

Nutrient enrichment and food chains: can evolution buffer top-down control?

Nicolas Loeuille* and Michel Loreau

Laboratoire d'Ecologie, Ecole Normale Supérieure, UMR 7625, 46 rue d'Ulm, F-75230 Paris, Cedex 05, France

Received 24 July 2003

Abstract

We show how evolutionary dynamics can alter the predictions of classical models of the effects of nutrient enrichment on food webs. We compare an ecological nutrient–plant–herbivore food-chain model without evolution with the same model, including herbivore evolution, plant evolution, or both. When only herbivores are allowed to evolve, the predictions are similar to those of the ecological model without evolution, i.e., plant biomass does not change with nutrient addition. When only plants evolve, nutrient enrichment leads to an increase in the biomass of all compartments. In contrast, when plants and herbivores are allowed to coevolve, although these two classical patterns are common, a wide variety of other responses is possible. The form of the trade-offs that constrain evolution of the two protagonists is then critical. This stresses the need for experimental data on phenotypic traits, their costs and their influence on the interactions between organisms and the rest of the community.

© 2004 Elsevier Inc. All rights reserved.

Keywords: Nutrient enrichment; Bottom-up effect; Plant–herbivore coevolution; CSS; Adaptive dynamics

Introduction

Together with global climate change, nutrient enrichment is receiving increasing scientific attention (Boesch et al., 2001; Kaiser, 2001). The importance of this environmental problem is due both to its spatial scale (the majority of the Earth's ecosystems), to its consequences in terms of loss of biodiversity and changes in species dominance (Dyer and Letourneau, 2003; Hillebrand, 2003), and to more specific problems such as harmful algae blooms (Anderson et al., 2002). In spite of international efforts to understand the effects of nutrient enrichment on ecosystems, the variety of responses observed in nature or in experiments seems to defy predictions (e.g., Carpenter et al., 1987; Brett and Goldman, 1997; Forkner and Hunter, 2000; Persson et al., 2001; Dawes-Gromadzki, 2002; Dyer and Letourneau, 2003).

During the 1970s and 1980s, the management of eutrophic lakes and rivers arose as a major ecological problem, and boosted the controversy about the factors

that determine the abundance of species in food webs. The biomass of a species in a community depends on the reproduction and survival of its individuals, which, among other factors, depend on the availability of resources and the risk of predation. As ecologists sought to determine which of these two factors is the most critical in natural ecosystems, the “bottom-up control” versus “top-down control” controversy grew.

Bottom-up as well as top-down controls have been shown to be important for a wide variety of systems (e.g., bottom-up: Coe et al., 1976; Chase et al., 2000; Hansson, 1979; top-down: Estes and Palmisano, 1974; Carpenter et al., 1987), and theories such as the Green World Hypothesis (Hairston et al., 1960) or the Exploitation Ecosystem Hypothesis (Oksanen et al., 1981; Oksanen, 1983; Fretwell, 1987) are based on the dominance of top-down control in structuring the whole community.

However, there is growing evidence that both types of control are present in for most ecosystems (Hansson, 1979; Carpenter et al., 1987; McQueen et al., 1989; Hunter and Price, 1992; Brett and Goldman, 1997; Jarvinen, 2002) and that the primacy of one or the other is dependent on biotic and abiotic conditions. This made it necessary to understand the factors influencing the

*Corresponding author. Fax: +33-1-44-32-38-85.

E-mail addresses: loeuille@biologie.ens.fr (N. Loeuille), loreau@biologie.ens.fr (M. Loreau).

relative strength of the two types of control. Theoretical studies (Hunter and Price, 1992; Abrams, 1993; Hulot et al., 2000), experiments (Hunter and Price, 1992; Hulot et al., 2000; Schmitz et al., 2000; Persson et al., 2001; Moon and Stiling, 2002) and observations (Polis, 1994; Gange, 1997) agree that the heterogeneity, or functional diversity, of the various trophic levels has an important effect on the strengths of bottom-up and top-down controls. Omnivory also modifies the distribution of biomasses in a community compared with simple food-chain models (Polis, 1994; Diehl and Feissel, 2000; Schmitz et al., 2000).

The top-down versus bottom-up control controversy also suffers from confusion between “control” and “effect”. “Control” indicates the factor (resource or predator) that limits the abundance or biomass of a trophic level; “effect” describes the consequence of perturbing the system at either the top or the bottom. Consider for example the fertilization process. Its propagation along the food chain is typically a bottom-up effect. The way fertilization will affect the food web, however, is dependent on the type of control that governs the abundance of the various trophic levels. If bottom-up control is dominant, i.e. the biomass of each trophic level is controlled by the amount of its resources, the biomass of all trophic levels will increase. On the contrary, if top-down control is dominant, i.e. the biomass at each trophic level is controlled by the level above it if the latter is not itself top-down controlled, nutrient enrichment will increase the biomass of top predators and all odd-numbered lower trophic levels, but it will leave even-numbered compartments of the food chain unaffected (Smith, 1969; Oksanen et al., 1981). Thus, predator removal is expected to yield a top-down effect on the biomass of other trophic levels which is dependent on the type of control that governs the food chain (small effects of predator removal if bottom-up control prevails, major effects if top-down control prevails).

An additional complication arises from the presence of species adaptation under natural conditions. Classical ecological theories and hypotheses assume fixed species traits. Species, however, have evolved different phenotypes or strategies in response to interspecific interactions or abiotic conditions depending on the assembly and evolutionary history of the community. Species adaptation potentially influences top-down and bottom-up effects (Abrams, 1995, 1996). This underlines the need for more theoretical studies on the implications of evolution on top-down and bottom-up effects.

The present article aims at understanding how species evolution and coevolution affects the response of a simple food chain subject to fertilization (bottom-up effect). The model without evolution is top-down controlled as in Oksanen et al.’s (1981) classical model. We show how evolution, or adaptive dynamics, affects

the phenotypic traits at the various trophic levels, and thereby deeply alters the predictions of the top-down model on the effects of fertilization in such a system. We show that, even in a simple food-chain model, the possible outcomes are numerous. Forecasting the outcome of nutrient enrichment requires knowledge of the costs of phenotypic traits as well as their exact influence on interspecific interactions.

1. A simple food-chain model

The ecological model describes a simple food chain consisting only of a plant and a herbivore compartment in addition to the inorganic nutrient pool (Fig. 1). This model has already been used in a previous work to assess the importance of nutrient dynamics in plant–herbivore coevolution (Loeuille et al., 2002). It includes both the plant and herbivore population dynamics and their feedback on nutrient availability. The nutrient–plant and plant–herbivore interactions are modelled using linear functional and numerical responses. *Per capita* growth rate of the consumers are not density dependent. Part of the dead biomass of both plants and herbivores are recycled into the inorganic nutrient compartment. In addition to this recycling, nutrient availability depends on the balance between the input, I , and output, eN , of the nutrient. The various parameters and variables are defined in the Table 1 (a) and (b).

The model contains features of both community (species interactions) and ecosystem (nutrient recycling) processes. We made it very simple to keep it mathematically tractable, since the aim of the present work is to provide analytical results on the effects of nutrient enrichment on the various compartments of the food

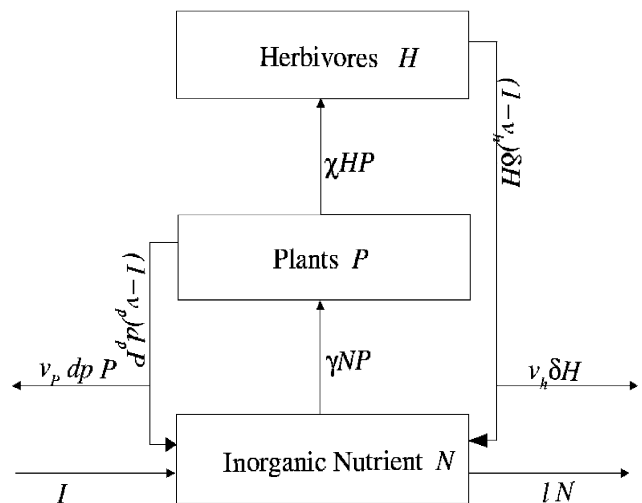


Fig. 1. Ecological model for the plant–herbivore interaction in a nutrient limited ecosystem. Variables and parameters are defined in Table 1a and b.

