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

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8 *equal contribution

9 **Running title:** Plant-herbivore eco-evolutionary dynamics

10

11 **Abstract**

12   Plant defenses are very diverse and often involve contrasted costs and benefits.

13   Quantitative defenses, whose protective effect is dependent on the dose, are effective

14   against a wide range of herbivores, but often divert energy from growth and reproduction.

15   Qualitative defenses often have little allocation costs. However, while deterrent to some

16   herbivores, they often incur costs through other interactions within the community (eg,

17   decrease in pollination or attraction of other enemies). In the present work, we model the

18   evolutionary dynamics of these two types of defenses, as well and the evolutionary

19   dynamics of the herbivore niche. We assess the effects of such evolutionary dynamics for

20   the maintenance of diversity within the plant-herbivore system, and for the functioning of

21   such systems under various levels of resource availability. We show that the two types of

22   defenses have different implications. Evolution of quantitative defenses often helps to

23   maintain or even increase diversity, while evolution of qualitative defenses most often has

24   a detrimental effect on species coexistence. From a functional point of view, increased

25   resource availability selects for higher levels of quantitative defenses, which reduces top-

26   down controls exerted by herbivores. Resource availability does not affect qualitative

27   defenses, nor the evolution of the herbivore niche. The growing evidence that plant

28   defenses are diverse in types, benefits and costs has large implications not only for the

29   evolution of these traits, but also for their impacts on community diversity and ecosystem

30   functioning.

31 **Keywords:** quantitative defenses, qualitative defenses, resource availability, diversity

32 maintenance

33Introduction

34Understanding the evolution of plant defenses is of great importance for ecology and its 35applications. Because plants serve as the energetic basis of most ecosystems, defenses, by 36modifying the strength of top-down controls (Chase et al., 2000; Loeuille and Loreau, 2004; 37Schmitz et al., 2000) may alter the availability of this energy for higher trophic levels 38(Dickman et al., 2008). Plant defenses also play a critical role in the community composition, 39not only of herbivores (Becerra, 2007; Kessler et al., 2004; Robinson et al., 2012; van Zandt 40and Agrawal, 2004; Whitham et al., 2003), but also of higher trophic levels (Halitschke et al., 412008; Poelman et al., 2008; Xiao et al., 2012) and of pollinator assemblages (Adler et al., 422006, 2012; Herrera et al., 2002).

43While many works study the coevolution of plants and enemies (Agrawal and Fishbein, 442008; Bergelson et al., 2001; Carroll et al., 2005; Cornell and Hawkins, 2003; Loeuille et 45al., 2002; Rausher, 2001, 1996), current ecological theory linking the evolution of plant 46defenses to community structure in general is scarce. Also, from an evolutionary point of 47view, the fitness components incorporated in such studies are often too simplistic to 48account for community aspects efficiently. Particularly, most studies focus on the 49evolution of plant defenses assuming allocation costs (de Mazancourt et al., 2001; 50Loeuille and Loreau, 2004; Loeuille et al., 2002), proposing that additional defenses 51divert energy from growth and reproduction (Coley, 1986; Herms and Mattson, 1992; 52Züst et al., 2011). Such defenses have far reaching implications for ecosystem 53functioning because they largely decrease the availability of energy for higher trophic 54levels in two ways. First, by protecting plant biomass, these defenses constrain the 55proportion of productivity transmitted up the food chains. Second, these defenses 56reduce the productivity, because of direct allocation costs.

57When food chain length is constrained by energy availability (Dickman et al., 2008; Oksanen

58et al., 1981; Pimm and Lawton, 1977; Wollrab et al., 2012), such costs ultimately modify the

59structure of ecological networks.

60While allocation costs have been widely observed for such quantitative defenses (Müller-

61Schärer et al., 2004; Strauss et al., 2002), whose efficiency is typically dependent on the dose

62produced by the plant (for chemical defenses) or for the quantity of protective structures (eg,

63hair, spines), several studies failed to detect such allocation costs (Häring et al., 2008;

64Koricheva et al., 2004). A possibility is that allocation costs exist but were not properly

65detected, these defenses may also be constrained by alternative costs, for instance through

66other ecological interactions (ecological costs: Müller-Schärer et al., 2004; Strauss et al.,

672002). A higher investment in such defenses can be efficient against some enemies, but incurs

68costs by attracting other enemies or by rendering the plant less attractive to mutualists (e.g.,

69Adler *et al*. 2012; Xiao *et al*. 2012). Ecological costs may be particularly suitable for

70qualitative defenses (Müller-Schärer et al., 2004; Strauss et al., 2002), for which the presence

71of the compound rather than its concentration matters for herbivore deterrence. For instance,

72some volatile compounds seem to be very variable and efficient only against a given

73herbivore specialist (Becerra, 2003). Many closely related volatile organic compounds exist

74(Courtois, 2010), involving similar chemical structures and enzymatic pathways. Switching

75from one to another likely does not incur a large cost in terms of growth or reproduction.

76While defenses with ecological costs do not have the direct energetic implications of defenses

77based on allocation costs, their variations largely impact relative interaction strengths within

78the community. They can also play a crucial role in the diversification of herbivore and plant

79clades (Becerra, 2007, 2003).

80In the present article, we aim at understanding the interplay of these two defense types as well

81as their implications for the evolution of the herbivore. The model we develop contains a

82qualitative defense that is intimately linked to the herbivore niche, thereby allowing for

83ecological costs (in the sense that efficiency against one herbivore will come at a cost given

84another herbivore), and a quantitative defense that reduces any herbivore pressure, whose

85allocation cost entails a decrease in the plant biomass production. We investigate how

86evolution of these two defense types and of the herbivore, affect the functioning and structure 87of the community. More specifically, we ask:

88   1.   Whether the evolution of each defense type alter the persistence of the herbivore in
89   different ways. According to observations detailed earlier, we hypothesize that
90   qualitative defenses may allow the herbivore persistence while quantitative defenses
91   can only be detrimental to it by reducing energetic availability.

