

## GRAZING OPTIMIZATION, NUTRIENT CYCLING, AND SPATIAL HETEROGENEITY OF PLANT-HERBIVORE INTERACTIONS: SHOULD A PALATABLE PLANT EVOLVE?

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**Abstract.**—Can the evolution of plant defense lead to an optimal primary production? In a general theoretical model, Loreau (1995) and de Mazancourt et al. (1998, 1999) have shown that herbivory could increase primary production up to a moderate rate of grazing intensity through recycling of a limiting nutrient, provided several conditions are fulfilled. In the present paper, we assume: (1) grazing intensity is controlled by plants through their level of palatability; and (2) plant fitness is determined by its productivity. We explore the conditions under which such an optimal production may be reached through natural selection. We model two competing plant types that differ only in palatability and are distributed in a patchy landscape determined by the plant-herbivore interaction. Patch size is determined by herbivore behavior: herbivores recycle nutrient homogeneously within patches, but recycle nutrient proportionally to consumption between patches. The model shows that a strategy of intermediate palatability can be adaptive in response to a small herbivore that lives on and recycles nutrient around one or a few individual plants. For moderately small herbivores, plant palatability may evolve towards one of two local convergent strategies, depending on the initial conditions. For medium- to large-sized herbivores, the nonpalatable strategy is always selected. We discuss the functional and evolutionary implications of these results, and suggest that the traditional dichotomy describing antagonistic and mutualistic interactions may be misleading.

**Key words.**—Antagonism, grazing optimization, group selection, indirect effect, maximum power principle, mutualism, patchy environment, plant defense, plant palatability, primary production, spatial heterogeneity.

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Can plant-herbivore interaction be mutualistic? Plant-herbivore interactions have traditionally been considered antagonistic because herbivores have a negative direct effect on plants through biomass consumption. This assumption has been challenged by the grazing optimization hypothesis, which states that herbivores can enhance plant primary production (McNaughton 1979; Hilbert et al. 1981; Dyer et al. 1986): primary production can increase with low grazing intensity and reach an optimum at intermediate grazing, before production decreases again when grazing intensity becomes too high. Several authors have gone further and have suggested that grazing optimization can lead to mutualistic interactions between plants and their herbivores (Owen and Wiegert 1981, 1982; Petelle 1982; Vail 1992), based on a few studies that show a positive effect of herbivory on plant fitness (Paige and Whitham 1987; but see Bergelson and Crawley 1992; Paige 1992; Bergelson et al. 1996; Grone-meyer et al. 1997; Lennartsson et al. 1997, 1998). Such a claim has attracted a lot of criticism (Silvertown 1982; Belsky et al. 1993; Mathews 1994). According to Belsky et al. (1993), no plausible explanation of a real benefit for the individual plant from herbivory has ever been proposed, and plants “always have an interest in developing a defense strategy.”

One possible mechanism that could explain a positive effect of herbivory on primary production under certain conditions is the positive indirect effects of herbivores through nutrient cycling, as was investigated by theoretical models (Loreau 1995; de Mazancourt et al. 1998, 1999). Such mechanism could be at work in two systems where herbivores have been shown to increase primary production, the Ser-

engeti in Tanzania (McNaughton 1985) and the La Pouse Bay in Canada (Cargill and Jefferies 1984a; Bazely and Jefferies 1989; but see Bakker and Loonen 1998). However, such indirect positive effect might not be possible under evolving plant defense. The main argument against plant-herbivore mutualism mediated by nutrient cycling is that recycling of a limiting nutrient by herbivores should favor unpalatable plants because they benefit from nutrient cycling without suffering from any herbivory (Westoby 1989). Because plant defenses diminish the amount of nutrient cycling through the herbivore population, they decrease or prevent the realization of the positive indirect effects of herbivory. Therefore, even when in principle herbivory could lead to grazing optimization, optimal plant primary production may never be reached under evolving plant defenses.

In previous models, we considered grazing intensity as an ecological parameter and studied the effect of herbivores on the nutrient cycle and primary production (de Mazancourt et al. 1998, 1999). We also studied the effect of plant replacement induced by herbivory on grazing optimization (de Mazancourt and Loreau, unpubl. ms.). In the present model, we consider only one plant species, whose palatability is allowed to evolve, so that grazing intensity is the result of plant evolution.

Levels of plant defense do indeed vary within plant species (Karban 1992), and intraspecific variation in plant toxins is found at all spatial scales investigated, between individual plants as well as among plant populations (Hoy et al. 1998). We address the effects of the environment on the evolution of plant defense in another paper (Loreau and de Mazancourt 1999). In the present paper, we study how an ecosystem process, that is, nutrient cycling and the spatial heterogeneity of the interaction affect the outcome of evolution. To our knowledge, it is the first time that the effect of spatial heterogeneity and herbivore behavior on the evolution of plant palatability has been addressed.

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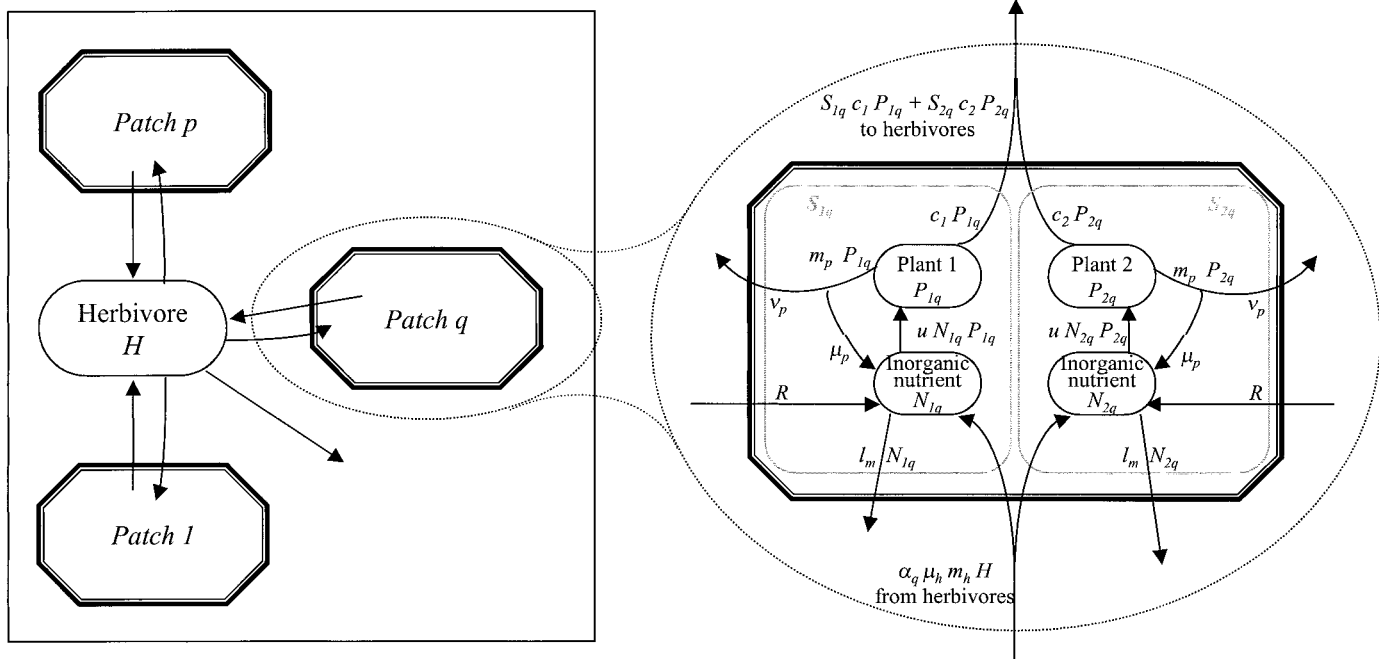


FIG. 1. The model: Two plant types are distributed in a landscape among patches. They are mixed in the patches and each type occupies a total fraction  $S_{iq}$  of soil surface. The two plant types differ only in their palatability, represented by their consumption rates,  $c_i$ . Inside the gray squares, stocks and fluxes are expressed per unit of surface occupied by plant  $i$ ; outside they are expressed per unit of patch surface.

