Multidimensionality of plant defenses and herbivore niches: implications for eco-evolutionary dynamics

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Abstract

Plant defenses are very diverse and often involve contrasted costs and benefits. Quantitative defenses, whose protective effect is dependent on the dose, are effective against a wide range of herbivores, but often divert energy from growth and reproduction. Qualitative defenses do not have such allocation costs. However, while deterrent to some herbivores, they often incur costs through other interactions within the community (eg, decrease in pollination or attraction of other enemies). In the present work, we model the evolutionary dynamics of these two types of defenses, as well and the evolutionary dynamics of the herbivore niche. We also assess the effects of such evolutionary dynamics for the maintenance of diversity within the plant-herbivore system, and for the functioning of such systems (effects of nutrient enrichment). We show that the two types of defenses have different implications. Evolution of quantitative defenses may help to maintain or even increase diversity, while evolution of qualitative defenses most often has a detrimental effect on species coexistence. From a functional point of view, nutrient enrichment selects for higher levels of quantitative defenses, which reduces top-down controls exerted by herbivores. Enrichment does not affect qualitative defenses, nor the evolution of the herbivore niche. We finally discuss the implications of these results for the management of ecosystems.

Introduction

Understanding the evolution of plant defenses is of great importance for ecology and its applications. Because plants serve as the energetic basis of most ecosystems, defenses, by modifying the strength of top-down controls (Chase et al., 2000; Loeuille and Loreau, 2004; Schmitz et al., 2000) may alter the availability of this energy for higher trophic levels (Dickman et al., 2008). Plant defenses also play a critical role in the community composition, not only of herbivores (Becerra, 2007; Kessler et al., 2004; Robinson et al., 2012; van Zandt and Agrawal, 2004; Whitham et al., 2003), but also of higher trophic levels (Halitschke et al., 2008; Poelman et al., 2008; Xiao et al., 2012) and of pollinators (Adler et al., 2006, 2012; Herrera et al., 2002).

While many works study the coevolution of plants and enemies (Agrawal and Fishbein, 2008; Bergelson et al., 2001; Carroll et al., 2005; Cornell and Hawkins, 2003; Loeuille et al., 2002; Rausher, 2001, 1996), current ecological theory linking the evolution of plant defenses to community structure in general is scarce. Also, from an evolutionary point of view, the fitness components incorporated in such studies are often too simplistic to account for community aspects efficiently. Particularly, most studies focus on the evolution of plant defenses assuming allocation costs (de Mazancourt et al., 2001; Loeuille and Loreau, 2004; Loeuille et al., 2002), meaning that they assume that additional defenses divert energy from growth and reproduction (Coley, 1986; Herms and Mattson, 1992; Züst et al., 2011). Such defenses have far reaching implications for ecosystem functioning because they largely decrease the availability of energy for higher trophic levels in two ways. First, by protecting plant biomass, thereby reducing the proportion of productivity transmitted up the food chains. Second, by reducing the productivity, due to allocation costs. When food chain length is constrained by energy availability (Dickman et al., 2008; Oksanen et al., 1981; Pimm and Lawton, 1977;

Wollrab et al., 2012), such costs may ultimately affect food chain length, hence the structure of ecological networks.

While allocation costs have been widely observed for such quantitative defenses (Müller-Schärer et al., 2004; Strauss et al., 2002), whose efficiency is typically dependent on the dose produced by the plant (for chemical defenses) or for the quantity of protective structures (eg, hair, spines), several studies have failed at detecting such allocation costs for different defense strategies (Häring et al., 2008; Koricheva et al., 2004). Such defenses may instead incur ecological costs (Müller-Schärer et al., 2004; Strauss et al., 2002), in the sense that a higher investment in such defenses can be efficient against some enemies, but incurs costs through other interactions in the community (eg, by attracting other enemies or by rendering the plant less attractive to mutualists). Such ecological costs are consistent with several empirical studies (e.g., Adler *et al.* 2012; Xiao *et al.* 2012)□□. They may be particularly suitable for qualitative defenses (Müller-Schärer et al., 2004; Strauss et al., 2002)□, for which the presence of the compound rather than its concentration matters for herbivore deterrence. For instance, some volatile compounds seem to be very variable and associated with a given herbivore specialist (Becerra, 2003)□. Many closely related volatile organic compounds exist (Courtois, 2010)□, involving similar chemical structures and enzymatic pathways and switching from one to another likely does not incur a large cost in terms of growth or reproduction. While defenses with ecological costs do not have the direct energetic implications of defenses based on allocation costs, their variations largely impact relative interaction strengths within the community, and they can play a crucial role in the diversification of herbivore and plant clades (Becerra, 2007, 2003)□. Therefore we expect that such defenses will play a crucial role in the overall maintenance of diversity in the plant-arthropod community.

Implications for the management of ecosystems are widespread. Consider three of the ecosystem services listed in Costanza *et al.* (1997): biological control, pollination and resource provisioning. In an agricultural context, choice of a well-defended cultivar reduces the need for effective biological control, though productivity may be reduced if the defenses divert much energy from individual growth. Also, when plant defenses impact predator and pollinator communities (Xiao et al., 2012), they may couple pollination and biological control in synergistic or antagonistic ways. The three ecosystem services may then be managed quite differently depending on the type of defense used by the plant •(Denison et al., 2003; Loeuille et al., 2013; Xiao et al., 2012).

In the present article, we aim at understanding the interplay of these two defense types as well as their implications for the evolution of the herbivore. The model we develop contains a qualitative defense that is intimately linked to the herbivore niche, thereby allowing for ecological costs, and a quantitative defense that reduce the overall herbivory pressure, whose allocation cost entails a decrease in the plant biomass production. We investigate how evolution of these two defense types and of the herbivore, affect the functioning and total diversity of the community. More specifically, we ask:

1. Whether the evolution of each defense type increases or decreases the diversity of the herbivore compartment. According to observations detailed earlier, we hypothesize that qualitative defenses may maintain herbivore diversity while quantitative defenses can only be detrimental to it by reducing energetic availability.
2. Whether the evolution of each defense types produces diversification in the plant compartment.

