2S}-C_{zS}, where all consumers are specialists (Fig. 7a, b), is feasible. In this section, we study the food webs R-P_1-P_2-H_1-H_2-C_{zS} (Fig. 7c and 7d), where the herbivores are generalists. Because of many interactions of unequal strength, the communities where a specialist carnivore C_{zS} preys either upon H_1 or upon H_2 are not simple symmetric cases. We analyse in the following these two alternative food webs.

First we make the hypothesis in the following that the carnivore C_{zS} invades the R-P_1-P_2-H_1-H_2 food web (Fig. 7c-d). Therefore the conditions insuring the stability of the R-P_1-P_2-H_1-H_2 food webs and defined above (conditions 1-5'-6-7 or conditions 1-7, Table 1) are met. Other sequences of invasion are possible and we analyse them below. To study the feasibility and the stability of the R-P_1-P_2-H_1-H_2-C_{zS} food web, we conduct a graphical analysis of the ZNGP of the two herbivores in the (P_1, P_2, C_{zS}) space. The equation of herbivore H_j's ZNGP in the (P_1, P_2, C_{zS}) space is:

$$\sum_i a_{ij} b_{ij} P_i^* - d_j - e_{jz} C_{zS}^* = 0 \tag{4}$$

Depending on the slopes of the herbivore ZNGPs in the (P_1, P_2, C_{zS}) space and their intersections with the axes, four alternative cases arise. If one of the two herbivores is a better exploiter of the two plants, either the carnivore C_{1S} preys upon the worse grazer and the herbivore ZNGPs do not cross in the positive (P_1, P_2, C_{zS}) orthant (Fig. 8a, b), or the carnivore C_{1S} preys upon the better grazer, and the herbivore ZNGPs do cross in the positive (P_1, P_2, C_{zS}) orthant (Fig. 8c, d). Nevertheless, in both cases, the herbivore ZNGPs do not cross in the (P_1, P_2) plane and the R-P_1-P_2-H_1-H_2 food web is not feasible (Fig. 8a-d). As a consequence, a carnivore cannot invade it. However, the latter case suggests that the R-P_1-P_2-H_1-H_2-C_{zS} food web is feasible despite the unfeasibility of the R-P_1-P_2-H_1-H_2 food web (Fig. 8c, d). The last two alternative cases correspond to the situations where the herbivore ZNGPs do cross in the (P_1, P_2) plane (Fig. 8e-h), which implies that the R-P_1-P_2-H_1-H_2-C_{zS} food web is feasible. The carnivore may control either herbivore H_1, which is the better exploiter of the most competitive plant P_1 (Fig. 8e, f) or herbivore H_2, which is the better exploiter of the least competitive plant P_2 (Fig. 8g, h). Theses two cases correspond to the food webs with a carnivore C_{1S} or C_{2S}, respectively, as depicted in the Fig. 7c and 7d. We study the stability of these two food webs in the following section.

4.2.1. *Communities with a specialist carnivore* C_{1S}

The analysis of the dynamical system (Appendix C) shows that the external nutrient input should be bounded to ensure positive equilibrium values for the plants and the specialist carnivore ($I' < I < I''$ with $I' = (a_{12}b_{12}q + k_1 d_2)R^*_{(1,2;1,2;1S)}/a_{12}b_{12}$ and $I'' = (a_{22}b_{22}q + k_2 d_2)R^*_{(1,2;1,2;1S)}/a_{22}b_{22}$). The equilibrium value of herbivore H_1, $H^*_{1(1,2;1,2;1S)}$, is always positive but the equilibrium values of the resource pool, $R^*_{(1,2;1,2;1S)}$, and of herbivore H_2, $H^*_{2(1,2;1,2;1S)}$, depend on the properties of the food web without the carnivore. If the plants trade off nutrient exploitation and resistance to grazing by the two herbivores in the R-P_1-P_2-H_1-H_2 food web (Condition 5, Table 1), $R^*_{(1,2;1,2;1S)}$ and $H^*_{2(1,2;1,2;1S)}$ are both positive if $H^*_{1(1;1;1)} < H^*_{1(1,2;1)}$ with $H^*_{1(1,2;1,2;1S)} = H^*_{1(1;1;1)} = H^*_{1(2;1;1)}$ (Appendix C). The feasibility condition $H^*_{1(1;1;1)} < H^*_{1(1,2;1)}$ depends on the equilibrium values of H_1 in food webs without H_2 and reads as follows: the equilibrium value of H_1 in the food chain R-P_1-H_1-C_1 should be smaller than that in the food web R-P_1-P_2-H_1 where it is a keystone herbivore. In other words, if the carnivore C_1 is very efficient in its prey exploitation, it decreases the equilibrium value of H_1 to a level $H^*_{1(1;1;1)}$ inferior to the value $H^*_{1(1,2;1)}$ necessary to insure the keystone role of the herbivore in the R-P_1-P_2-H_1 food web. Therefore, to be feasible, the R-P_1-P_2-H_1-H_2 food web with two trade-offs should be invaded by a very efficient specialist carnivore preying upon H_1. This efficiency leads to suppress the keystone role of herbivore H_1. However, the R-P_1-P_2-H_1-H_2-C_{1S} food web is still feasible: it relies on the R-P_1-P_2-H_2 sub-system in which H_2 is a keystone herbivore. Conversely, if the plants trade off nutrient exploitation and resistance to grazing by herbivore H_1 only in the R-P_1-P_2-H_1-H_2 food web (Condition 5', Table 1), $R^*_{(1,2;1,2;1S)}$ and H^*_2 are both positive if $H^*_{1(1;1;1)} > H^*_{1(1,2;1)}$ (Appendix C). The feasibility condition implies that, in the R-P_1-P_2-H_1-H_2-C_{1S} food web where the herbivore H_2 is not a keystone herbivore, this function is still insured by herbivore H_1 even if carnivore C_1 controls it. This feasibility condition requires that the specialist carnivore is not too efficient in its prey exploitation. In conclusion, the feasibility of the R-P_1-P_2-H_1-H_2-C_{1S} food web depends on the efficiency on the specialist carnivore and the structure of the food web without the carnivore: either the carnivore is very efficient and it may invade food webs with two trade-offs, or it is poorly efficient and it may invade food webs with one trade-off only.

The stability analysis is performed by the analysis of the herbivore impact vectors in the (P_1, P_2, C_{1S}) space. As in the food webs without carnivore (previous section), we compare the components of the impact vectors in planes parallel to the reference planes (P_1, P_2), (P_1, C_1) and (P_2, C_1) and crossing the intersection between the herbivore ZNGPs. The stability of the R-P_1-P_2-H_1-H_2-C_{1S} food web is insured if stability conditions in the three planes are fulfilled. In the plane parallel to the (P_1, P_2) plane, the impact vector of herbivore H_j is $C_{H_j} = a_{1j}/a_{2j}$. The necessary condition to insure stability is $C_{H_1} > C_{H_2}$ (Fig. 9a) and corresponds to Condition 7 (Table 1). In the planes parallel to the (P_i, C_1) planes, the impact vector of herbivore H_j is $C_{H_j} = e_{j1} f_{j1} / a_{ij}$. Because the carnivore does not prey upon herbivore H_2, the vertical component of its impact vector is zero, implying that $C_{H1} > C_{H2}$ (Fig. 9b, c). Consequently, H_1 has a greater impact on the factor that most limits its growth (C_{1S} predation) and the conditions insuring stability are met in the planes parallel to the (P_1, C_1) and (P_2, C_1) planes (Fig. 9b, c). In conclusion, the R-P_1-P_2-H_1-H_2-C_{1S} food web is stable if conditions 1-7 or 1-5'-7 are met.

The analysis of the effects of nutrient enrichment reveals interesting results (Appendix C). The resource pool and the two herbivores do not respond to nutrient enrichment (Table 2), P_2^* responds positively, and P_1^* and C_{1S}^* respond negatively to nutrient enrichment. A negative response of the top carnivore to nutrient enrichment means that it settles with a high abundance in a community with a low nutrient status (i.e. closed to the threshold level I' allowing C_1 invasion) and with a low abundance in a community with a high nutrient status (i.e. closed to the threshold level I'' beyong which C_1 is excluded). In the R-P_1-P_2-H_1-H_2-C_{1S} food web, plant P_2 drives the dynamics of the food web at the expense of P_1 and C_{1S}, which echoed the response of P_1. The effect of nutrient enrichment on total plant biomass depends on the relative net growth rates of H_2 due to the two plants (Appendix B). Either total plant biomass increases with nutrient enrichment if the effect of P_1 on the net growth rate of H_2 is higher than that of P_2 ($a_{12}b_{12} > a_{22}b_{22}$), or it decreases in the opposite case ($a_{12}b_{12} < a_{22}b_{22}$).

The R-P_1-P_2-H_1-H_2-C_{1S} food web can be assembled from the invasion of the R-P_1-P_2-H_1-H_2 food web with two trade-offs by the specialist carnivore C_{1S}. We explore now other sequences of invasions to assemble the food web. First, the herbivore H_2 may invade the food web R-P_1-P_2-H_1-C_{1S} but, as showed previously, this food web is not feasible. Therefore this assembly sequence is not possible. Plant P_1 may also invade the food web R-P_2-H_1-H_2-C_{1S}, or plant P_2 may invade the food web R-P_1-H_1-H_2-C_{1S}. The invasion of plant P_1 does not raise any problem. However the food web R-P_2-H_1-H_2-C_{1S} is not feasible because the carnivore controls H_1, the worse exploiter of plant P_2. Therefore this invasion sequence is also impossible. Possible invasion sequences to assemble the R-P_1-P_2-H_1-H_2-C_{1S} food web are either P_1, H_1, P_2, H_2 and C_{1S}, or P_1, H_1, C_{1S}, H_2 and P_2. In addition, in the food web with two trade-offs, the sequence relying on the keystone herbivore H_2 (P_1, H_2, P_2, H_1 and C_{1S}) is also possible. What happens then if a species gets extinct? If plant P_1 gets extinct, the better and the worse exploiters of the other plant P_2 remain, the latter herbivore supporting the specialist carnivore. As a consequence, we expect the extinction of herbivore H_1 and carnivore C_{1S}. If plant P_2 gets extinct, plant P_1 supports two herbivores, the better exploiter H_1 being controlled by the carnivore. Therefore we expect no secondary extinction. If herbivore H_1 gets extinct, its specialist predator also gets extinct. If the plants trade off competitive ability and resistance to predation by the two herbivores, the remaining sub-system R-P_1-P_2-H_2 will suffer no further extinction. Otherwise, plant P_2 gets extinct. If herbivore H_2 gets extinct, either one of the plants or the carnivore disappears: because of cascade competition the remaining food web R-P_1-P_2-H_1-C_{1S} is not feasible. Finally, if carnivore C_{1S} gets extinct, there should be no further extinction because the R-P_1-P_2-H_1-H_2 food web is feasible and stable (see Table 3 for a summary).