92   2.   Whether the evolution of each defense types produces diversification in the plant
93   compartment (ie, the coexistence of different defensive strategies).

94   3.   How the evolution of each defense type affects the functioning of the system, that is
95   the distribution of biomasses among the two trophic levels and its changes with
96   resource availability. We hypothesize that investment in quantitative defenses, by
97   reducing overall vulnerability, will lower top-down controls therefore allowing plant
98   biomass increase (and low response of herbivore biomass).

99**Ecological model**

100We model the dynamics of plant and herbivore biomass (P and H respectively) within an 101isolated ecosystem. In the absence of herbivores, we assume that the plant biomass is 102constrained by a limiting factor (e.g., energy, limiting nutrient, space) and reaches an 103equilibrium constrained by K (carrying capacity).

104The intrinsic growth rate of plants is noted r. Herbivores consume plants at a rate β and 105converts a proportion f of consumed plant biomass into herbivore biomass. We assume 106that plant growth is limited by direct competition among plants (α/K: *per capita* 107competition rate). Herbivore mortality rate m is constant.

108Accounting for these hypotheses, we model the variations in plant and herbivore 109biomasses over time through a simple Lotka-Volterra system:

110
$$\frac{dP}{dt} = P\left(r\left(1 - \frac{\alpha P}{K}\right) - \beta H\right)$$
$$\frac{dH}{dt} = H\left(f\beta P - m\right)$$
(1)

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

	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	Plant quantitative defenses	$]-\infty, +\infty[$	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

112 **Table 1: Notation, name and dimension of variables and parameters**

113 Traits and trade-offs

114 Because plants are consumed by herbivores, herbivores exert a selective pressure on

115 plant defensive traits. The traits of herbivores, whose reproduction and growth depend

116 on the plants they consume, are similarly likely to evolve in response to plant defenses.

117 Hence, the consumption rate of herbivores β is shaped by both plant and herbivore

118 traits. We consider that plants are characterized by two defense traits noted x and y. The

119consumption strategy of herbivores is characterized by two traits p and g. Hence, the

120consumption rate of herbivores β is a function of these four traits:

121$\beta = \beta_0 \beta_1(y) \beta_2(x,p,g)$ (2)

122, where β_0 is the basal rate of consumption.

123Trait y represents a quantitative defense that has an allocative cost (Müller-Schärer et al.,

1242004). The efficiency of trait y depends on its amount within each plant. We assume it

125decreases the herbivore consumption rate:

126$\beta_1(y) = e^{-ay}$ (3)

127We suppose that allocative costs affect the plant competitive ability (Agrawal et al., 2012):

128$K(y) = K_0 e^{-by}$ (4)

129Combining (3) and (4) allows flexible trade-off shapes between investment in defenses

130(-β) and K: concave ($a>b$), linear ($a=b$) or convex ($a<b$) (Fig 1A).

131Trait x represents a qualitative defense. For instance, x may be construed as a particular

132assembly of defensive compounds (*e.g.,* a given chemical bouquet of volatile organic

133compounds). Each plant is characterized by one qualitative defense value. This

134qualitative defense x defines one dimension of the ecological niche of herbivores (Fig

1351B). Along this niche dimension, we consider that herbivore consumption is described

136by two traits, p the preference of the herbivore for a given chemical bouquet and g the

137degree of generalism ($g>0$). The further the herbivore preference p is from plant trait x,

138the lower its consumption rate (ie, qualitative defenses affect herbivore consumption

139through trait matching rules). Herbivore generalism g describes the range of trait x that

140can be efficiently consumed by the herbivore. We assume a trade-off between the

141generalism g and the maximal consumption rate (Craig MacLean et al., 2004), so that the

142consumption rate is normalized and remains globally constant when g varies.

143Accounting for these constraints, the herbivore niche is (Fig 1B):

144$\beta_2(x,p,g)=\dfrac{1}{g\sqrt{2\pi}}e^{\frac{-(p-x)^2}{2g^2}}$ (5)

145Note that trait x does not entail any direct cost. However, changes in x may be

146constrained by ecological costs (ie, by increasing interaction with other herbivores). For

147instance, if plant trait x is between the traits of two herbivores (p_1 and p_2 respectively),

148then any variation of x will decrease the interaction with one herbivore, but attract the

149other (eg, as on Fig 1B). As a result of equations 4 and 5, we have two traits for defense:

150one with allocation costs and no ecological cost (y), while the other has only ecological

151costs and no allocation costs (x). We acknowledge that in nature, defense traits are not

152likely to be as clear cut, and that qualitative defenses may actually involve weak

153allocation costs or quantitative defense may be counteracted by some herbivores.

154However, this simplification allows us to fully describe resulting evolutionary dynamics

155and to highlight the consequences of various cost structures for plant defenses.