3. How the evolution of each defense type affects the functioning of the system, that is the distribution of biomasses among the two trophic levels. We hypothesize that investment in quantitative defenses, by reducing overall vulnerability, may affect top-down controls and largely impact the distribution of nutrient among the two trophic levels.

Ecological model

We model the dynamics of plant and herbivore biomass (*P* and *H* respectively) within an isolated ecosystem. In absence of herbivores, we assume that the plant biomass is constrained by a limiting factor (e.g., energy, limiting nutrient, space) and reaches an equilibrium constrained by *K* (carrying capacity) in the absence of herbivores. We assume that the factor limiting plant biomass is positively related to carrying capacity *K* (e.g., Kaunzinger and Morin, 2008) and does not affect other parameters of the model.

The intrinsic growth rate of plants is noted r. Herbivores consume plants at a rate β and converts a proportion *f* of plants eaten into herbivore biomass. We assume that plant growth is limited by direct competition among plants (α/K: *per capita* competition rate). Herbivore mortality rate *m* is constant.

According to these hypotheses, variations in plant and herbivore biomasses over time follow the system of differential equations:

$$\begin{aligned} \frac{dP}{dt} &= P\left(r\left(1-\frac{\alpha P}{K}\right)-\beta H\right) \\ \frac{dH}{dt} &= H(f\beta P - m) \end{aligned} \qquad (1)$$

For more details on parameters and variables, see Table 1.

Traits and trade-offs

Because plants are consumed by herbivores, herbivores exert a selective pressure on plant defensive traits. The traits of herbivores, whose reproduction and growth depend on the plants they consume, are similarly likely to evolve in response to plant defenses. Hence, the consumption rate of herbivores β is shaped by both plant and herbivore traits. We consider that plants are characterized by two defense traits noted *x* and *y*. The consumption strategy of herbivores is characterized by two traits *p* and *g*. Hence, the consumption rate of herbivores β is a function of these four traits:

$$\beta = \beta_0 \beta_1(y) \beta_2(x, p, g) \qquad (2)$$

, where β_0 is the basal rate of consumption.

Trait *x* represents a qualitative defense that has an ecological cost and trait *y* represents a quantitative defense that has an allocative cost (Müller-Schärer et al., 2004). The efficiency of trait *y* depends on its amount within each plant. We assume it decreases the herbivore consumption rate:

$$\beta_1(y) = e^{-ay} \qquad (3)$$

Trait *y* is supposed costly in term of plant competitive ability (Agrawal et al., 2012) thereby negatively affecting plant carrying capacity:

$$K(y) = K_0 e^{-by} \qquad (4)$$

Combining (3) and (4) allows flexible trade-off shapes between investment in defenses (-β) and *K*: concave ($a>b$), linear ($a=b$) or convex ($a<b$) (Fig.1a).

Trait *x* represents a qualitative defense. Each value of *x* corresponds to a particular assembly of defensive compound that plants may produce (*e.g.*, a given chemical bouquet of volatile

organic compounds). Each plant is characterized by one qualitative defense value. This qualitative defense *x* defines one dimension of the ecological niche of herbivores (Fig.1b). Along this niche dimension, we consider that herbivore consumption is described by two traits, *p* the preference of the herbivore for a given chemical bouquet and *g* the degree of generalism (*g*>0). The further the herbivore preference *p* is from plant trait *x*, the lower its consumption rate. Herbivore generalism *g* describes the range of trait *x* that can be efficiently consumed by the herbivore. We assume a trade-off between the generalism *g* and the maximal consumption rate (Craig MacLean et al., 2004), so that the consumption rate is normalized and remains globally constant when *g* varies. Accounting for these constraints, the herbivore niche is (fig 1b):

$$\beta_2(x,p,g) = \frac{1}{g\sqrt{2\pi}} e^{\frac{-(p-x)^2}{2g^2}} \qquad (5)$$

We studied two competitive scenarios: (1) α=1; (2) direct competition is enhanced when traits are similar (Brännström et al., 2011; Kisdi, 1999; Loeuille and Loreau, 2005; Yoder and Nuismer, 2010). We modeled the relationship between the direct competition coefficient α and plant traits using a Gaussian function. Similarity is defined by the Euclidean distance *D* between plant traits:

$$\alpha\left(x_i - x_j, y_i - y_j\right) = \frac{\alpha_0}{\sigma\sqrt{2\pi}} e^{\frac{-D^2}{2\sigma^2}} \qquad (6), \text{ with } D = \sqrt{(x_i - x_j)^2 + \left(y_i - y_j\right)^2}$$

Evolutionary dynamics

We studied the evolution of plants and herbivores traits using adaptive dynamics methods (Dieckmann and Law, 1996; Geritz et al., 1998). While all trait may coevolve, we here study the evolution of the different species and traits separately, to contrast the implications of the different evolutionary dynamics. The relative fitness of a mutant population in a resident population, denoted W_m, depends on both the mutant and the resident trait. It is defined as the

per capita growth rate of a rare mutant population in a resident population at equilibrium (P^*, H^*). For instance, considering the trait y, a mutant plant has a relative fitness:

$$W_m(y_m, y_r) = \frac{1}{P_m}\frac{dP_m}{dt}\bigg|_{\substack{P_m \to 0 \\ P_r \to P^*}} \qquad (7)$$

where y_m is the trait of the mutant population while the resident population P_r is assumed to be at equilibrium (ecological dynamics are therefore assumed faster than evolutionary dynamics).