4.2.2. *Communities with a specialist carnivore* C_{2S}

In this section we analyse the R-P_1-P_2-H_1-H_2-C_{2S} food web where the carnivore C_{2S} preys upon the herbivore, H_2, that is the better exploiter of the less competitive plant P_2 (Fig. 8g, h, Fig. 10a). Because of the asymmetry of interaction strengths within the food web, we address the question whether the invasion of carnivore C_{2S}, preying on H_2, would require the same conditions as the invasion by C_{1S} preying upon H_1. The feasibility analysis (Appendix C) shows that the external resource input should be bounded to ensure positive equilibrium values for P_1, P_2 and C_{2S}. $H^*_{2(1,2;1,2;2S)}$ and $R^*_{(1,2;1,2;2S)}$ equilibrium values are always positive. The equilibrium value of H_1 is positive only if $H^*_{2(1;2;2)} < H^*_{2(1,2;2)}$ with $H^*_{2(1,2;1,2;2S)} = H^*_{2(1;2;2)} = H^*_{2(2;2;2)}$ and $\gamma > 0$ (Appendix C). This condition implies that the plants trade off competitive ability and resistance to the two herbivores and that the carnivore is efficient enough to decrease the equilibrium value of its prey below the level allowing the herbivore H_2 to play its keystone role. Therefore, in contrast to the food web with a carnivore C_{1S} preying upon H_1, the feasibility of the R-P_1-P_2-H_1-H_2-C_{2S} food web requires that plants always trade off competitive ability and resistance to the two herbivores. The stability analysis of the R-P_1-P_2-H_1-H_2-C_{2S} food web is analogous to that of the food web with C_{1S}. In the plane parallel to the (P_1, P_2) plane, the two herbivores have a greater impact on the plant that most limits their growth if condition 7 is satisfied ($C_{H_1} > C_{H_2}$ with $C_{H_j} = a_{1j}/a_{2j}$, Fig. 10b). In the plane parallel to the (P_1, C_{2S}) and (P_2, C_{2S}) planes, herbivore H_1 has no effect on C_{2S}, implying that $C_{H_2} > C_{H_1}$ (Fig. 10c, d). Thus the R-P_1-P_2-H_1-H_2-C_{2S} food web is stable if condition 7 is satisfied. Nutrient enrichment has no effect on the resource pool and the two herbivores. The response to nutrient enrichment of plants and the specialist carnivore differs from the community with C_{1S}: P_1^* responds negatively and P_2^* and C_{2S}^* respond positively (Table 2). However, similarly to the R-P_1-P_2-H_1-H_2-C_{1S} food web, the effect of nutrient enrichment on total plant biomass depends on the relative effects of the plants on the growth rate of the unconsumed herbivore H_1. If the effect of P_1 on the net growth rate of H_1 is higher than that of P_2 ($a_{11}b_{11} > a_{21}b_{21}$), total plant biomass increases with nutrient enrichment; in the opposite case ($a_{11}b_{11} < a_{21}b_{21}$), it decreases.

The R-P_1-P_2-H_1-H_2-C_{2S} food web may result from the invasion of the R-P_1-P_2-H_1-H_2 food web with two trade-offs by the specialist carnivore C_{2S} (invasion sequences P_1, H_1, P_2,

H_2 and C_{2S} or P_1, H_2, P_2, H_1 and C_{2S}) but also from the invasion sequence P_2, H_2, C_{2S}, H_1 and P_1. What can we expect after a species extinction? If plant P_1 or carnivore C_{2S} gets extinct, the remaining food web is feasible and stable and we expect no further extinction. If plant P_2, herbivore H_1 or herbivore H_2 gets extinct, secondary extinctions will follow. In the first case, herbivore H_2 and carnivore C_{2S}, supported by P_2, will get extinct. In the second case, because of cascade competition and the absence of a trade-off in plants mediated by H_2, either P_1, P_2, or C_{2S} will get extinct. In the third case, extinction of H_2 will be followed by that of its specialist predator C_{2S} (see Table 3 for a summary).

In conclusion, because of the asymmetry of interaction strengths in the food webs, the addition of a specialist carnivore leads to two contrasting food webs depending on whether it is supported by the herbivore that is a better or worse exploiter of the more competitive plant. The food webs differ by the plants' trade-off between competitive ability and resistance to herbivory: either they trade off resistance with the two herbivores or with only one herbivore. These qualitative differences have consequences in terms of assembly rules and risks of secondary extinctions after a primary extinction.

4.3. Communities with two herbivores and a generalist carnivore C_1

We may now ask whether a food web with a generalist top carnivore is feasible. The food web with two generalist herbivores and a generalist carnivore is the general case of the food webs with one specialist carnivore C_{ZS}. Again, we analyse graphically the herbivore ZNGPs in the (P_1, P_2, C_1) space (Fig. 11). The equation for the ZNGP of herbivore H_j is:

$$\sum_i a_{ij} b_{ij} P_i^* - d_j - e_{jz} C_z^* = 0 \qquad (5)$$

Four situations arise regarding how these planes cross. In the first case, the two herbivores trade off plant exploitation and resistance to predation (Fig. 11a: H_2 is a better exploiter of the plants and H_1 is more resistant to predation; the food web with H_1 as a better exploiter of plants and H_2 more resistant to predation is not represented). These food webs are *a priori* feasible although they may not result from the invasion of C_1 in the R-P_1-P_2-H_1-H_2 food web where each herbivore should be a better exploiter of one of the two plants.

In the second case (Fig. 11b), each herbivore is a better exploiter of one or both plants but herbivores do not trade off predation resistance and competitive ability. In the graphical analysis, the ZNGIs of H_1 and H_2 do not cross in the (P_1, C_1) and (P_2, C_1) planes. This is possible only if the herbivores have the same resistance to C_1. This situation is highly unlikely. The third case (Fig. 11c) is characterised by the existence of a trade-off between plant exploitation and resistance to predation in only one of the two R-P_i-H_1-H_2-C_1 (with i = 1, 2) sub-food webs. For instance, in the R-P_1-H_1-H_2-C_1 sub-food web, H_1 is a better exploiter of P_1 and H_2 is more resistant to predation by C_1 (Fig. 11c; the alternative case where H_2 is a better exploiter of P_1 and H_1 is a more resistant to predation by C_1 is not represented). The two food webs, which differ by the herbivore trade-off in the R-P_i-H_1-H_2-C_1 sub-food web, can result from the invasion of the R-P_1-P_2-H_1-H_2 community by the generalist carnivore C_1. The fourth case where there is a trade-off between competition and resistance to predation in the two R-P_i-H_1-H_2-C_1 (with i = 1, 2) food webs is not possible because the two herbivore ZNGPs could no longer be planes with the following constraints (Fig. 11d): each herbivore is a better competitor for one plant (their isoclines cross in the [P_1, P_2] plane) and the herbivores trade off competitive ability and resistance to predation in the two sub-food webs R-P_i-H_1-H_2-C_1 (with i = 1, 2) (their isoclines cross in the [P_1, C_1] and [P_2, C_1] planes).

We provide equilibrium values of the variables in Appendix C. However, because of the complexity of the food web and the high number of possible alternative cases, we do not further analyse the feasibility and stability conditions of the food web with a generalist carnivore.

4.4. Communities with two herbivores and two carnivores C_1 *and* C_2

Grover (1997, p. 160) showed that a food web with two specialist herbivores and two specialist carnivores is not feasible because of cascade competition between the two carnivores. We extend here this conclusion to food webs with generalist consumers. In the *R*-P_1-P_2-H_1-H_2-C_1-C_2 food web, the equilibrium value of the resource $R^*_{(1,2;1,2;1,2)}$ should satisfy two values (Appendix C, equations C12 and C13), which is infinitely unlikely. Because of cascade competition between the two carnivores, the P_1-P_2-H_1-H_2-C_1-C_2 food web is not feasible.

5. Discussion

While conditions to assemble nutrient-based food webs with two plants and one generalist herbivore have been described before (Holt et al., 1994; Leibold, 1996; Grover, 1997; Chase et al., 2000), here we have extended this body of theory considerably by analysing the feasibility, stability and assembly rules of nutrient-based food webs with up to three trophic levels and two species per trophic level. Our analysis shows the following:
(1) The addition of a generalist herbivore to a food web with two plants competing for a limiting resource and sharing a generalist herbivore does not necessarily require that the plants' nutrient exploitation ability trades off with resistance to predation by the second herbivore.
(2) Nutrient-based food webs with either two plants, one generalist herbivore and a carnivore or two plants, two generalist herbivores and two generalist carnivores are not feasible. Cascade competition (Grover 1997, p. 160) between the carnivore and the less competitive plant in the former food web and between the two carnivores in the latter food web prevents the feasibility of the food webs.

(3) Nutrient-based food webs with two plants, two generalist herbivores and a specialist carnivore are feasible and stable under certain conditions. If the carnivore preys upon the herbivore that is the better exploiter of the more competitive plant, either the plants must trade off competitive ability and resistance to the two herbivores and the carnivore should be very efficient, or the plants must trade off competitive ability and resistance to one herbivore only and the carnivore should be poorly efficient. If the carnivore preys upon the herbivore that is the worse exploiter of the more competitive plant, the plants must trade off competitive ability and resistance to the two herbivores.

(4) Nutrient enrichment is a necessary condition to allow species invasion in some food webs, but it may lead to species exclusion in others. In particular, in the food webs with a specialist carnivore, nutrient enrichment may lead to its exclusion.

