



Consequences of Plant-Herbivore Coevolution on the Dynamics and Functioning of Ecosystems

NICOLAS LOEUILLÉ*†, MICHEL LOREAU† AND RÉGIS FERRIÈRE†

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

(Received on 13 September 2001, Accepted in revised form on 11 February 2002)

The potential consequences of plant–herbivore coevolution for ecosystem functioning are investigated using a simple nutrient-limited ecosystem model in which plant and herbivore traits are subject to adaptive dynamics. Although the ecological model is very simple and always reaches a stable equilibrium in the absence of evolution, coevolution can generate a great diversity of dynamical behaviors. The evolutionary dynamics can lead to a stable equilibrium. If the evolution of plants is fast enough, certain values of the trade-off parameters lead to complex evolutionary cycles bounded by physiological constraints. The dynamical behavior of the model is very different when the dynamics of inorganic nutrient is ignored and plant competition is modeled by a logistic growth function. This emphasizes the importance of including explicit nutrient dynamics in studies of plant–herbivore coevolution.

© 2002 Elsevier Science Ltd. All rights reserved.

Introduction

Herbivory is the basis of classical food webs, and is therefore important for the understanding of ecosystem functioning. Many studies have been devoted to this biological interaction. They are usually focused on internal (plant or herbivore traits) and external (nutrient supply, predators) factors that influence herbivory. A number of dynamical models have been developed to analyse the functional role of herbivory in ecosystems (see for example, Loreau, 1995; de Mazancourt *et al.*, 1998, 1999). In these models, the interactions between species and with the environment are expressed by constant parameters. Many factors, however, such as environmental changes (Kesh *et al.*, 2000; Leibold, 1996;

Post *et al.*, 1999) or the evolution of species' behavior, physiology or morphology, are likely to influence these parameters (Abrams, 1996).

Here, we consider that herbivory acts as a selective pressure on plants. Plants that experience herbivory may evolve physical or chemical defenses (Rausher, 1996; Westoby, 1989) or compensatory responses to herbivory (Mc Naughton, 1983). Herbivores may then evolve in response to these defenses. As described in Krieger *et al.* (1971) and Seldal *et al.* (1994), they may improve their digestion and detoxification capacities. Thus, both species are allowed to evolve, leading to plant–herbivore coevolution. Since this coevolution affects the strength of the plant–herbivore interaction, the parameters that govern ecosystem stocks and fluxes are not fixed, they evolve with species. A comparison of the model with fixed (ecological dynamics) and changing (evolutionary dynamics) parameters

*Corresponding author. Tel.: +33-0-1-44-32-38-08; fax: +33-0-1-44-32-38-85.

E-mail address: loeuille@biologie.ens.fr (N. Loeuille).

shows the importance of coevolution in both the population dynamics of the interacting species and the dynamics of ecosystem processes.

Herbivores are not simply predators. They eat plants, but do not kill them. Moreover, as they digest plants and release nutrients, they can increase nutrient recycling efficiency, which has a positive effect on neighboring plants. When inorganic nutrient dynamics is taken into account, the herbivore–plant interaction may even be seen as a form of indirect mutualism under certain conditions (Loreau, 1995; de Mazancourt *et al.*, 1998, 1999, 2001), although the empirical evidence for this hypothesis is controversial (Belsky, 1986; Belsky *et al.*, 1993; McNaughton 1979, 1983; McNaughton *et al.*, 1997). As the effect of the herbivore on the nutrient cycle is important to understand the plant–herbivore interaction, nutrient dynamics may also be important to understand the coevolution of the two species. In the present article, we compare two models, of which one includes this feedback, whereas the other does not take it explicitly into account. In the latter model, plant competition is expressed through a logistic growth function. This comparison allows us to investigate the role of nutrient dynamics on the ecological and the evolutionary dynamics of the system.

Thus, the objective of this work is two-fold. It aims, first, to understand the consequences of plant–herbivore coevolution on the dynamics and functioning of the system, and, second, to assess the importance of considering explicitly nutrient dynamics on the dynamics of the system on both ecological and evolutionary time-scales.

The Ecological Model

Our ecological model describes a spatially homogeneous, nutrient-limited ecosystem (Fig. 1). There are three nutrient compartments, namely inorganic nutrient (N), plants (P) and herbivores (H). Nutrient uptake by plants and plant consumption by herbivores are assumed to be simple Lotka–Volterra functions. Consequently, the food web is top-down structured. The nutrient is released by plants and herbivores following simple, linear donor-controlled functions. Only part of the released nutrient is

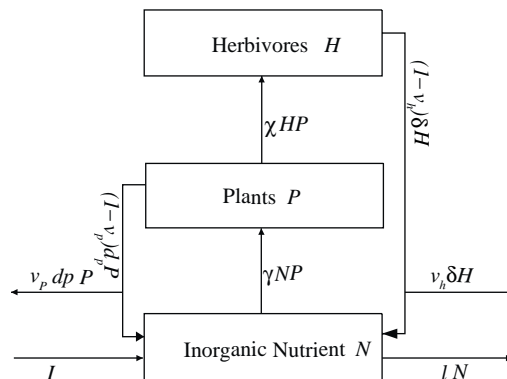


FIG. 1. Ecological model for the plant–herbivore interaction in a nutrient-limited ecosystem. Variables and parameters are defined in Table 1.

recycled in the inorganic nutrient pool (v_P and v_H determining the fractions of nutrient that are lost to the system during the recycling process).

The model is described by the following differential equations:

$$\frac{dN}{dt} = I - IN + (1 - v_P)d_P P + (1 - v_H)\delta H - \gamma NP,$$

$$\frac{dP}{dt} = P(\gamma N - d_P - \chi H),$$

$$\frac{dH}{dt} = H(\chi P - \delta). \quad (1)$$

The various parameters and variables are defined in Table 1.