The evolution of a trait is modeled using the canonical equation of the adaptive dynamics which assumes that the amplitude of mutation effect on phenotype ω is small. For trait y:

$$\frac{dy}{dt} = k\mu\omega^2 P^*(y)\frac{\partial W_m}{\partial y_m}\bigg|_{y_m \to y_r} \qquad (8)$$

where μ is the mutation rate, ω^2 is the variance of mutation effect, and k is a scaling parameter. The selection gradient $\partial W_m/\partial y_m\big|_{y_m \to y_r}$, embodies the slope of the local adaptive landscape (ie, close to the resident trait) and constrains the direction of evolution. Singular strategies, therefore correspond to:

$$\frac{\partial W_m}{\partial y_m}\bigg|_{y_m \to y_r} = 0 \qquad (9)$$

Evolutionary dynamics around the singular strategies can be analyzed through the computation of second derivatives of the fitness function (Dieckmann and Law, 1996; Geritz et al., 1998). Singular strategy y^*, cannot be invaded by nearby mutants, provided:

$$\frac{\partial^2 W_m}{\partial y_m^2}\bigg|_{y_m \to y_r \to y^*} < 0 \qquad (10)$$

This equilibrium satisfies the convergence criteria (ie, selection favors mutant closer to the singularity in its vicinity) provided:

$$\left.\frac{\partial^2 W_m}{\partial y_r^2}\right|_{y_m \to y_r \to y^*} > \left.\frac{\partial^2 W_m}{\partial y_m^2}\right|_{y_m \to y_r \to y^*} \qquad (11)$$

When an evolutionary equilibrium satisfies both the non-invasibility and the convergence criteria, it is called a Convergence Stable Strategy or CSS (Eshel, 1983). When an evolutionary equilibrium satisfies the convergence condition but is invasible, the selection near the equilibrium is disruptive and evolutionary branching will eventually occur, creating a diversification in the corresponding trait. Finally, we also encountered singularities that were invasible and non convergent, called repeller.

Results

We here describe the main results of the analysis, while more details, including regarding the formulation of fitness functions, fitness gradients and evolutionary singularities are shown in the supplementary information.

Ecological dynamics

The model described by the system of equation (1), has a single equilibrium in which both plants and herbivores coexist at the following densities:

$$P^* = \frac{m}{f\beta}$$
$$H^* = \frac{r\left(1 - \frac{P^*}{K}\right)}{\beta} \qquad (12)$$

From the Jacobian matrix of (1) estimated at equilibrium (12), it is possible to show that this coexistence equilibrium is stable when it is feasible, i.e. when

$$\frac{K}{\alpha} > \frac{m}{f\beta} \qquad (13)$$

When $\frac{K}{\alpha} < \frac{m}{f\beta}$, herbivores go extinct and plants reaches $\frac{K}{\alpha}$.

Effects of enrichment on equilibrium (12) can be studied from derivatives:

$$\frac{\partial P^*}{\partial K} = 0 \text{ and } \frac{\partial H^*}{\partial K} = \frac{r\alpha m}{f\beta^2 K^2} \quad (14)$$

Thus, when considering only ecological dynamics, as plants limiting factor increases (*K* increases), herbivore biomass increases whereas plant biomass remains constant (Fig. 4A).

Evolution of quantitative defenses

When the carrying capacity of plants is sufficiently high to maintain herbivores, the consumption of plants by herbivore may depend on quantitative defense of plants (y) that has an allocative cost (see M&M). Incorporating trait y in equation (13), one gets that herbivore coexist with plants when

$$y < \frac{ln\left(\frac{\beta f_0 K_0}{m}\right)}{a+b} = y_{feas} \qquad (15)$$

The fitness of plant mutant of trait y_m in the resident plant population of trait y_r is then:

$$W(y_m, y_r) = r\left(1 - \frac{\alpha(0, y_m - y_r)P^*(y_r)}{K(y_m)}\right) - \beta(y_m)H^*(y_r) \qquad (16)$$

The evolutionary dynamic of the quantitative defense y is described by the canonical equation (8)

The associated singular strategy is:

$$y^* = \frac{ln\left(\frac{a\beta f_0 K_0}{m(a+b)}\right)}{a+b} \qquad (17)$$

Comparing (17) and (15) shows that the evolutionary singular strategy is always feasible ($y^* < y_{feas}$). The properties of this evolutionary equilibrium (invasibility and convergence criteria) depend on the hypothesis about direct competition between plants. When α=1, the singular strategy satisfies both the convergence (eq 11) and the non-invasibility (eq 10) criteria, being therefore a Continuously Stable Strategy, or CSS (Marrow et al., 1996). Thus the quantitative defense y evolves until it reaches y^* at which point the evolutionary dynamics stabilizes. Note that the selected amount of quantitative defenses increases with energetic parameters of the plant population (eg, K_0) and with herbivore consumption pressures ($ß\ f_0$).

By contrast, when the direct competition between plants increases with trait similarity (eq 6), the evolutionary outcome depends on the following condition:

- If $\sigma > \frac{1}{\sqrt{ab+b^2}}$, the singular strategy y^* remains a CSS (Fig.2A,B).

- If $\sigma < \frac{1}{\sqrt{ab+b^2}}$, the singular strategy y^*, while still convergent becomes invasible. In such instances, disruptive selection yields evolutionary branchings leading to the coexistence of a diversity of quantitative defense strategies, ie the coexistence of differentially defended plant phenotypes (Fig.2C,D).

Variations in biomasses P^* and H^* and in trait y^* with plant limiting factor can be studied by differentiating with respect of K_0 (see appendix). Contrary to the pattern observed for the purely ecological model, when the evolution of the quantitative defense y leads to a CSS, the plant biomass P^*, herbivore biomass H^* and the level of defense y^* at the evolutionary equilibrium all increase with K_0 (Fig. 4B).