Our analysis shows that nutrient enrichment has different effects on species diversity depending on the structure and relative strength of species interactions in food webs. The importance of heterogeneity (i.e. different species) within trophic levels was first showed by Abrams (1993). Later, Leibold (1996) showed that, in food webs with two plants and one keystone herbivore, nutrient enrichment leads to species replacement within the plant trophic level and maintains constant species diversity in the community. In food webs with two generalist herbivores, species replacement is observed within the herbivore trophic level if plants trade off competitive ability and resistance to the two herbivores. Otherwise, nutrient enrichment leads to an increase in species diversity, without species replacement, within the trophic level of herbivores. The effect of nutrient enrichment on herbivore biomass is positive in food webs with one trade-off and undetermined in food webs with two trade-offs. Therefore, in these two-trophic-level food webs, the relative strength of species interactions is the key factor governing the response to nutrient enrichment. When a specialist carnivore preying upon one or the other herbivore is added, the effect of nutrient enrichment on the third trophic level depends on the structure of the food web. If the carnivore preys upon the better exploiter of the more competitive plant, nutrient enrichment has a negative effect on the third trophic level; on the contrary, if the carnivore preys upon the worse exploiter of the more competitive plant, nutrient enrichment has a positive effect on the carnivore level. If we consider the plant trophic level, the effects of nutrient enrichment are undetermined and depend on the relative interaction strengths of the plants with the unconsumed herbivore. Therefore, nutrient enrichment has contrasting effects on the first and third trophic levels depending on relative interaction strengths and food-web structure, respectively. The effect of nutrient enrichment on the top trophic level gives the potential for matter flow extension with an addition of a supplementary trophic level: if the biomass of the top trophic level is high enough to support a consumer, matter flow may lengthen with the addition of a trophic level. We show mechanistically here how this potential hinges upon food-web structure and how it may explain contradictory results observed in experimental communities (see for instance Hulot et al., 2000; Post, 2002).

In the present analysis, we have defined conditions for new species to invade existing communities and form new communities with the species initially present. These conditions provide values that life-history parameters combined with the nutrient status of the community should or should not exceed. Thus several species might candidate for a place in the community as far as their parameters do not cross these bounds. Because the species already present in the community constrain the range of parameters allowing a successful species invasion, the order of invasion and the history of the community are of great importance (Drake, 1991; Drake et al., 1993; Grover, 1997). For instance, a carnivore can settle in a two-trophic-level food web only if the primary producers are controlled by herbivores. If the community is formed by two plants and two generalist herbivores, the success of invasion of a specialist carnivore will depend on its diet (identity of the prey and predation efficiency) and on whether the plants trade off competitive ability and resistance to one or two herbivores. If a species reaches a community while its parameters do not allow the feasability and the stability of the final community, the invasion fails. Our analysis shows how the assembly and the structure of simple food webs depend on the history of community organization and resource availability.

The analysis also shows how the structure of a community brings about cascades of extinctions. The extinction of a prey leads to the extinction of its predator, and the extinction of a keystone consumer leads to the extinction of the worse competitor(s) among its prey (Paine, 1966). However, in addition to the collapse of an arch, the extinction of a keystone species may also lead to the collapse of a neighbouring building. The reason is that the neighbouring building may be supported by indirect interactions mediated by the keystone species and be unfeasible if alone. This situation is illustrated by food webs with two plants, two generalist herbivores and a specialist carnivore. If the unconsumed herbivore gets extinct, whether it is a keystone species or not, cascade competition is not impeded anymore and leads to further extinctions. Therefore, a keystone species is not only a predator that directly mediates the coexistence of its competing prey but it is also a species whose presence counteract indirect effects that propagate within the food web and may induce species exclusion.

Assembly rules (Drake et al., 1999)show that both competition and predation are important in shaping communities. Recent experiments conducted in microcosms have showed that the R^* rule and other rules defined for simple systems (one resource, two prey species and a consumer) could match experimental results (Kraaijeveld et al., 1997; Bohannan et al., 1999; Bohannan et al., 2000; Fox, 2002). However, these rules and the ones derived in this paper hinge on two important assumptions: a homogeneous environment and equilibrium conditions (a new community emerges after invasion of a species in a community at equilibrium). These two assumptions should be approximately valid in microcosm experiments in which the medium is often considered homogeneous and species are added sequentially (Petchey et al., 2002, p. 128). Assembling experimental food webs (Weatherby et al., 1998) and understanding their functioning (Naeem et al., 1998) under these conditions often prove to be a difficult task. This difficulty can be explained by the restrictive conditions under which food webs can be assembled as we showed in this paper. Natural ecosystems, however, often present transient, nonequilibrium dynamics; spatial heterogeneity is the rule rather than the exception; and depending on their connections with other ecosystems, the propagule rain may be more or less continuous. Under natural conditions, therefore, one may expect the restrictive assumptions of our model to be relaxed and coexistence to be easier, as was shown for instance in the case of spatial heterogeneity by Loreau (1996) and Leibold (1996).

6. Conclusion

Our analysis studies mechanistically the feasibility, stability and assembly rules of resource-based food webs with up to three trophic levels. The critical factors for these processes are the relative strength of species interactions and the relative impacts of plants and herbivores on factors which control their growth. Analysis of these critical factors allows to understand how the history of community constrains order of invasions and cascades of extinctions and how nutrient enrichment distributes among the populations

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Table 1. Summary of the conditions defined in the text to ensure species persistence in food webs. (See text for explanation.)

N°	Condition	Mathematical notation
1	P_1 better exploiter of the resource R than P_2.	$R^*_{(P_1)} < R^*_{(P_2)}$, that is $m_1/k_1l_1 < m_2/k_2l_2$
2	P_2 ZNGI is steeper than P_1 ZNGI in the (R, H_1) plane.	$\frac{k_2l_2}{a_{21}} > \frac{k_1l_1}{a_{11}}$; $\alpha = a_{11}k_2l_2 - a_{21}k_1l_1$, $\alpha > 0$
3	$C_{P_1} > C_{P_2}$ in the (R, H_1) plane.	$\frac{a_{11}b_{11}}{k_1} > \frac{a_{21}b_{21}}{k_2}$; $\beta = k_2a_{11}b_{11} - k_1a_{21}b_{21}$, $\beta > 0$
4	H_1 is limited by P_1 and H_2 is limited by P_2.	$\frac{d_1}{a_{11}b_{11}} < \frac{d_2}{a_{12}b_{12}}$ and $\frac{d_2}{a_{22}b_{22}} < \frac{d_1}{a_{21}b_{21}}$; $\omega = a_{11}b_{11}a_{22}b_{22} - a_{12}b_{12}a_{21}b_{21}$, $\omega > 0$
5	P_2 ZNGI is steeper than P_1 ZNGI in the (R, H_2) plane.	$\frac{k_2l_2}{a_{22}} > \frac{k_1l_1}{a_{12}}$; $\gamma = a_{12}k_2l_2 - a_{22}k_1l_1$, $\gamma > 0$
5’	P_2 ZNGI is shallower than P_1 ZNGI in the (R, H_2) plane.	$\frac{k_2l_2}{a_{22}} < \frac{k_1l_1}{a_{12}}$; $\gamma' = a_{22}k_1l_1 - a_{12}k_2l_2$, $\gamma' > 0$
6	P_1 ZNGI is steeper in the (R, H_2) than in the (R, H_1) plane and P_2 ZNGI is shallower in the (R, H_2) than in the (R, H_1) plane.	$a_{11}a_{22} > a_{12}a_{21}$
7	$C_{P_1} > C_{P_2}$ in the (R, H_2) plane.	$\frac{a_{12}b_{12}}{k_1} > \frac{a_{22}b_{22}}{k_2}$; $\varepsilon = k_2a_{12}b_{12} - k_1a_{22}b_{22}$, $\varepsilon > 0$

Table 2. Plants and specialist carnivore's responses to nutrient enrichment in the *R*-*P*₁-

	C_{1S} food web	C_{2S} food web
P_1^*	↘	↘
P_2^*	↗	↗
C_{zS}^*	↘	↗

Table 3. Primary and secondary extinctions in R-P_1-P_2-H_1-H_2-C_{zS} food webs. 2 TO and 1 TO refer to food webs with two trade-offs and food webs with one trade-off respectively (see text for explanation).

Primary extinction	Secondary extinction(s)	
	R-P_1-P_2-H_1-H_2-C_{1S}	R-P_1-P_2-H_1-H_2-C_{2S}
P_1	H_1 and C_{1S}	no
P_2	no	H_2 and C_{2S}
H_1	2 TO: C_{1S} 1 TO: C_{1S} and P_2	P_1 or P_2 or C_{2S} and P_2
H_2	P_1 or P_2 or C_{1S}	C_{2S}
C_{1S} or C_{2S}	no	no

Figure legends.

Fig. 1. Isocline analysis of plants P_1 and P_2 in the (R, H_1) plane. (a) The coexistence equilibrium is stable. (b) The coexistence equilibrium is unstable. Plain line: ZNGI of plant P_1; dashed line: ZNGI of plant P_2. Closed circles: stable equilibrium points; open circles: unstable equilibrium points. Dotted line: projection of the impact vectors. Roman numbers refer to the analysis of the outcome (see text).

Fig. 2. R-P_1-P_2-H_1-H_2 food web. R: limiting resource; P_i: plant; H_j: herbivore. Arrows represent resource-consumer interactions; they point toward the consumer.

Fig. 3. ZNGP of P_1 and P_2 in (R, H_1, H_2) space (first column) and ZNGI of P_1 and P_2 in (R, H_2) plane (second column). The plant ZNGIs cross in the (R, H_1) plane and either cross in the positive (R, H_2) plane (a-b) or do not cross in the positive (R, H_2) plane (c-d). Black plane: P_1 ZNGP; grey plane: P_2 ZNGP. Plain line: P_1 ZNGI; dashed line: P_2 ZNGI. Bold lines: projection of the intersection between the ZNGPs in the (H_1, H_2) plane.

Fig. 4. Graphical analysis of the plant ZNGPs in the (R, H_1, H_2) space.
The graphs correspond to the R-P_1-P_2-H_1-H_2 food webs where the plants trade off nutrient exploitation and resistance to grazing by the two herbivores (a-d) or by herbivore H_1 (e-f). The graphs display the intersection of the plant ZNGPs with the (R, H_1) and (R, H_2) planes and the intersection between the two ZNGPs (a, c and e) and with the (H_1, H_2) plane (b, d, and f). Plain lines: P_1 ZNGI; dashed line: P_2 ZNGI. Bold line: intersection of the plant ZNGPs. In b, d and f, the direction of the intersection of the plant ZNGPs is illustrated such that the bold

extremity is in front of the page and the dotted extremity is the prolongation toward the back of the page.

Fig. 5. Effects of nutrient enrichment on the nutrient pool R, the plants P_1 and P_2 and the herbivores H_1 and H_2.

(a) R-P_1-P_2-H_1-H_2 food web where the plants trade off nutrient exploitation and resistance to grazing by the two herbivores. (b) R-P_1-P_2-H_1-H_2 food web where the plants trade-off nutrient exploitation and resistance to grazing by herbivore H_1. (See text for explanation.)