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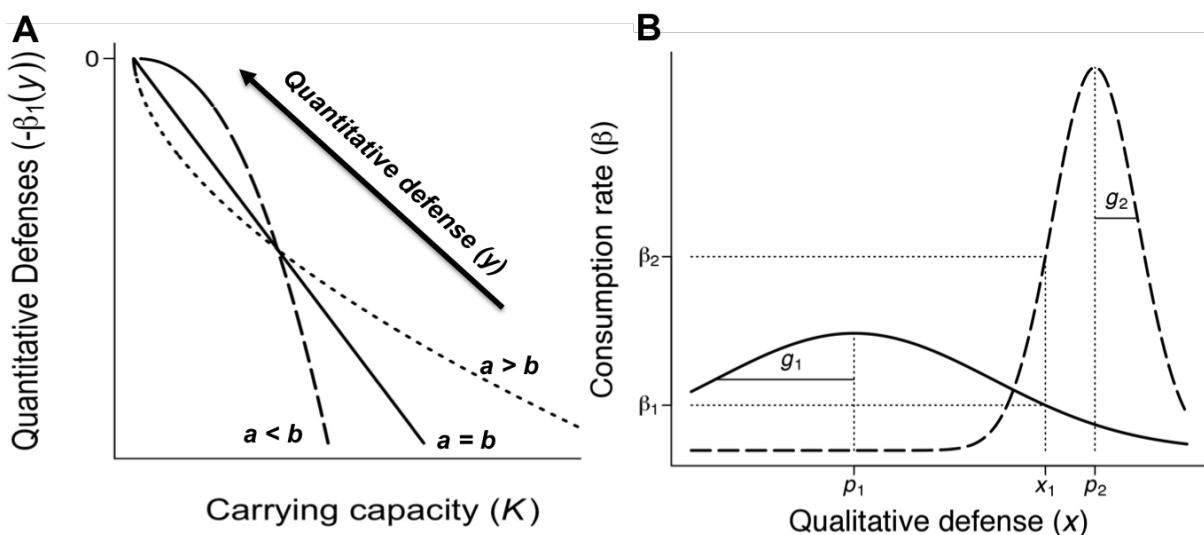
157**Figure 1. Types of defense and their costs.** A. The quantitative defense trait y

158decreases consumption β of plants by herbivores and affects competitive ability,

159lowering the plant carrying capacity K. The trade-off can be concave (dashed line, $a<b$),

160linear (solid line, $a=b$) or convex (dotted line, $a>b$). B. Plant qualitative defense trait x of

161plants defines one dimension of the herbivore niche. Herbivore niche is described by

162two consumption traits: p and g. Herbivore preference p, is the x value at which the

163consumption rate of the herbivore is maximal (trait matching). The generalism of the

164herbivore, denoted g, sets the ability of the herbivore to consume plants a given range of

165x around p. The herbivore defined by (p_1,g_1) is a generalist (solid line) whereas the

166herbivore (p_2,g_2) is a specialist (dashed line). The more generalist the herbivore, the

167lower is its maximal consumption rate.

168We studied two competitive scenarios: (1) $\alpha=1$; (2) direct competition is enhanced when traits

169are similar (Brännström et al., 2011; Kisdi, 1999; Loeuille and Loreau, 2005; Yoder and

170Nuismer, 2010). We modeled the relationship between the direct competition coefficient α

171and plant traits using a Gaussian function. Similarity is defined by the Euclidean distance D

172between plant traits:

173$\alpha\left(x_i-x_j, y_i-y_j\right)=\dfrac{\alpha_0}{\sigma\sqrt{2\pi}}e^{\frac{-D^2}{2\sigma^2}}(6)$, with $D=\sqrt{\left(x_i-x_j\right)^2+\left(y_i-y_j\right)^2}$

174**Evolutionary dynamics**

175We studied the evolution of plant and herbivore traits using adaptive dynamics methods

176(Dieckmann and Law, 1996; Geritz et al., 1998). While all traits may coevolve, we here

177study the evolution of each species and each trait separately, to contrast the implications

178of the different evolutionary dynamics. Therefore, for each trait, we consider a

179monomorphic population and determine a fitness of a mutant whose value for the given

180trait slightly differs.

181The relative fitness of a mutant population in a resident population, denoted W_m,

182depends on both the mutant and resident traits. It is defined as the *per capita* growth

183rate of a rare mutant population in a resident population at equilibrium (P_{eq}, H_{eq}). For

184instance, considering the trait y, a mutant plant has a relative fitness:

$$185 W_m(y_m, y_r) = \frac{1}{P_m} \frac{dP_m}{dt} \bigg|_{\substack{P_m \to 0 \\ P_r \to P_{eq}}} (7)$$

186where y_m is the trait of the mutant population while the resident population P_r is

187assumed to be at equilibrium (ecological dynamics are therefore assumed faster than

188evolutionary dynamics).

189The evolution of a trait is modeled using the canonical equation of the adaptive

190dynamics, which assumes that the amplitude of mutation effects, ω, is small. For trait y:

$$191 \frac{dy}{dt} = k\mu \omega^2 P_{eq}(y) \frac{\partial W_m}{\partial y_m} \bigg|_{y_m \to y_r} (8)$$

192where μ is the *per capita* mutation rate, ω^2 is the variance of mutation effect, and k is a

193scaling parameter. The selection gradient $\dfrac{\partial W_m}{\partial y_m} \bigg|_{y_m \to y}$ corresponds to the slope of the local

194adaptive landscape (ie, close to the resident trait) and constrains the direction of

195evolution. Singular strategies y^*, therefore correspond to:

$$196 \frac{\partial W_m}{\partial y_m} \bigg|_{y_m \to y_r} = 0 (9)$$

197Evolutionary dynamics around the singular strategies can be analyzed by computing the

198second derivatives of the fitness function (Dieckmann and Law, 1996; Geritz et al.,

1991998). Singular strategy $y*$, cannot be invaded by nearby mutants, provided:

$$200 \left. \frac{\partial^2 W_m}{\partial y_m^2} \right|_{y_m \to y_r \to y*} < 0 \quad (10)$$

201Moreover, singular strategies satisfy the convergence criteria (ie, selection favors

202mutant closer to the singularity in its vicinity) provided:

203

$$204 \left. \frac{\partial^2 W_m}{\partial y_r^2} \right|_{y_m \to y_r \to y*} > \left. \frac{\partial^2 W_m}{\partial y_m^2} \right|_{y_m \to y_r \to y*} \quad (11)$$

205When an evolutionary equilibrium satisfies both the non-invasibility and the

206convergence criteria, it is called a Convergence Stable Strategy or CSS (Eshel, 1983).