At the ecological equilibrium, the rate of increase of all the compartments is zero. Solving eqns (1) then provides the equilibrium nutrient stocks:

$$\begin{aligned} N^0 &= \frac{\chi I + \delta d_P (v_H - v_P)}{\chi I + \delta \gamma v_H}, \\ P^0 &= \frac{\delta}{\chi}, \\ H^0 &= \frac{\chi(I\gamma - d_P I) - \delta \gamma d_P v_P}{\chi(\chi I + \delta \gamma v_H)}. \end{aligned} \quad (2)$$

As in previous studies (Loreau, 1995; de Mazancourt *et al.*, 1998, 1999, 2001), we assume that plant and herbivore biomasses are

TABLE 1
Definitions and units of the different variables of the model

Variable	Dimension	Definition
P	Quantity of nutrient per unit of area	Stock of plant nutrient of the system
N	Quantity of nutrient per unit of area	Stock of inorganic nutrient in plants' absorption pool of the system
H	Quantity of nutrient per unit of area	Stock of herbivores nutrient of the system
ϕ	Quantity of nutrient per unit of area and per unit of time	Primary production of plants of the system
s_P	Dimensionless	Plants' defense capacity (both chemical and physical) submitted to evolution
s_H	Dimensionless	Part of the herbivore's voracity submitted to evolution
χ	(Quantity of nutrient per unit of area \times time) ⁻¹	Consumption rate of plants by herbivores
δ	Time ⁻¹	Detritus production rate of herbivores
γ	(Quantity of nutrient per unit of area \times time) ⁻¹	Rate of nutrient uptake by plants

proportional to their nutrient stocks, after multiplication by a suitable C:N ratio.

Note from eqns (2) that there is a minimum value of nutrient input, I , below which the ecological dynamics leads the herbivore to extinction. The analysis of the Jacobian matrix easily shows that the ecological equilibrium is stable whenever I is sufficient to maintain the herbivore population. Thus, the ecological dynamics never leads to cyclic behaviors in the absence of evolution.

Evolutionary Dynamics

TRAITS SUBJECTED TO EVOLUTION

For plants, the trait s_P subjected to evolution represents the production of antiherbivore defenses. These defenses can be either physical (e.g. production of thorns) or chemical (e.g. production of tannins) (du Toit, 1990). Another form of defense is the attraction by plants of the herbivores' predators, using these predators as bodyguards (Takabayashi *et al.*, 1994; Kessler & Baldwin, 2001). For herbivores, the trait s_H subjected to evolution determines the herbivore's voracity.

The parameters symbolized by Greek letters in the ecological model are assumed to be modified by the evolution of plant and herbivore traits. Parameter χ , which measures the rate of plant consumption by herbivores, increases with s_H and decreases with s_P . We chose the following expression for this parameter (Abrams &

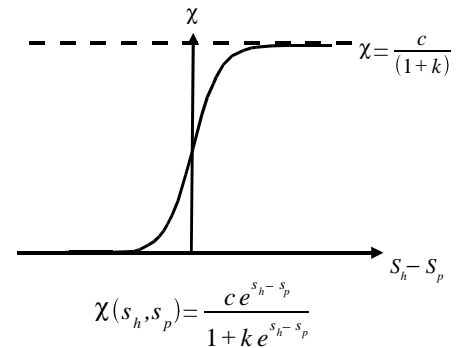


FIG. 2. Variations of the parameter describing the plant-herbivore interaction depending on the difference between the trait s_H (herbivore voracity) and s_P (plant defense).

Matsuda, 1997b) (Fig. 2):

$$\chi(s_P, s_H) = \frac{c \text{EXP}(s_H - s_P)}{1 + k \text{EXP}(s_H - s_P)}. \quad (3)$$

Thus, as one would expect, χ is always non-negative, it grows with the difference between the two traits and remains finite even when the difference between the two traits is large.

We assume that both traits are costly. This assumption has often been made (and debated) for plants (Herms & Matson, 1992; Levin, 1991; Rauscher, 1996). The basic idea is that the plants have a certain amount of nutrient and energy available and that the nutrient and energy they devote to defense is lost for growth and reproduction. Possible costs for herbivore

evolution have seldom been addressed. In the present model, we assume that the greater the voracity of the herbivore, the greater is its nutrient losses, through either increased mortality due to a lower attention to predators (Illius & Fitzgibbon, 1994) or increased respiratory and excretory losses.

Mathematically speaking, these trade-offs are expressed through δ and γ :

$$\begin{aligned}\gamma(s_P) &= u \text{EXP}(-as_P), \\ \delta(s_H) &= d_H \text{EXP}(gs_H).\end{aligned}\quad (4)$$

Parameters a and g are called trade-off parameters and describe how heavy the costs of the evolving traits are. Note that the special cases where one or both of the traits are cost-free can be modeled using the particular case a and/or $g=0$. These particular cost functions are chosen for mathematical convenience. Whatever be the values of the two traits, they are positive and monotonous, and they permit a certain number of simplifications. There are no general results regarding the shape of the plant trade-off between growth and defense in the literature (Mauricio, 1998; Herms & Mattson, 1992). The herbivore trade-off is even less studied; we were unable to find data on the shape of the trade-off between herbivore voracity and mortality (however, see Illius & Fitzgibbon, 1994).

These trade-offs also avoid that the traits take too large values. They give ‘‘smooth’’ maximum limits to the values of the two traits. They do not introduce minimum limits to these traits, however, and infinitely negative values of the two traits are also biologically irrelevant. To avoid such biases, while keeping the model tractable, we chose to introduce a ‘‘harsh’’ minimum limit to the traits. This limit is fixed to zero for simplicity, but we checked that this value does not influence the qualitative results of the model.

ANALYSIS OF EVOLUTIONARY DYNAMICS USING THE THEORY OF ADAPTIVE DYNAMICS

The model is analysed using the theory of adaptive dynamics (Metz *et al.*, 1996, Geritz *et al.*, 1997). The main hypothesis made in this theory is that the time-scale of evolutionary

dynamics is much greater than the time-scale of ecological dynamics. With this simplification, the analysis of the model can be split into different steps.

In the first step, the ecological dynamics leads system (1) to its ecological equilibrium described by eqns (2).

In the second step, the mutation process takes place. For example, let us suppose a plant mutant whose trait s_{Pm} is close to the trait s_P of the plant resident. The fitness of this mutant is then defined by its growth rate in the resident population:

$$\begin{aligned}W_{Pm}(s_{Pm}, s_P, s_H) &= \frac{1}{P_m} \frac{dP_m}{dt} = uN^0 \text{EXP}(-as_{Pm}) \\ &\quad - d_P - \frac{cH^0 \text{EXP}(s_H - s_{Pm})}{1 + k \text{EXP}(s_H - s_{Pm})}.\end{aligned}\quad (5a)$$

The mutant is able to invade the resident population if and only if this function is positive. In this case, s_{Pm} will become the new resident trait for the plant population. The new situation corresponds to a new ecological equilibrium (2), in which the Greek-letter parameters are modified by the new trait value. The appearance of a herbivore mutant is treated the same way, its fitness being

$$\begin{aligned}W_{Hm}(s_{Hm}, s_P, s_H) &= \frac{1}{H_m} \frac{dH_m}{dt} = \frac{cP^0 \text{EXP}(s_{Hm} - s_P)}{1 + k \text{EXP}(s_{Hm} - s_P)} \\ &\quad - d_H \text{EXP}(gs_{Hm}).\end{aligned}\quad (5b)$$