The model links the description of nutrient cycling with evolutionary aspects of plant-herbivore interactions. Such an approach is innovative because it encompasses these two fundamental levels of ecological research, allowing the exploration of both the evolutionary consequences of ecological interactions and the ecological implications of evolutionary change. We show that a palatable strategy may be adaptive in the case of a small herbivore relative to plant size, when the grazing optimization conditions are fulfilled. Thus, if herbivores recycle nutrients in the surroundings of the grazed plants, grazing optimization becomes conceivable again, even when taking, as demanded by Belsky et al. (1993), the evolution of plant defense into account. We discuss the implications of our results in terms of plant-herbivore interaction.

#### MODEL DESCRIPTION

To keep it mathematically tractable, we made a simple compartment model of the nutrient cycle in a theoretical system (Fig. 1). Stocks and fluxes are expressed in units of the limiting nutrient (kg of nutrient/ha and kg of nutrient  $\text{ha}^{-1} \text{year}^{-1}$ , respectively). All the parameters are defined in Table 1.

#### Plant Defense

We consider the simple case of a system composed of one plant species, comprising two plant types, and one herbivore species. Plant type is indicated by a subscript  $i$ , where  $i = 1$  or  $2$ . The two types differ only in palatability, represented in a palatability index,  $c_i$ , which determines the rate at which they are consumed. We define palatability as an intrinsic feature of the plant type toward that particular herbivore.

Plants control their palatability through their level of defense, which include mechanical defenses, such as thorns, as well as chemical defense such as tannins or alkaloids.

The fitness of defended plants might be decreased if plant defense are costly, and we explore the consequences of such cost of plant defense in another paper (C. de Mazancourt, M. Loreau, and U. Dieckmann, unpubl. ms.). However, despite the general belief that plant defense do bear costs, disagreements persist about their frequency and prevalence. Evidence for costs of defense is extremely scant (Simms and Rausher 1987; Mole 1994). In a review, Bergelson and Purrington (1996) analyzed 88 published comparisons to explore trade-offs between resistance and fitness traits. They showed that less than half of resistant plants only show costs of resistance. According to Simms and Rausher (1987), costs of resistance are not universal; at least for some systems, a framework other than cost-benefit theory must be found to account for the levels of plant defense and resistance found in natural plant populations.

The present model also assumes that the palatability of a plant type does not depend on its nutrient supply. This is the simplest assumption, and it does not have any consequence on the model results as long as plant defense bears no cost.

#### Patch Structure

Plants are distributed in a landscape among  $p$  patches, and each patch contains  $n$  plants in a mixture of the two plant types in various proportions. Landscape structure is generated by the interaction of plants with the herbivore. On a small spatial scale (within a patch), herbivores do not differentiate between plants with regard to recycling. On a larger scale

TABLE 1. Parameters and variables of the model.

Variable	Definition (dimension)
$P_{iq}$	plant $i$ nutrient stock per unit of occupied surface by this plant in patch $q$ (kg of nutrient/ha occupied by plant $i$ )
$N_{iq}$	soil mineral nutrient stock in the local pool of plant $i$ in patch $q$ per unit of occupied surface by this plant in this patch (kg of nutrient/ha occupied by plant $i$ )
$H$	herbivore density in terms of nutrient stock per hectare (kg of nutrient/ha)
$\Phi_{iq}$	plant $i$ productivity in patch $q$ per unit of occupied surface by plant $i$ , in terms of the limiting nutrient (kg of nutrient per year and per ha occupied by plant $i$ )
$F_i^*$	plant $i$ overall equilibrium productivity per unit of occupied surface by plant $i$ in the whole landscape, in terms of the limiting nutrient (kg of nutrient per year and per hectare)
Parameter	Definition (dimension)
$R$	input of inorganic nutrient in the ecosystem per unit of surface per year (kg of nutrient per year and per hectare)
$l_m$	loss rate of mineral nutrient (per year)
$u$	plant nutrient uptake rate (per year and per kg of nutrient/ha occupied by plant $i$ )
$c_i$	plant $i$ consumption rate, that is, plant $i$ palatability index (per year)
$m_p$	plant detritus production rate (per year)
$\mu_p(v_p)$	fraction of nutrient recycled in (respectively lost for) the ecosystem along the plant pathway (dimensionless) $\mu_p + v_p = 1$
$m_h$	herbivore detritus production rate (per year)
$\mu_h(v_h)$	fraction of nutrient recycled in (respectively lost for) the ecosystem along the herbivore pathway (dimensionless) $\mu_h + v_h = 1$
Spatial description	Definition (dimension)
$S_{iq}$	fraction of occupied surface by plant $i$ in patch $q$ (dimensionless)
$\bar{S}_i$	plant $i$ mean frequency in the landscape
	$\bar{S}_i = \frac{\sum_{q=1}^p S_{iq}}{p} \quad (\text{dimensionless})$
$\sigma^2$	variance of plant distribution between patches
	$\sigma^2 = \frac{\sum_{q=1}^p (S_{1q} - \bar{S}_1)^2}{p} = \frac{\sum_{q=1}^p (S_{2q} - \bar{S}_2)^2}{p} \quad (\text{dimensionless})$
$\alpha_q$	relative contribution of patch $q$ to herbivore food
	$\alpha_q = p \frac{S_{1q}c_1P_{1q} + S_{2q}c_2P_{2q}}{\sum_{r=1}^p (S_{1r}c_1P_{1r} + S_{2r}c_2P_{2r})} \quad (\text{dimensionless})$

(between patches), herbivores recycle the limiting nutrient proportionally to the amount of food they obtain in this patch. Such recycling behavior might be generated by herbivore spatial distribution: on a small scale (within a patch), herbivores are distributed or move at random, whereas on a larger scale (between patches), herbivores have an ideal free distribution, that is, they are distributed proportionally to the amount of food they obtain in a patch.

We should expect that a small herbivore, such as a caterpillar, stays very close to the grazed plant and thus has a small, delimited recycling patch. Patch size would therefore

be close to a single plant. In contrast, a large herbivore, such as a buffalo, is unlikely to recycle nutrients near the plant it grazes. Consequently, its patch size will obviously be much larger. Thus, the patchy structure of our model results from herbivore behavior, and patch size should be linked to the size of herbivores relative to the size of the grazed plants.

Plant growth and consequent aggregation determines the distribution of plant types over the patches. If plants are distributed uniformly over the patches, all patches contain the same proportion of the two plant types. The opposite, extreme case is such that every patch contains a single plant type. An intermediate state assumes a random distribution of plant types over the patches.