207When an evolutionary equilibrium satisfies the convergence condition but is invasible,

208the selection near the equilibrium is disruptive and an evolutionary branching

209eventually occurs, creating a diversification in the corresponding trait (ie, the

210coexistence of two or more phenotypes exhibiting different defense levels). Finally, we

211also encountered singularities that were invasible and non convergent, called repeller.

212Note that the framework we use here can be extended to account for variations not in

213one trait at a time, but of multiple traits simultaneously (eg, Loeuille et al. 2002). It can

214also be extended to follow the evolution of traits along branches passed the first

215branching point. Our study can then be thought as the first step of a more complete

216evolutionary analysis. Our analysis of single traits however allows a complete

217mathematical analysis of the singularities and associated evolutionary dynamics

218(detailed in the appendix). More complex coevolutionary scenarios do not allow a

219tractable analysis of the evolutionary trajectories, as convergence and invasibility

220criteria cannot be easily extended in such instances (Kisdi 2006).

221**Results**

222We here describe the main results of the analysis. More details, including regarding the

223formulation of fitness functions, fitness gradients and evolutionary singularities are

224shown in the supplementary information.

225**Ecological dynamics**

226The model described by the system of equation (1), has a single equilibrium allowing the

227coexistence of plants and herbivores:

228
$$P_{eq} = \frac{m}{f\beta}$$
$$H_{eq} = \frac{r\left(1 - \frac{P_{eq}}{K}\right)}{\beta} \quad (12)$$

229

230From the Jacobian matrix of (1) estimated at equilibrium (12), it is possible to show that

231this coexistence equilibrium is stable when it is feasible, i.e. when

232$$\frac{K}{\alpha} > \frac{m}{f\beta} \quad (13)$$

233When $\frac{K}{\alpha} \leq \frac{m}{f\beta}$, herbivores go extinct and plants reaches $\frac{K}{\alpha}$.

234

235Effects of enrichment on equilibrium (12) can be studied from derivatives:

236$$\frac{\partial P_{eq}}{\partial K} = 0 \text{ and } \frac{\partial H_{eq}}{\partial K} = \frac{r\alpha m}{f\beta^2 K^2} \quad (14)$$

237Thus, when considering only ecological dynamics, as plants limiting factor increases (K

238increases), herbivore biomass increases whereas plant biomass remains constant (Fig.

2394A), stressing the importance of top-down controls in the ecological model.

240Evolution of quantitative defenses

241When the carrying capacity of plants is sufficiently high to maintain herbivores, the

242consumption of plants by herbivores depends on the level of quantitative defense of

243plants y. Incorporating trait y in equation (13), one gets that herbivore coexist with

244plants when

$$245 \quad y < \frac{\ln\left(\dfrac{\beta f_0 K_0}{m}\right)}{a+b} = y_{feas} \,(15)$$

246The fitness of a rare plant mutant of trait y_m in the resident plant population of trait y_r is

247then:

$$248 W\left(y_m, y_r\right) = r\left(1 - \frac{\alpha\left(0, y_m - y_r\right) P_{eq}\left(y_r\right)}{K\left(y_m\right)}\right) - \beta\left(y_m\right) H_{eq}\left(y_r\right) \,(16)$$

249The evolutionary dynamics of the quantitative defense y are described by the canonical

250equation (8)

251The associated singular strategy is:

$$252 \quad y* = \frac{\ln\left(\dfrac{a\beta f_0 K_0}{m(a+b)}\right)}{a+b} \,(17)$$

253Comparing (17) and (15) shows that the evolutionary singular strategy is always

254feasible ($y^* < y_{feas}$). The properties of this evolutionary equilibrium (invasibility and

255convergence criteria) depend on the competition scenario that is considered. When

256competition does not depend on trait similarity ($\alpha=1$), the singular strategy satisfies

257both the convergence (eq 11) and the non-invasibility (eq 10) criteria, being therefore a

258Continuously Stable Strategy, or CSS (Marrow et al., 1996). Quantitative defense levels

259then evolve to reach y^* at which point the evolutionary dynamics stabilize. Note that the

260selected amount of quantitative defenses increases with energetic parameters of the

261plant population (eg, K_0) and with herbivore consumption pressures (βf_0).