Evolution of qualitative defenses

Now fixing y, we turn to the analysis of the evolution of qualitative defenses. Incorporating x in the feasibility condition (13), coexistence is possible if:

$$x \in \left]p - g\sqrt{2ln(A)}, p + g\sqrt{2ln(A)}\right[\qquad (18)$$

(A>1). When direct competition between plants is independent on x (α=1), $A = \beta_0 f K / (mg\sqrt{2\pi})$. When direct competition between plants depend on plants similarity $A = \beta_0 f K \sigma / (mg\alpha_0)$.

Evolutionary dynamics may be analyzed as we did above for y.

The only possible singular strategy is $x^* = p$ (independent of the competitive scenario). Convergence and non-invasibility criteria are always violated; making this singular strategy a repeller (Geritz et al., 1998). Thus, evolutionary dynamics always move away from herbivore preference *p*. Because of the selective pressure of herbivores, the qualitative defense *x* always increases or always decreases depending on the initial position of *x* with respect of herbivore preference *p*. Eventually, the evolution of the qualitative defense leads to herbivores extinction (evolutionary murder *sensu* Dercole et al., 2006), when *x* reaches the feasility boundaries (eq 18). It is possible to understand how enrichment affects the ecological and evolutionary states, by differentiating equilibrium biomasses and trait with respect to *K*. An increase of *K* leads to an increase of herbivore biomass while plant biomass and plant qualitative defenses *x** remain unaffected (see appendix & Fig. 4C).

Evolution of herbivore preference

When the carrying capacity of plants is sufficiently high to maintain herbivores, the consumption of plants by herbivores is constrained by the difference *p*-*x*. Herbivore biomass is strictly positive if $x - g\sqrt{2\ln(A)} < p < x + g\sqrt{2\ln(A)}$ where *A*>1 and $A = \beta_0 \, f \, K \big/ (mg\sqrt{2\pi})$.

Only one evolutionary equilibrium then exists, $p^* = x$, which is always convergent and cannot be invaded (CSS). Evolution eventually leads to this value. Thus, herbivore preference *p* increases or decreases depending on its initial position with respect to *x* until herbivore preference matches plant qualitative defenses *x*. It is possible to understand how enrichment affects the ecological and evolutionary states, by differentiating equilibrium biomasses and trait with respect to *K*. An increase of *K* leads to an increase of herbivore biomass while plant biomass and herbivore preference *p** are unaffected (see appendix & Fig. 4D).

Evolution of herbivore generalism

It is possible to show that the equilibrium value of herbivore biomass as defined by equation (12) can be defined as a function of trait *g*, and that this function reaches a peak at |p-x|. This peak is positive (ie, herbivore population can be positive), only if $|p-x| < B$ where $B = \beta_0 \, f \, k / (m\sqrt{2\pi e})$. Under this condition *g* is constrained to an interval $[g_{feas}^{min}, g_{feas}^{max}]$ that allows both plant and herbivore populations to be positive.

The canonical equation has one evolutionary equilibrium, which is positive, $g^* = |p-x|$. This singularity is by definition feasible (see the argument above). This equilibrium satisfies non-invasibility and convergence criteria and is thus a CSS (Fig.3B). Evolution of herbivore generalism *g* therefore converges toward g^* (Fig.3A). This means that selection acts to match the degree of the generalism of the herbivore with the difference that exists between its preference and the trait of the available plant population.

Differentiating with respect of *K*, it may be shown that any increase in *K* leads to an increase in herbivore biomass while plant biomass and herbivore generalism g^* remain constant (appendix & Fig. 4E).

Discussion

The aim of the present work is to understand how the evolution of plant defenses and of herbivore consumption strategies may alter the maintenance of diversity and the functioning of plant-herbivore systems. More particularly, we want to assess whether different types of defenses (in terms of costs and effects) have similar implications for community structure and functioning. These two types of defenses have been proposed based on reviews of many different empirical systems (Müller-Schärer et al., 2004; Strauss et al., 2002) that propose to distinguish quantitative defenses (efficient against all herbivores, but having allocative costs

that reduce growth or productivity) and qualitative defenses (whose costs are not allocative, but happens through the modifications of other interactions). Most theoretical works on plant defenses focus on the former type (de Mazancourt et al., 2001; Levin et al., 1990; Loeuille and Loreau, 2004; Loeuille et al., 2002; Loreau and Mazancourt, 1999), while the evolution of qualitative defenses has received far less attention (but see Loeuille and Leibold, 2008). Here we show that the evolution of these two defenses have very different implications both in terms of diversity maintenance and in terms of ecosystem functioning.

Concerning the maintenance of diversity, evolution of quantitative defenses has only positive effects. First, contrary to our prediction, maintenance of the plant-herbivore system is warranted at the evolutionary equilibrium. This is simply due to the fact that evolution of defenses decreases the herbivore population. At some point, herbivore population becomes too low and selection of higher levels of defense would incur too much intrinsic costs for little benefits. Next to maintaining the different trophic levels, the evolution of quantitative defenses may also allow an increase in the plant phenotypic diversity, when disruptive selection allows the coexistence of high, low and intermeditate levels of defense. Such a diversification within the plant compartment however requires that plants of similar trait compete more intensively. These results are consistent with other models that predict branching in defense strategies (Costa et al., 2016; Ito and Ikegami, 2006), but also, from an empirical point of view, with the widespread coexistence of contrasted investment in defenses within natural ecosystems (Züst et al., 2012).