Table 1
Definition and units of (a) the variables of the model, (b) the parameters of the model

Parameter	Dimension	Definition
<i>Variable</i>		
<i>N</i>	Quantity of nutrient per unit of area	Stock of inorganic nutrient in plant's absorption pool of the system
<i>P</i>	Quantity of nutrient per unit of area	Stock of plant nutrient of the system
<i>H</i>	Variable	Stock of herbivore nutrient of the system
<i>s_p</i>	Dimensionless	Amount of defenses produced by plants against herbivory
<i>s_h</i>	Dimensionless	Herbivore's capacity to consume plants
<i>χ</i>	(Quantity of nutrient per unit of area × time) ⁻¹	Consumption rate of plants by herbivores
<i>δ</i>	Time ⁻¹	Detritus production rate of herbivores
<i>γ</i>	(Quantity of nutrient per unit of area × time) ⁻¹	Rate of nutrient uptake by plants
<i>I</i>	Quantity of nutrient per unit of area/time	Total input of inorganic nutrient for the global system
<i>e</i>	Time ⁻¹	Inorganic nutrient output rate for the global system
<i>d_p</i>	Time ⁻¹	Detritus production rate for plants
<i>v_p</i>	Dimensionless	Fraction of nutrient lost along the plant recycling pathway
<i>v_h</i>	Dimensionless	Fraction of nutrient lost along the herbivore recycling pathway

chain. Nutrient enrichment is here introduced through an increase of the parameter *I*.

2. Responses of the food chain to nutrient enrichment

2.1. Model without evolution

The model is described by the following dynamical equations:

$$\begin{aligned} \frac{dN}{dt} &= I - eN - \gamma NP + (1 - v_p)d_p P + (1 - v_h)\delta H, \\ \frac{dP}{dt} &= P(\gamma N - d_p - \chi H), \\ \frac{dH}{dt} &= H(\chi P - \delta). \end{aligned} \tag{1}$$

In this model, *N*, *P*, and *H* stand for the total amount of nutrient in the inorganic, the plant and the herbivore compartment, respectively. This system has a single feasible equilibrium in which both plants and herbivores are present:

$$\begin{aligned} N^0 &= \frac{\chi I + \delta d_p (v_h - v_p)}{\chi e + \delta \gamma v_h}, \\ P^0 &= \frac{\delta}{\chi}, \\ H^0 &= \frac{\gamma N^0 - d_p}{\chi}. \end{aligned} \tag{2}$$

It is easy to show, using a study of the Jacobian matrix corresponding to system (1) at the equilibrium point (2), that this equilibrium is always stable. Note that nutrient input, *I*, has to be sufficiently large to sustain the herbivore population. The variations of the various equilibrium stocks with nutrient enrichment

Table 2
Effects of an increase in nutrient input *I* on the equilibrium stocks and traits of the food chain in three cases: no evolution, plant evolution alone and herbivore evolution alone

	No evolution	Plant evolution	Herbivore evolution
<i>N</i>	+	+	+
<i>P</i>	0	+	0
<i>H</i>	+	+	+
<i>s_p</i>		+	
<i>s_h</i>			0

can easily be determined by differentiation of the equilibrium position depending on *I*:

$$\begin{aligned} \frac{\partial N^0}{\partial I} &= \frac{\chi}{\chi e + \delta \gamma v_h}, \\ \frac{\partial P^0}{\partial I} &= 0, \\ \frac{\partial H^0}{\partial I} &= \frac{\gamma}{\chi} \frac{\partial N^0}{\partial I}. \end{aligned} \tag{3}$$

Thus, as nutrient input increases, the inorganic nutrient and herbivore equilibrium stocks increase, while plant biomass remains constant (Table 2). This result is in accordance with classical models in which predators control their prey (Smith, 1969; Fretwell, 1977; Oksanen et al., 1981).

2.2. Model with plant evolution

In the model above, plant survival is determined by grazing intensity. Grazing thereby exerts a selective pressure on plants, which may result in a modification of their traits, such as size, chemical or physical defenses (Simms and Rausher, 1987; Herms and Mattson, 1992; Tuomi, 1992; Steinberg et al., 1995; Rausher, 1996; Mauricio, 1998). This trait, denoted *s_p*, has an influence

on the rate of herbivory, $\chi(s_p)$. In the rest of the article (except in the third example below), we assume that this plant trait represents a defense against herbivory, which means that the parameter χ decreases with the trait s_p . This trait is supposed to have a cost, diminishing the efficiency of nutrient absorption by the plant, $\gamma(s_p)$ (allocation cost see Angilletta et al., 2003). This type of cost is typically linked to resistance of plants to herbivory (Herms and Mattson, 1992; Rausher, 1996; Mauricio, 1998). As a result, the parameter γ is a decreasing function of the plant trait. This means that the only conditions for the functions γ and χ are their positivity and the sign of their derivatives. We want to keep the study of the plant evolution as general as possible. For this reason, the phenotypic trait is not further defined, and no exact shape is postulated for the functions γ and χ .

We make the assumption that although the stocks P and H stand for amounts of nutrients, they are proportional to the plant and herbivore populations, respectively. Evolution of the plant trait will be modeled using the canonical equation of the adaptive dynamics (Dieckmann and Law, 1996; Champagnat et al., 2001):

$$\frac{ds_p}{dt} = K\mu_p\sigma_p^2 P^0 \left(\frac{\partial W_{Pm}(s_{pm}, s_p)}{\partial s_{pm}} \right)_{spm \rightarrow sp}, \quad (4)$$

where K is a parameter that scales plant biomass in traits values, μ_p is the mutation rate per individual, σ_p^2 is the variance of the mutational effects, and W_{Pm} is the fitness of a plant mutant characterized by its trait s_{pm} in the resident population s_p . This fitness is defined by the rate of variation of the mutant in the resident population, i.e.

$$W_{Pm}(s_{pm}, s_p) = \frac{1}{P_m} \frac{dP_m}{dt} = \gamma(s_{pm})N^0 - d_p - \chi(s_{pm})H^0. \quad (5)$$

The evolution of the plant trait is accurately approximated by Eq. (4) under several assumptions:

- μ_p is small, that is, the time scale of evolutionary dynamics is much longer than that of ecological dynamics;
- the mutation amplitude σ_p^2 is small;
- the mutant is initially rare.

If the equilibrium of the evolutionary dynamics (4) satisfies both the convergence and the non-invasibility conditions, then it is called a Convergence Stable Strategy, or CSS (Eshel, 1983; Marrow et al., 1996).

This adaptive dynamics framework seems to be restrictive, but Eq. (4) derived from this theory is often a good approximation of quantitative genetic models (Abrams, 2001), and may be a good approximation for many types of adaptation (Abrams et al., 1993).

The analysis of evolutionary dynamics and of the effects of nutrient enrichment on equilibrium stocks is

described in Appendix A, and summarized in Table 2. When evolution leads to a CSS, nutrient enrichment always increases both the equilibrium stocks of all compartments and the level of plant defense.

2.3. Model with herbivore evolution

As herbivore growth and reproduction depend on plant consumption, herbivores are also likely to adapt to plant availability. Herbivore traits that influence plant consumption are numerous; they include size (Neubert et al., 2000), detoxification capacities (Krieger et al., 1971; Musser et al., 2002), and behavioral investment between searching for plants and being vigilant (Illius and Fitzgibbon, 1994). Let us note the herbivore trait s_h . This trait affects the plant consumption rate, $\chi(s_h)$. Except in the third example below, we assume that this herbivore trait always has a positive effect on herbivore voracity, which means that χ is increasing with this trait. The trait is assumed to be costly in terms of mortality, $\delta(s_h)$ (Illius and Fitzgibbon, 1994), because the energy and time that herbivores invest in plant searching and consumption is not available for the vigilance to predators (acquisition cost see Angilletta et al., 2003). Here again, we do not constrain the expressions of the two functions except for giving the sign of their derivatives, and ensuring that they remain positive. It is then possible to model the evolution of the herbivore trait, using the same framework as in the plant case:

$$\frac{ds_h}{dt} = K\mu_H\sigma_H^2 H^0 \left(\frac{\partial W_{Hm}(s_{hm}, s_h)}{\partial s_{hm}} \right)_{shm \rightarrow sh}. \quad (6)$$

The fitness of herbivores is defined by

$$W_{Hm}(s_{hm}, s_h) = \frac{1}{H_m} \frac{dH_m}{dt} = \chi(s_{hm})P^0 - \delta(s_{hm}). \quad (7)$$

Evolutionary dynamics results in a CSS under certain conditions. Since the per capita growth rate of the herbivore is purely a function of plant density and plant density does not depend on the level of fertilization (see Eq. (2)), the changes in the various equilibrium stocks driven by nutrient input are qualitatively similar to those obtained in the model without evolution.