Fig. 6. R-P_1-P_2-H_1-C_{1S} food web. R: limiting resource; P_i: plant; H_j: herbivore; C_{1S}: specialist carnivore. Arrows represent resource-consumer interactions; they point toward the consumer. This food web is not feasible. (See text for explanation.)

Fig. 7. R-P_1-P_2-H_1-H_2-C_{zS} food webs. The herbivores H_j are specialist and the specialist carnivore C_{zS} preys upon (a) H_1 or (b) H_2 (Grover, 1997). The two herbivores are generalist and the specialist carnivore preys upon (c) H_1 or (d) H_2. (See Fig. 6 for the legend)

Fig. 8. H_1 and H_2 ZNGPs in the (P_1, P_2, C_{ZS}) space (first column) and their intersection with the (P_1, P_2) plane (second column). Black plane: H_1 ZNGP. Grey plane: H_2 ZNGP. Plain line and dotted line: H_1 and H_2 ZNGI in the (P_1, P_2) plane respectively. $P^*_{i(H_i)}$: P_i equilibrium value in presence of the herbivore H_j. (See text for explanation.)

Fig. 9. Impact vectors of the herbivores H_1 and H_2 in the (a) (P_1, P_2), (b) (P_1, C_{1S}) and (c) (P_2, C_{1S}) planes. Plain lines: H_1 ZNGI; dashed line: H_2 ZNGI. Bold line: intersection of the plants' ZNGP. In (c), the direction of the intersection of the herbivore ZNGPs is illustrated

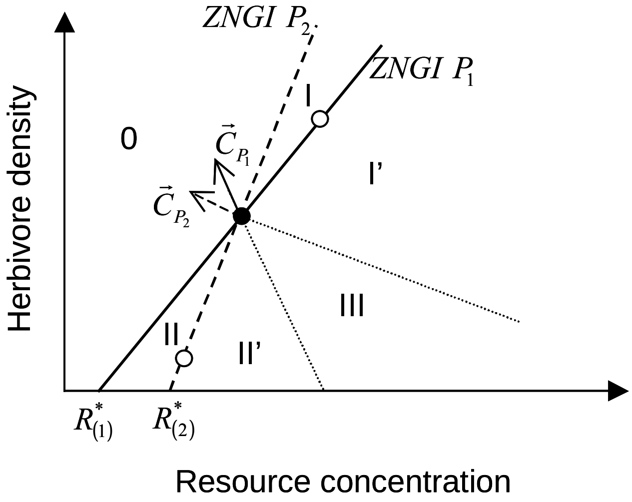
such that the bold extremity is in front of the page and the dotted extremity is toward the back of the page.

Fig. 10. ZNGP of H_1 and H_2 in the (P_1, P_2, C_{2S}) space (a) and impact vectors of the herbivores H_1 and H_2 in the (b) (P_1, P_2), (c) (P_1, C_{2S}) and (d) (P_2, C_{2S}) planes.

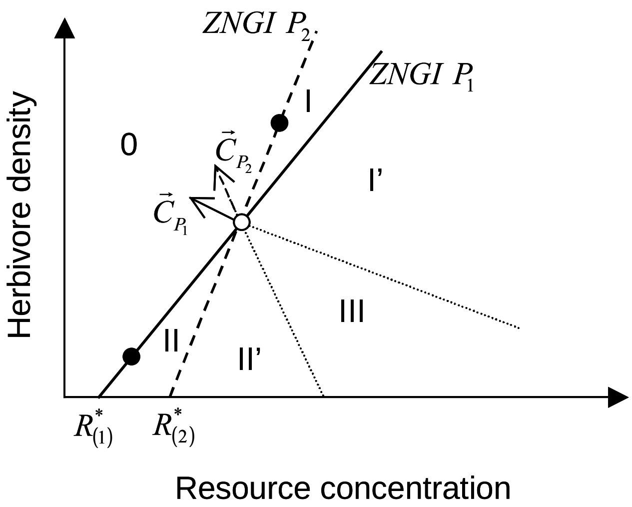
Fig. 11. H_1 and H_2 ZNGPs in the (P_1, P_2, C_1) space where C_1 is a generalist carnivore. Black plane: H_1 ZNGP. Grey plane: H_2 ZNGP. Plain line and dashed line are respectively H_1 and H_2 isoclines in the (P_1, P_2), (P_1, C_1) and (P_2, C_1) planes. Dots indicate H_1 isocline intersections with axes and H_2 isoclines. Circles are H_2 isocline intersections with axes and H_1 isoclines. (See text for explanation.)

Fig. 1.

(a)


ZNGI P_2
ZNGI P_1
I
0
$\vec{C}_{P_1}$
I'
$\vec{C}_{P_2}$
III
II
II'
Herbivore density
$R^*_{(1)}$
$R^*_{(2)}$
Resource concentration

(b)


ZNGI P_2
ZNGI P_1
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0
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III
II
II'
Herbivore density
$R^*_{(1)}$
$R^*_{(2)}$
Resource concentration

Fig. 2.

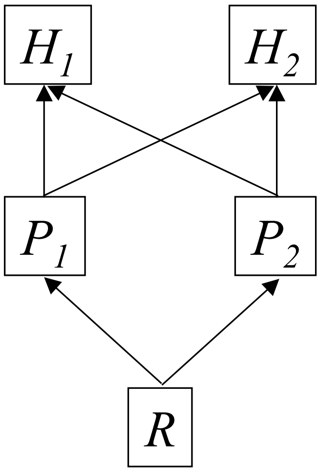
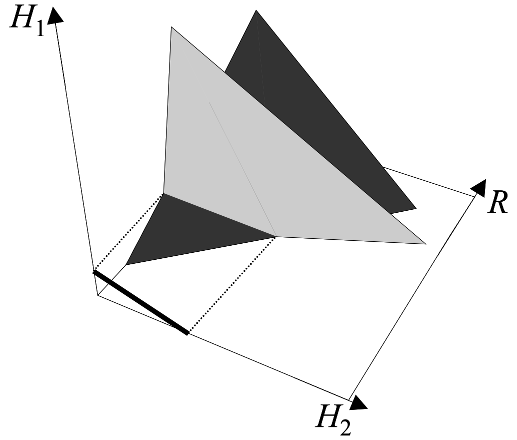


Fig. 3.

(a)



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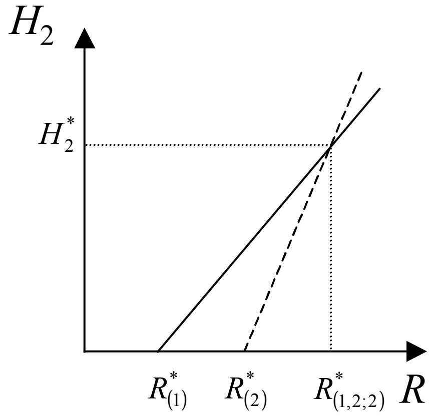

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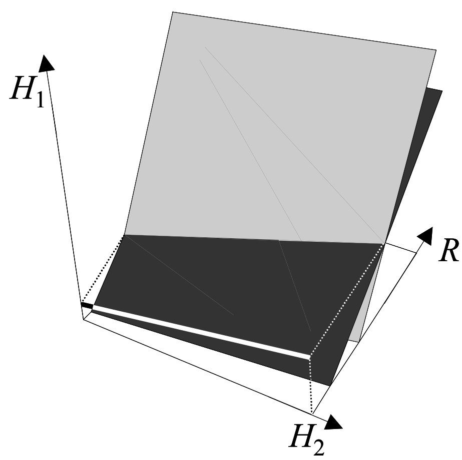


(d)

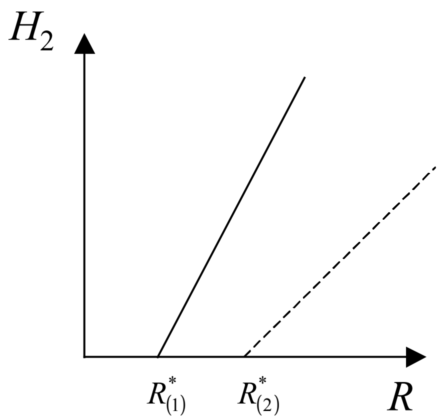


Fig. 4.