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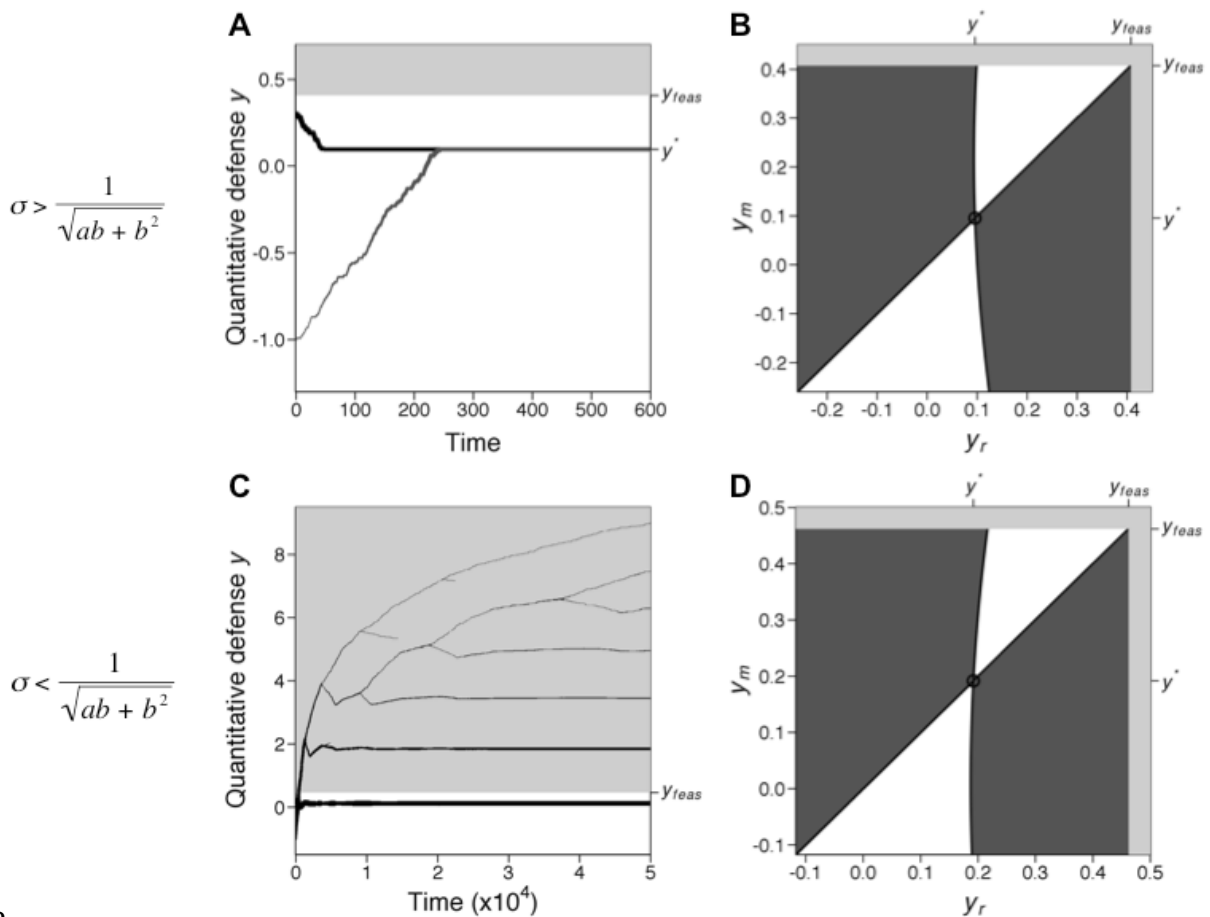
263**Figure 2. Evolution of quantitative defenses y assuming that competition increases**

264**with trait similarity.** The herbivore, feeding on one plant, maintains a positive biomass

265H_{eq} if the quantitative defense y is below y_{feas} ($H_{eq}<0$, light grey background; $H_{eq}>0$ white

266background). When σ is high (A, B), trait difference has small effects on the direct

267competition, the quantitative defense y converges to the evolutionary equilibrium y^*

268which is a CSS. When σ is low (C, D), similar morphs compete very strongly, yielding

269disruptive selection and successive evolutionary branchings. On A and C, the thickness

270of lines is proportional to plant biomass. (B, D) Pairwise Invasibility Plots show the sign

271(+: dark grey area; -: white area) of mutant fitness as a function of the trait of the

272resident γ_r and of the mutant γ_m. Parameter values (A, B, C and D): $r=1$, $K_0=10$, $\alpha_0=1$,

273$\sigma=0.4$, $\beta_0=1$, $f=0.1$, $m=0.5$, $b=1$. (A,B): $a=0.7$. (C,D): $a=0.5$

274By contrast, when the direct competition between plants increases with trait similarity

275(eq 6), the evolutionary outcome depends on the following condition:

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

277• If $\sigma < \dfrac{1}{\sqrt{ab+b^2}}$, the singular strategy γ^*, while still convergent becomes invasible. In

278   such instances, disruptive selection yields successive evolutionary branchings

279   leading to the coexistence of a diversity of quantitative defense strategies, ie the

280   coexistence of plant phenotypes exhibiting contrasted levels of quantitative defenses

281   (Fig.2C,D). Note that in such instances, values of the trait γ can become larger that the

282   limit value γ_{feas} (eq 15). Eq 5 is indeed computed from the one plant-one herbivore

283   system (eq 12), while on Fig 2C, the herbivore consumes a set of plants exhibiting

284   various defense traits γ, including one abundant plant species that is palatable (the γ

285   of the lower branch allows a feasible system).

286Variations in biomasses P_{eq} and H_{eq} and in trait γ^* with plant limiting factor can be

287studied by differentiating with respect of K_0 (see appendix). Contrary to the pattern

288observed for the purely ecological model, when the evolution of the quantitative defense

289γ leads to a CSS, the plant biomass P_{eq}, herbivore biomass H_{eq} and the level of defense γ^*

290at the evolutionary equilibrium all increase with K_0 (Fig. 4B). Evolution of quantitative

291defenses therefore allows the plants to reduce top down controls exerted by the

292herbivore.

293Evolution of qualitative defenses

294Now fixing quantitative defense level γ, we analyze the evolution of qualitative defenses.

295Incorporating x in the feasibility condition (13), coexistence is possible if:

296$x \in \,]\,p - g\sqrt{2\ln(A)}, p + g\sqrt{2\ln(A)}\,[$¿

297($A>1$). When direct competition between plants is independent on x ($\alpha=1$), $A = \dfrac{\beta_0 f K}{m g \sqrt{2\pi}}$.

298When direct competition between plants depend on plants similarity $A = \dfrac{\beta_0 f K \sigma}{m g \alpha_0}$.

299The only possible singular strategy is $x* = p$ (independent of the competitive scenario).

300Convergence and non-invasibility criteria are always violated; making this singular

301strategy a repeller (Geritz et al., 1998). Thus, evolutionary dynamics always move away

302from herbivore preference p. Such an outcome is intuitive. As we assume no direct costs

303of qualitative defenses x, they may only be counterselected when they increase

304consumption by other herbivores. As our model here just considers one herbivore, plant

305evolution is continuous and directional. Eventually, the evolution of the qualitative

306defense leads to herbivores extinction (evolutionary murder *sensu Dercole et al., 2006)*,

307when x reaches the feasibility boundaries (eq 18). It is possible to understand how

308resource availability affects the ecological and evolutionary states, by differentiating

309equilibrium biomasses and trait with respect to K. Higher levels of resources increase

310herbivore biomass while plant biomass and plant qualitative defenses x^* remain

311unaffected (see appendix & Fig. 4C).