Step-by-step, the values of the traits s_H and s_P change on the evolutionary dynamical time-scale. As demonstrated in Marrow *et al.* (1996), these discrete trait changes can be put in a continuous form. The corresponding equations are

$$\begin{aligned}\frac{Ds_P}{Dt} &= K_P \mu_P \sigma_P^2 P^0 \left(\frac{\partial W_{Pm}}{\partial s_{Pm}} \right)_{spm \rightarrow s_P} \\ \frac{Ds_H}{Dt} &= K_H \mu_H \sigma_H^2 H^0 \left(\frac{\partial W_{Hm}}{\partial s_{Hm}} \right)_{shm \rightarrow s_H}\end{aligned}\quad (6)$$

K is a parameter scaling plant and herbivore biomass to trait values, μ the mutation rate and σ^2 the genetic variability of the corresponding population. The product $\mu\sigma^2$ measures the rate of evolution of the species (Marrow *et al.*, 1996). Equations (6) imply that the rate of change of the two traits is proportional to the fitness gradient in each species. Although these equations are introduced through the adaptive dynamics theory, they can also be obtained from quantitative genetics models as an approximation (Abrams, 2001).

The analysis these equations (6) yields the evolutionary outcome of the plant-herbivore interaction. We first find the fixed points of eqns (6), which are the evolutionary equilibria of the system.

$$\begin{aligned} \left(\frac{\partial W_{Pm}}{\partial s_{Pm}}\right)_{spm \rightarrow sp} &= 0, \\ \left(\frac{\partial W_{Hm}}{\partial s_{Hm}}\right)_{shm \rightarrow sh} &= 0. \end{aligned} \tag{7}$$

We then determine their stability using the Jacobian matrix evaluated at the equilibrium points. An evolutionary equilibrium will be stable if and only if (Marrow *et al.*, 1996)

$$\begin{aligned} Trace(J) &< 0, \\ Det(J) &> 0, \end{aligned} \tag{8}$$

where J is the Jacobian matrix of system (6):

$$J = \begin{bmatrix} \mu_P \sigma_P^2 P \left(\frac{\partial^2 W_P}{\partial^2 s_{Pm}^2} + \frac{\partial^2 W_P}{\partial s_{Pm} \partial s_P} \right) & \mu_P \sigma_P^2 P \left(\frac{\partial^2 W_P}{\partial s_{Pm} \partial s_H} \right) \\ \mu_H \sigma_H^2 H \left(\frac{\partial^2 W_H}{\partial s_{Hm} \cdot \partial s_P} \right) & \mu_H \sigma_H^2 H \left(\frac{\partial^2 W_H}{\partial^2 s_{Hm}^2} + \frac{\partial^2 W_H}{\partial s_{Hm} \partial s_H} \right) \end{bmatrix}_{sm \rightarrow s} \tag{9}$$

Evolutionary Outcomes of the Adaptive Model

EVOLUTIONARY ISOCLINES

In what follows, the isocline of each species is defined as the ensemble of the traits (s_P, s_H) such that the fitness gradient for that species' trait in eqns (6) is zero. These isoclines, linked to the evolutionary dynamics of the system, should not

be mistaken for the ones corresponding to the ecological dynamics of the system [eqns (1)].

Determining the fixed points of system (6) is equivalent to finding the intersection of the isoclines of the fitness gradients. In order to get a full comprehension of what happens, let us fix one of the two traits and analyse the two isoclines separately. It is easy to find an analytical expression for the herbivore fitness isocline from eqns (7):

$$s_H = s_P + \text{LN} \left(\frac{1-g}{gk} \right) \quad (0 < g < 1). \tag{10}$$

This equation is a straight line with slope 1 [Fig. 3(A)]. It is easy to demonstrate that this isocline is stable, i.e., if the trait s_P is fixed, the herbivore trait s_H will tend to this isocline by successive mutation-invasion processes. The role of the herbivore trade-off parameter g in evolutionary dynamics is made clear by considering the y -intercept. The greater g , the smaller this intercept, and the smaller the herbivore voracity. This result is rather intuitive since a larger g means a higher cost in terms of nutrient losses. Note that the intercept depends also on k . The role of this parameter is very similar to that of g in most of the results of the model. In many ways, it can also be considered as a trade-off parameter of the herbivore.

The determination of the plant isocline is not possible analytically. Figure 3(B) displays this isocline as determined numerically. The isocline is bell shaped. This shape is robust to changes of

parameters, but the exact position of the isocline depends on the trade-off parameters a and g . The isocline is a boundary between an inner space where plant fitness increases with s_P and an outer space where it decreases. Consequently, the isocline is stable on its right part and unstable on its left part. There is no isocline for positive traits values if parameter a is larger

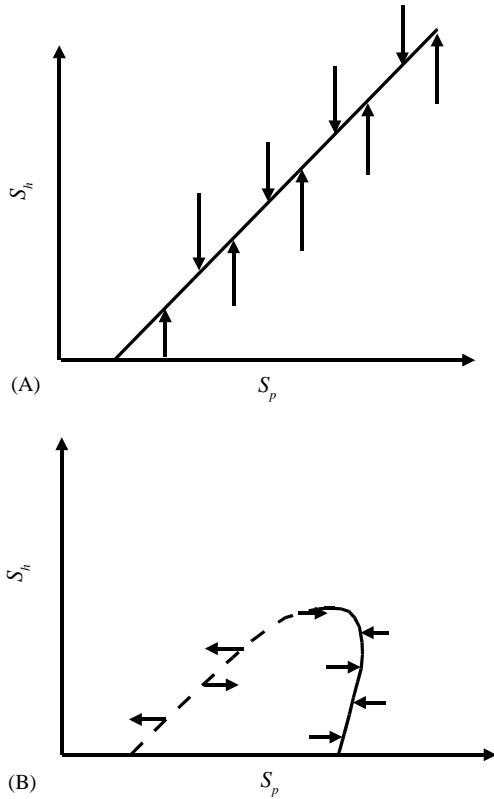


FIG. 3. (A) Isocline of herbivore fitness. This isocline is always stable. (B) Isocline of the plant fitness. The stable part of the isocline is shown by the solid line whereas its unstable part is shown by the dashed line. Although this isocline cannot be determined analytically, its bell shape and stability do not change with parameters.

than a threshold depending on the values of the various parameters.