As stated above, plant type is indicated by a subscript  $i$ , where  $i = 1$  or  $2$ ; patch number is indicated by a subscript  $q$ , with  $1 \leq q \leq p$ . Each plant type occupies a fraction of soil surface  $S_{iq}$  in patch  $q$ . Plants are assumed to occupy all the available surface in each patch:

$$S_{1q} + S_{2q} = 1 \quad (1)$$

### Nutrient Dynamics

The model is illustrated in Figure 1.

The system is open with regard to the nutrient cycle, and we assume a constant input of nutrient in an inorganic form,  $R$ .

The soil mineral nutrient pool is not assumed to be homogeneous. Each plant has a local nutrient depletion zone, which is located under its roots. Such a model is a simplified version of Huston and DeAngelis's (1994) model and allows two different plant types to coexist by preventing competitive exclusion (Huston and DeAngelis 1994; Loreau 1996).

Plant nutrient can then be recycled through two different pathways, termed the "plant pathway" and the "herbivore pathway." The plant pathway represents the fate of nutrient that is not consumed by the herbivore. Detritus dynamics involved with differential lag effects are not represented in this model, assuming that the nutrient is immediately mineralized. At steady state, the assumption of immediate release does not change the results (de Mazancourt et al. 1998). A fraction of mineralized nutrient is recycled in the local pool of nutrients of the plant, that is, in the vicinity of the plant, whereas the rest is lost and leaves the ecosystem. This assumption of local recycling is conservative.

Nutrients consumed by herbivores follow the herbivore pathway. As with plant detritus, we assume that herbivore detritus is immediately mineralized. The resulting mineralized nutrient supplies the different local pools of mineralized nutrient according to their spatial distribution. A fraction of nutrient  $v_h$  leaves the ecosystem during this process. Note that all detritus that herbivores distribute in other systems is to be considered as a loss of nutrient for the system composed of the  $p$  patches and accounted for in the fraction of nutrient lost,  $v_h$ . Most functions used for the fluxes are linear, except for nutrient uptake. They can be found in Figure 1.

Herbivore consumption is proportional to the plant palatability index and plant nutrient stock per unit of occupied surface in patch  $q$ :  $c_i P_{iq}$ . The proportion of the standing biomass that is consumed does not depend on herbivore density. This assumption is made for simplicity's sake, but our results

are robust to a change of the consumption function, in particular to a change into a Lotka-Volterra interaction (see Appendix 2).

Herbivores are assumed to be very selective in their foraging within a patch. This is a conservative assumption because herbivores should eat less of the more-palatable plant type when it is growing in the middle of less-palatable plants and eat more of the less-palatable type when it is mixed with more-palatable ones. Such protection has been shown to occur for palatable plants when surrounded by unpalatable ones (Atsatt and O'Dowd 1976; Hay 1986; Pfister and Hay 1988; Hjältén et al. 1993; Tuomi et al. 1994), but our assumption is reasonable if individual plants are big when compared with herbivore mouth size or if herbivores are sufficiently selective (McNaughton 1978).

We assume that the amount of nutrient recycled by herbivores in any given patch is proportional to the amount of nutrient consumed in this patch. Mineralized nutrients are then divided among patches proportionally to  $\alpha_q$ , the relative contribution of patch  $q$  to herbivore food:

$$\alpha_q = p \frac{S_{1q}c_1P_{1q} + S_{2q}c_2P_{2q}}{\sum_{r=1}^p (S_{1r}c_1P_{1r} + S_{2r}c_2P_{2r})}. \quad (2)$$

At a small, within-patch scale we assume that herbivores recycle nutrient evenly. Thus, recycled nutrients are distributed between the two plant types proportionally to the occupied surface  $S_{iq}$ . (This factor does not appear in the equations for plant types in each patch  $q$  because these are given per unit of surface occupied by plant  $i$  in the patch.)

The equations representing the dynamics of plant type  $i$  in patch  $q$  then become:

$$\frac{dN_{iq}}{dt} = R - l_m N_{iq} - u N_{iq} P_{iq} + \mu_p m_p P_{iq} + \mu_h m_h \alpha_q H \quad (3)$$

and

$$\frac{dP_{iq}}{dt} = u N_{iq} P_{iq} - m_p P_{iq} - c_i P_{iq}, \quad (4)$$

and the equation for herbivore dynamics (per unit of patch surface) is:

$$\frac{dH}{dt} = \frac{\sum_{q=1}^p (S_{1q}c_1P_{1q} + S_{2q}c_2P_{2q})}{p} - m_h H. \quad (5)$$

All the variables and parameters are defined in Table 1.

### Dynamics of Site Occupation

At a small time scale, we assume that plant distribution is constant and the nutrient cycle reaches a steady state. However, on a longer time scale, plant seed production governs changes in the distribution of plant types. We assume that herbivores do not have any influence on plant lifespan. We chose the simplest assumption because the effects of herbivory on differential plant survival have scarcely been addressed.

We consider two alternative possible scenarios for plant

seed production: (1) it is proportional to plant biomass; or (2) it is proportional to plant primary production, measured by the rate of nutrient absorption. On the one hand, plant nutrient stock is positively correlated with plant standing biomass; it is this biomass that can be re-allocated to seed production at the end of each season. Such a scenario is likely for an annual plant. On the other hand, the amount of nutrient that a plant absorbs per unit time is positively correlated with plant primary production and characterizes the amount of resources that plants can continuously divert to seed production during the season. Such a scenario is likely for a perennial plant. This relationship between production and seed output is likely in the case of intermediate grazing intensities, as long as plant biomass is not depressed too much. This corresponds to classical physiological allocation models describing the pattern of resource allocation between different functions (Mole 1994).

Both scenarios result in a positive correlation between seed production and plant biomass, which is found in many empirical studies (Aarssen and Taylor 1992). Therefore, most empirical studies of plant seed production cannot discriminate between these two alternatives. However, Obeso and Grubb (1994) show that seed production of the annual plant *Senecio vulgaris* was not decreased with defoliation, although plant biomass was decreased. Such a result is not consistent with a correlation between plant biomass and seed production, whereas it is consistent with a correlation between primary production and seed production. Both scenarios assume a constant allocation of plant resource to seed production and leaf production, and we do not explore the consequences of a trade-off between these two functions for simplicity's sake.

If plant seed production is proportional to plant size, then our previous models (Loreau 1995; de Mazancourt et al. 1998, 1999) show that herbivory will always decrease plant seed production in spite of nutrient cycling. The conclusions of our present study are then trivial: the most defended plants are always selected for.

In the following, we assume that seed output is proportional to primary production. With this assumption, herbivores then do have a positive net effect on plant absolute fitness when the grazing optimization conditions are fulfilled (de Mazancourt et al. 1998).

For a given proportion and distribution of plant types among patches, we obtain the steady-state value of each plant type's primary productivity per unit of occupied surface in each patch in terms of the limiting nutrient:

$$\Phi_{iq}^* = u N_{iq}^* P_{iq}^* \quad (6)$$

where the asterisk denotes a steady-state value.

We assume that seed dispersal occurs between patches, so that a seed that comes from any other patch can colonize a free site in a patch. Thus, each plant type may be considered to have a common seed pool, to which each patch  $q$  contributes in proportion to its net production,  $S_{iq} \Phi_{iq}^*$ . Each plant type's total seed production is proportional to its total primary productivity per unit of occupied surface throughout the landscape:

TABLE 2. Relatedness describes the mean genetic similarity between plants of the same patch, when compared to the population mean: It is zero if the composition of the patch is the mean composition of the population. It is proportional to the variance in the distribution of plant types between patches, which depends on patch size and spatial aggregation of plant types.