Evolution of qualitative defenses does not have such intrinsic positive effects on the maintenance of diversity. First, our results suggest that, *per se*, the evolution of such defenses should lead to defense strategies that ever diverge from the herbivore preference. Because evolution away from the herbivore does not involve costs in itself, evolution eventually

allows for plant that will be too little consumed by the herbivore to match its mortality rate. Evolution of plant then kills the herbivore (evolutionary murder *sensu* Dercole et al., 2006) thereby constraining the maintenance of diversity within the community. Also, we note that, in the case of qualitative defenses, diversification is never observed, even when similar plants compete more strongly. We therefore suggest that, intrinsically (ie, under the assumption of a simple one plant-one predator community), evolution of qualitative defenses may constrain diversity while the evolution of quantitative defenses ultimately favors diversity. Finally, note that, when allowing for herbivore evolution in response to qualitative defenses, we predict that evolution of herbivore, either through variations in its preference or through variations in its generalism, always allows the coexistence of the plant-herbivore community.

In terms of ecosystem functioning, we uncover the impact of nutrient enrichment on the eco-evolutionary dynamics of the plant-herbivore system. Enrichment always increases herbivore biomass. From an ecological point of view, we observe that such enrichment yields an increase of the herbivore biomass, while the plant biomass remains constant. Such a pattern is expected, as our model formulation allows for strong top-down effects (Hairston et al., 1960; Oksanen and Oksanen, 2000; Oksanen et al., 1981). We also show that the evolution of herbivore strategies or of plant qualitative defenses do not alter this pattern. Indeed, evolution of these traits is independent of nutrient supply, as qualitative defenses do not hinge on allocative costs and herbivore traits define the niche of herbivores based on such qualitative defenses. Evolution of quantitative defenses, on the other hand, may change the effects of nutrient enrichment. Higher nutrient supplies relax the allocation constraints that affect quantitative defenses. Therefore, nutrient supply allows for the production of higher quantities of defenses, which in turn decreases the effects of top down controls by modulating the herbivore consumption rate. In such a scenario, plant biomass then increases when enrichment occurs. Such a weakening of top-down controls due to plant defenses is in good agreement

with other theoretical/conceptual works (Armstrong, 1979; Leibold, 1996; Loeuille and Loreau, 2004; Strong, 1992), and has been suggested as an important mechanism for the mitigation of trophic cascades in nature (Borer et al., 2005; Polis et al., 2000). Our results again highlight that considering different types of defenses is especially important to understand the fate of ecosystems undergoing environmental change. Whether plants are defending themselves with qualitative or quantitative defenses acutally leads to contrasted outcome in terms of ecosystem functioning here.

We however stress that the model we use here is deliberately simple as its goal is mostly to contrast the different eco-evolutionary dynamics linked to various plant-herbivore traits. We expect that two levels of complexity, not considered here, will indeed matter much for most empirical situations. First, it seems likely that most plants do not use quantitative defenses or qualitative defenses, but actually use the two types of defenses simultaneously. Also, while the quantitative/qualitative dichotomy is useful, it may well be that costs and effects are actually varying in a more continuous fashion so that defenses actually follow a continuum between the two extremes (qualitative/quantitative) used to structure the present model. In any case, if considering the coevolution of quantitative and qualitative defenses, we expect strong interactions between their evolutionary dynamics. Consider for instance that the cost of qualitative defenses is to attract another herbivore. Then, a plant that would have high levels of quantitative defenses would not pay much of such a cost, for it is protected against such alternative herbivores. Also, if one imagines a fast variation in qualitative defenses (for they are initially cost-free), we expect a decrease in the herbivore population, hence a decrease in the selective pressures for quantitative defenses. We therefore expect that quantitative and qualitative defenses create evolutionary feedbacks on one another, so that the study of their coevolution is especially interesting.

A second important simplification lies in the ecological system we use for our analysis. We have considered one single plant and herbivore population, to allow for a more thorough and tractable analysis of the consequences of the evolution of the different traits. An important perspective is to relax such a hypothesis and to consider the diffuse coevolution of plants and herbivores within diverse communities. Consider for instance the implications of qualitative defenses for diversity. As mentioned at the beginning of this discussion part, the evolution of such defenses ultimately constrains the diversity in our system, the plant eventually "killing" the herbivore through its evolutionary dynamics. We expect this conclusion to differ when a diversity of herbivores is considered.

Consider that, next to the herbivore we modeled in the result part (that has a preference p_1), we now consider also a second herbivore, whose preference is p_2. Note that, under such conditions, we expect that the most efficient herbivore will win the competition and eventually exclude the other herbivore (R* rule, Tilman, 1982). For the sake of the argument, suppose that ecological and evolutionary dynamics of the plant is however faster than the herbivore dynamics (*e.g.*, because the generation time of herbivores and plants are vastly different), so that, on a first approximation, we may consider the herbivore population fixed and study the evolution of defenses x in this context. Evolution of qualitative plant defenses x in the one herbivore context, as earlier, selects for traits that diverge from the herbivore preference p_1 (hence an expected evolutionary murder of this herbivore, figure 5A). The presence of the second herbivore however halts this runaway evolution (figure 5B) and allows the first herbivore to remain in the system (at least on this timescale). Similarly, the evolution of the plant due to the first herbivore facilitates the maintenance of the second herbivore (as the plant trait becomes more similar to its preference p_2). Because this evolution actually leads to an equivalent consumption of the plant by the two herbivores, a neutral coexistence is then possible, so that the two herbivores eventually remain in the system. Indirect effects

happening between the two herbivores due to the plant evolution are positive on both sides, a situation we call “evolutionary facilitation”. Such positive effects due to evolution have already been shown in other contexts. For instance, Abrams and Matsuda (2005) show that adaptation in the prey can facilitate the persistence of its predator. Moreover, indirect interactions between herbivores through plant defenses have been suggested in empirical works. Expression of plant defenses following herbivore consumption has been shown to facilitate some other herbivores, while deterring others, so that such defenses strongly affect herbivore diversity maintenance (Poelman et al., 2008). The extension of the model we present here, in a more complex network context, may allow a better understanding regarding the role of plant defenses and of herbivore consumption traits in the maintenance of diversity within natural communities, but also help the management of biological control, in an agricultural context (Loeuille et al., 2013).