COEVOLUTIONARY DYNAMICS

If the two traits are allowed to change simultaneously, coevolution takes place. The dynamics then depends strongly on the values of the trade-off parameters a and g . The isoclines intersect only if g is larger than a , i.e., if herbivore voracity is more costly than plant defense. The equilibrium obtained in these cases can be stable or unstable depending on the way the two isoclines intersect and the respective rates of evolution of plants and herbivores (Fig. 4).

If the two isoclines intersect in the stable part of the plant isocline, the evolutionary equilibrium is globally stable (ESS). Evolution seen always leads to this equilibrium whatever the

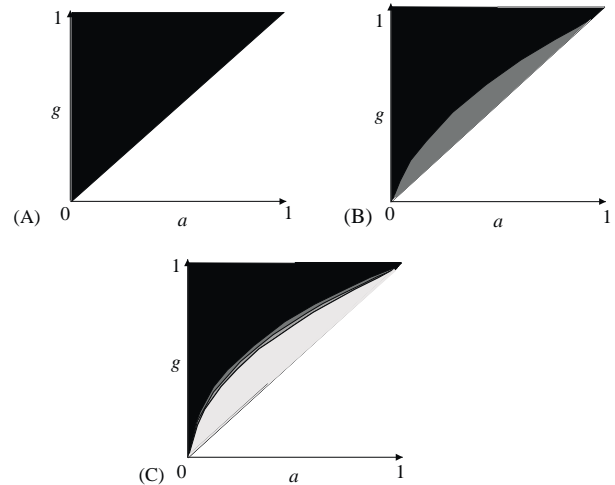


FIG. 4. Bifurcation diagrams for different evolution speeds: (A) $\mu_p \sigma_p^2 = 0.1 \mu_H \sigma_H^2$, (B) $\mu_p \sigma_p^2 = \mu_H \sigma_H^2$, (C) $\mu_p \sigma_p^2 = 10 \mu_H \sigma_H^2$. The black part corresponds to parameter values leading to a stable evolutionary node. The intermediate gray [particularly visible in (B)] indicates a stable evolutionary spiral. If the plant evolves faster than the herbivore, unstable cases appear. In figure C, darkest gray corresponds to the parameters values leading to unstable evolutionary nodes whereas the intermediate gray corresponds to parameters values leading to unstable evolutionary spirals. The values of the parameters other than a and g are: ($I = 60$, $l = 0.05$, $u = 0.1$, $c = 1$, $v_H = 0.25$, $v_P = 0.2$, $d_P = 0.3$, $d_H = 0.275$, $k = 1$).

initial point (s_{P0}, s_{H0}) . If the two isoclines intersect in the unstable part of the plant isocline, the stability of the equilibrium depends on the relative rates of evolution of plants and herbivores. If the rate of plant evolution is high enough compared with that of herbivore evolution, the instability of the plant isocline prevails over the stability of the herbivore isocline, and the equilibrium is unstable. Otherwise, the equilibrium is stable. Figures 4(A)–(C) show that the greater the rate of plant evolution compared with the rate of herbivore evolution, the greater the likelihood of finding an unstable equilibrium. All the unstable equilibria observed in the model yield stable limit cycles. In these cases, all the evolutionary trajectories lead to this cycle independent of the initial point (s_{P0}, s_{H0}) (Fig. 5). After a transient state, the dynamics of both traits becomes periodic. The amplitude of the limit cycle depends on the trade-off parameter values. Since we fixed a minimum value for the two traits, however, the evolutionary

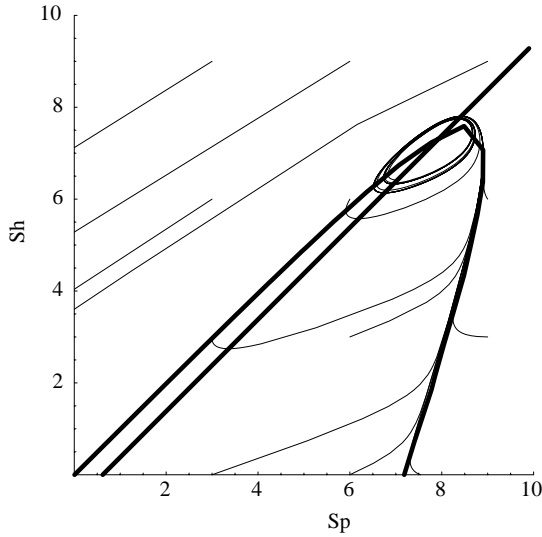


FIG. 5. Coevolutionary cycles, in which traits vary periodically. In this figure, the values of trade-off parameters are $a=0.5$, $g=0.65$, evolution rates are such that $\mu_P\sigma_P^2 = 2\mu_H\sigma_H^2$, and the other parameters have the same values as in Fig. 4. The two isoclines are also drawn. The unstable evolutionary equilibrium lies at their intersection.

cycle is bound to stay in the positive quadrant of the (s_P, s_H) plane.

In a large number of cases, the isoclines do not intersect. In these cases, the evolutionary equilibrium is what we call a “physiological equilibrium”, because it is determined by the physiological constraints $s_P \geq 0$ and $s_H \geq 0$.

If $g \geq 1$, the herbivore isocline does not exist. The herbivore fitness decreases with the trait s_H whatever be the trait value [Fig. 6(A)]. Since the trait s_H is to remain non-negative, three evolutionary equilibria appear, two of which are stable. The outcome of coevolution is then one of the alternative stable equilibria depending on the initial point (s_{P0}, s_{H0}) . If the two isoclines exist but do not intersect, there is a single stable equilibrium point [Figure 6(B)].

Although the shape of the two isoclines depends on the choice we made for the trade-off functions, these functions permit all the stability regimes by only ranging the two parameters a and g .

CONSEQUENCES FOR ECOSYSTEM FUNCTIONING

The previous section shows that a wide variety of evolutionary outcomes is possible depending