312**Evolution of herbivore preference**

313When the carrying capacity of plants is sufficiently high to maintain herbivores, the

314consumption of plants by herbivores is constrained by the difference *p-x*. Herbivore

315biomass is strictly positive if $x - g\sqrt{2\ln(A)} < p < x + g\sqrt{2\ln(A)}$ where $A > 1$ and $A = \dfrac{\beta_0 f K}{m g \sqrt{2\pi}}$.

316Only one evolutionary equilibrium then exists, $p* = x$, which is always convergent and

317cannot be invaded (CSS). Evolution eventually leads to this value. Thus, herbivore

318preference *p* increases or decreases depending on its initial position with respect to *x*

319until herbivore preference matches plant qualitative defenses *x*. As for plants, such

320simple dynamics would be altered in more complex communities. A herbivore

321consuming several plants differing in their trait *x* would face a trade-off between the

322consumption of one plant and the other.

323Higher resource availability leads to an increase of herbivore biomass while plant

324biomass and herbivore preference *p** are unaffected (see appendix & Fig. 4D).

325**Evolution of herbivore generalism**

326Equilibrium value of herbivore biomass as defined by equation (12) can be defined as a

327function of trait *g,* and that this function reaches a peak at |p-x|. This peak is positive (ie,

328herbivore population can be positive), only if $|p - x| < B$ where $B = \dfrac{\beta_0 f K}{m \sqrt{2\pi e}}$. Therefore, *g*

329is constrained to an interval $\left[g_{feas}^{min}, g_{feas}^{max} \right]$ that allows both plant and herbivore populations

330to be positive.

331The singular strategy associated with herbivore specialization is $g* = |p - x|$. This

332singularity is by definition feasible (see the argument above). This equilibrium satisfies

333non-invasibility and convergence criteria and is thus a CSS (Fig.3B). Evolution of

334herbivore generalism g therefore converges toward g^* (Fig.3A). Selection acts to match

335the degree of the generalism of the herbivore with the difference that exists between its

336preference and the trait of the available plant population. Differentiating with respect of

337K, it may be shown that any increase in K leads to an increase in herbivore biomass

338while plant biomass and herbivore generalism g^* are not affected by resource

339availability (appendix & Fig. 4E).
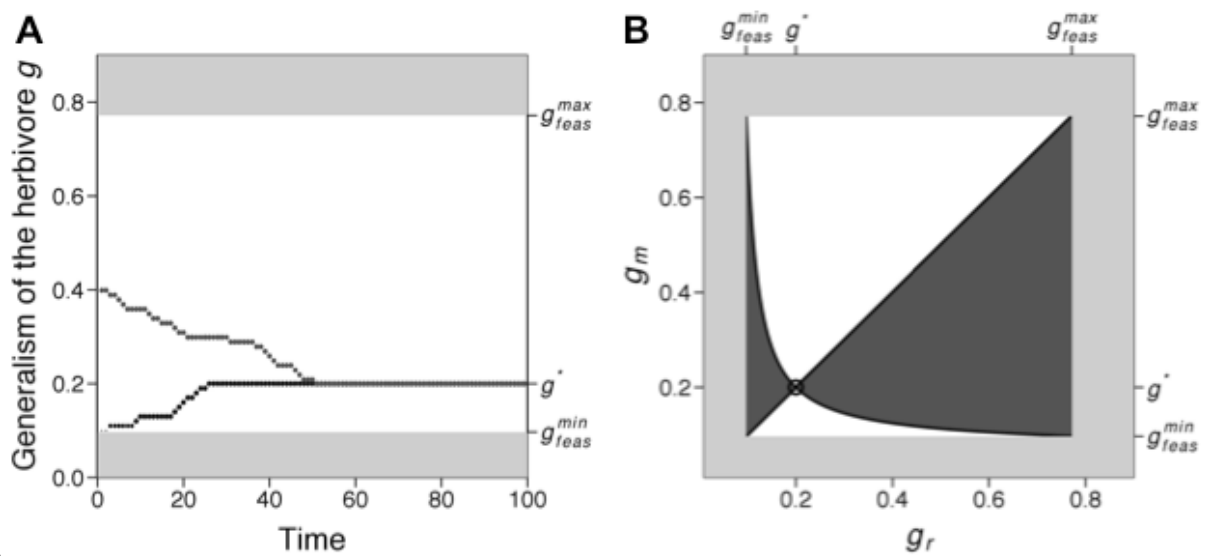
340

341**Figure 3: Evolution of herbivore generalism g**. The herbivore maintains a positive

342biomass H^* if its generalism g is between g_{feas}^{min} and g_{feas}^{max} ($H^*<0$, light grey area; $H^*>0$ white

343area). Generalism converges to an evolutionary equilibrium $g* = |p - x|$ that is a CSS. (A)

344Two examples of evolutionary dynamics for two initial values of g (g_0=0.1; g_0=0.4). (B)

345Pairwise Invasibility Plots near represent the sign (+: dark grey area; -: white area) of

346mutant fitness as a function of the trait of the resident g_r and of the mutant g_m.

347Parameter 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.