2.4. Model with plant–herbivore coevolution

Unless one has good reasons to think that one of the two protagonists is evolving much faster than the other (e.g., a large difference in the generation times or mutation rates of the two protagonists), considering the coevolution of the two protagonists is a priori more satisfying than separating them as done above. In this case, we assume that the herbivory rate depends on the difference between the plant and herbivore traits, i.e., $\chi(s_h - s_p)$. To keep the model consistent with the models where only one of the two protagonists evolves, we

Table 3

Possible effects of an increase in nutrient input I when plants and herbivores coevolve. The only constraint is that the equilibrium plant stock and the plant trait vary similarly

Coevolution																
N	+	–	+	+	–	+	–	+	–	+	+	–	–	–	+	–
P	+	+	+	+	+	–	+	+	–	–	–	+	–	–	–	–
H	+	+	–	+	–	+	+	–	+	–	+	–	–	+	–	–
s_p	+	+	+	+	+	–	+	+	–	–	–	+	–	–	–	–
s_h	+	+	+	–	+	+	–	–	+	+	–	–	+	–	–	–

assume that the parameter χ is an increasing function of the difference between the two traits. This assumption is relaxed only in the third example below. As above, the uptake of nutrient by plants decreases with s_p , and the death rate of the herbivore increases with s_h . The trait dynamics is modeled via the canonical equations of the adaptive dynamics:

$$\begin{aligned} \frac{ds_p}{dt} &= K_P \mu_P \sigma_P^2 P^0 \left(\frac{\partial W_{Pm}(s_{pm}, s_p, s_h)}{\partial s_{pm}} \right)_{s_{pm} \rightarrow s_p}, \\ \frac{ds_h}{dt} &= K_H \mu_H \sigma_H^2 H^0 \left(\frac{\partial W_{Hm}(s_{hm}, s_h, s_p)}{\partial s_{hm}} \right)_{s_{hm} \rightarrow s_h}, \end{aligned} \tag{8}$$

where the fitnesses are:

$$\begin{aligned} W_{Pm}(s_{pm}, s_p, s_h) &= \frac{1}{P_m} \frac{dP_m}{dt} = \gamma(s_{pm})N^0 - d_p \\ &\quad - \chi(s_h - s_{pm})H^0, \\ W_{Hm}(s_{hm}, s_h, s_p) &= \frac{1}{H_m} \frac{dH_m}{dt} = \chi(s_{hm} - s_p)P^0 - \delta(s_{hm}). \end{aligned} \tag{9}$$

The analysis of evolutionary dynamics is detailed in Appendix B. Under certain conditions, the model also yields a CSS. The effects of nutrient enrichment in this case are summarized in Table 3.

The potential consequences of nutrient enrichment when there is coevolution are much more complex and diverse than in the previous models. There are 16 possible cases, depending on the sign of the second derivatives of the $\chi(s_h - s_p)$, $\delta(s_h)$ and $\gamma(s_p)$ (see Appendix B). The only common feature of all these possible cases is the parallel variations of equilibrium plant biomass and plant trait. This parallelism is due to the assumption that $\chi'(s_h - s_p)$ is positive. The various cases depend on the shape of the functions $\chi(s_h - s_p)$, $\delta(s_h)$ and $\gamma(s_p)$. This stresses the need for an improvement in the knowledge of the physiological traits and trade-offs of organisms within a community context.

In the following part, we analyze three possible examples for these functions. These examples are intended to illustrate the general analysis above and to give an idea of the probabilities associated with the various outcomes in the coevolutionary model.

3. Three examples of trade-offs between traits

The following examples were treated numerically. In each case, we performed 100,000 simulations. We then determined if the ecological equilibrium (2) was feasible. If it was feasible, we determined the position of the evolutionary equilibrium (given by the intersection of the null isoclines of Eqs. (8)), and the nature of this equilibrium. If it was a CSS, we determined how a change in nutrient input affected the position of this CSS in terms of trait values and equilibrium stocks. We did not consider evolutionary outcomes other than CSSs since we were unable to make predictions about the effects of nutrient enrichment on unstable regimes, and simple objective measures of these effects are much more difficult. We also checked that 100,000 simulations were enough to get precise values for the different probabilities. Values of the parameters are $l=0.1$, $v_h=0.5$, $v_p=0.5$, $d_p=1$ for the parameters of the ecological model. Parameters of the trade-off functions were drawn randomly in intervals mentioned below. The results are presented in Tables 4a,b and in Figs. 2–4.

3.1. Interaction parameters are linear functions of the traits

Linear trade-offs are suggested by some experimental results. For example, Thrall and Burdon (2003) noted that there was a linear trade-off between spore production of *Melampsora lini* and resistance to parasites. In this example, the trait-dependent parameters are defined by

$$\begin{aligned} \chi(s_h - s_p) &= a(s_h - s_p) + b, \\ \gamma(s_p) &= -cs_p + d, \\ \delta(s_h) &= fs_h + g. \end{aligned} \tag{10}$$

The various parameters (a, b, c, d, e, f) are positive. In this case, the function χ increases with $(s_h - s_p)$, which conforms to the hypothesis made earlier that herbivory rate increases with the herbivore trait and decreases with the plant trait. The plant trait represents plant defense against herbivory, and the herbivore trait is correlated with the energy herbivores invest in plant consumption. Plant defense has a cost in terms of nutrient absorption

Table 4

(a) Responses of the equilibrium stocks and traits following nutrient enrichment in the three examples studied^a

	Coevolution, example 1		Coevolution, example 2
<i>N</i>	+	–	+
<i>P</i>	0	0	+
<i>H</i>	+	–	+
<i>S_p</i>	0	0	+
<i>S_h</i>	+	–	+
Probability	Almost 100%	Close to 0%	100.00%

(b) Effect of the nutrient enrichment on the food chain^b

Coevolution, example 3						
<i>N</i>	+	+	+	+	+	
<i>P</i>	+	+	+	–	+	27 other possible outcomes
<i>H</i>	+	+	+	+	+	
<i>S_p</i>	+	+	–	+	–	
<i>S_h</i>	+	–	–	–	+	
Probability	34.7%	28.2%	21.8%	9.10%	3.73%	2.47%

^aThe parameters are either linear (example 1) or exponential (example 2) functions of the traits.

^bThe interaction parameter is a Gaussian function of the traits difference. The traits are supposed to be body sizes.

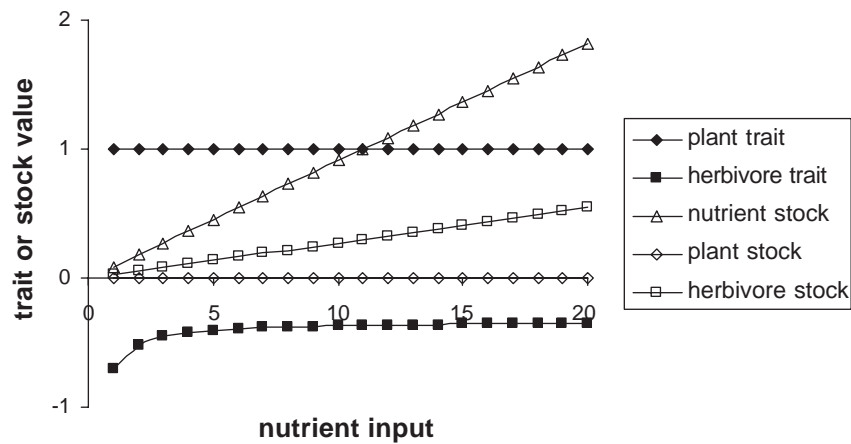


Fig. 2. Trait and stock values at the evolutionary equilibrium as nutrient input varies, when trade-off functions are linear (Section 3.1). For the sake of clarity, stocks have been divided by 100. Parameters values: $a=1, b=2, c=0.3, d=0.5, f=0.1, g=0.1$. As mentioned in the text and demonstrated in Appendix C, another outcome is possible, but marginal.

capacity (Herms and Mattson, 1992; Rausher, 1996; Mauricio, 1998). Consequently, the parameter γ is a decreasing function of the plant trait. The herbivore trait also has a cost in terms of mortality (Illius and Fitzgibbon, 1994): the parameter δ is increasing with s_h . Because the various interaction parameters are to be positive, the traits values are bounded:

$$\begin{aligned}
 s_p &< \frac{d}{c}, \\
 s_h &> \frac{-g}{f}, \\
 s_h - s_p &> \frac{-b}{a}.
 \end{aligned}
 \tag{11}$$

Conditions (11) were also checked for each simulation. The different possible responses of the coevolutionary model under such an assumption are summarized in Table 4a. As shown in Appendix C, only two cases turn out to be possible: an increase in the herbivore stock and trait and in the nutrient stock, or a decrease in all these variables. Plant biomass and plant defense are never affected by nutrient supply. In the vast majority of the simulations yielding a CSS, the nutrient stock, the herbivore stock and the herbivore trait increase with nutrient input and plant trait and biomass are not affected. In very few cases (Table 4a), however, the model yields opposite, counterintuitive results. Decreases are then very weak, and only happen for very limited ranges of nutrient inputs. Fig. 2 illustrates the main outcome obtained in this case.