Within-patch relatedness	$\frac{\sigma^2}{\bar{S}_1 \bar{S}_2}$
All patches contain each plant type with average frequency, for example, uniform distribution of plants between patches or infinite number of plants per patch ( $n = \infty$ )	0
Random distribution of plant types and there are $n$ plants per patch	$\frac{1}{n}$
There is only one plant type per patch, for example, plant types are completely aggregated or there is only one plant per patch ( $n = 1$ )	1

$$F_i^* = \frac{\sum_{q=1}^p S_{iq} \Phi_{iq}^*}{\sum_{q=1}^p S_{iq}}. \quad (7)$$

The plant with the largest  $F_i^*$  will be assumed to increase in abundance. The underlying assumption is that the dynamics of plant site occupation is slow compared to the ecological dynamics of nutrient cycling.

## RESULTS

### *Model Analysis*

This  $F_i^*$  criterion allows us to calculate the local fitness gradient,  $f$ , around a given strategy with palatability  $c_1$  (see Appendix 1). The sign of  $f$  describes the direction of selection: if it is positive, there is selection for a greater palatability index, if it is negative, there is selection for a lower palatability index.

After algebraic manipulation, the local fitness gradient,  $f$ , can be shown to depend only on the palatability index of the strategy considered,  $c_1$ , and on a parameter that describes the spatial distribution of plant types or within patch relatedness,  $\sigma^2/\bar{S}_1\bar{S}_2$  (Table 2), where  $\bar{S}_1$  is the mean frequency of plant 1 in the landscape,  $\bar{S}_2$  is the mean frequency of a strategy that is close to  $c_1$ , and  $\sigma^2$  is the variance of the plant distribution between patches (see Table 1 for formulas):

$$f\left(c_1, \frac{\sigma^2}{\bar{S}_1 \bar{S}_2}\right) = -a(c_1) + \frac{\sigma^2}{\bar{S}_1 \bar{S}_2} b(c_1) \quad (8)$$

where  $a$  and  $b$  are functions of the model's parameters (see Appendix 1).

This equation is very similar to Hamilton's rule (Grafen 1985), where  $a$  is the cost of the interaction with the herbivore and  $b$  is its benefit for a neighboring individual. Unfortunately, the equations for  $a$  and  $b$  are extremely complicated and no direct interpretations of these costs and benefits in terms of nutrient fluxes could be inferred. The term  $\sigma^2/\bar{S}_1\bar{S}_2$  is plant within-patch relatedness; it measures the genetic similarity between plants in the same patch, here with respect to their palatability index. Relatedness is a measure of the deviation of patch composition from the average population (Grafen 1985): it is zero if all patches have the average plant type frequencies and one if every patch contain a single plant type (Table 2).

An interesting feature is that, apart from relatedness, the

local gradient of fitness  $f$  is independent of  $\bar{S}_i$ . Invasion of a mutant strategy into a resident strategy results in the exclusion of the latter, as long as the pattern of spatial distribution as described by within-patch relatedness stays constant: there cannot be coexistence of two close strategies.

The local fitness gradient allows us to find local convergent strategies (Geritz et al. 1996; Dieckmann 1997). A convergent strategy (CS) is an evolutionary attractor in the sense that a population that starts off with a different strategy can always be invaded by close strategies nearer to the CS: selection tends toward that strategy through successive invasions by close strategies.

The nonpalatable strategy ( $c_1 = 0$ ) is a local CS if  $f$  is negative for low positive values of the palatability index,  $c_1$ . A palatable strategy  $c_1$  ( $c_1 > 0$ ) is a local CS if the local fitness gradient is positive for less palatable plants and negative for more palatable ones:

$$\begin{aligned} f\left(c_1, \frac{\sigma^2}{\bar{S}_1 \bar{S}_2}\right) &> 0 && \text{when } c_1 < c_{CS}, \\ f\left(c_1, \frac{\sigma^2}{\bar{S}_1 \bar{S}_2}\right) &= 0 && \text{when } c_1 = c_{CS}, \\ f\left(c_1, \frac{\sigma^2}{\bar{S}_1 \bar{S}_2}\right) &< 0 && \text{when } c_1 > c_{CS}. \end{aligned} \quad (9)$$

We will not prove that a CS is an evolutionary stable strategy (Maynard Smith and Price 1973), that is, that it is immune to invasion by neighboring strategies. We do not know whether it is capable of invading all its neighboring types or whether a pair of neighboring phenotypes lying either side of a convergent strategy can invade each other and lead to a stable dimorphism. All those questions are independent of each other (Dieckmann 1997), but the mathematical criteria necessary to answer these questions (Geritz et al. 1996) do not simplify and cannot be handled analytically, except in the case when plant types are completely segregated between patches. In the latter case, we can show that the CS is also an ESS, it can invade all its neighboring types, and a pair of neighboring phenotypes lying either side of it cannot invade each other, so that there is no dimorphism.

The calculation of the zeros of the local fitness gradient and the analysis of its sign is given in Appendix 1. Here, we present the CS palatability index as a function of within-patch relatedness. This parameter depends on two factors: herbivore recycling behavior (which determines patch size)

and plant aggregation (which determines the distribution of plant types over patches).

Grazing optimization occurs only if herbivores limit the export of the limiting nutrient from the ecosystem (de Mazancourt et al. 1998). In this case, there exists a value of the palatability index, which we call optimal, at which primary production is maximized.

#### CS Palatability Index as a Function of Within-Patch Relatedness of Plant Types

CS palatability index is a function of within-patch relatedness,  $\sigma^2/S_1S_2$ . The parameter  $v_h$ , the fraction of nutrient lost along the herbivore pathway, is then a major determinant of the results of the model. Three cases are possible, depending on its value (Figure 2).

*Large losses along the herbivore pathway ( $v_h > v_{h0}$ ).*—If the fraction of nutrient lost along the herbivore pathway is greater than a threshold value  $v_{h0}$  (see Appendix 1), herbivory does not reduce exportation of the limiting nutrient from the system sufficiently and no grazing optimization is possible. This threshold determines the occurrence of grazing optimization for a community with a single plant type (de Mazancourt et al. 1998). The herbivore ecological effect is then negative (primary production is decreased), and there is never any advantage in being eaten. In this case, the CS is always the nonpalatable type (Fig. 2A).

*Moderate losses along the herbivore pathway ( $v_{h0} > v_h > v_{h1}$ ).*—If the fraction of nutrient lost along the herbivore pathway lies between two threshold values  $v_{h0}$  and  $v_{h1}$  (see Appendix 1), the CS palatability index is an increasing function of relatedness (Fig. 2B).

For small within-patch relatedness, the nonpalatable type is selected for, that is, herbivores recycle nutrients on the two plant types in a way that is too similar for a palatable type to be favored.

At the right end of the x-axis (Fig. 2B), relatedness is one, that is, every patch contains a single plant type. Herbivores recycle on each plant type an amount of nutrient proportional to consumption, and the optimal palatability index is selected for.

*Small losses along the herbivore pathway ( $v_h < v_{h1}$ ).*—When the fraction of nutrient lost along the herbivore pathway is smaller than the lower threshold value,  $v_{h1}$ , CS palatability is no longer a simple increasing function of relatedness (Fig. 2C). When within-patch plant relatedness is small, there is selection for the nonpalatable plant type. When within-patch relatedness is one, with only one plant type per patch, there is selection for the optimal palatability index. But for intermediate relatedness, there can be two CS strategies (Fig. 2C). The arrows in Figure 2 show the directions of selection through invasion of close strategies for a given within-patch relatedness. Thus, it can be seen from Figure 2C that each CS strategy has its attraction basin and the selected palatability index depends on the initial type of the population.