348
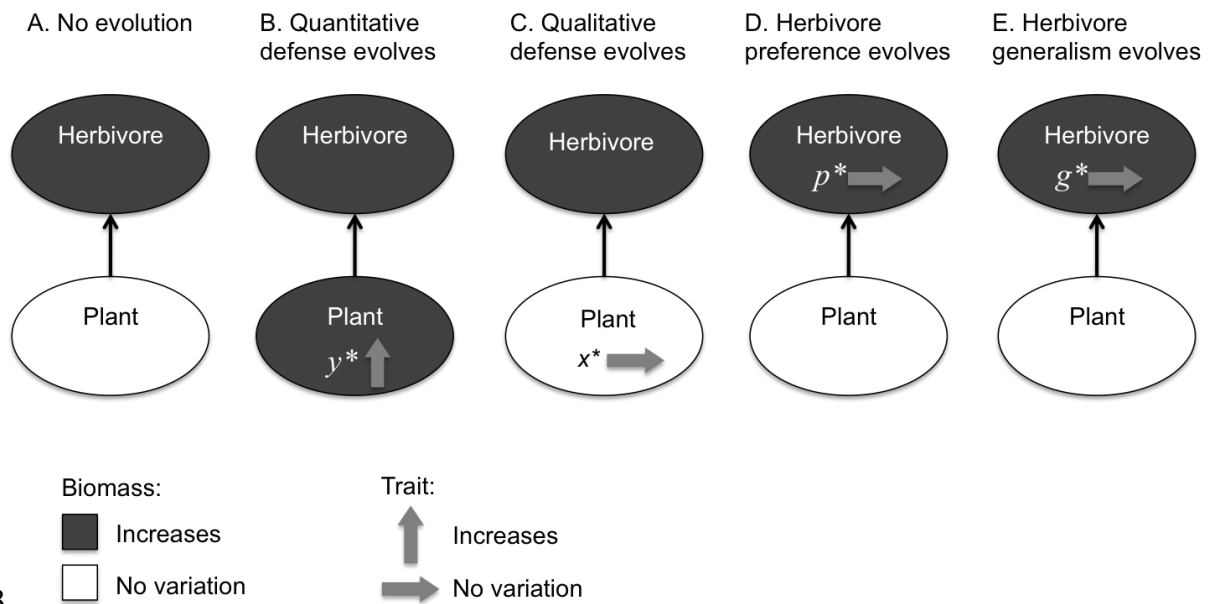
Figure 4. Effects of increases in resource availability, depending on the eco-evolutionary scenario. Without evolution, enrichment has a positive effect on the density of herbivores (A). This pattern remains when the herbivore evolves (D, E) or when qualitative defenses evolve (C). Quantitative defenses (B) are increased when resource levels are higher, allowing for an increase in plant biomass.

Discussion

The aim of the present work is to understand how the evolution of various types of plant defenses and of herbivore consumption strategies alters the structure and the functioning of plant-herbivore systems. The two types of defenses we consider have been proposed based on reviews of many different empirical systems (Müller-Schärer et al., 2004; Strauss et al., 2002) that 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).

366Concerning the structure of the community, evolution of quantitative defenses tends to

367increase the complexity of the system. First, contrary to our prediction, coexistence of

368the plant-herbivore system is warranted at the evolutionary equilibrium. Evolution of

369quantitative defenses indeed decreases the herbivore population. At some point,

370herbivore population becomes too low and selection of higher levels of defense incurs

371too much intrinsic costs for little benefits. Evolution then stops, but the herbivore persist

372(through at smaller biomass). Next to maintaining the different trophic levels, the

373evolution of quantitative defenses also increases the plant phenotypic diversity, when

374disruptive selection allows the coexistence of plant phenotypes that have contrasted

375levels of defenses. Such a diversification within the plant compartment however

376requires that plant competition is partly linked to trait similarity. These results are

377consistent with other models that predict branching in defense strategies (Costa et al.,

3782016; Ito and Ikegami, 2006), but also, from an empirical point of view, with the

379widespread coexistence of contrasted investment in defenses within natural ecosystems

380(Züst et al., 2012).

381Evolution of qualitative defenses, on the contrary, leads the system to simpler structures. Our

382results suggest that, *per se*, the evolution of such defenses should lead to strategies that ever

383diverge from the herbivore preference. Because evolution away from the herbivore does not

384involve costs in itself, evolution eventually allows the existence of plants that will be too little

385consumed to compensate the herbivore intrinsic mortality rate. Evolution of plant then kills

386the herbivore (evolutionary murder *sensu Dercole et al., 2006)* thereby constraining the

387maintenance of diversity within the community. Also, we note that, in the case of qualitative

388defenses, diversification of defense strategies is never observed, even when similar plants

389compete more strongly. We therefore suggest that, intrinsically (ie, under our assumption of a

390simple one plant-one predator community), evolution of qualitative defenses may limit

391diversity (both in terms of species coexistence and in terms of phenotypic variability) while
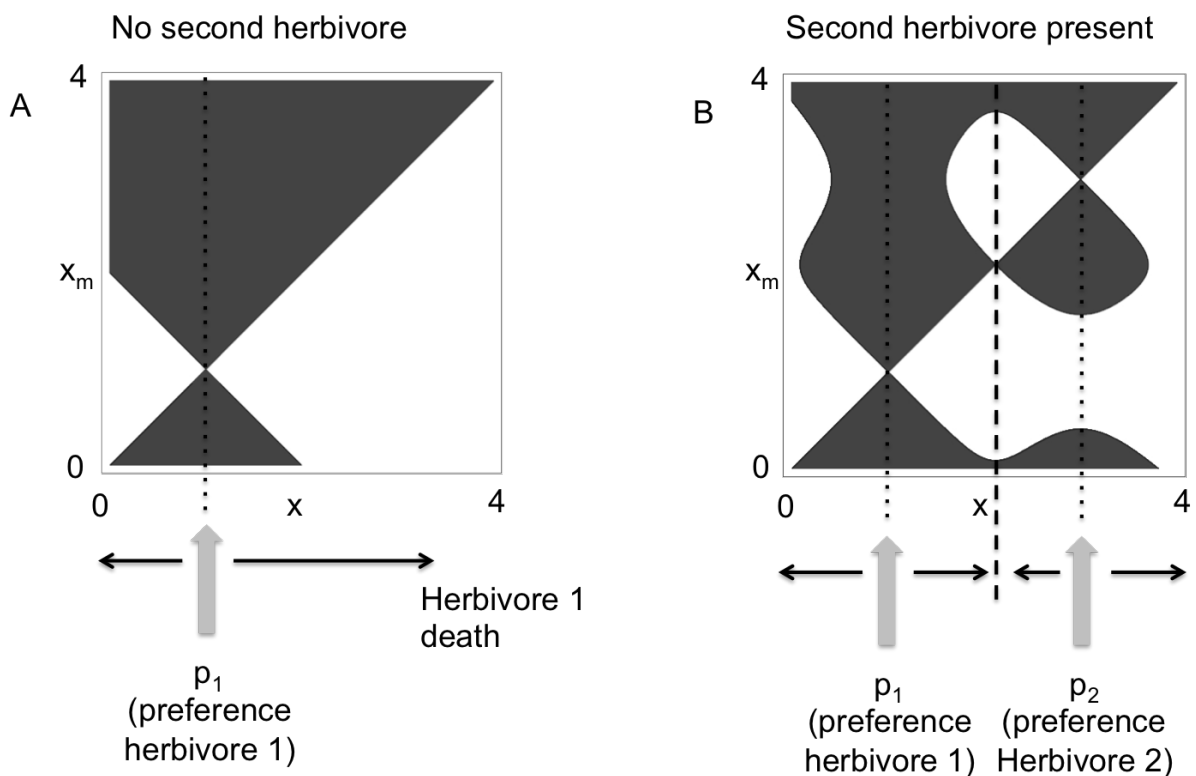
392the evolution of quantitative defenses ultimately favors diversity. Finally, note that, herbivore