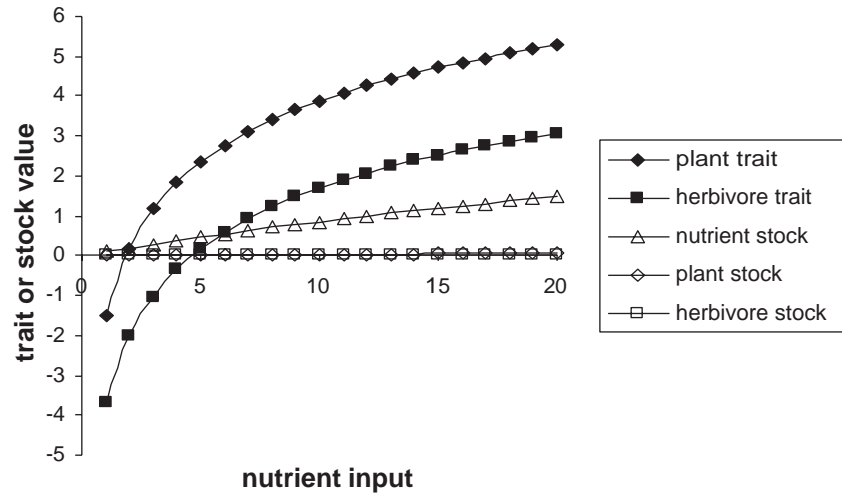


Fig. 3. Trait and stock values at the evolutionary equilibrium as nutrient input varies, when trade-off functions are exponential (Section 3.2). For the sake of clarity, stocks have been divided by 100. Parameters values: $u=0.1$, $c=1$, $k=1$, $d_h=0.1$, $c=2$, $g=0.9$, $a=0.4$.

3.2. Interaction parameters are exponential functions of the traits

Using the same meaning for the traits and similar trade-offs (absorption-defense for plants, voracity-mortality for herbivores), it is also possible to link the traits and the interaction parameters with exponential functions. The function used to describe the herbivory rate χ was suggested by Abrams and Matsuda (1997):

$$\begin{aligned} \chi(s_h - s_p) &= \frac{c \exp(s_h - s_p)}{1 + k \exp(s_h - s_p)}, \\ \gamma(s_p) &= u \exp(-as_p), \\ \delta(s_h) &= d_h \exp(gs_h), \end{aligned} \tag{12}$$

where u is the rate of nutrient absorption by plants when these do not defend themselves, d_h is the rate of mortality and detritus production of herbivores when the herbivore trait is zero, c is the basic consumption rate of plants by herbivores, and k is the saturation parameter of the consumption function of plants by herbivores.

The χ function is always positive, and, in accordance with the general hypothesis, it is an increasing function of the difference between the two traits. Even though we are not able to provide experimental results matching this function, it makes more biological sense than does the function used in the previous example. Indeed, it is S shaped, the consumption rate reaches smoothly a maximum (resp. minimum) when $s_h \gg s_p$ (resp. $s_h \ll s_p$). Since the parameters are by definition positive, no bounds are necessary for the traits s_p and s_h .

The analysis of this example (using the general framework summarized in Appendix B) yields a very simple result: all the stocks and traits increase simulta-

neously when nutrient input increases. This result is akin to the one obtained using the model with plant evolution alone. The results are summarized in Table 4a and plotted in Fig. 3.

3.3. Herbivory depends on body size

Consumption intensity can also be dependent on the relative body sizes of the two protagonists (Neubert et al., 2000). This size dependence can be modeled using a Gaussian function (Marrow et al., 1996). This means that we suppose that consumers may eat a limited range of prey size, because of morphological and behavioral constraints:

$$\begin{aligned} \chi(s_h - s_p) &= \exp(-a(s_h - s_p)^2), \\ \gamma(s_p) &= k_1 - (b - ds_p)^2, \\ \delta(s_h) &= k_2 - (c - fs_h)^2. \end{aligned} \tag{13}$$

The parabolic form of the functions describing nutrient absorption by plants and the death rate of herbivores is also taken from Marrow et al. (1996), who suggested that prey mortality was a parabolic function of the prey trait. Because of these parabolic functions, there is a stabilizing selection on the phenotypic traits in the absence of the interacting species. This example relaxes the hypothesis that χ is an increasing function of the difference between the two traits. Consequently, and contrary to the cases presented in Table 2 and in the previous examples, the variations of the plant trait and of the plant biomass are not a priori linked as in Table 3. This means that the potential results of such a model are more numerous: 32 outcomes are possible. The ability of plants to absorb nutrient is optimal for an intermediate body size, as is the death rate of herbivores (large

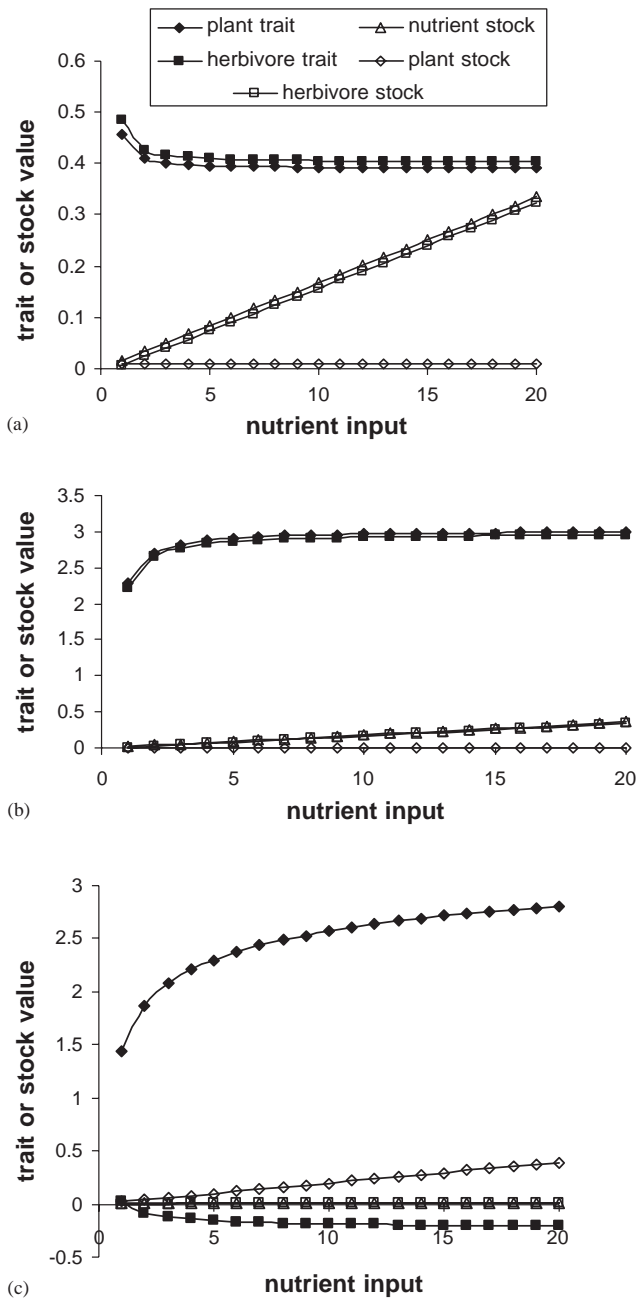


Fig. 4. Trait and stock values at the evolutionary equilibrium as nutrient input varies, when trade-off functions are based on body size (Section 3.3). For the sake of clarity, stocks have been divided by 100. Parameters values:

(a) $a=0.5$, $b=0.1$, $c=0.1$, $d=0.1$, $e=0.3$, $k_1=1$, $k_2=1$.