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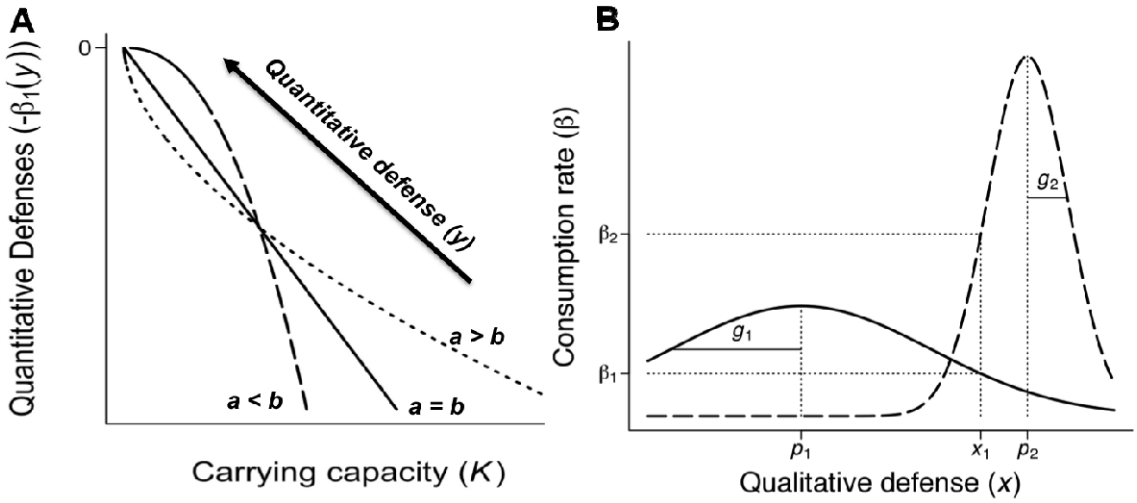

Figure 1. Types of defense and their costs. A. The quantitative defense trait *y* decreases consumption β of plants by herbivores and affects competitive ability, lowering the plant carrying capacity *K*. The trade-off can be concave (dashed line, $a<b$), linear (solid line, $a=b$) or convex (dotted line, $a>b$). B. Plant qualitative defense trait *x* of plants defines one dimension of the herbivore niche. Herbivore niche is described by two consumption traits: *p* and *g*. Herbivore preference *p*, is the *x* value at which the consumption rate of the herbivore is maximal. The generalism of the herbivore, denoted *g*, sets the ability of the herbivore to consume plants a given range of *x* around *p*. The herbivore defined by (p_1,g_1) is a generalist (solid line) whereas the herbivore (p_2,g_2) is a specialist (dashed line). The more generalist the herbivore, the lower is its maximal consumption rate.