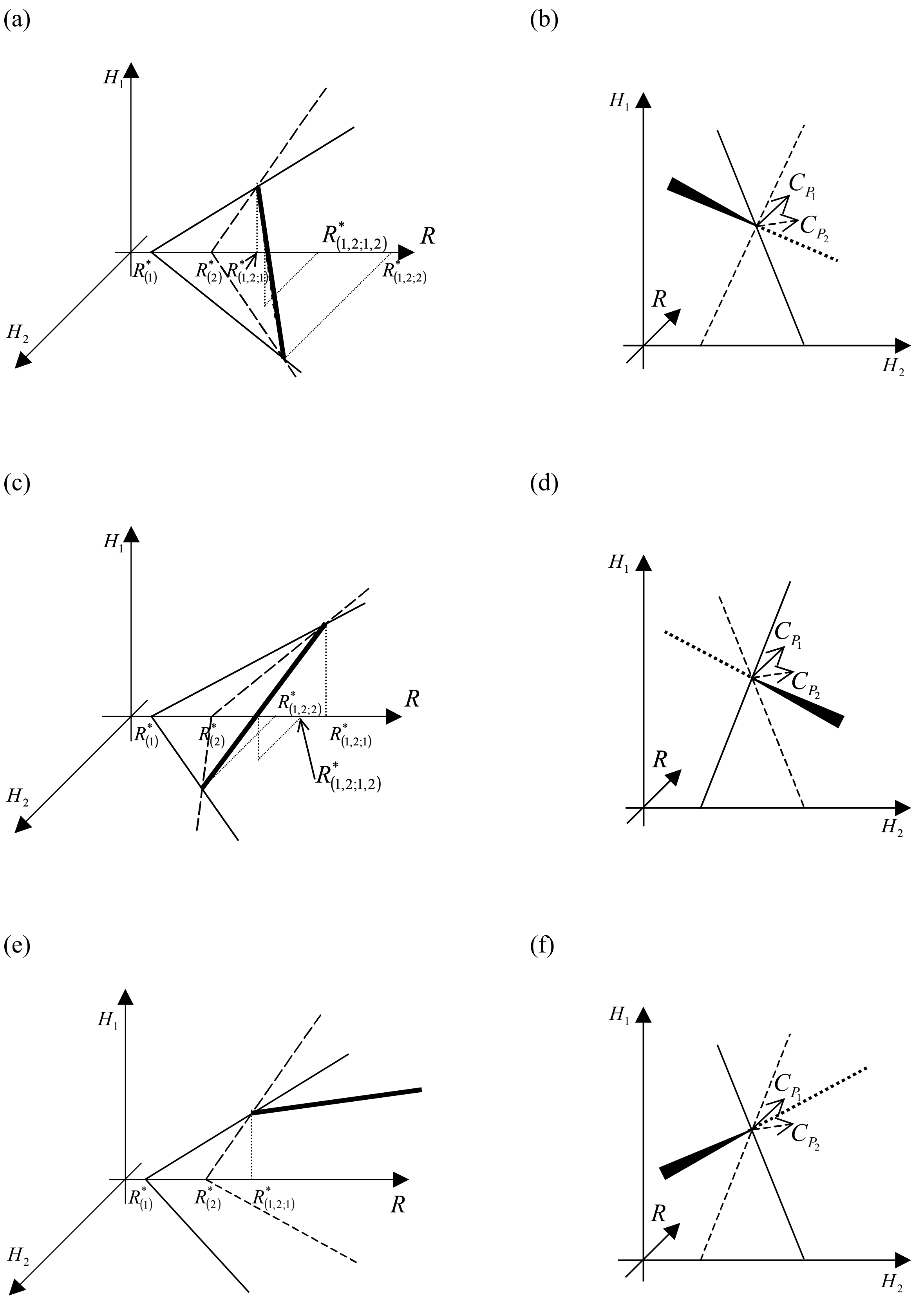
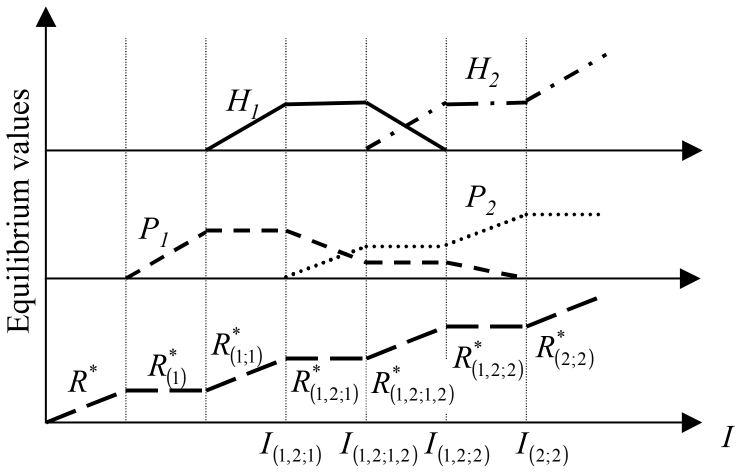
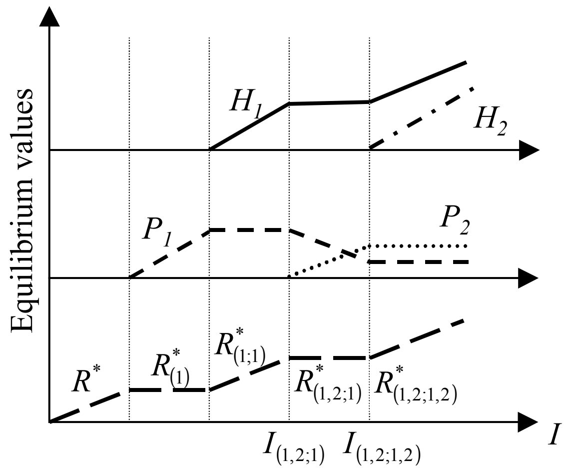

(a)
H_1
R
H_2
$R^*_{(1)}$
$R^*_{(2)}$
$R^*_{(1,2;1)}$
$R^*_{(1,2;1,2)}$
$R^*_{(1,2;2)}$
(b)
H_1
C_{P_1}
C_{P_2}
R
H_2
(c)
H_1
R
H_2
$R^*_{(1)}$
$R^*_{(2)}$
$R^*_{(1,2;2)}$
$R^*_{(1,2;1)}$
$R^*_{(1,2;1,2)}$
(d)
H_1
C_{P_1}
C_{P_2}
R
H_2
(e)
H_1
R
H_2
$R^*_{(1)}$
$R^*_{(2)}$
$R^*_{(1,2;1)}$
(f)
H_1
C_{P_1}
C_{P_2}
R
H_2

Fig. 5.

(a)


Equilibrium values
H_1
H_2
P_1
P_2
R^*
$R^*_{(1)}$
$R^*_{(1;1)}$
$R^*_{(1,2;1)}$
$R^*_{(1,2;1,2)}$
$R^*_{(1,2;2)}$
$R^*_{(2;2)}$
$I_{(1,2;1)}$ $I_{(1,2;1,2)}$ $I_{(1,2;2)}$ $I_{(2;2)}$
I

(b)


Equilibrium values
H_1
H_2
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P_2
R^*
$R^*_{(1)}$
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$R^*_{(1,2;1,2)}$
$I_{(1,2;1)}$ $I_{(1,2;1,2)}$
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Fig. 6.

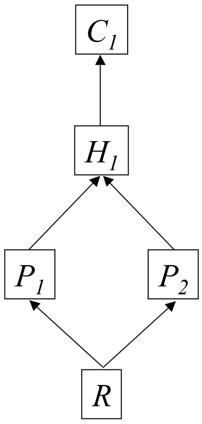
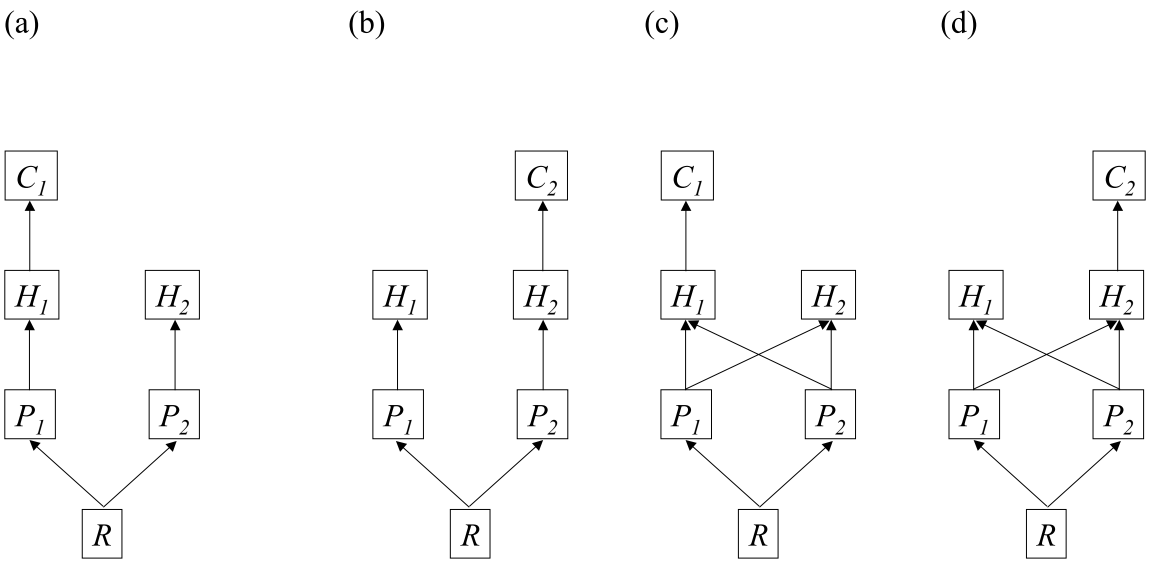

C_1
H_1
P_1
P_2
R

Fig. 7.


(a)
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C_1
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R
C_2
H_1
H_2
P_1
P_2
R

Fig. 8.

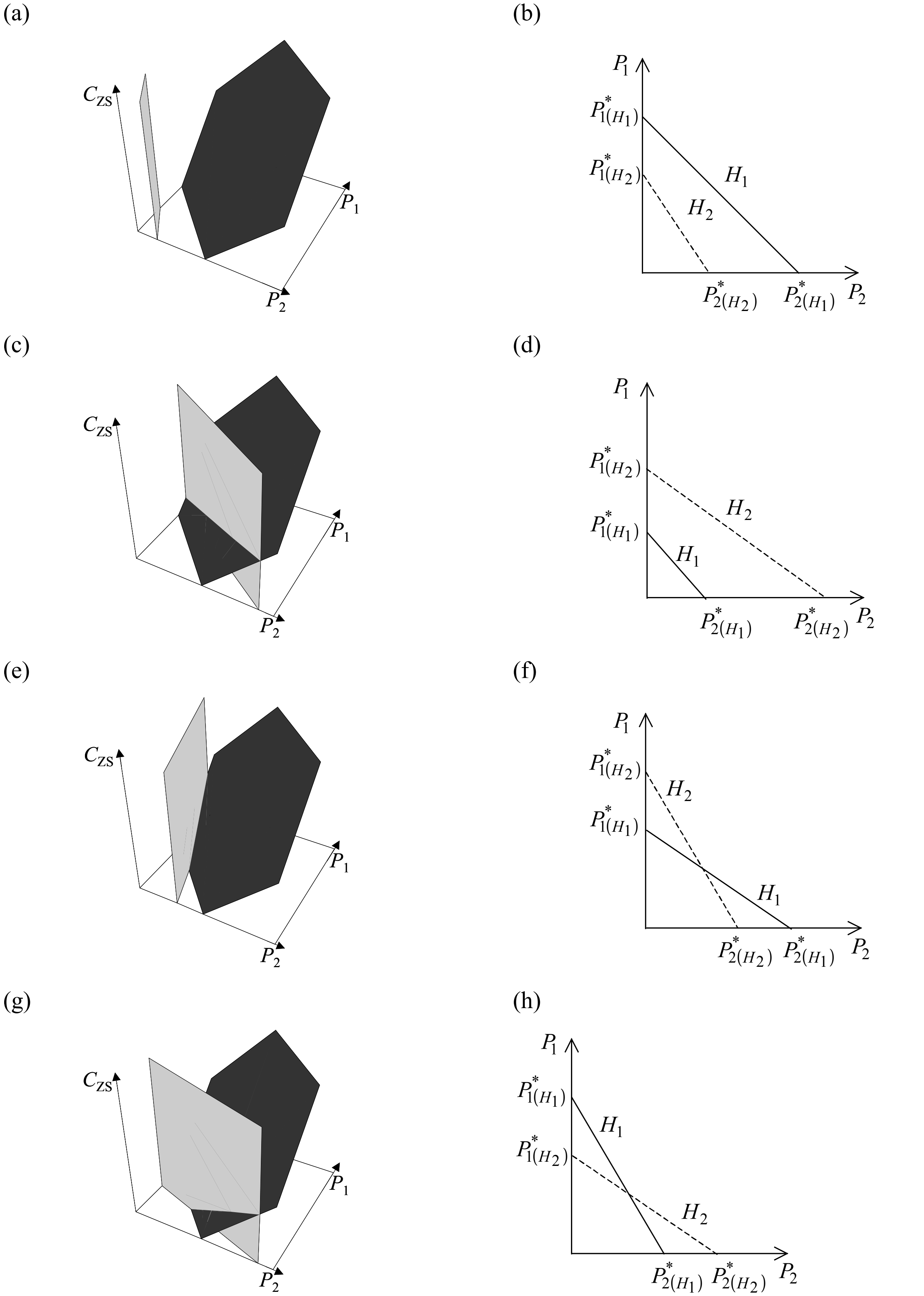
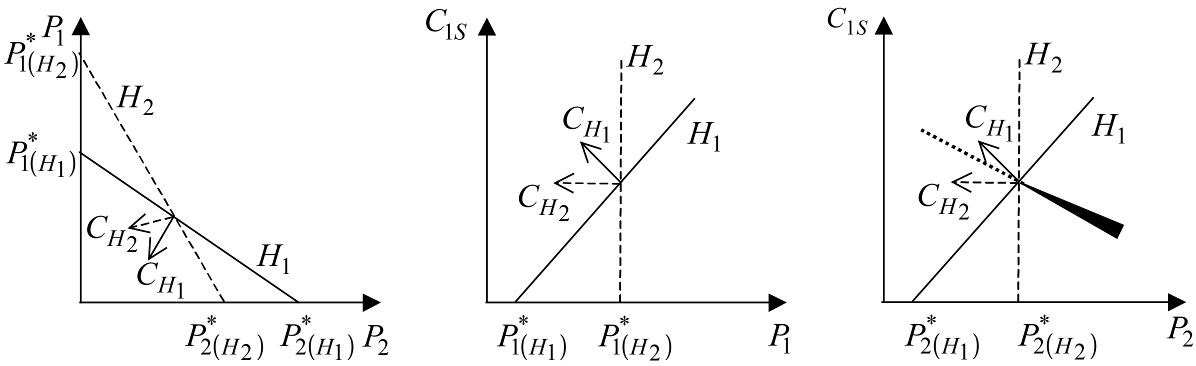