(b) $a=0.5$, $b=0.1$, $c=0.5$, $d=0.1$, $e=0.1$, $k_1=1$, $k_2=1$.

(c) $a=0.5$, $b=0.1$, $c=0.6$, $d=0.1$, $e=0.8$, $k_1=1$, $k_2=1$.

Note that other outcomes are possible when this kind of trade-off is considered. See the text and Table 4b for more details.

herbivore body sizes would lead to a greater sensitivity to certain predators). Parameters are clearly positive whatever the traits.

The Gaussian function used for χ is only one possibility for an interaction based on size. In some

cases, the predator consumes a large spectrum of prey sizes. Then this function may not be an accurate description of the interaction.

As no simple analytical results emerged from the analysis of this example, we studied the outcome of 100,000 simulations in which the parameters of the Eqs. (13) were drawn randomly between 0 and 1. The results of this model are summarized in Table 4b. The diversity of outcomes is greater than in the other examples, but here again, the biomass of all trophic levels increased in more than 85% of the cases. Some of these possible outcomes are reported in Fig. 4. The dominance of the outcomes detailed in Table 4b is robust. We tried different intervals for the parameters (particularly the parameters k of the parabolic functions): although the percentages of these outcomes vary, their rank in importance remains the same.

A potential problem in the case of size evolution is the fact that the link between stocks P and H and plant and herbivore populations change during the evolution process. This would imply that K_P (resp. K_H) in the Eqs. (8) will depend on s_p (resp. s_h). This modifies the evolutionary dynamics, but it does not change the position of the evolutionary equilibrium. As the study focuses on the position of the equilibrium and as Table 4b only considers stable evolutionary equilibria, we do not expect this to change the frequencies reported in the Table 4b.

4. Discussion

Hunter (2001), when studying the various factors that influence top-down and bottom-up controls, made it clear that generalities were hard to obtain due to the multiplicity of these factors. He also suggested that including adaptation may help to find such generalities. The present study gives new answers about the possibility of such generalities. Table 3 shows that 16 responses to enrichment may be observed in the case of coevolution in a simple nutrient–plant–herbivore food chain. Therefore, coevolution seems to multiply the different outcomes rather than leading to generalities. On the other hand, two patterns emerge as being much more frequent than the others:

- (1) An increase in the biomass of all compartments. This is the only possible result when plant evolution alone occurs (Table 2) and when coevolution with exponential trade-offs occurs (Table 4a, example 2). This outcome is also dominant in the third example, where both traits are supposed to be size dependent (Table 4b). This pattern has already been obtained in other theoretical models (Arditi and Ginzburg, 1989; Leibold, 1996; Leibold et al., 1997) and in natural observations or experiments (e. g., Leibold,

1989; Leibold et al., 1997) based on pure ecological hypotheses. Note that this type of outcome is similar to those obtained when one considers that bottom-up control is dominant along the food chain.

- (2) An increase in herbivore biomass and in the stock of inorganic nutrient, but no variation in plant biomass. This pattern, obtained in the case when no evolution was considered (Table 2), accords with Oksanen's hypothesis (Oksanen et al., 1981; Oksanen, 1983). It is also expected when herbivore evolution alone occurs (Table 2) and is the most frequent outcome when coevolution is taken into account with linear trade-offs (Table 4a, example 1). This pattern is similar to those obtained in models in which top-down control is strong, and bottom-up effects such as enrichment therefore benefit the top of the food chain, which controls the level below it.

Thus, even though the 16 possible results make predictions difficult, the most frequent outcomes are similar to the familiar outcomes of other experiments, observations, and models of nutrient enrichment. Which of these outcomes occurs, however, depends on where evolution takes place in the system (plant evolution, herbivore evolution, or coevolution) and on the efficiency and costs of the various traits. The comparison between the three examples clearly underlines this, as the exact shape of the trade-off functions determines the biomass variations of the compartments.

While comparison of the present results to other theoretical models is easy, comparison with natural and experimental data is trickier, because of the differences in the time scales considered. As noted by Schmitz et al. (2000), experiments conducted to understand the importance of trophic cascades rarely last longer than a few years. This makes the observation of changes in the biomass of the various trophic levels difficult, and may be a reason why observed trophic cascades are more often species-level cascades than community-level cascades (see Polis et al., 2000). If generation times are shorter in aquatic than in terrestrial systems (Chase, 2000), this may also be a reason why trophic cascades are more easily detectable in aquatic systems. If the time scale considered in experimental studies is not sufficient to see these community-level changes in biomass, variations of the phenotypic traits will be all the more difficult to detect. This underlines the need for more long-term experiments to test both ecological and evolutionary models. Even though changes in evolutionary trait are hard to detect under these conditions, several authors noted the importance of such traits in determining the strength of the bottom-up and top-down controls (edibility: Power, 1990; Carpenter et al.,

1987; Lacroix et al., 1996; Leibold, 1996; Mikola and Setälä, 1998; Chase, 1998; size: Hulot et al., 2000; Chase, 2003). For example, in the experiment made by Chase (2003), the strength of the top-down control depended on productivity and on the size of the herbivores. Depending on enrichment, the size of the dominant species within a trophic level changed, which means that the average trait was also changing. The framework of adaptive dynamics mimics the replacement of mutants under selective pressures. This can be to some extent related to the replacement of species observed by Chase (2000). The fact that the strength of the top-down effect depended on species traits in his study is in agreement with our results (Table 3), in which we see that the control exerted by herbivores on plants may be buffered because of plant–herbivore coevolution (if the plant trait increases and the herbivore trait decreases or varies only slightly).

More generally, as only stable evolutionary equilibria are considered in the present model, the results are qualitatively the same as those of any adaptive model whose equilibrium involves maximization of fitness costs and benefits that are described by fitness functions that are similar in form to those explored here. Therefore a link can easily be made with models of other types of adaptation, even when the adaptation process considered is not evolution but behavioural adaptation or species replacement. Abrams (1984, 1992, 1995) showed that adaptation at the intermediate level will modify Oksanen et al.'s predictions about trophic level responses to fertilization. All the same, models and data considering species replacement displayed a wide variety of qualitatively different outcomes in case of enrichment (Armstrong, 1979; Leibold, 1996; Leibold et al., 1997; Abrams, 1993; Chase et al., 2000). For example, Leibold (1996) analyzed replacement of prey species with a trade-off between edibility and resource access. This makes his model very similar to our model of plant evolution, since the trade-off he chose is similar to ours. The effect of nutrient enrichment is then positive on all trophic levels in both models. Leibold et al. (1997) provided experimental results showing that species turnover may influence top-down and bottom-up effects. Our coevolutionary model may be seen as a model of replacement of species at two trophic levels, and may be related to Abrams (1993). Abrams (1993) includes two species on each trophic level, allowing shifts in the relative abundance of these two species. Abrams found a large variety of the possible responses in case of fertilization, which can be easily related to the variety of outcomes displayed by Table 3.

As noted by Power (1992), there is an apparent paradox between the local variations of biomass within communities subjected to nutrient enrichment (frequently showing trophic cascades, especially in aquatic systems), and the variations of biomass across different

communities with different nutrient loads (usually showing an increase of all trophic levels along productivity gradients). Power (1992) proposed that this paradox is due to both the mobility of consumers and the diffuse gradients of nutrient loading. In the light of the present work, an alternative explanation is that the variation observed across ecosystems (such as different lakes) could also be associated to divergences in the local evolution of the two separate systems. As shown in the case of the plant evolution or in some cases of coevolution (examples 2 and 3), enrichment may produce an increase in the biomass of all trophic levels even if the associated ecological model shows a cascade-like pattern. Thus, the differences observed between different lakes may be linked to the fact that these lakes have reached different states in their evolutionary or successional (through replacement of species) dynamics under the influence of different nutrient loads.