#### CS Palatability Index as a Function of Patch Size

Within-patch relatedness depends on patch size (Table 2). When the spatial distribution of plant types in the landscape

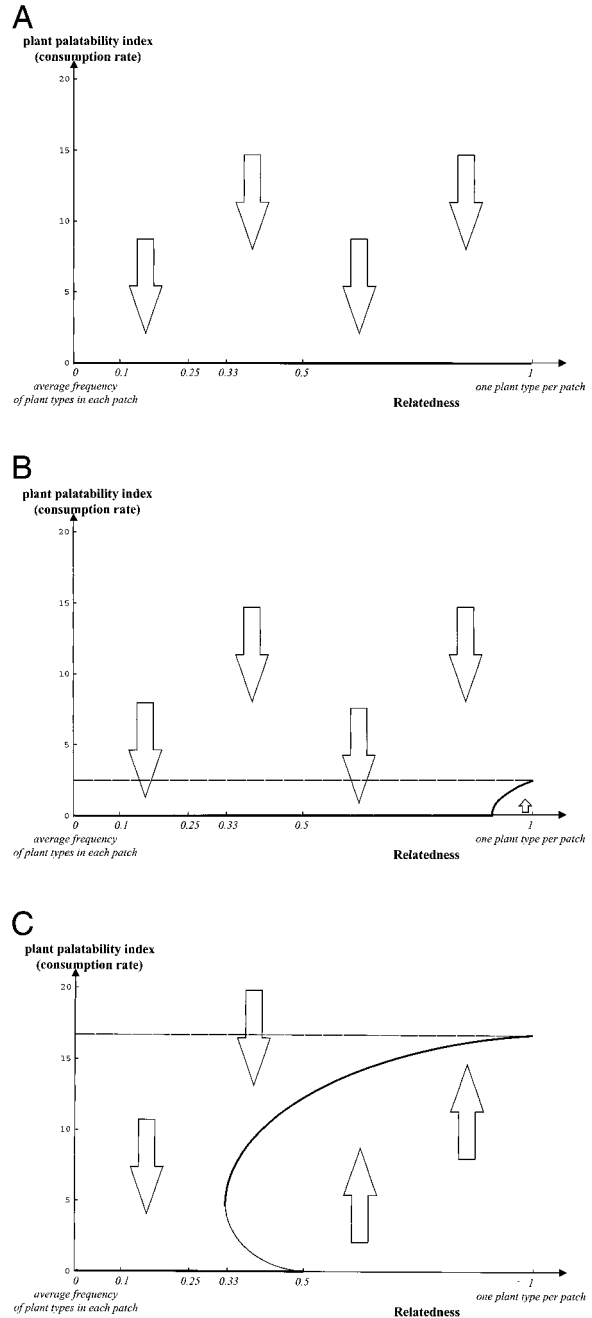


FIG. 2. Convergence stable strategy of palatability (in bold) is given as a function of the parameter describing within patch relatedness,  $\sigma^2/S_1S_2$  (Table 2). Arrows show the direction of selection as given by the sign of the fitness gradient for a given relatedness (eq. 8). The convergent strategy is the unpalatable plant type if the fitness gradient is negative for low positive values of palatability. The other convergent strategies are obtained for zero values of the fitness gradient  $f$  (eq. 9). (A) Large losses along the herbivore pathway: the fraction of nutrient loss along the herbivore pathway,  $v_h$ , is greater than the first threshold value:  $v_h > v_{h0}$  (here,  $v_h = 0.6$ ). (B) Moderate losses along the herbivore pathway: the fraction of nutrient loss along the herbivore pathway  $v_h$  is comprised between the two threshold values:  $v_{h0} > v_h > v_{h1}$  (here,  $v_h = 0.55$ ). (C) Small losses along the herbivore pathway: the fraction of nutrient loss along the herbivore pathway  $v_h$  is smaller than the second threshold value:  $v_{h1} > v_h$  (here,  $v_h = 0.2$ ). Other parameter values:  $R = 25 \text{ kgN ha}^{-1} \text{ year}^{-1}$ ,  $l_m = 0.2 \text{ year}^{-1}$ ,  $d_p = 2 \text{ year}^{-1}$ ,  $u = 1 \text{ year}^{-1}/(\text{kg of nutrient/ha occupied by plant } i)$ ,  $v_p = 0.6$ .

is random, relatedness is a simple function of the number of plants per patch,  $n$  (Table 2):

$$\frac{\sigma^2}{S_1 S_2} = \frac{1}{n}. \quad (10)$$

The CS palatability index then depends on  $n$ , the number of plants per patch, and  $v_h$ , the fraction of nutrient lost along the herbivore pathway.

Thus, provided that the fraction of nutrient lost along the herbivore pathway is smaller than the threshold  $v_{h0}$ , there can be selection for an intermediate value of the palatability index if patch size is sufficiently small, that is, for a relatively small herbivore. If the herbivore is very small and recycles nutrients in the immediate vicinity of the consumed plant, the patch size is one and the optimal palatability index is selected for. When the fraction of nutrient lost along the herbivore pathway is smaller than the lower threshold value,  $v_{h1}$ , there can be two CS strategies for medium-sized patches and the selected palatability index depends on the initial type of the population.

#### *CS Palatability Index as a Function of Plant Aggregation*

When the number of plants per patch,  $n$ , is fixed, the CS palatability index may also be considered a function of plant aggregation among patches. Thus, we find exactly the same results as above (see Fig. 2). Relatedness is zero when plant types are distributed uniformly among patches, that is, there is exactly the same number of each plant type in all patches. Herbivores then recycle indifferently on the two plant types, as if the environment was homogeneous, and the nonpalatable plant type is always selected for. In contrast, if plant types are totally aggregated, that is, plants of the same type are clumped together, so that each patch contains only one type, relatedness is one. Thus, if (1)  $v_h$ , the fraction of nutrient lost along the herbivore pathway, is smaller than the threshold  $v_{h0}$ ; (2) the number of plants per patch is not too high; and (3) a palatable plant type is aggregated, this can be selected for (Fig. 2).

## DISCUSSION

We have shown that under certain conditions, an ecosystem process, that is, nutrient cycling, can affect the evolution of plant defense: individual plants may have an interest in tolerating some grazing, even if defenses are costless. Plants that tolerate some grazing have a higher fitness than better-defended plants when the following conditions are fulfilled: (1) herbivores recycle the limiting nutrient sufficiently more efficiently than do plants; (2) herbivores do not recycle nutrients homogeneously, but recycle more in the vicinity of more grazed plants; (3) plants allocate a constant proportion of the resources they absorb to reproduction. Here we discuss these conditions for such an evolutionary outcome and its implications on ecosystem processes and the nature of plant-herbivore interaction.

#### *The Paradox of Within- and Between-Patch Fitness*

Our results show that plants can be selected to result in an intermediate defense strategy. This may seem paradoxical

because, within patches, herbivores recycle nutrients on both plant types indifferently, so that it is always the less-palatable plant that has the greater productivity. However, between patches, herbivores recycle proportionally to consumption. The most productive patches are those that contain more-palatable plants. Thus, most of the more-palatable plants are in very productive patches, whereas most of the less-palatable plants are in less productive patches. At the between-patch level, plants close to the optimal grazing intensity are selected for. As a result, at the level of the overall population, an intermediate palatability can be selected for.