Fig. 9

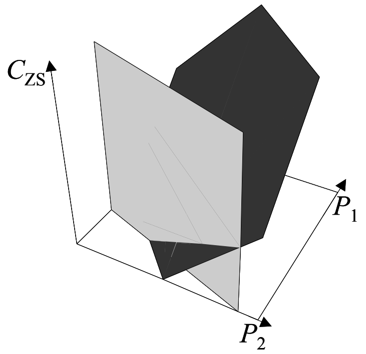
(a) (b) (c)



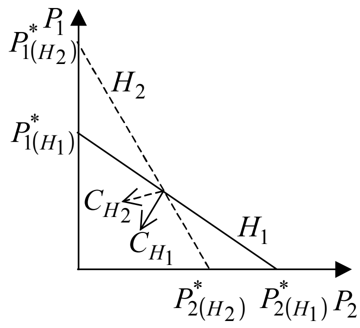
P_1
$P^*_{1(H_2)}$
H_2
$P^*_{1(H_1)}$
C_{H_2}
C_{H_1}
H_1
$P^*_{2(H_2)}$
$P^*_{2(H_1)}$
P_2
C_{1S}
H_2
C_{H_1}
H_1
C_{H_2}
$P^*_{1(H_1)}$
$P^*_{1(H_2)}$
P_1
C_{1S}
H_2
C_{H_1}
H_1
C_{H_2}
$P^*_{2(H_1)}$
$P^*_{2(H_2)}$
P_2

Fig. 10.

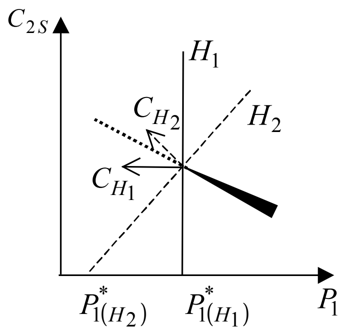
(a)


C_{ZS}
P_1
P_2

(b)


P_1
$P^*_{1(H_2)}$
H_2
$P^*_{1(H_1)}$
C_{H_2}
C_{H_1}
H_1
$P^*_{2(H_2)}$
$P^*_{2(H_1)}$
P_2

(c)


C_{2S}
H_1
C_{H_2}
H_2
C_{H_1}
$P^*_{1(H_2)}$
$P^*_{1(H_1)}$
P_1

(d)

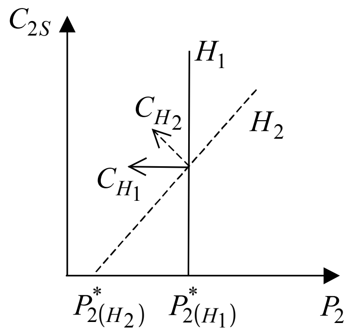
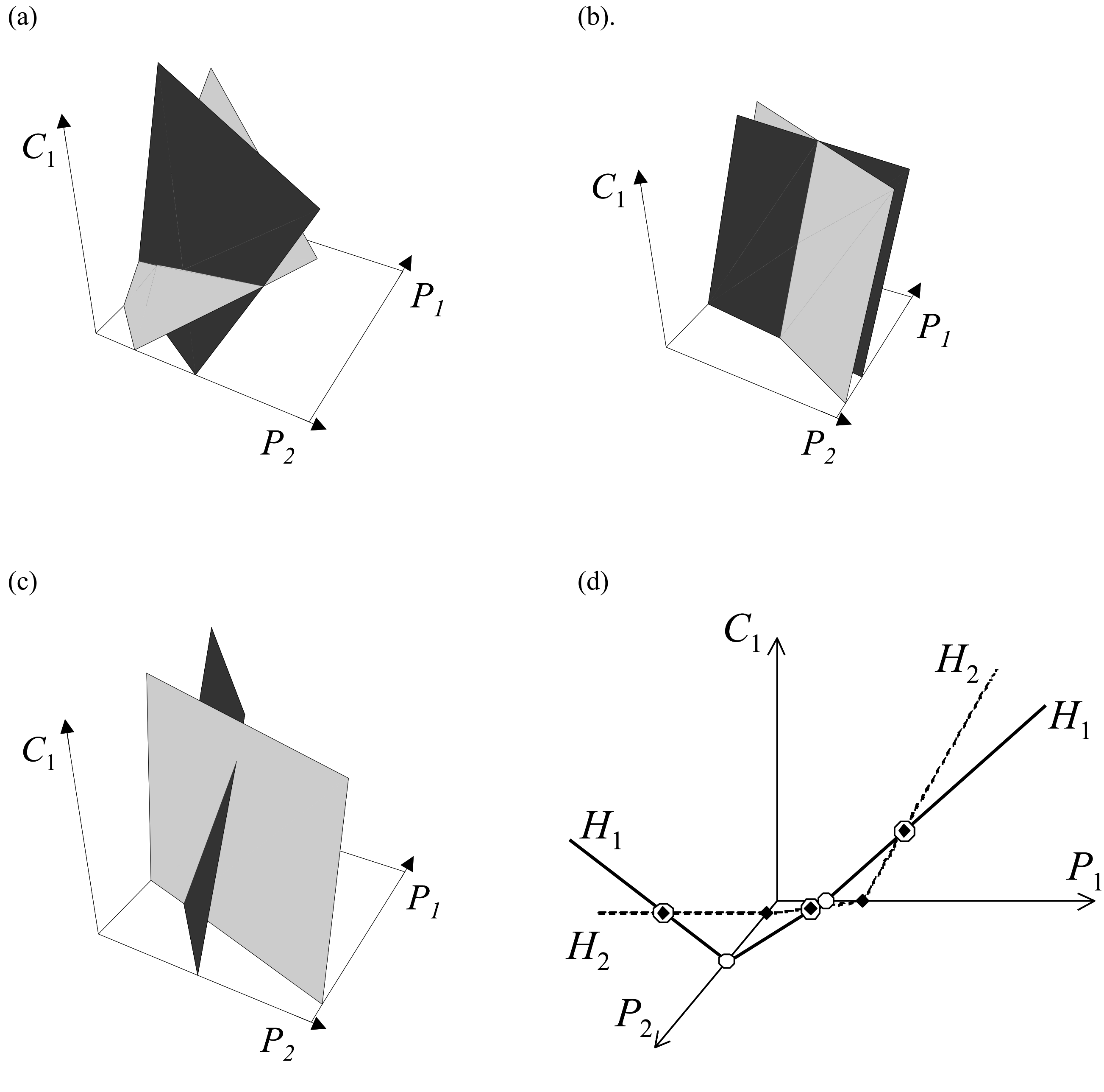

C_{2S}
H_1
C_{H_2}
H_2
C_{H_1}
$P^*_{2(H_2)}$
$P^*_{2(H_1)}$
P_2

Fig. 11.



Appendix A: the *R*-P_1-P_2-H_1 food web

The equilibrium values of the model discussed in the text are

$$R^*_{(1,2;1)} = \frac{a_{11}m_2 - a_{21}m_1}{a_{11}k_2l_2 - a_{21}k_1l_1}$$

$$P_1^* = -\frac{a_{21}b_{21}\left(I - qR^*\right) - k_2d_1R^*}{\alpha R^*} \tag{A1}$$

$$P_2^* = \frac{a_{11}b_{11}\left(I - qR^*\right) - k_1d_1R^*}{\alpha R^*}$$

$$H_1^* = \frac{k_1l_1m_2 - k_2l_2m_1}{a_{11}k_2l_2 - a_{21}k_1l_1}$$

with $\alpha = a_{11}k_2l_2 - a_{21}k_1l_1$ and α>0.