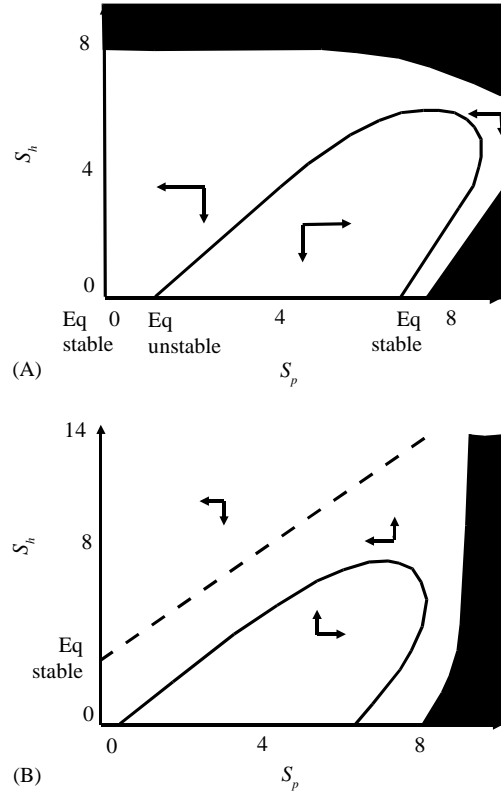


FIG. 6. (A) When $g \geq 1$, herbivore fitness always decreases with s_H . There are three evolutionary equilibria, of which two are ESS (and therefore possible outcomes of evolution, depending on the initial point of evolution). Here, the trade-off parameter $a=0.6$, and the other parameters are the same as in the previous figures. The plant isocline is drawn in solid line. The black areas are the points (s_P, s_H) for which the herbivore goes extinct. (B) The isoclines do not intersect. The only evolutionary equilibrium is $(0, s_{Hiso})$, and is always stable. All evolutionary trajectories converge to that point (ESS). The herbivore isocline is the dashed line, whereas the plant isocline is the solid line. Values of trade-off parameters used here are $g=0.1$, $a=0.4$. The other parameters are the same as before.

on the values of the trade-off parameters. We now explore their implications for ecosystem functioning.

Stable Evolutionary Equilibrium

The evolutionary dynamics may lead to a stable equilibrium (ESS) at the intersection of the two isoclines. Fig. 7 shows how the nutrient stocks at the ESS change with the two trade-off parameters a and g . Plants are dominant (in

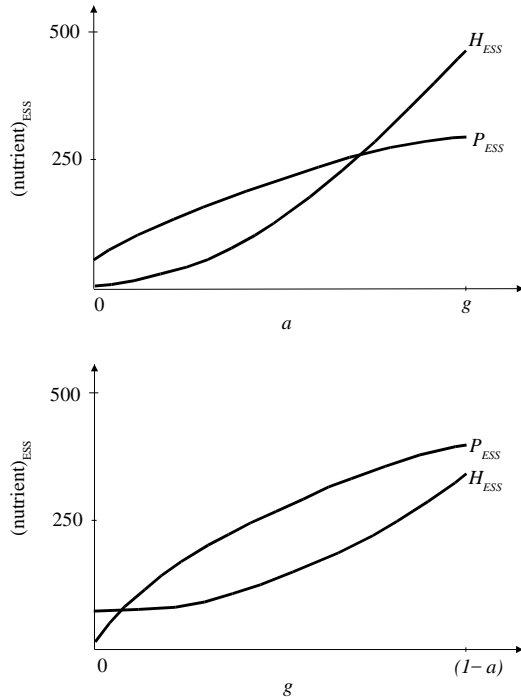


FIG. 7. Values of the plants and herbivores stocks at the ESS for different values of a and g , all other parameters being fixed. Here, the rates of evolution of the plant and the herbivore are equal, so all the intersections of the two isoclines lead to a stable evolutionary equilibrium. Depending on the values of the cost parameters (a, g), either the herbivore or the plant may dominate at the ESS.

terms of nutrient quantity) at the ESS when a is small, whereas herbivores become dominant when a is large. This is understood easily. When a is small, the cost for the plants defenses is small, and inorganic nutrient is easily absorbed. Thus, the conditions are favorable for plant growth, which leads to plant dominance. In the same way, herbivores are dominant at the ESS when g is small, whereas plants become dominant when g is large. Thus, coevolution has a large effect on the overall functioning of the ecosystem, the distribution of nutrient among trophic levels being very different depending on the trade-off parameters.

Stable Evolutionary Cycle

When coevolution leads to a stable limit cycle, nutrient stocks vary periodically on the evolutionary time-scale. For some values of the

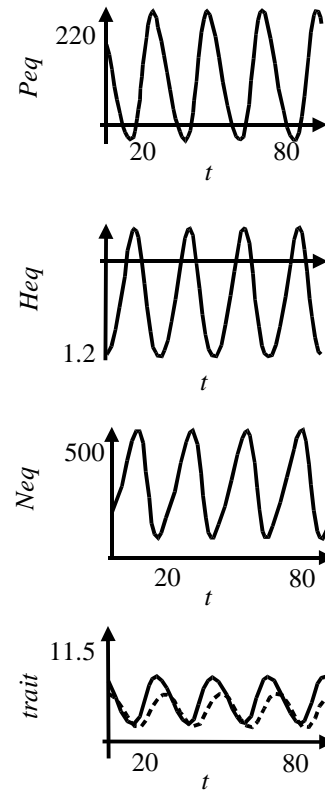


FIG. 8. Variations of ecological equilibrium stocks along the evolutionary cycle presented in Fig. 5. Both traits values and nutrient stocks vary periodically.

trade-off parameters a and g , the amplitude of the cycle is small. The cycle is then a regular ellipse along which the dynamics of both traits and nutrient stocks is sinusoidal (Figs. 5 and 8). Slight variations in trade-off parameter values, however, may increase the amplitude of the cycle. Since the two traits must remain non-negative, the cycle is then limited by the axes, which can generate more irregular dynamics.

What is the Effect of Inorganic Nutrient Dynamics?

Our model incorporates nutrient recycling and inorganic nutrient dynamics explicitly. If the inorganic nutrient stock is fixed, the model becomes very similar to classical prey-predator coevolution models. The analysis of such a model is detailed in Appendix A. The assumption that the inorganic nutrient is fixed means

that nutrient dynamics is fast, and is mainly governed by the plant composition. Plant-growth limitation is then expressed by a logistic growth function whose saturation is determined by the amount of available nutrient. If the nutrient input is sufficient to maintain the herbivores, the ecological equilibrium is also always stable. But the evolutionary outcomes are very different from those of the model with nutrient dynamics. The two isoclines of plant and herbivore fitness gradients are parallel, and their y -intercept depends on the costs of the two traits. The plant fitness isocline is unstable whereas the herbivore gradient fitness isocline is stable. It means that, depending on the values of the two trade-off parameters, the evolutionary outcome is either a stable equilibrium or a simple arms race between the plant and the herbivore. Evolutionary cycles never occur. Thus, the outcome of coevolution is very different if nutrient dynamics is considered explicitly or if plant competition is simply modeled by a logistic growth.

Discussion

COMPLEXITY OF EVOLUTIONARY DYNAMICS

Consequences of Coevolution on the Dynamics of Population and Nutrient Stocks

Our model provides new insights into the understanding of populations cycles. Population time-series such as fur time-series in North America (U.S.A. and Canada) display some low-amplitude, long-period variations in addition to yearly variations in population size (Keith, 1963). A spectral analysis of these series show long-period cycles (more than 30 years). Although these cycles are difficult to analyse due to their length relative to the length of the time series, they are likely to be produced by long-period processes, which can be either abiotic (climate or slow change of the environment) or biotic (evolutionary processes, as suggested above).