Spatial structure results in multiple levels of selection (Levontin 1970; Wilson and Sober 1989; Olivieri et al. 1995) and allows a character to be counterselected or neutral at a first level of selection, but nevertheless be selected for at the level of the overall population (Wilson 1980; Frank 1994; Hamilton 1996).

#### *Herbivore Size*

Selection for an intermediate palatability appears to depend on herbivore size. Our results show that a palatable strategy can be adaptive in the case of very small herbivores (as compared with plant size), which recycle nutrients on the much grazed plant. Thus, if small herbivores do sufficiently recycle a limiting nutrient, then plants should allow some herbivory, even if defense bears no cost. The effects of large herbivores on nutrient cycles is well documented in the Serengeti savanna in Tanzania (McNaughton 1976, 1979, 1985; Ruess 1984; Ruess and McNaughton 1984, 1987, 1988; McNaughton et al. 1997). The effect of snow geese on the nitrogen cycle in the La Perouse Bay salt marsh in Canada is also well documented (Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985; Ruess et al. 1989; Hik and Jefferies 1990; Bakker and Loonen 1998), and these herbivores can sometimes lead to increased primary production, probably through their effect on the nutrient cycle. Do small herbivores recycle nutrients sufficiently to lead to an increased primary production? We know of no studies of the effects of small herbivores on nutrient cycles. However, grazing optimization was demonstrated for big-headed grasshoppers (*Aulocara elliotti* Thomas) grazing on blue grama (*Bouteloua gracilis*; Williamson et al. 1989). If large herbivores may increase recycling of a limiting nutrient, small herbivores may do as well. Primary production is difficult to measure in the presence of large herbivores (McNaughton et al. 1996), and it is even more difficult in the case of small ones because they are difficult to exclude from small enclosure plots. We would like to emphasize that it would be interesting to search for such patterns with small herbivores.

For moderately small herbivores (patch size of two to four plants), plant palatability may evolve toward one of two local convergent singular strategies, depending on the initial conditions. For medium- to large-sized herbivores, the nonpalatable strategy should always be selected. Thus, even if large herbivores recycle nutrient such that grazing optimization conditions are fulfilled, plant evolution should not lead to a palatable plant strategy, but to maximization of defense, at least when the latter is costless. There can then be no ‘‘mu-

tualistic'' interaction, although there is a positive ecological effect of herbivores on plants.

#### *Aggregation of Plant Types*

The CS of palatability also depends on the spatial distribution of plant types among patches: plant aggregation favors more palatable plant types (Fig. 2). Many studies of plant species distribution conclude that clumped patterns are the rule, rather than the exception (Forman and Hahn 1980; Wright 1982; Wei and Skarpe 1995; Husband and Barrett 1996). A patchy distribution of plants might result from spatial distribution of local habitats (Forman and Hahn 1980; Duncan 1991; Husband and Barrett 1996). Here, we are interested in the pattern of distribution of two different genotypes rather than simple spatial distribution. A clumped distribution of genotypes in a population might, for example, arise due to local seed or pollen dispersal (Turner et al. 1982; Wei and Skarpe 1995; Husband and Barrett 1996; McFadden 1997; Peres and Baider 1997), or clonal reproduction (Peterson and Squires 1995).

The present model assumes that seed dispersal occurs between patches, so that a seed that comes from patch can colonize a free site in any patch. The effects of local dispersion, or ''population viscosity'' on the evolution of plant defense in our model are likely to be complex and depend on the scale at which density dependence operates (Kelly 1994).

#### *Slow Dynamics of Site Occupation versus Fast Dynamics of Nutrient Cycling*

A major assumption of the model is that the dynamics of plant site occupation is slow compared with the dynamics of nutrient cycling. Given a distribution of plant types in the landscape, we assume that the steady state of the system for nutrient cycling is reached before there is a change in frequency of plant types. The fitness of each plant type is then measured at steady state, and the type that has the greatest fitness is assumed to increase in abundance. Our model seems to be adapted for a plant with a long lifespan when compared with the time scale of nutrient cycling, such as a long-lived perennial.

In fact, as we discuss in de Mazancourt et al. (1998), nutrient turnover rates determine transient dynamics, which are likely to enhance the positive effect of herbivores on plant productivity. Thus, if the system were not at steady state, the patterns found here should be reinforced.

#### *Generalization of the Results*

In our model, the essential difference between herbivores and plant detritus is their recycling properties. The nutrient in plant detritus is assumed to be entirely recycled in the local pool of the plant, whereas herbivores divide up the amount of nutrient consumed between the  $n$  plants of the patch. Thus, the difference between plants and herbivores lies in the spatial scale at which recycling occurs.

In fact, our herbivore pathway could represent any pathway of nutrient cycling that shares its characteristics, that is, the same fraction of recycled nutrient and the same spatial pattern

of recycling among plant types. Thus, our results can be interpreted as follows: a plant should favor the recycling pathway that prevents nutrient from leaving the ecosystem the most, as long as it is recycled sufficiently locally.

#### *Optimization of Primary Production and Evolution of Plant Defense*

Except in the extreme case where the herbivore recycles nutrient on the much-grazed plant, we show that plants following the CS are less palatable than those following the optimal strategy. Thus, selection for plant palatability results in a primary productivity that is lower than the maximum possible productivity.

This contradicts Lotka's (1922) principle, according to which ''evolution proceeds in such direction as to make the total energy flux through the system a maximum compatible with the constraints.'' Other authors later claimed that systems should tend to run at maximum power output (Odum and Pinkerton 1955) or reproductive power (Brown et al. 1993). Their laws are expressed in terms of energy, but they should apply equivalently to the fluxes of a limiting nutrient. In the present model, reproductive power would stand for the flow of nutrient used for reproduction, which is assumed to be proportional to primary production. According to these maximum principles, the system should tend toward the maximum primary production. When grazing optimization conditions are fulfilled, selection does not lead to the maximum primary production because, when the two plant types are mixed in the patches, a conflict between the two levels of selection occurs (Loreau 1998). These maximum principles do not take into account competition between different individuals, which can prevent the evolution toward a maximum.

#### *Plant-Herbivore Mutualism and Plant-Herbivore Coevolution?*

An interaction is mutualistic if the performance of each partner is increased in the other's presence. In the present case, the plant-herbivore interaction becomes mutualistic if the conditions for evolution of palatability are fulfilled and evolution does lead to a grazing intensity that is not too high.

We have shown that plants should favor herbivory up to a grazing intensity that corresponds to the CS of palatability and defend themselves above this consumption rate. Plant-herbivore coevolution also depends on the selection pressure exerted on the herbivores. If herbivores are submitted to a fitness gradient that drives them toward a lower consumption rate than the CS of plants, then plants should always encourage consumption. However, if the selection pressure leads herbivores to a higher consumption rate than the CS of plants, then plants should always defend themselves and herbivores should fight against plant defenses. In the absence of costs for herbivore defense, this results in the traditional arms race between plants and herbivores. But here, plants aim at limiting consumption to a threshold. In such a context, plant defense does evolve to limit consumption, as suggested by McNaughton (1983), not to eradicate it completely.