If the conditions 1 and 2 (see text and Table 1) are met then $R^*_{(1,2;1)} > 0$ and $H_1^* > 0$. P_1^* and P_2^* are positive if the external nutrient input *I* is in the interval between the values $I_{(1,2;1)}$ and $I_{(2;1)}$:

$$P_1^* > 0 \Leftrightarrow I < I_{(2;1)} \text{ with } I_{(2;1)} = \frac{R^*_{(1,2;1)}\left(\alpha + a_{21}b_{21}q + k_2d_1\right)}{a_{21}b_{21}} \tag{A2}$$

$$P_2^* > 0 \Leftrightarrow I > I_{(1,2;1)} \text{ with } I_{(1,2;1)} = \frac{R^*_{(1,2;1)}\left(\alpha + a_{11}b_{11}q + k_1d_1\right)}{a_{11}b_{11}} \tag{A3}$$

Response to nutrient enrichment is given by the partial derivative of the populations with respect to nutrient input: $\partial R^*_{(1,2;1)} / \partial I = 0$, $\partial P_1^* / \partial I = -\left(a_{21}b_{21} / \alpha R^*_{(1,2;1)}\right) I$, $\partial P_2^* / \partial I = \left(a_{11}b_{11} / \alpha R^*_{(1,2;1)}\right) I$ and $\partial H_1^* / \partial I = 0$. The zeros indicate that the nutrient pool and the herbivore do not respond to nutrient enrichment. P_1 and P_2 respond respectively negatively and positively to nutrient enrichment .

Appendix B: R-P_1-P_2-H_1-H_2 food webs

In this appendix, we analyse the equilibrium values of R-P_1-P_2-H_1-H_2 food webs and their response to nutrient enrichment.

B.1. Equilibrium values of the resource pool, the plants and the herbivores

The equilibrium values are

$$
\begin{aligned}
R^*_{(1,2;1,2)} &= \frac{I}{q + k_1 P_1^* + k_2 P_2^*}. \\
P_1^* &= \frac{d_1 a_{22} b_{22} - d_2 a_{21} b_{21}}{a_{11} b_{11} a_{22} b_{22} - a_{12} b_{12} a_{21} b_{21}} \\
P_2^* &= \frac{d_2 a_{11} b_{11} - d_1 a_{12} b_{12}}{a_{11} b_{11} a_{22} b_{22} - a_{12} b_{12} a_{21} b_{21}} \\
H_1^* &= \frac{(a_{22} k_1 l_1 - a_{12} k_2 l_2) R^*_{(1,2;1,2)} + a_{12} m_2 - a_{22} m_1}{a_{11} a_{22} - a_{12} a_{21}} \\
H_2^* &= \frac{(a_{11} k_2 l_2 - a_{21} k_1 l_1) R^*_{(1,2;1,2)} + a_{21} m_1 - a_{11} m_2}{a_{11} a_{22} - a_{12} a_{21}}
\end{aligned}
\tag{B1}
$$

The equilibrium values of P_1^* and P_2^* are positive if their numerators and their common denumerator are of the same sign. We make the hypotheses that H_1 decreases plant P_1 more than does H_2 ($d_1 a_{22} b_{22} - d_2 a_{21} b_{21} > 0$, condition 4, Table 1) and that H_2 decreases plant P_2 more than does H_1 ($d_2 a_{11} b_{11} - d_1 a_{12} b_{12} > 0$, condition 4, Table 1). After mathematical manipulation, these hypotheses can be shown to imply that $a_{11} b_{11} a_{22} b_{22} - a_{12} b_{12} a_{21} b_{21} > 0$. Therefore the equilibrium value of P_1^* and P_2^* are positive if each herbivore is a better exploiter of one of the two plants (i.e. H_1 is a better exploiter of P_1 than is H_2 and H_2 is a better exploiter of P_2 than is H_1.) The equilibrium value of the resource $R^*_{(1,2;1,2)}$ is positive if the condition 4 (Table 1) is met.

To study the equilibrium values of the herbivores, let $X = a_{12}m_2 - a_{22}m_1$, $X' = a_{21}m_1 - a_{11}m_2$ and $W = a_{11}a_{22} - a_{21}a_{12}$ with $X > 0$ (conditions 1 and 5) and $X' < 0$ (conditions 1 and 2, Table 1). The equilibrium values are $H_1^* = \left(-\gamma R^*_{(1,2;1,2)} + X\right)/W$ and $H_2^* = \left(\alpha R^*_{(1,2;1,2)} + X'\right)/W$. We show in the main text that the stability of the food web requires that $W > 0$. Therefore the equilibrium values are positive if

$$-\gamma R^* + X > 0 \text{ and } \alpha R^* + X' > 0 \tag{B2}$$

After mathematical manipulation, conditions ensuring positive equilibrium values become:

$$H_1^* > 0 \text{ if } I < I_{(1,2;2)} \text{ with } I_{(1,2;2)} = \frac{\left(a_{12}m_2 - a_{22}m_1\right)\left(q + k_1P_1^* + k_2P_2^*\right)}{\gamma} \tag{B3}$$

$$H_2^* > 0 \text{ if } I > I_{(1,2;1,2)} \text{ with } I_{(1,2;1,2)} = \frac{\left(a_{11}m_2 - a_{21}m_1\right)\left(q + k_1P_1^* + k_2P_2^*\right)}{\alpha} \tag{B4}$$

H_1^* and H_2^* are positive if $I_{(1,2;1,2)} < I < I_{(1,2;2)}$, with $I_{(1,2;1,2)} < I_{(1,2;2)}$ true if $W > 0$.

B.2. Food web where the plants trade off competitive ability and resistance to grazing by herbivore H*1*

Only the equilibrium value of herbivore H_1 differs from the previous analysis. In this case, $H_1^* = \frac{\gamma' R^*_{(1,2;1,2)} + X}{W}$ where $\gamma' = a_{22}k_1l_1 - a_{12}k_2l_2$ ($\gamma' > 0$, condition 5', Table 1, $X = a_{12}m_2 - a_{22}m_1$ and $W = a_{11}a_{22} - a_{21}a_{12}$). A positive equilibrium value of H_1 requires

$$I > \frac{\left(a_{12}m_2 - a_{22}m_1\right)\left(q + k_1P_1^* + k_2P_2^*\right)}{\gamma} \tag{B5}$$

The threshold value of external nutrient input ensuring herbivore H_2 persistence (Eq. B4) is inferior to the threshold value for H_1 (Eq. B5). Therefore the equilibrium value of herbivores are positive if the external nutrient input is superior to the threshold defined in Eq. B4.

B.3. Effects of nutrient enrichment

Partial derivatives with respect to nutrient input of the resource and the plants show that $\partial P_1^* / \partial I = 0$, $\partial P_2^* / \partial I = 0$ and $\partial R_{(1,2;1,2)}^* / \partial I > 0$. Thus the plants do not respond to nutrient enrichment and the resource pool responds positively to nutrient enrichment. Herbivores' response to nutrient enrichment is:

1. H_1^* response to nutrient enrichment in the food webs with two (Eq. B6) or one trade-off (Eq. B7) respectively:

$$\frac{\partial H_1^*}{\partial I} = \frac{\partial}{\partial I}\left(\frac{-\gamma R_{(1,2;1,2)}^*}{W}\right) \text{ with } \gamma > 0 \text{ and } W > 0 \text{ (conditions 5 and 6, Table 1)} \quad \text{(B6)}$$

$$\frac{\partial H_1^*}{\partial I} = \frac{\partial}{\partial I}\left(\frac{\gamma' R_{(1,2;1,2)}^*}{W}\right) \text{ with } \gamma' > 0 \text{ and } W > 0 \text{ (conditions 5' and 6, Table 1)} \quad \text{(B7)}$$

2. H_2^* response to nutrient enrichment in the two food webs:

$$\frac{\partial H_2^*}{\partial I} = \frac{\partial}{\partial I}\left(\frac{\alpha R_{(1,2;1,2)}^*}{W}\right) \text{ with } \alpha > 0 \text{ (condition 2, Table 1)} \quad \text{(B8)}$$

Therefore, the response to nutrient enrichment of H_1^* is negative in the food web with two trade-offs and positive in the food web with one trade-off while the response of H_2^* is positive in either type of food web.

The effects of nutrient enrichment on the trophic level of the herbivores H is given by: $\frac{\partial H}{\partial I} = \frac{\partial (H_1 + H_2)}{\partial I}$. After mathematical manipulation:

$$\frac{\partial H}{\partial I}=\frac{\partial}{\partial I}\left(\frac{\alpha-\gamma}{W}R^{*}_{(1,2;1,2)}\right), \text{ with } \alpha>0 \text{ (condition 2, Table 1)} \tag{B9}$$

In the food web with two trade-offs $\gamma>0$ whereas in the food web with one trade-off $\gamma<0$ (Conditions 5 and 5', Table 1, respectively). In conclusion, the effect of nutrient enrichment on the trophic level of herbivores is undetermined in the food web with two trade-offs while it is positive in the food web with one trade-off.

Appendix C: *R*-*P*$_1$-*P*$_2$-*H*$_1$-*H*$_2$-*C*$_z$ communities

C.1. Communities with a specialist carnivore preying upon H$_1$ *(*R-P$_1$-P$_2$-H$_1$-H$_2$-C$_{1S}$*) (Fig. 8)*

For this community, the equilibrium value are

$$R^*_{(1,2;1,2;1s)} = \frac{(a_{21}a_{12} - a_{11}a_{22})H_1^* + m_2a_{12} - m_1a_{22}}{\gamma}$$

$$P_1^* = -\frac{a_{22}b_{22}I - (a_{22}b_{22}q + k_2d_2)R^*_{(1,2;1,2;1S)}}{\varepsilon R^*_{(1,2;1,2;1S)}}$$

$$P_2^* = \frac{a_{12}b_{12}I - (a_{12}b_{12}q + k_1d_2)R^*_{(1,2;1,2;1S)}}{\varepsilon R^*_{(1,2;1,2;1S)}} \tag{C1}$$

$$H_1^* = \frac{\mu_1}{e_{11}f_{11}}$$

$$H_2^* = \frac{-\alpha H_1^* + m_2k_1l_1 - m_1k_2l_2}{\gamma}$$

$$C_{1S}^* = -\frac{\omega I - R^*_{(1,2;1,2;1S)}(\omega q + \beta d_2 - \varepsilon d_1)}{\varepsilon e_{11}R^*_{(1,2;1,2;1S)}}$$

Equilibrium values of the resource pool and herbivores: The equilibrium value of $H^*_{2(1,2;1,2;1S)}$ and $R^*_{(1,2;1,2;1S)}$ depend on interactions within the communities without the specialist carnivore. As shown before, in such food webs the plants trade off resource exploitation and resistance to either one ($\gamma < 0$; condition 5', Table 1) or two ($\gamma > 0$; condition 5, Table 1) herbivores.

In the food web with two trade-offs ($\gamma > 0$; condition 5, Table 1), $R^*_{(1,2;1,2;1S)} > 0$ and $H^*_{2(1,2;1,2;1S)} > 0$ if $H^*_{1(1,2;1,2;1S)} < \dfrac{m_2a_{12} - m_1a_{22}}{a_{11}a_{22} - a_{12}a_{21}}$ and $H^*_{1(1,2;1,2;1S)} < \dfrac{m_2k_1l_1 - m_1k_2l_2}{\alpha}$ respectively.