Our work suggests that such long-period variations could be linked to the transient phase of an evolutionary process or to stable evolutionary cycles. This role of coevolution in populations cycles was suggested in the case of

lemmings (Seldal *et al.*, 1994). Many other explanations have been suggested for population cycles, such as interactions between species (Baltensweiler & Fischlin, 1988; Garding, 2000; Keith, 1963), maternal effects (Inchausti & Ginzburg, 1998) harvesting (Basson & Fogarty, 1997; Clark, 1976; Gamarra & Sole, 2000), food supply (Baltensweiler & Fischlin, 1988; Garding, 2000; Keith, 1963), dispersal (Baltensweiler & Fischlin, 1988), and climate variability (Keith, 1963).

Other models showed that the evolution destabilize prey-predator models. Prey evolution alone may induce population cycles (Abrams & Matsuda, 1997a), and so does predator-prey coevolution (Abrams & Matsuda, 1997b; Marrow *et al.*, 1996; Abrams, 2000). Our model, however, shows that prey-predator coevolution alone may not be sufficient to explain the cycles and that the nutrient dynamics can play a critical role in this regard.

Abrams (1984) suggested that considering parameters of food-web models as variable might provide new insights into the understanding of food webs. The results of the present model show that incorporating coevolution yields a unified view of a wide range of possible population dynamics on evolutionary time-scales. As in the Khibnik & Kondrashov (1997) model, the interplay of ecological and evolutionary dynamics is potentially important to fully understand the plant-herbivore interaction. A natural example of the effect of plant-enemy coevolution on the dynamics and distribution of the various species is presented by Benkman (1999).

Importance of Inorganic Nutrient Dynamics

The variety of possible evolutionary dynamics is conditioned by the consideration of inorganic nutrient dynamics in the model. If inorganic nutrient is fixed and plant competition is modeled using a logistic function, evolutionary dynamics is much simpler because of the simplification of the costs of the two evolving traits. These costs have a direct influence on the nutrient cycle, and thus fixing the level of inorganic nutrient reduces the impacts of these

costs on the system. When the nutrient is fixed, the model is very similar to some prey-predator coevolutionary models in its mathematical expressions and results (Abrams & Matsuda, 1997b; Marrow *et al.*, 1992; Marrow & Cannings, 1993; Marrow *et al.*, 1996). The comparison between the models emphasizes the importance of incorporating an explicit dynamics of the nutrient in our understanding of the evolution of plant-herbivore interactions, and species interactions more generally (Loreau & de Mazancourt, 1999; Loreau, 2002; de Mazancourt *et al.*, 2001).

LIMITATIONS OF THE MODEL

Separation of Ecological and Evolutionary Time-Scales

As is traditional in the theory of adaptive dynamics, we have assumed separation between the time-scales of ecological and evolutionary dynamics in the analysis of our model. This hypothesis simplifies the analysis since the fitnesses are evaluated at the ecological equilibrium. A number of recent studies have suggested that evolution is sometimes rapid, so that the time-scales of evolution and population dynamics may not be so clearly separated (Hendry *et al.*, 2000; Huey *et al.*, 1999; Grant & Grant, 1995; Reznick *et al.*, 1997).

Our model shows that coevolution may play an important role in the dynamics of plant and herbivore populations and the whole ecosystem. If evolution is faster than that assumed here, its consequences on ecosystem functioning are likely to be all the more important. If the ecological and evolutionary time-scales are approximately equal, however, the theoretical framework of the present study can no longer be used. To assess the consequences of evolution under these conditions, population dynamics and trait dynamics should be considered simultaneously. A few theoretical studies have attempted to do this (Abrams, 1995). The problem with such models is that they are less tractable analytically. If we were to apply this approach to our model, this would comprise five simultaneous differential equations, which would preclude a stability analysis. The alternative would be to use a discrete-time simulation model in

which a mutant would be introduced according to a defined probability at each time step. When we simulated our plant-herbivore model in this way, we found that the qualitative features of the results presented here hold even if the two time-scales are similar.

Are Results Robust to a Change in the Herbivore Trade-Off?

The plant trade-off between growth and defense is well documented, but the herbivore trade-off between consumption and nutrient loss or mortality is less so. How robust are the results presented in the present paper to the trade-off considered? To answer this question we considered another possible cost for the herbivore trait, i.e., a decrease in the herbivore assimilation efficiency. The more the herbivore is able to eat, the less it is able to efficiently turn the consumed plants into the production of new tissues for growth and reproduction.

With this kind of cost, the herbivore nutrient loss rate δ , and hence also nutrient recycling by the herbivore, is no longer dependent on the evolution of the herbivore trait, and the production rate in the herbivore equation in eqns (1) is no longer χ , but $\chi \text{EXP}(-gs_H)$.

These changes do not alter the position of the ecological and evolutionary equilibria. But, for a given ratio between the rates of evolution of plants and herbivores, the probability to obtain an evolutionary cycle proves to be higher in the new model. In particular, in this model, cycles are obtained even when the rates of evolution of plants and herbivores are equal, which is not the case for the previous model [Figure 4(B)]. Thus, when the evolution of herbivores has a direct impact on nutrient recycling, the stability of the evolutionary equilibrium is enhanced compared with the case where evolution has no direct consequence on nutrient recycling.

A Step to Understand a Complex Changing World

Abrams (1995) regretted that in most of the theoretical studies of food webs, the parameters describing the interactions between two species are fixed. The present model adds to a rapidly

TABLE 2
Definitions and units for the different parameters of the model

<i>P</i>	Dimension	Definition
<i>I</i>	(Quantity of nutrient per unit of area)/time	Total input of inorganic nutrient for the global system
<i>l</i>	Time ⁻¹	Inorganic nutrient output rate for the global system
<i>u</i>	(Quantity of nutrient per unit of area × time) ⁻¹	Absorption of nutrient by plants, when plants do not defend themselves
<i>c</i>	(Quantity of nutrient per unit of area × time) ⁻¹	Basic value of the consumption of plants
<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>d_H</i>	Time ⁻¹	Detritus production rate of herbivores when <i>s_H</i> is null
<i>v_H</i>	Dimensionless	Fraction of nutrient lost along the herbivore recycling pathway
<i>k</i>	Dimensionless	Parameter of saturation of the consumption of plants by herbivores, in the course of the evolution
<i>a</i>	Dimensionless	Cost parameters for the plant defense determining the decrease of growth of the plant as a function of its defenses
<i>g</i>	Dimensionless	Cost parameters for the herbivore trait determining the increase of the herbivore mortality as a function of the herbivore trait <i>s_H</i>

growing body of literature in which evolutionary and ecological dynamics are combined. It emphasizes the role of the nutrient dynamics in the outcome of the plant-herbivore coevolution. Evolution is only one way in which species traits can vary, however. The interaction coefficients used in ecological models may also vary following behavioral and physiological changes and species replacement, or depend on species population densities and on the environment.