Here we have only explored selection acting on one plant characteristic, and we saw that it should lead to a smaller



grazing intensity than that maximizing primary production. According to the hypothesis of resource management by mammalian herbivores, they manage their resource utilization to maximize the flow of nutrient from these resources. Gordon and Lindsay's (1990) review suggests instead that no resource management is likely to have evolved because cheaters could easily invade it. If herbivores are resource limited, selection on individual herbivores is likely to lead to an overexploitation of their resource, providing that this exploitation bears no cost. In a model of plant-herbivore coevolution, Hartvigsen and Levin (1997) showed that coevolution led to a maximum herbivore population, thus maximizing the flux to herbivore population. Should this occur, selection pressure should lead herbivores to a higher consumption rate than the CS of plants and plants should evolve defense to limit consumption. Thus, we see that under several conditions, herbivores may have a beneficial effect on plant performance, while at the same time an arms race between the two may occur.

The above shows that the coevolutionary outcome of interactions is much more complex than the traditional dualism of a positive-positive or positive-negative interaction, representing either mutualism or antagonism. Conflicts are well known in the case of mutualisms (Anstett et al. 1997), and a mutualistic interaction between plants and herbivores would not mean that plants absolutely aim at being consumed, as Belsky et al. (1993) seem to believe. When the conditions for evolution of a palatable CS are fulfilled, herbivores may have positive or negative effects on plant fitness depending on interaction strength as measured by grazing intensity. The traditional classification of interactions with simple signs ignores such variations in their outcomes (Thompson 1988; Cushman 1991; Bronstein 1994), and thus both mutualism and antagonism may be too simplistic and misleading terms.

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#### APPENDIX 1

##### *Analysis of the Model*

Solving equations (3–5) where all time derivatives are set to zero leads to the following steady-state values of primary productivities in terms of the limiting nutrient in patch  $q$ :

$$\Phi_{1q}^* = (d_p + c_1) \frac{\tau_{2q}R_1 + S_{2q}\mu_h c_2 R_2}{\tau_{1q}\tau_{2q} - S_{1q}S_{2q}\mu_h^2 c_1 c_2} \quad (\text{A1})$$

and

$$\Phi_{2q}^* = (d_p + c_2) \frac{\tau_{1q}R_2 + S_{1q}\mu_h c_1 R_1}{\tau_{1q}\tau_{2q} - S_{1q}S_{2q}\mu_h^2 c_1 c_2}, \quad (\text{A2})$$

where:

$$R_i = R - l_m N_i^*, \quad (\text{A3})$$

$$N_i^* = \frac{m_p + c_i}{u}, \quad (\text{A4})$$

$$\tau_{iq} = v_p m_p + v_h c_i + (1 - S_{iq})\mu_h c_i. \quad (\text{A5})$$

Here,  $R_i$  represents the net input into the local mineral nutrient pool of plant  $i$  per unit of surface occupied,  $\mu_h$  is the fraction of nutrient recycled in the ecosystem along the herbivore pathway and  $\tau_{iq}$  is the loss rate of nutrient from plant  $i$  in patch  $q$  to its local mineral nutrient pool along both plant detritus and herbivore pathways.

The success of strategy  $i$  is measured by its total productivity over the landscape,  $F_i^*$  (eq. 7), the plant with the largest  $F_i^*$  increasing in abundance. Let us call  $\Delta F^*$  the difference between the two  $F_i^*$ s:

$$\Delta F^* = F_2^* - F_1^*. \quad (\text{A6})$$

The sign of  $\Delta F^*$  determines which is the winning strategy. When it is positive, plant type 2 increases in abundance; when it is negative, plant type 1 increases in abundance.

We then address the following question: will a given strategy 1 (with palatability index  $c_1$ ) be outcompeted by a close strategy 2 ( $c_2 = c_1 + \Delta_c$ , where  $\Delta_c \cong 0$ )? For that purpose, we use the function  $f$  to represent the local fitness gradient:

$$f = \left( \frac{\partial \Delta F}{\partial \Delta_c} \right)_{\Delta_c=0}. \quad (\text{A7})$$

When  $\Delta_c$  is in the neighborhood of zero,

$$\Delta F^* \cong f \Delta_c. \quad (\text{A8})$$

The local gradient of fitness  $f$  is given by the following equation:

$$f = \left( \frac{\partial \Delta F}{\partial \Delta_c} \right)_{\Delta_c=0} = \frac{1}{\sum_{q=1}^p S_{2q}} \left( \frac{\partial \left( \sum_{q=1}^p S_{2q} \Phi_{2q}^* \right)}{\partial \Delta_c} \right)_{\Delta_c=0} - \frac{1}{\sum_{q=1}^p S_{1q}} \left( \frac{\partial \left( \sum_{q=1}^p S_{1q} \Phi_{1q}^* \right)}{\partial \Delta_c} \right)_{\Delta_c=0}. \quad (\text{A9})$$

After algebraic manipulation, this reduces to:

$$f \left( c_1, \frac{\sigma^2}{S_1 S_2} \right) = -a(c_1) + \frac{\sigma^2}{S_1 S_2} b(c_1), \quad (\text{A10})$$

where

$$a(c_1) = \frac{\mu_p d_p \left( R - l_m \frac{d_p + c_1}{u} \right) + l_m \frac{d_p + c_1}{u} (v_p d_p + v_h c_1)}{(v_p d_p + c_1)(v_p d_p + v_h c_1)} \quad (\text{A11})$$

and

$$b(c_1) = \frac{\mu_h (d_p + c_1) \left[ v_p d_p \left( R - l_m \frac{d_p + c_1}{u} \right) - l_m \frac{c_1}{u} (v_p d_p + v_h c_1) \right]}{(v_p d_p + c_1)(v_p d_p + v_h c_1)^2}. \quad (\text{A12})$$

We are interested in the sign of the local fitness gradient: When

it is positive, there is selection toward a higher palatability; whereas when it is negative, there is selection toward a lower palatability.

First note that when palatability  $c_1$  is large, the local fitness gradient  $f$  is always negative:

$$\lim_{c_1 \rightarrow +\infty} f \left( c_1, \frac{\sigma^2}{S_1 S_2} \right) = -\frac{l_m}{u} \left[ 1 + \frac{\sigma^2}{S_1 S_2} \frac{\mu_h}{v_h} \right] < 0 \quad (\text{A13})$$

and there is selection for a lower palatability.

We now search for the solutions of the equation  $f(c_1, \sigma^2/S_1 S_2) = 0$  as a function of relatedness,  $\sigma^2/S_1 S_2$ .

(1) Within-patch relatedness is zero, that is, each patch contains plant types at their average frequency. Then:

$$f(c_1, 0) = -\frac{\mu_p d_p \left( R - l_m \frac{d_p + c_1}{u} \right) + l_m \frac{d_p + c_1}{u} (v_p d_p + v_h c_1)}{(v_p d_p + c_1)(v_p d_p + v_h c_1)}, \quad (\text{A14})$$

which is always negative. The only CS is the nonpalatable strategy.