The separation of the temporal scales of ecological and evolutionary dynamics may be a limitation of the adaptive dynamics framework used here. As suggested by Thompson (1998) and demonstrated in a certain number of cases (Grant and Grant, 1995; Reznick et al., 1997; Huey et al., 2000; Hendry et al., 2000; Heath et al., 2003; Reale et al., 2003), evolution can sometimes take place rather quickly compared with the time scale at which population dynamics occurs. The canonical equation of adaptive dynamics is then no longer valid. Even though the conditions under which this equation was derived (Diekmann and Law, 1996; Champagnat et al., 2001) are quite restrictive, however, its range of application may be larger. Abrams et al. (1993) suggested that it may be a good approximation for other types of adaptation than evolution. As mentioned by Le Galliard et al. (2003), the canonical equation may also be a good approximation to reality even when the separation of the two time scales is not strictly warranted. Therefore, the results presented here may be relevant even when the speed of evolution is not as low as considered in the initial demonstration of the canonical equation. Moreover, in the case of our models, considering evolution and demography on the same time scale would be equivalent, to considering the equations describing the changes of nutrient stocks (1) and the equations describing the changes of traits (8) simultaneously. The nutrient stocks included in the evolutionary dynamics (8) would then be instantaneous stocks instead of equilibrium stocks (2). This change would not affect the position of the evolutionary equilibrium, but only the evolutionary dynamics. As the present work only discusses the variation of the position of the evolutionary equilibrium with enrichment, this change would not affect the results, as long as the equilibrium remains stable.

Another limitation of the present model is the use of linear functions for the numerical and functional

responses (see Eq. (1)). Alternatives such as logistic growth or Holling type II or III functions would have produced instabilities in the ecological dynamics, which would have made the adaptive dynamics such as described in the present model inadequate (Diekmann and Law, 1996; Champagnat et al., 2001). Although we acknowledge that non-linearities may be preferable to accurately describe population dynamics, they would not affect the diversity of outcomes predicted by our coevolutionary model. Indeed, Table 3 shows that we obtain 16 possible outcomes, and the only reason why we do not get the maximal number of possible outcomes (*i.e.*, 32), is because $\chi(s_h - s_p)$ is supposed to be an increasing function of $s_h - s_p$, which generates parallel variations in plant biomass and plant trait when nutrient enrichment occurs (see Appendix B). On the other hand, the frequency of the different patterns observed and reported in the different tables, is likely to change when such numerical and/or functional responses are not linear. For example, Abrams (1995) and Abrams and Vos (2003) include such non-linearities. These models exhibit outcomes that are qualitatively different to the dominant patterns of the present article.

As underlined in the introduction, nutrient enrichment is a global change affecting a wide range of ecosystems. This means that spatial structure should be included, for example by the means of the geographic mosaic model (Thompson, 1997, 1999; Nuismer et al., 1999, 2000; Gomulkiewicz et al., 2000; Thompson and Cunningham, 2002). Hochberg and van Baalen (1998) studied the effect of environmental richness on prey–predator coevolution using this kind of approach. The present model would then describe evolution in one patch in the geographic mosaic, and would be linked to other similar systems via gene flow.

Ignoring these complexities of spatial and temporal scales made the model simple enough to show clearly that another critical element required to predict evolutionary dynamics is actually missing, *i.e.*, detailed knowledge of the effects of phenotypic traits on interspecific interactions and of the costs of these traits. Abrams (1986, 2000) also discussed the importance of the dependence of the capture rate on the traits in the coevolutionary dynamics of predator–prey systems. In the present article, however, no hypothesis is made on how the different components of the trade-off functions are linked to the traits. The importance of the shape of these components emerges from the analysis (see the various appendices).

The exact effect of phenotypic traits on interspecific interactions remains largely unknown. Even for traits as simple and directly measurable as size, several studies stressed the potential importance of this effect (Power, 1990; Leibold, 1996; Hulot et al., 2000; Chase, 2003), but none of them quantified it. Similarly, allocation costs (such as those considered here for plants) or

acquisition costs (such as those considered here for herbivores) of the traits are very often assumed in evolutionary models, but knowledge of these costs remains sketchy. Knowledge of the shape of cost functions, such as the linearity observed by Thrall and Burdon (2003), is required to predict the outcome of coevolution in our models. Two well-known patterns (increase in the biomass of all trophic levels, and increase in the biomass of the top trophic level and all other odd levels) emerge as being dominant in the three examples of coevolution presented here, thus providing some hope to find generalities when considering coevolution and fertilization together. However, knowing the exact costs of the traits involved in trophic interactions will be needed to properly address this question. This result underlines the need for more experimental studies about costs and benefits of traits, if reliable, long-term predictions of responses of ecosystem to environmental changes are to be made.

5. Conclusion

Including evolution in a very simple food-chain model modifies the potential effects of nutrient enrichment on this food chain. Predicting these effects requires a precise knowledge of the relevant phenotypic traits, their effects on interspecific interactions, and their costs. Although we acknowledge the existence of studies of such costs and effects (e.g., Mauricio, 1998), these studies are based on significance tests in extreme scenarios. The present article shows that more information is critically needed about these effects and costs.

Provided this information is available, the present framework might prove very useful to understand and predict long-term effects of nutrient enrichment on ecosystems. This framework can also be adapted to studying the effects of other long-term perturbations such as pollutions or global warming. For example, one could include the effect of temperature on life-history traits of plants and herbivores, and study how changes in temperature modify the position of the evolutionary equilibrium.

Once trade-off functions are known, space and time structure could also be considered. Coupling local adaptation within patches, such as described in the present model, and gene flow between patches, such as developed in the geographic mosaic models, would permit a better understanding of the effects of environmental changes on large spatial scales. Models of this kind would be useful to explore the idea that the grain of patchiness of nutrient load can play a role in the observed patterns of biomass across ecosystems (Power, 1992).

Acknowledgments

We thank Peter Abrams, Blandine Descamps-Julien, Gérard Lacroix, Elisa Thébault, Matthew Leibold and three anonymous referees for providing helpful comments on an earlier version of this manuscript.

Appendix A. Analysis of the model with plant evolution

At the evolutionary equilibrium, Eq. (4) vanishes. Substituting the expression for plant fitness (5) into (4), the evolutionary equilibrium becomes

$$\gamma'(s_p^{ESS})N^0 - \chi'(s_p^{ESS})H^0 = 0. \quad (\text{A.1})$$

Since s_p measures the level of plant defense, χ' is assumed to be negative. s_p is costly in terms of nutrient absorption, which means that γ' is negative too. The values of the equilibrium stocks (N^0 , H^0) are given by Eqs. (2). The derivatives of Eqs. (2) and (A.1) with respect to nutrient input I yield the variations of the various stocks (N^{ESS} , P^{ESS} , H^{ESS}) and of s_p^{ESS} with nutrient supply:

$$\begin{aligned} \frac{\partial N^{ESS}}{\partial I} &= K_1 + K_2 \frac{\partial s_p^{ESS}}{\partial I}, \\ \frac{\partial P^{ESS}}{\partial I} &= \frac{P^{ESS} \chi' \partial s_p^{ESS}}{\chi \partial I}, \\ \frac{\partial H^{ESS}}{\partial I} &= \frac{\gamma \partial N^{ESS}}{\chi \partial I}, \\ \frac{\partial s_p^{ESS}}{\partial I} &= \frac{K_1(-\gamma' + \frac{\chi' \gamma}{\gamma'})}{\gamma'' N^{ESS} - \chi'' H^{ESS} + K_2(-\gamma' + \frac{\chi' \gamma}{\gamma'})}. \end{aligned} \quad (\text{A.2})$$

In these expressions, K_1 and K_2 are positive and defined by:

$$\begin{aligned} K_1 &= \frac{\chi}{\chi e + \delta \gamma v_h}, \\ K_2 &= \frac{I \chi' - N^{ESS}(\chi' e + \delta \gamma' v_h)}{\chi e + \delta \gamma v_h}. \end{aligned} \quad (\text{A.3})$$

Eq. (A.2) implies that the plant biomass and the plant trait vary similarly following addition of nutrient. Using (2) and (A.1), that $(-\gamma' + \frac{\chi' \gamma}{\chi}) < 0$.

According to Marrow et al. (1996), the condition for the stability of the evolutionary equilibrium is

$$\begin{aligned} \left(\frac{\partial^2 W_{Pm}}{\partial s_{pm}^2} \right)_{spm \rightarrow sp} + \left(\frac{\partial^2 W_{Pm}}{\partial s_{pm} \partial s_p} \right)_{spm \rightarrow sp} < 0 \Leftrightarrow \gamma'' N^{ESS} \\ - \chi'' H^{ESS} + \frac{K_2 d_p \chi - \chi'^2 H^{ESS'}}{\chi} < 0 \end{aligned} \quad (\text{A.4})$$

while the condition to get no evolutionary branching is

$$\left(\frac{\partial^2 W_{pm}}{\partial s_{pm}^2}\right)_{spm \rightarrow sp} < 0 \Leftrightarrow \gamma'' N^{ESS} - \chi'' H^{ESS} < 0. \quad (A.5)$$

Using these stability conditions, it is possible to prove that all the expressions in (A.2) are positive. This means that if the evolutionary equilibrium is stable, and if there is no evolutionary branching, then the plant trait is increasing when nutrient supply increases. The equilibrium stocks of all the compartments as well as the plant trait increase together with nutrient input.