Given the significant potential consequences of coevolution on the dynamics of species and ecosystems, many new questions arise. Coevolution is likely to modify the traditional view of top-down or bottom-up controls of food webs. It could also provide new insights into the responses of ecosystems to environmental changes. Consequently, the application of new theoretical approaches such as the one proposed in this paper might be particularly useful in the understanding and conservation of natural and managed ecosystems (Table 2).

REFERENCES

- ABRAMS, P. A. (1984). Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80–96.
- 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. A. (1996). Dynamics and interactions in food webs with adaptive foragers. In: *Food Webs, Integration of Patterns and Dynamics* (Polis, G. A. & Winemiller, K. O., eds), pp. 113–121. London: Chapman & Hall.
- ABRAMS, P. A. (2000). Character shifts of species that share predators. *Am. Nat.* **156**, S45–S61.
- ABRAMS, P. A. (2001). Modelling the adaptive dynamics of evolving traits involved in inter and intraspecific interactions: an assessment of three methods. *Ecol. Lett.* **4**, 166–175.
- ABRAMS, P. A. & MATSUDA, H. (1997a). Prey adaptation as a cause of predator-prey cycles. *Evolution* **51**, 1742–1750.
- ABRAMS, P. A. & MATSUDA, H. (1997b). Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evol. Ecol.* **11**, 1–20.
- BALTENSWEILER, W. & FISCHLIN, A. (1988). The larch bud moth in the Alps. In: *Dynamics of Forest Insect Populations* (Berryman A., ed), pp. 331–351. New York: Plenum Publishing Corporation.
- BASSON, M. & FOGARTY, M. (1997). Harvesting in discrete-time predator-prey systems. *Math. Biosci.* **141**, 41–74.
- BELSKY, A. J. (1986). Does herbivory benefit plants? A review of the evidence. *Am. Nat.* **127**, 870–892.
- BELSKY, A. J., CARSON, W. P., JENSE, C. L. & FOX, G. A. (1993). Overcompensation by plants: herbivore optimization or red herring? *Evol. Ecol.* **7**, 109–121.
- BENKMAN, C. W. (1999). The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.* **153**, 75–91.
- CLARK, C. W. (1976). *Mathematical Bioeconomics, the Optimal Control of Renewable Resources*. Wiley editions. New York: Wiley.
- DE MAZANCOURT, C., LOREAU, M. & ABBADIE, L. (1998). Grazing optimization and nutrient cycling: when do

- herbivores enhance plant production? *Ecology* **79**, 2242–2252.
- DE MAZANCOURT, C., LOREAU, M. & ABBADIE, L. (1999). Grazing optimization and nutrient cycling: potential impacts of large herbivores on savanna systems. *Ecol. Appl.* **9**, 784–797.
- DE MAZANCOURT, C., LOREAU, M. & DIECKMANN, U. (2001). Can the evolution of plant defense lead to plant–herbivore mutualism? *Am. Nat.* **158**, 109–203.
- DU TOIT, J. T. (1990). Regrowth and palatability of acacia shoots following the pruning by african savanna browsers. *Ecology* **71**, 149–154.
- GAMARRA, J. G. & SOLE, R. V. (2000). Bifurcation and chaos in ecology: lynx return revisited. *Ecol. Lett.* **3**, 114–121.
- GARDING, L. (2000). A simple model for the interplay of predators, rodents and food. *J. theor. Biol.* **206**, 73–80.
- GERITZ, S. A. H., METZ, J. A. J., KISDI, E. & MESZENA, G. (1997). Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* **78**, 2024–2027.
- GRANT, P. R. & GRANT, B. R. (1995). Predicting microevolution responses to directional selection on heritable variation. *Evolution* **49**, 241–251.
- HENDRY, A. P., WENBURG, J. K., BENTZEN, P., VOLK, E. C. & QUINN, T. P. (2000). Rapid evolution of reproductive isolation in the wild: evidence for introduced salmon. *Science* **290**, 516–518.
- HERMS, D. A. & MATTSON, W. J. (1992). The dilemma of plants: to grow or to defend. *Q. Rev. Biol.* **67**, 283–335.
- HUEY, R. B., GILCHRIST, G. W., CARLSON, M. L., BERRIGAN, D. & SERRA, L. (1999). Rapid evolution of a geographic cline in size and introduced fly. *Science* **287**, 308–310.
- ILLIUS, W. A. & FITZGIBBON, C. (1994). Costs of vigilance in foraging ungulates. *Anim. Behav.* **47**, 481–484.
- INCHAUSTI, P. & GINZBURG, L. R. (1998). Small mammals in northern Europe: patterns and evidence for maternal effects hypothesis. *J. Anim. Ecol.* **67**, 180–194.
- KEITH, L. B. (1963). *Wildlife's Ten-year Cycles*. Wisconsin: University of Wisconsin Press.
- KESH, D., SARKAR, A. K. & ROY, A. B. (2000). Succession processes in a food-web of a two autotroph-one herbivore system. *Biosystems* **57**, 129–138.
- KESSLER, A. & BALDWIN, I. T. (2001). Defensive function of herbivore-induced plant volatile emissions in nature. *Science* **291**, 2141–2144.
- KHIBNIK, A. & KONDRASHOV, A. S. (1997). Three mechanisms of Red-Queen dynamics. *Proc. R. Soc. London B.* **264**, 1049–1056.
- KRIEGER, R. I., FEENY, P. P. & WILKINSON, C. F. (1971). Detoxification enzymes in the guts of caterpillars: an evolutionary answer to plant defenses. *Science* **172**, 579–580.
- LEIBOLD, M. A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *Am. Nat.* **147**, 784–812.
- LEVIN, S. A., SEGEL, L. A. & ADLER, F. R. (1991). Diffuse coevolution in plant herbivore communities. *Theor. Popul. Biol.* **37**, 171–191.
- LOREAU, M. (1995). Consumers as maximizers of matter and energy flow in ecosystems. *Am. Nat.* **145**, 22–42.
- LOREAU, M. (2002). Evolutionary processes in ecosystems. In: *Encyclopedia of Global Environmental Change* (Munn, T., Mooney, H. A. & Canadell, J., eds), Vol. 2, pp. 292–297 London: John Wiley & Sons.
- LOREAU, M. & DE MAZANCOURT, C. (1999). Should plants in resource-poor environments invest more in antiherbivore defence? *Oikos* **87**, 195–200.
- MAURICO, R. (1998). Costs of resistance to natural enemies in field populations of the annual plant *Arabidopsis thaliana*. *Am. Nat.* **151**, 20–28.
- MARROW, P. & CANNINGS, C. (1993). Evolutionary instability in prey–predator systems. *J. theor. Biol.* **160**, 135–150.
- MARROW, P., DIECKMANN, U. & LAW, R. (1996). Evolutionary dynamics of predator–prey systems: an ecological perspective. *Math. Biol.* **34**, 556–578.
- MARROW, P., LAW, R. & CANNINGS, C. (1992). The coevolution of prey–predator interaction: ESSs and red queen dynamics. *Proc. R. Soc. London B* **250**, 133–141.
- MCNAUGHTON, S. J. (1979). Grazing as an optimization process: grass ungulates relationships in the Serengeti. *Am. Nat.* **113**, 691–703.
- MCNAUGHTON, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos* **40**, 329–336.
- MCNAUGHTON, S. J., BANYIKWA, F. F. & MCNAUGHTON, M. M. (1997). Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**, 1798–1800.
- METZ, J. A. J., GERITZ, S. A. H., MESZENA, G., JACOBS, F. J. A. & VAN HEERVAARDEN, J. S. (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems* (van Strien, S. J. & Verduyn, S. M. eds), pp. 183–231. Amsterdam: Lunel, KNAW Verhandlingen.
- POST, E., PETERSON, R. O., STENSETH, N. C. & MCLAREN, B. E. (1999). Ecosystem consequences of wolf behavioural responses to climate. *Nature* **401**, 905–907.
- RAUSHER, D. M. (1996). Genetic analysis of coevolution between plants and their natural enemies. *TIG* **12**, 212–217.
- 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.
- Seldal, T., Andersen, K. J. & Hogstedt, G. (1994). Grazing-induced proteinase inhibitors: a possible cause for Lemming populations cycles. *Oikos* **70**, 3–11.
- TAKABAYASHI, J., DICKE, M. & POSTHUMUS, M. A. (1994). Volatile herbivore-induced terpenoids in plant-mite interactions: variation caused by biotic and abiotic factors. *J. Chem. Ecol.* **20**, 1329–1354.
- WESTOBY, M. (1989). Selective Forces Exerted by Vertebrate Herbivores on Plants. *TREE* **4**, 115–117.