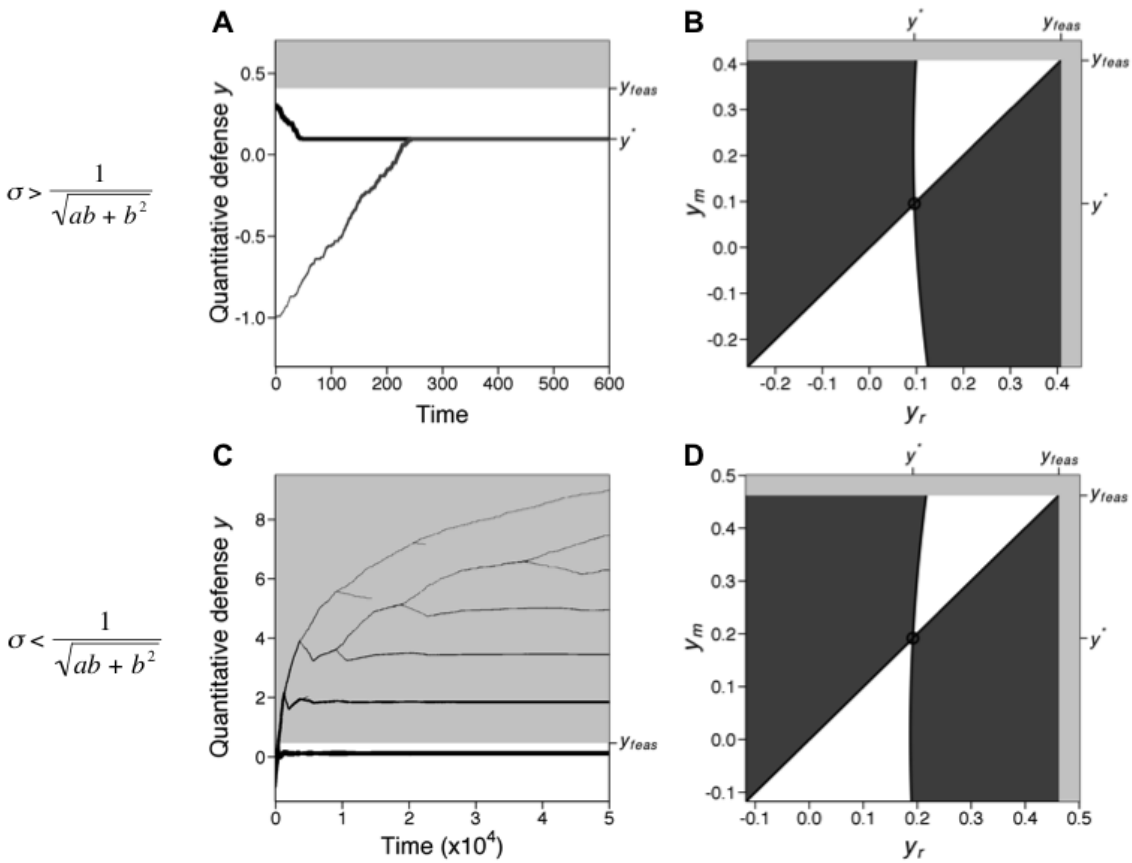

Figure 2. Evolution of quantitative defenses *y* assuming that competition increases with trait similarity. The herbivore, feeding on one plant, maintains a positive biomass H^* if the quantitative defense y is below y_{feas} ($H^*<0$, light grey background; $H^*>0$ white background). When σ is high (A, B), trait difference has small effects on the direct competition, the quantitative defense y converges to the evolutionary equilibrium y^* which is a CSS. When σ is low (C, D), similar morphs compete very strongly, yielding disruptive selection and successive evolutionary branchings. On A and C, the thickness of lines is proportional to plant biomass. (B, D) Pairwise Invasibility Plots show the sign (+: dark grey area; -: white area) of mutant fitness as a function of the trait of the resident y_r and of the mutant y_m. Parameter values (A, B, C and D): r=1, K_0=10, α_0=1, σ=0.4, β_0=1, f=0.1, m=0.5, b=1. (A,B): a=0.7. (C,D): a=0.5

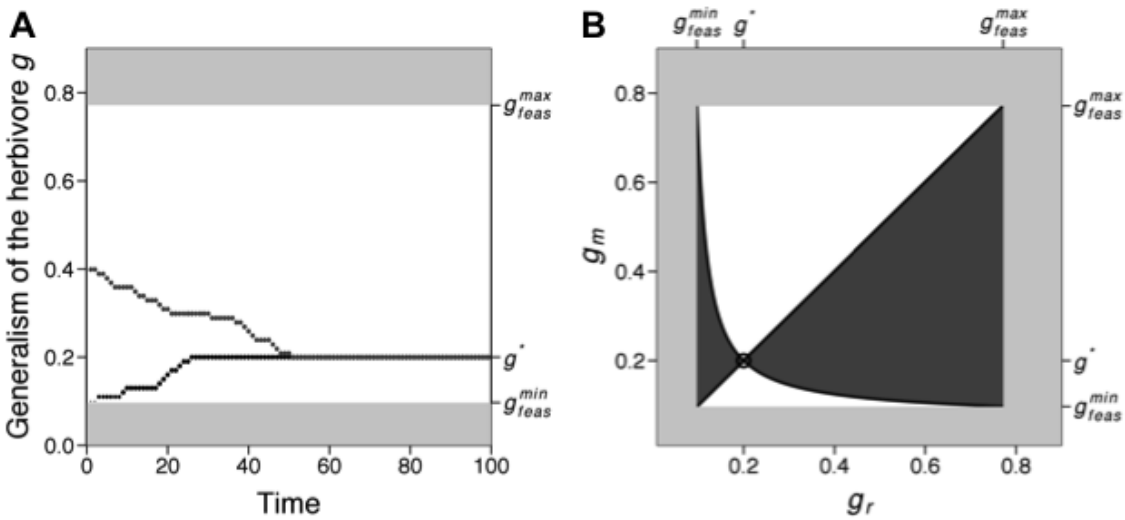

Figure 3: Evolution of herbivore generalism *g*. The herbivore maintains a positive biomass H^* if its generalism g is between $g_{feas}^{\min}$ and $g_{feas}^{\max}$ ($H^*<0$, light grey area; $H^*>0$ white area). Generalism converges to an evolutionary equilibrium $g^* = |p - x|$ that is a CSS. (A) Two examples of evolutionary dynamic for two initial values of g (g_0=0.1; g_0=0.4). (B) Pairwise Invasibility Plots near represent the sign (+: dark grey area; -: white area) of mutant fitness as a function of the trait of the resident g_r and of the mutant g_m. Parameter values (A, B): r=1, K=10, α_0=1, σ=0.4, β_0=1, f=0.1, m=0.5, p=0.3, x=0.5.

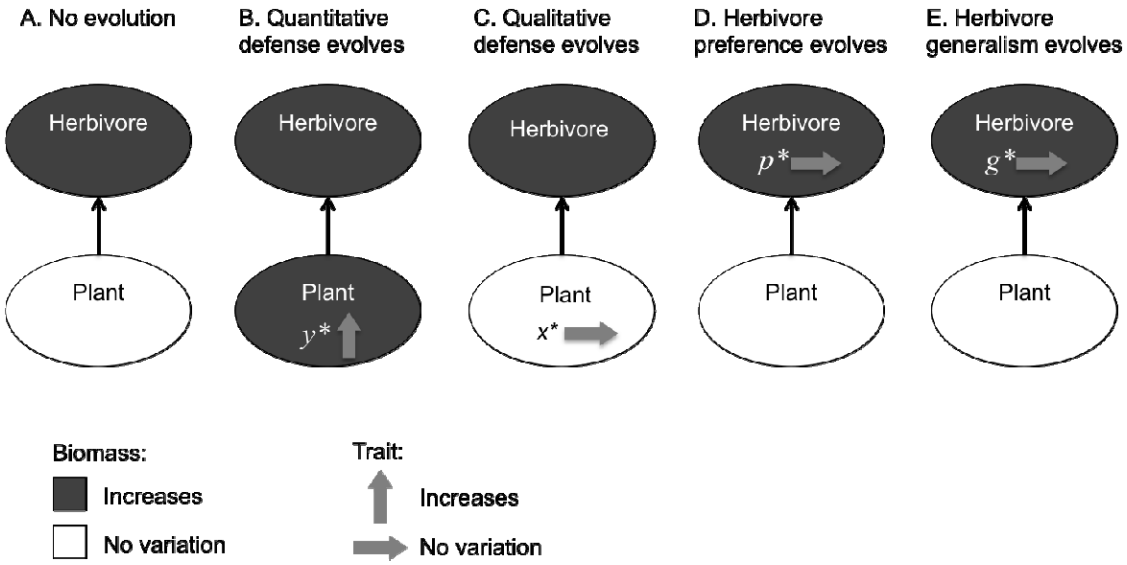

Figure 4. Effects of enrichment, depending on the eco-evolutionary scenario. Without evolution, enrichment has a positive effect on the density of herbivores (A). This pattern remains when the herbivore evolves (D, E) or when qualitative defenses evolve (C). Quantitative defenses (B) are increased through enrichment, allowing for an increase in plant biomass.