Evolutionary branching occurs when the system converges to the evolutionary equilibrium but does not halt at this point. The coexistence of mutants with different phenotypes then becomes possible, and the evolutionary trajectory continues with the two phenotypes (“species”) diverging from one another.

Appendix B. Analysis of the model with plant–herbivore coevolution

The variations of the various equilibrium stocks and of the plant and herbivore traits with nutrient input are given by the derivatives of Eqs. (2) and (B.1) which describe the evolutionary equilibrium conditions:

$$\begin{aligned} \gamma'(s_p^{ESS})N^{ESS} + \chi'(s_h^{ESS} - s_p^{ESS})H^{ESS} &= 0, \\ \chi'(s_h^{ESS} - s_p^{ESS})P^{ESS} - \delta'(s_h^{ESS}) &= 0. \end{aligned} \quad (B.1)$$

These derivatives yield the following results:

$$\begin{aligned} \frac{\partial N^{ESS}}{\partial I} &= K_1 + K_3 \frac{\partial s_p^{ESS}}{\partial I}, \\ \frac{\partial P^{ESS}}{\partial I} &= \frac{P^{ESS} \chi'}{\chi} \frac{\partial s_p^{ESS}}{\partial I}, \\ \frac{\partial H^{ESS}}{\partial I} &= \frac{\gamma}{\chi} K_1 + \frac{\gamma K_3 - H^{ESS} \chi' K_2}{\chi} \frac{\partial s_p^{ESS}}{\partial I}, \\ \frac{\partial s_h^{ESS}}{\partial I} &= K_2 \frac{\partial s_p^{ESS}}{\partial I}, \\ \frac{\partial s_p^{ESS}}{\partial I} &= \frac{-K_1 \chi' d_p}{\gamma'' N^{ESS} - \chi'' H^{ESS} (K_2 - 1) + \frac{K_3 \chi' d_p}{\chi}}. \end{aligned} \quad (B.2)$$

$$\begin{aligned} \frac{\partial s_p^{ESS}}{\partial I} &= 0, \\ \frac{\partial N^{ESS}}{\partial I} &= \frac{a H^{ESS} N^{ESS}}{d_p} \frac{\partial s_H^{ESS}}{\partial I}, \\ \frac{\partial s_H^{ESS}}{\partial I} &= \frac{\chi}{\frac{a H^{ESS}}{d_p} (\chi I + \delta d_p (v_h - v_p)) - a(I - e N^{ESS}) - f(d_p (v_h - v_p) - \gamma v_h N^{ESS})}. \end{aligned} \quad (C.3)$$

where K_1 , K_2 and K_3 are defined by

$$\begin{aligned} K_1 &= \frac{\chi}{\chi e + \delta \gamma v_h}, \\ K_2 &= \frac{\delta' \chi' - \delta \chi''}{\delta'' \chi - \delta \chi''}, \\ K_3 &= \frac{I \chi' (K_2 - 1) - N^{ESS} (\chi' e (K_2 - 1) + \delta' K_2 \gamma v_h + \delta \gamma' v_h)}{\chi e + \delta \gamma v_h}. \end{aligned} \quad (B.3)$$

As in the other appendices, the evolutionary equilibrium has to be stable and there should not be evolutionary branching. If one of these two conditions is not met, then derivatives (B.2) are useless. Contrary to the case analyzed in Appendix A, the conditions for the stability of the evolutionary equilibrium do not provide the sign of K_2 and K_3 . This is why we do not detail them here, but the assessment of the evolutionary stability was made using the Jacobian matrix of system (8) (Marrow et al., 1996). Thus, the only general result in the case of the coevolutionary model is that plant biomass and plant defense vary similarly when nutrient supply is modified. Concerning the other compartments and the herbivore trait, no general rule can be given, as the variation will depend on the form of the functions χ , γ and δ

Appendix C. Analysis of the model with linear trade-offs (example 1)

When trade-offs are linear, the analysis of coevolution is quite simple. The position of the equilibrium is given by the canonical equations:

$$\begin{aligned} -c N^{ESS} + a H^{ESS} &= 0, \\ a P^{ESS} - f &= 0. \end{aligned} \quad (C.1)$$

Then, the derivative of the equation (C.1) regarding to I yields

$$\begin{aligned} \frac{\partial P^{ESS}}{\partial I} &= 0, \\ \frac{\partial H^{ESS}}{\partial I} &= \frac{c}{a} \frac{\partial N^{ESS}}{\partial I}. \end{aligned} \quad (C.2)$$

Using the position of the ecological equilibrium (2), the derivative of this equilibrium with respect to I is

From this analysis, we can draw the following conclusions:

- Plant trait and plant biomass do not vary with fertilization when trade-offs are linear.
- Variations of the herbivore and nutrient stocks are correlated with the variations of the herbivore trait.
- Variations of the herbivore traits with nutrient enrichment may be positive or negative.

These analytical results are in accordance with the results of Table 4a. This table suggests that variations of herbivore traits are rarely negative, which is fairly intuitive when (C.3) and (2) are considered together.

References

- Abrams, P.A., 1984. Foraging time optimization and interactions in food webs. *Am. Nat.* 124, 80–96.
- Abrams, P.A., 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. *Evolution* 40 (6), 1229–1247.
- Abrams, P.A., 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *Am. Nat.* 140, 573.
- Abrams, P.A., 1993. Effect of increased productivity on the abundance of trophic levels. *Am. Nat.* 141 (3), 351–371.
- Abrams, P.A., Matsuda, H., Harada, Y., 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* 7, 465–487.
- Abrams, P.A., 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *Am. Nat.* 146, 112–134.
- Abrams, P., 1996. Dynamics and interactions in food webs with adaptive foragers. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, USA, pp. 113–121.
- Abrams, P.A., Matsuda, H., 1997. Prey adaptation as a cause of predator–prey cycles. *Evolution* 51, 1742–1750.
- Abrams, P.A., 2000. The evolution of predator–prey systems: theory and evidence. *Annu. Rev. Ecol. Syst.* 31, 79–105.
- Abrams, P.A., 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: an assessment of three methods. *Ecol. Lett.* 4 (2), 166–175.
- Abrams, P.A., Vos, M., 2000. Adaptation, density dependence, and the responses of trophic level abundances to mortality. *Evol. Ecol. Res.* 5, 1113–1132.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* 25 (4B), 704–726.
- Angilletta, M.J., Wilson, R.S., Navas, C.A., James, R.S., 2003. Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol. Evol.* 18 (5), 234–240.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326.
- Armstrong, R.A., 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* 60 (1), 76–84.
- Boesch, D., Burreson, E., Dennison, W., Houde, E., Kemp, M., Kennedy, V., Newell, R., Paynter, K., Orth, R., Ulanowicz, R., 2001. Factors in the decline of coastal ecosystems. *Science* 293 (5535), 1589–1590.
- Brett, M.T., Goldman, C.R., 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* 275 (5298), 384–386.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, D.M., Lodge, M.M., Kretchmet, D., He, X., von Ende, C.N., 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68, 1863–1876.
- Champagnat, N., Ferrière, R., Ben Arous, G., 2001. The canonical equation of adaptive dynamics: a mathematical view. *Selection* 2, 73–84.
- Chase, J.M., 1998. Central-place forager effects on food web dynamics and spatial pattern in Northern California meadows. *Ecology* 79 (4), 1236–1245.
- Chase, J.M., 2000. Are there real differences among aquatic and terrestrial food webs? *Trends Ecol. Evol.* 15 (10), 408–412.
- Chase, J.M., 2003. Strong and weak trophic cascades along a productivity gradient. *Oikos* 101, 187–195.
- Chase, J.M., Leibold, M.A., Downing, A.L., Shurin, J.B., 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 81 (9), 2485–2497.
- Coe, M.J., Cumming, D.M.H., Phillipson, J., 1976. Biomass and production of large herbivores in relation to rainfall and primary production. *Oecologia* 22, 341–354.
- Dawes-Gromadzki, T.Z., 2002. Trophic trickles rather than cascades: conditional top-down and bottom-up dynamics in an Australian chenopod shrubland. *Aust. Ecol.* 27, 490–508.
- Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34, 579–612.
- Diehl, S., Feissel, M., 2000. Effects of enrichment on three-level food chains with omnivory. *Am. Nat.* 155 (2), 200–218.
- Dyer, L.A., Letourneau, D.K., 2003. Top-down and bottom-up diversity cascades in detrital versus living food webs. *Ecol. Lett.* 6, 60–68.
- Eshel, I., 1983. Evolutionary and continuous stability. *J. Theor. Biol.* 103, 99–111.
- Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structuring nearshore communities. *Science* 185, 1058–1060.
- Forkner, R.E., Hunter, M.D., 2000. What goes up must come down? Nutrient addition and predation pressure on oak insects. *Ecology* 81, 1588–1600.
- Fretwell, S.D., 1977. Regulation of plant communities by food-chains exploiting them. *Perspect. Biol. Med.* 20 (2), 169–185.
- Fretwell, S.D., 1987. Food chain dynamics: the central theory of ecology. *Oikos* 50, 291–301.
- Gange, A.C., 1997. *Multitrophic Interactions in Terrestrial Systems*. Blackwell, Oxford.
- Gomulkiewicz, R., Thompson, J.N., Holt, R.D., Nuismer, S.L., Hochberg, M.E., 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. *Am. Nat.* 156, 156–174.
- Grant, P.R., Grant, B.R., 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49, 241–251.
- Hairton, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *Am. Nat.* 94, 421–425.
- Hansson, L., 1979. Food as a limiting factor for small rodent numbers. Test of two hypotheses. *Oecologia* 37 (3), 297–314.
- Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M., Fox, C.W., 2003. Rapid evolution of egg size in captive salmon. *Science* 299, 1738–1740.
- Hendry, A., Wenburg, J.K., Bentzen, P., Volk, E.C., Quinn, T.P., 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290, 516–518.
- Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67 (3), 283–335.
- Hillebrand, H., 2003. Opposing effects of grazing and nutrients on diversity. *Oikos* 100, 592–600.