Appendix A

A Model Without Nutrient Dynamics

To assess the role of nutrient dynamics is modeled on plant–herbivore coevolution, we build a simplified version of our model with a fixed level of inorganic nutrient. Since the plant is limited by a single nutrient, the fixed level of inorganic nutrient defines the carrying capacity

of the plant population.

$$\begin{aligned} \frac{dP}{dt} &= P \left(\gamma \left(1 - \frac{P}{N} \right) - \chi H \right), \\ \frac{dH}{dt} &= H(\chi P - \delta). \end{aligned} \tag{A.1}$$

We introduce a logistic growth for plant biomass to account for plant resource limitation. The definitions of parameters remain the same. N is now fixed and can be considered as another parameter of the system. This model has one non-trivial equilibrium:

$$\begin{aligned} P^0 &= \frac{\delta}{\chi}, \\ H^0 &= \gamma \frac{N - P^0}{\chi N}. \end{aligned} \tag{A.2}$$

The analysis of the Jacobian matrix at this equilibrium shows that it is always stable as long as the nutrient level is sufficient to sustain the herbivore population at the equilibrium.

The fitness of a plant or herbivore mutant is defined by their rate of increase in the resident population:

$$\begin{aligned} W_{Pm} &= \gamma_{spm} \left(1 - \frac{P^0}{N} \right) - \chi_{spm} H^0, \\ W_{Hm} &= \chi_{shm} P^0 - \delta_{shm}. \end{aligned} \tag{A.3}$$

The continuous evolution of the traits can be modeled again with eqns (6). The isoclines of the fitness gradients are much simpler than in the full model studied in the main text:

$$\begin{aligned} \left(\frac{\partial W_{Pm}}{\partial s_{Pm}} \right)_{spm \rightarrow sp} = 0 &\Leftrightarrow s_H = s_P + \log \left(\frac{1 - a}{ak} \right), \\ \left(\frac{\partial W_{Hm}}{\partial s_{Hm}} \right)_{shm \rightarrow sh} = 0 &\Leftrightarrow s_H = s_P + \log \left(\frac{1 - g}{gk} \right). \end{aligned} \tag{A.4}$$

In the space of the two traits (s_P, s_H) the two isoclines are parallel lines. A simple study of fitness gradients shows that the plant isocline is

unstable whereas the herbivore isocline is stable. Consequently, there are several possibilities:

(1) If $a = g$, the two isoclines are identical. The outcome of coevolution is then an evolutionary arms race in which both traits increase. At a certain point, this arms race leads to an evolutionary suicide of herbivores (their population can no longer be maintained). This result does not depend on either the ecological parameters or the speed of evolution of plants and herbivores.

(2) If the cost parameters are different, the outcome depends on the relative position of the two isoclines and on the relative speed of evolution of the two species. If the isocline of the plant fitness gradient is above that of the herbivore (i.e., $g > a$), then whatever be the ecological parameters and the relative speed of evolution of the two partners, coevolution leads to an arms race, and finally to an evolutionary suicide of the herbivore. If the herbivore isocline is above that of the plant (i.e., $g < a$) then there are two possible outcomes, depending on the speed of evolution of the two species. If the plant evolves much faster than the herbivore and that the initial traits are noted (s_{P0}, s_{H0}) , we get the same arms race and evolutionary suicide of the herbivore as in the previous cases. In all other cases, the final point of the coevolution is $(s_P = 0, s_H = \text{Max}(0, \ln(1 - g)/gk))$. This point is an ESS, which is determined by either the stability of the herbivore isocline or the condition of nonnegativity of the two traits.

To conclude, the evolutionary dynamics is much simpler in this model where plant competition is expressed through a logistic function than in the full model in which nutrient dynamics is explicit. Fixing the level of nutrient implies the introduction of a density dependence, which modifies the expression of the plant mutant fitness. There are then only two possible outcomes, i.e., either an ESS with no plant defense against the herbivore or an arms race leading to the evolutionary suicide of the herbivore. In this case, coevolution cannot lead to limit cycles.