Because $\dfrac{m_2k_1l_1 - m_1k_2l_2}{\alpha} < \dfrac{m_2a_{12} - m_1a_{22}}{a_{11}a_{22} - a_{12}a_{21}}$ (Conditions 1 and 2, Table 1), $R^*_{(1,2;1,2;1S)}$ and

$H^*_{2(1,2;1,2;1S)}$ are positive if $H^*_{1(1,2;1,2;1S)} < \dfrac{m_2k_1l_1 - m_1k_2l_2}{\alpha}$ with $H^*_{1(1,2;1)} = \dfrac{m_2k_1l_1 - m_1k_2l_2}{\alpha}$.

Therefore, $R^*_{(1,2;1,2;1S)}$ and $H^*_{2(1,2;1,2;1S)}$ are positive if $H^*_{1(1,2;1,2;1S)} < H^*_{1(1,2;1)}$. Inversely, in the food web with one trade-off ($\gamma < 0$; condition 5', Table 1), $R^*_{(1,2;1,2;1S)} > 0$ and $H^*_{2(1,2;1,2;1S)} > 0$ if $H^*_{1(1,2;1,2;1S)} > H^*_{1(1,2;1)}$.

Equilibrium values of the plants and the specialist carnivore are

$$P_1^* > 0 \text{ if } I < I_{P_1} \text{ with } I_{P_1} = \frac{(a_{22}b_{22}q + k_2d_2)R^*_{(1,2;1,2;1S)}}{a_{22}b_{22}} \tag{C2}$$

$$P_2^* > 0 \text{ if } I > I_{P_2} \text{ with } I_{P_2} = \frac{(a_{12}b_{12}q + k_1d_2)R^*_{(1,2;1,2;1S)}}{a_{12}b_{12}} \tag{C3}$$

$$C_{1S}^* > 0 \text{ if } I < I_{C_{1S}} \text{ with } I_{C_{1S}} = \frac{(\omega q + \beta d_2 - \varepsilon d_1)R^*_{(1,2;1,2;1S)}}{\omega} \tag{C4}$$

It can be shown that $I_{P_2} < I_{P_1} < I_{C_{1S}}$ (Conditions 4 and 6, Table 1). Therefore these equilibrium values are all positive if $I_{P_2} < I < I_{P_1}$.

Effects of nutrient enrichment: Responses of the populations' equilibrium values to nutrient enrichment are: $\partial R^*_{(1,2;1,2;1S)}/\partial I = 0$, $\partial P_1^*/\partial I < 0$, $\partial P_2^*/\partial I > 0$, $\partial H_1^*/\partial I = 0$, $\partial H_2^*/\partial I = 0$ and $\partial C_{1S}^*/\partial I < 0$, whatever the interactions in the communities without the specialist carnivore. The effects on the total equilibrium value of plants is given by $\partial(P_1^* + P_2^*)/\partial I = (a_{12}b_{12} - a_{22}b_{22})/\varepsilon R^*_{(1,2;1,2;1S)}$, whose sign is undetermined.

C.2. Communities with a specialist carnivore preying upon H_2 *(*R-P_1-P_2-H_1-H_2-C_{2S}) *(Fig. 7d)*

The equilibrium values are

$$R^*_{(1,2;1,2;2S)} = \frac{(a_{11}a_{22} - a_{21}a_{12})H_2^* + m_2 a_{11} - m_1 a_{21}}{\alpha}$$

$$P_1^* = -\frac{a_{21}b_{21}I - (a_{21}b_{21}q + k_2 d_1)R^*_{(1,2;1,2;2S)}}{\beta R^*_{(1,2;1,2;2S)}}$$

$$P_2^* = \frac{a_{11}b_{11}I - (a_{11}b_{11}q + k_1 d_1)R^*_{(1,2;1,2;2S)}}{\beta R^*_{(1,2;1,2;2S)}} \qquad \text{(C5)}$$

$$H_1^* = \frac{\gamma H_2^* + m_1 k_2 l_2 - m_2 k_1 l_1}{-\alpha}$$

$$H_2^* = \frac{\mu_2}{e_{22} f_{22}}$$

$$C_{2S}^* = \frac{\omega I - R^*_{(1,2;1,2;2S)}(\omega q + \beta d_2 - \varepsilon d_1)}{\beta e_{11} R^*_{(1,2;1,2;2S)}}$$

The equilibrium value of P_1, P_2 and C_{2S} are positive if $I < I'_{P_1}$, $I > I'_{P_2}$ and $I < I_{C_{2S}}$ with $I'_{P_1} = \frac{(a_{11}b_{11}q + k_1 d_1)R^*_{(1,2;1,2;2S)}}{a_{11}b_{11}}$, $I'_{P_2} = \frac{(a_{12}b_{12}q + k_1 d_2)R^*_{(1,2;1,2;1S)}}{a_{12}b_{12}}$ and $I_{C_{2S}} = \frac{(\omega q + \alpha d_2 - \varepsilon d_1)R^*_{(1,2;1,2;2S)}}{\omega}$ with $I'_{P_2} < I'_{P_1} < I_{C_{2S}}$ (Conditions 3 and 4, Table 1). Therefore the equilibrium value of P_1, P_2 and C_{2S} are positive if $I'_{P_2} < I < I'_{P_1}$.

The equilibrium values of the resource pool $R_{(1,2;1,2;2S)}$ and herbivore H_2 are always positive (Conditions 1 and 2, Table 1). The equilibrium value of herbivore H_1 depends on the interactions in the communities without C_{2S}. H_1^* is positive either if $H^*_{2(1,2;1,2;2S)} < H^*_{2(1,2;2)}$ and $\gamma > 0$ or if $H^*_{2(1,2;1,2;2S)} > H^*_{2(1,2;2)}$ and $\gamma < 0$. However, if $\gamma < 0$, R-P_1-P_2-H_2 food webs do not exist. Hence the equilibrium value $H^*_{2(1,2;2)}$ is irrelevant. Therefore, the R-P_1-P_2-H_1-H_2-C_{2S} food web is feasible only if the plants trade off competitive ability with resistance to grazing by the two herbivores ($\gamma > 0$).

The effects of nutrient enrichment do not depend on interactions within the communities without C_{2S}. The nutrient pool and the herbivores populations do not respond to nutrient enrichment. The response of the plants and the specialist carnivore are $\partial P_1^* / \partial I < 0$, $\partial P_2^* / \partial I > 0$ and $\partial C_{2S}^* / \partial I > 0$. The effect on the total plants equilibrium value is undetermined ($\partial\left(P_1^* + P_2^*\right) / \partial I = \left(a_{11}b_{11} - a_{21}b_{21}\right) / \varepsilon R^*_{(1,2;1,2;2S)}$).

*C.3. Communities with a generalist carnivore (*R-P$_1$-P$_2$-H$_1$-H$_2$-C$_1$*)*

The equilibrium values are

$$\begin{aligned}
R^*_{(1,2;1,2;1)} &= \frac{\mu_1\left(a_{11}a_{22} - a_{12}a_{21}\right) + e_{11}f_{11}\left(m_1 a_{22} - m_2 a_{12}\right) + e_{21}f_{21}\left(m_2 a_{11} - m_1 a_{21}\right)}{e_{21}f_{21}\alpha - e_{11}f_{11}\gamma} \\
P_1^* &= \frac{\left(a_{21}b_{21}e_{21} - a_{22}b_{22}e_{11}\right)\left(I - qR^*_{(1,2;1,2;1)}\right) + \left(e_{11}d_2 - e_{21}d_1\right)k_2 R^*_{(1,2;1,2;1)}}{\left(e_{11}\varepsilon - e_{21}\beta\right)R^*_{(1,2;1,2;1)}} \\
P_2^* &= \frac{\left(a_{11}b_{11}e_{21} - a_{12}b_{12}e_{11}\right)\left(I - qR^*_{(1,2;1,2;1)}\right) + k_1\left(e_{11}d_2 - e_{21}d_1\right)R^*_{(1,2;1,2;1)}}{\left(e_{21}\beta - e_{11}\varepsilon\right)R^*_{(1,2;1,2;1)}} \\
H_1^* &= \frac{e_{21}f_{21}\left(m_1 k_2 l_2 - m_2 k_1 l_1\right) + \gamma\mu_1}{\gamma e_{11}f_{11} - \alpha e_{21}f_{21}} \\
H_2^* &= \frac{e_{11}f_{11}\left(m_1 k_2 l_2 - m_2 k_1 l_1\right) + \alpha\mu_1}{\alpha e_{21}f_{21} - \gamma e_{11}f_{11}} \\
C_1^* &= \frac{\omega\left(I - qR^*_{(1,2;1,2;1)}\right) + \left[d_1\varepsilon - \beta d_2\right]R^*_{(1,2;1,2;1)}}{\left(e_{21}\beta - e_{11}\varepsilon\right)R^*_{(1,2;1,2;1)}}
\end{aligned} \tag{C6}$$

*C.4. Community with two generalist carnivores (*R-P$_1$-P$_2$-H$_1$-H$_2$-C$_1$-C$_2$*)*

The calculation of the equilibrium value of the resource pool leads to two different values:

$$R^*_{(1,2;1,2;1,2)} = \frac{\mu_1\left(a_{11}e_{22}f_{22} - a_{12}e_{12}f_{12}\right) + \mu_2\left(a_{12}e_{11}f_{11} - a_{11}e_{21}f_{21}\right) + m_1\left(e_{11}f_{11}e_{22}f_{22} - e_{12}f_{12}e_{21}f_{21}\right)}{k_1 l_1\left(e_{11}f_{11}e_{22}f_{22} - e_{12}f_{12}e_{21}f_{21}\right)}$$

(C7)

$$R^{*}_{(1,2;1,2;1,2)} = \frac{\mu_1\left(a_{21}e_{22}f_{22} - a_{22}e_{12}f_{12}\right) + \mu_2\left(a_{22}e_{11}f_{11} - a_{21}e_{21}f_{21}\right) + m_2\left(e_{11}f_{11}e_{22}f_{22} - e_{12}f_{12}e_{21}f_{21}\right)}{k_2 l_2\left(e_{11}f_{11}e_{22}f_{22} - e_{12}f_{12}e_{21}f_{21}\right)}$$
(C8)

Satisfying these two conditions simultaneously is infinitely unlikely in natural systems.