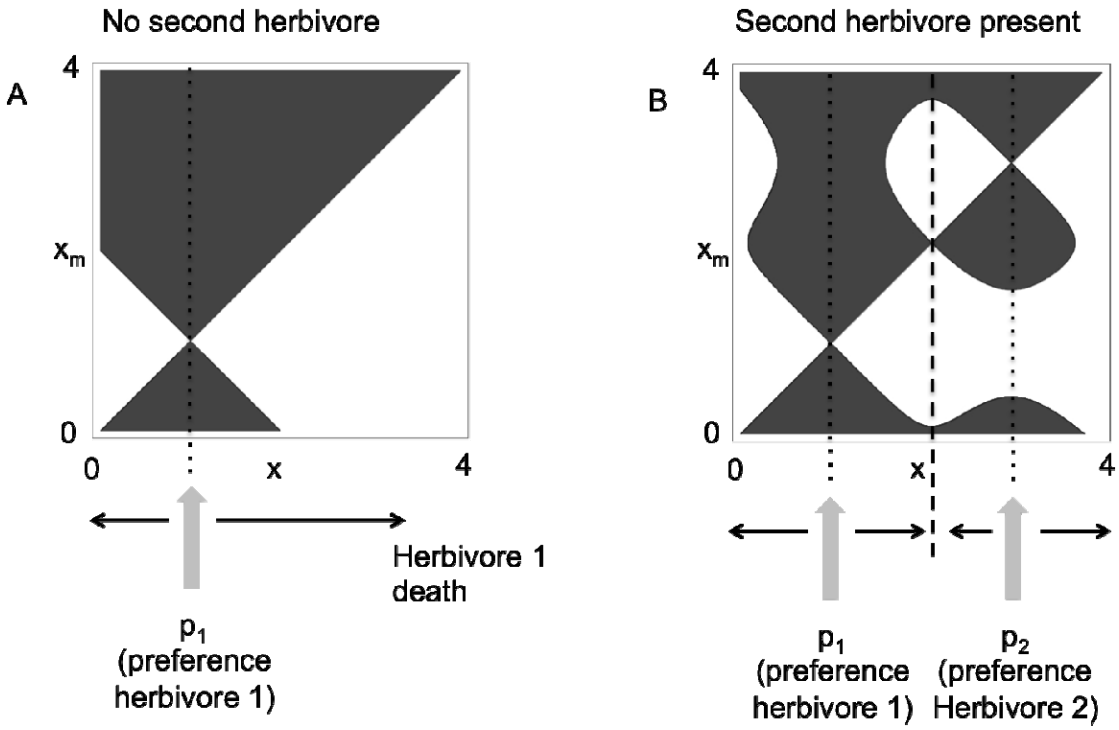

Figure 5: Effect of herbivore diversity on the evolution of qualitative defenses. Here, herbivore populations are considered constant (eg, herbivore populations vary on a much longer timescale). Thick grey arrows show the herbivore preferences. Black thin arrows the evolutionary dynamics of qualitative defenses. Dotted lines show the positions of the repellers and dashed line the position of the CSS. A) No second herbivore ($H_2=0$). Plants evolve away from preference p_1, decreasing the herbivore 1 feeding rate eventually threatening its maintenance. B) The second herbivore is present ($H_2=0.05$). Due to its preference p_2, evolution of the plant may settle between the two preferences, facilitating the coexistence of the two herbivores.

Table 1. Notation, name and dimension of variables and parameters.

	Name	Definition domain	Dimension
Variables			
P	Plant Biomass	$[0, +\infty[$	$kg.m^{-2}$
H	Herbivore Biomass	$[0, +\infty[$	$kg.m^{-2}$
x	Plant qualitative defenses	$]-\infty, +\infty[$	dimensionless
y	Amount of quantitative defenses	$[0, +\infty[$	dimensionless
p	Herbivore preference (preferred qualitative defenses)	$]-\infty, +\infty[$	dimensionless
g	Degree of generalism of the herbivore	$]0, +\infty[$	dimensionless
Functions			
K	Carrying capacity		$kg.m^{-2}$
β	Per capita consumption rate		$m^2.kg^{-1}.time^{-1}$
α	Trait dependent competition scaling		dimensionless
Parameters			
K_0	Basal carrying capacity of plant	$]0, +\infty[$	$kg.m^{-2}$
f	Conversion efficiency	$[0, +\infty[$	Dimensionless
m	Herbivore *per capita* mortality rate	$[0, +\infty[$	$time^{-1}$
r	Maximal plant intrinsic growth rate	$[0, +\infty[$	$time^{-1}$
a	Benefits of quantitative defenses in terms of reduced consumption	$[0, +\infty[$	dimensionless
b	Costs of quantitative defenses in terms of reduced competitive ability	$[0, +\infty[$	dimensionless
β_0	Basal herbivore consumption rate	$[0, +\infty[$	$m^2.kg^{-1}.time^{-1}$
σ	Variance of the competition kernel	$]0, +\infty[$	dimensionless