(2) Within-patch relatedness is one, that is, each patch contains only one plant type. Then:

$$f(c_1, 1) = \frac{\left( R - \frac{l_m}{u} (d_p + c_1) \right) (v_p - v_h) d_p - \frac{l_m}{u} (d_p + c_1) (v_p d_p + v_h c_1)}{(v_p d_p + v_h c_1)^2}. \quad (\text{A15})$$

The equation  $f(c_1, 1) = 0$  is a second-degree equation in  $c_1$ :

$$v_h l_m c_1^2 + 2l_m v_p d_p c_1 + [(v_h - v_p)(R u - l_m d_p) + l_m v_p d_p] d_p = 0. \quad (\text{A16})$$

This equation has two real solutions of opposite signs if and only if:

$$(v_h - v_p)(R u - l_m d_p) + l_m v_p d_p < 0. \quad (\text{A17})$$

As we assume that the condition for plant persistence when alone and ungrazed is fulfilled, that is:

$$R > l_m \frac{d_p}{u}, \quad (\text{A18})$$

condition (A17) is equivalent to the condition:

$$v_h < v_{h0}, \quad (\text{A19})$$

where

$$v_{h0} = v_p \frac{\left[ R - 2l_m \frac{d_p}{u} \right]}{\left[ R - l_m \frac{d_p}{u} \right]}. \quad (\text{A20})$$

When the fraction of nutrient lost along the herbivore pathway is greater than the threshold value  $v_{h0}$ , that is  $v_h > v_{h0}$ , there is no positive solution of equation (A16). Because  $f$  is negative when  $c_1$  becomes large (eq. A13),  $f$  is then negative for all positive values of  $c_1$ . There is always selection toward the less palatable type, the only CS being the nonpalatable strategy.

When the fraction of nutrient lost along the herbivore pathway is smaller than the threshold  $v_{h0}$ , that is,  $v_h < v_{h0}$ , equation (A16) has two real roots, one and only one of which is positive. This positive root is a CS indeed, as condition (9) is fulfilled:  $f$  is negative when  $c_1$  is greater than the CS (eq. A13), and since it changes sign between its two roots, it is positive for a palatability lower than the CS.

(3) Within-patch relatedness is intermediate. We look for the shape of the curve described by the equation:

$$f \left( c_1, \frac{\sigma^2}{S_1 S_2} \right) = 0. \quad (\text{A21})$$

When the fraction of nutrient lost along the herbivore pathway is smaller than the threshold value  $v_{h0}$ , this equation is a third-

degree equation in  $c_1$  and a first-degree equation in  $\sigma^2/\overline{S_1 S_2}$ , which gives only simple possible patterns, shown in Figure 2B and 2C.

When the fraction of nutrient loss along the herbivore pathway is smaller than the threshold value  $v_{h0}$ , we have:

$$f(0, 0) < 0 \quad \text{and} \quad (\text{A22})$$

$$f(0, 1) > 0 \quad (\text{A23})$$

Because  $f$  is continuous with respect to the second variable (i.e., relatedness), there is a value of this variable for which the nonpalatable strategy ( $c_1 = 0$ ) is a zero of the local fitness gradient.

$$f\left(0, \frac{\sigma^2}{\overline{S_1 S_2}}\right) = 0 \quad \text{yields:}$$

$$\frac{\sigma^2}{\overline{S_1 S_2}} = D_1 = \frac{\mu_p \left(R - 2l_m \frac{d_p}{u}\right) + l_m \frac{d_p}{u}}{\mu_h \left(R - l_m \frac{d_p}{u}\right)}. \quad (\text{A24})$$

This extremum is a CS if:

$$\left[\frac{\partial f}{\partial c_1}\right]_{c_1=0, \sigma^2/\overline{S_1 S_2}=D_1} < 0. \quad (\text{A25})$$

This condition leads to:

$$v_h > v_{h1}, \quad (\text{A26})$$

where:

$$v_{h1} = v_{h0} - \frac{l_m(2Ru - 2l_m d_p)v_p^2 d_p}{(Ru - l_m d_p)[(Ru - l_m d_p)\mu_p + 2l_m v_p d_p]}. \quad (\text{A27})$$

When the fraction of nutrient lost along the herbivore pathway is smaller than this second threshold, that is,  $v_h < v_{h1}$ , the nonpalatable strategy is a local evolutionary repeller when relatedness  $\sigma^2/\overline{S_1 S_2} = D_1$ . The pattern of CS palatability as a function of relatedness is similar to that of Figure 2C.

When the fraction of nutrient lost along the herbivore pathway is greater than this lower threshold, but smaller than the upper threshold, that is,  $v_{h1} < v_h < v_{h0}$ , the nonpalatable strategy is a local evolutionary attractor, that is, a CS when relatedness  $\sigma^2/\overline{S_1 S_2} = D_1$ . The pattern of CS palatability as a function of relatedness is then similar to that of Figure 2b.

When the fraction of nutrient lost along the herbivore pathway is greater than the upper threshold, that is,  $v_h > v_{h0}$ , the nonpalatable strategy is always the evolutionary attractor, whatever the distribution of plant types (Fig. 2a).

The value of  $v_h$  relative to the two threshold values  $v_{h0}$  and  $v_{h1}$  thus determines the pattern of CS as a function of within-patch relatedness.

## APPENDIX 2

### Generalization to a Lotka-Volterra Interaction

Let us consider the case of a Lotka-Volterra (LV) interaction. The two strategies have consumption rates  $\gamma_1$  and  $\gamma_2$ , and consumption of plant type  $i$  in patch  $q$  has the form:

$$\gamma_i P_{iq} H. \quad (\text{A28})$$

The equations of the LV system are then:

$$\frac{dN_{iq}}{dt} = R - l_m N_{iq} - u N_{iq} P_{iq} + \mu_p m_p P_{iq} + \mu_h m_h \alpha_q H,$$

$$\frac{dP_{iq}}{dt} = u N_{iq} P_{iq} - m_p P_{iq} - \gamma_i P_{iq} H,$$

$$\frac{dH}{dt} = \frac{\sum_{q=1}^p (S_{1q} \gamma_1 P_{1q} + S_{2q} \gamma_2 P_{2q}) H}{p} - m_h H, \quad (\text{A29})$$

where

$$\alpha_q = p \frac{S_{1q} \gamma_1 P_{1q} + S_{2q} \gamma_2 P_{2q}}{\sum_{r=1}^p (S_{1r} \gamma_1 P_{1r} + S_{2r} \gamma_2 P_{2r})}. \quad (\text{A30})$$

Let us consider the case of a resident strategy 1 with a consumption rate  $\gamma_1$  and a rare mutant with a consumption rate  $\gamma_2$  close to  $\gamma_1$ . At equilibrium, herbivore biomass can be approximated by:

$$H^* = \frac{R - l_m \frac{m_p}{u} - v_p \frac{m_p m_h}{\gamma_1}}{v_h m_h + l_m \frac{\gamma_1}{u}} = H^*(\gamma_1). \quad (\text{A31})$$

Let us now consider the system with donor-controlled (DC) herbivory with consumption rates:

$$c_1 = \gamma_1 H^*(\gamma_1), \quad \text{and} \quad c_2 = \gamma_2 H^*(\gamma_1). \quad (\text{A32})$$

The biomass  $P_{iq}$  and primary production  $\phi_{iq}$  of each plant type  $i$  in each patch  $q$  are determined by the same equations in both systems, hence they reach the same values. Thus, if there exists a mutant  $\gamma_2$  that can invade the resident  $\gamma_1$  in the LV system, then there exists a mutant  $c_2$  that can invade the resident  $c_1$  in the DC system, and vice versa. The invading mutants lie on the same side of the residents in both systems. Therefore, the two systems should evolve towards equivalent convergent strategies, with:

$$c_{CS} = \gamma_{CS} H^*(\gamma_{CS}). \quad (\text{A33})$$

A similar but more detailed proof can be found in de Mazancourt et al. (1998).