- Hochberg, M.E., van Baalen, M., 1998. Antagonistic coevolution over productivity gradients. *Am. Nat.* 152, 620–634.
- Huey, R.B., Gilchrist, G.W., Carlsen, M., Serra, L., 2000. Rapid evolution of a latitudinal cline in body size in an introduced fly. *Science* 287 (5451), 308–309.
- Hulot, F.D., Lacroix, G., Lescher-Moutoué, F., Loreau, M., 2000. Functional diversity governs ecosystem response to nutrient enrichment. *Nature* 405, 340–344.
- Hunter, M.D., 2001. Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic Appl. Ecol.* 4, 293–310.
- Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724–732.
- Illius, W.A., Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. *Anim. Behav.* 47, 481–484.
- Jarvinen, M., 2002. Control of plankton and nutrient limitation in small boreal brown-water lakes: evidence from small and large-scale manipulation experiments. Academic Dissertation.
- Kaiser, J., 2001. The other global pollutant: nitrogen proves tough to curb. *Science* 294, 1268–1269.
- Krieger, R.I., Feeny, P., Wilkinson, C.F., 1971. Detoxification enzymes in the guts of caterpillars: an evolutionary answer to plant defenses? *Science* 172, 579–581.
- Lacroix, G., Lescher-Moutoué, F., Pourriot, R., 1996. Trophic interactions, nutrient supply, and the structure of freshwater pelagic food webs. In: Hochberg, M.E., Clobert, J., Barbault, R. (Eds.), *Aspects of the Genesis and Maintenance of the Biological Diversity*. Oxford University Press, Oxford, pp. 162–179.
- Le Galliard, J.-F., Ferrière, R., Dieckmann, U., 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57 (1), 1–17.
- Leibold, M.A., 1989. Resource edibility and the effects of predators and productivity on consumer-resource interactions. *Am. Nat.* 134, 922–949.
- Leibold, M.A., 1996. A graphical model of keystone predation: effects of productivity on abundance, incidence and ecological diversity in communities. *Am. Nat.* 147, 784–812.
- Leibold, M.A., Chase, J.M., Shurin, J., Downing, A., 1997. Species turnover and the regulation of trophic structure. *Annu. Rev. Ecol. Syst.* 28, 467–497.
- Loeuille, N., Loreau, M., Ferrière, R., 2002. Consequences of plant-herbivore coevolution on the dynamics and functioning of ecosystems. *J. Theor. Biol.* 217, 369–381.
- Marrow, P., Dieckmann, U., Law, R., 1996. Evolutionary dynamics of predator-prey systems: an ecological perspective. *J. Math. Biol.* 34, 556–578.
- Mauricio, R., 1998. Costs of resistance to natural enemies in field populations of the annual plant, *Arabidopsis thaliana*. *Am. Nat.* 151, 20–28.
- McQueen, D.J., Johannes, M.R., Post, J.R., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* 59, 289–309.
- Mikola, J., Setälä, H., 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology* 79, 153–164.
- Moon, D.C., Stiling, P., 2002. Top-down, bottom-up, or side to side? Within-trophic-level interactions modify trophic dynamics of a salt marsh herbivore. *Oikos* 98, 479–489.
- Musser, R.O., Hum-Musser, S.M., Eichenseer, H., Peiffer, M., Ervin, G., Murphy, J.B., Felton, G.W., 2002. Herbivory: caterpillar saliva beats plant defences. *Nature* 416, 599–600.
- Neubert, M.G., Blumenshine, S.C., Duplisea, D.E., Jonsson, T., Rashleigh, B., 2000. Body size and food web structure: testing the equiprobability assumption of the cascade model. *Oecologia* 123, 241–251.
- Nuismer, S.L., Thompson, J.N., Gomulkiewicz, R., 1999. Gene flow and geographically structured coevolution. *Proc. R. Soc. London Ser. B: Biol. Sci.* 266, 605–609.
- Nuismer, S.L., Thompson, J.N., Gomulkiewicz, R., 2000. Coevolutionary clines across selection mosaics. *Evolution* 54, 1102–1115.
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118, 240–261.
- Oksanen, T., 1983. Trophic exploitation and arctic phytomass patterns. *Am. Nat.* 122, 45–52.
- Persson, A., Hansson, L.A., Brönmark, C., Lundberg, P., Pettersson, L.B., Greenberg, L., Nilsson, A.P., Nyström, P., Romare, P., Tranvik, L., 2001. Effects of enrichment on simple aquatic food webs. *Am. Nat.* 157 (6), 654–669.
- Polis, G.A., 1994. Food webs, trophic cascades and community structure. *Aust. J. Ecol.* 19 (2), 121–136.
- Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a trophic cascade a trophic cascade? *Trends Ecol. Evol.* 15, 473–475.
- Power, M.E., 1990. Resource enhancement by indirect effects of grazers – armored catfish, algae, and sediment ecology. *Ecology* 71, 897–904.
- Power, M.E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73 (3), 733–746.
- Rausher, M.D., 1996. Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* 12, 212–217.
- Reale, D., McAdam, A.G., Boutin, S., Berteaux, D., 2003. Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. London Ser. B: Biol. Sci.* 270, 591–596.
- Reznick, D.N., Shaw, F.H., Rodd, F.H., Shaw, R.G., 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275, 1934–1937.
- Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155, 141–153.
- Simms, E.L., Rausher, M.D., 1987. Costs and benefits of the evolution of plant defense against herbivory. *American naturalist* 130, 570–581.
- Smith, F.E., 1969. Effects of enrichment in mathematical models. In: *Eutrophication: Causes, Consequences, Correctives*. National Academy Press, Washington DC, pp. 631–645.
- Thompson, J.N., 1997. Evaluating the dynamics of coevolution among geographically structured populations. *Ecology* 78 (6), 1619–1623.
- Thompson, J.N., 1998. Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13 (8), 329–332.
- Thompson, J.N., 1999. Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.* 153, S1–S14.
- Thompson, J.N., Cunningham, B.M., 2002. Geographic structure and temporal dynamics of coevolutionary selection. *Nature* 417, 735–738.
- Thrall, P.H., Burdon, J.J., 2003. Evolution of virulence in a plant host-pathogen metapopulation. *Science* 299, 1735–1737.
- Tuomi, J., 1992. Toward integration of plant defence theories. *Trends in Ecology and Evolution* 11, 365–367.