393evolution in response to qualitative defenses, either through variations in its preference or

394through variations in its generalism, always allows the coexistence of the plant-herbivore

395community. It however does not lead to the coexistence of various herbivore strategies.

396In terms of ecosystem functioning, we uncover the impact of variation in resource availability

397on the eco-evolutionary dynamics of the plant-herbivore system. In all scenarios, higher levels

398of resources always increase herbivore biomass. When only ecological dynamics is allowed,

399the plant biomass remains constant. Such a pattern is expected, as our model formulation

400allows for strong top-down effects (Hairston et al., 1960; Oksanen and Oksanen, 2000;

401Oksanen et al., 1981). The evolution of herbivore strategies or of plant qualitative defenses

402does not alter this pattern. Indeed, evolution of these traits is independent of resource supply,

403as qualitative defenses do not hinge on allocative costs and herbivore traits define the niche of

404herbivores based on such qualitative defenses. Evolution of quantitative defenses, on the other

405hand, is expected to alter the pattern that would be expected when discarding evolution.

406Higher resource availability relaxes the allocation constraints that affect quantitative defenses.

407It then allows the production of higher levels of defenses, which in turn decreases the effects

408of top down controls by modulating the herbivore consumption rate. In such a scenario, plant

409biomass then increases when more resources are available. Such a weakening of top-down

410controls due to plant defenses is in good agreement with other theoretical/conceptual works

411(Armstrong, 1979; Leibold, 1996; Loeuille and Loreau, 2004; Strong, 1992), and has been

412suggested as an important mechanism for the mitigation of trophic cascades in nature (Borer

413et al., 2005; Polis et al., 2000). Our results again highlight that considering different types of

414defenses is especially important to understand the fate of ecosystems undergoing

415environmental change. Whether plants are defending themselves with qualitative or

416quantitative defenses eventually leads to contrasted outcomes in terms of ecosystem

417functioning here. Finally, note that the evolutionary part of these results may also be tested.

418Along environmental gradients of resources we for instance expect molecules acting as

419quantitative defenses will systematically increase, while molecules acting as qualitative

420defenses will remain approximately constant.

421While the two types of defenses have contrasted effects on coexistence, one may wonder how

422their evolutions affect system stability. As explained in the result section, in the case of our

423linear model, coexistence of the two species insures that the equilibrium is asymptotically

424stable. However, it is still possible to assess the return time to the equilibrium (assuming a

425small disturbance on the equilibrium), through the changes in the eigenvalues of the

426associated jacobian matrix (eg, Rip & McCann 2011). Earlier works have shown that the

427resilience of the system will increase when the consumer (here herbivore) death rate increases

428relative to the its attack rate (Rip & McCann 2011). Therefore, when evolution favors higher

429defenses, the system is stabilized (see appendix 2, fig S1, S2). This leads to interesting

430outcomes if one considers the effects of enrichment in our model (figure 4). Ignoring

431evolution, enrichment (eg, higher K) is destabilizing (appendix 2), as expected from the

432paradox of enrichment (Rosenzweig 1971). Now consider the evolution of quantitative

433defenses. Enrichment then leads to more defenses (Fig 4B), thus a lower attack rate, so that

434this evolutionary effect of enrichment is stabilizing. Interestingly, the direct (destabilizing)

435effect of enrichment is exactly compensated by the (stabilizing) effect of selecting higher

436defenses, so that enrichment is actually neutral for system stability (appendix 2). Conversely,

437in the case of qualitative defenses, enrichment does not lead to any change in evolved

438defenses (figure 4), so it remains destabilizing.

439We however stress that the model we use here is deliberately simple as its goal is mostly to

440contrast eco-evolutionary dynamics linked to various plant-herbivore traits. We expect that

441two levels of complexity, not considered here, will indeed matter much for most empirical

442situations. First, it seems likely that most plants do not use quantitative defenses or qualitative

443defenses, but actually use the two types of defenses simultaneously. Also, while the

444quantitative/qualitative dichotomy is useful as a first approximation, costs and effects are

445likely to vary in a more continuous fashion so that defenses actually follow a continuum

446between the two extremes (qualitative/quantitative) used to structure the present work. When

447considering the coevolution of quantitative and qualitative defenses, we expect strong

448interactions between their evolutionary dynamics. Consider for instance that the cost of

449qualitative defenses is to attract another herbivore. A plant having high levels of quantitative

450defenses would not pay much of such a cost, for it is protected against such alternative
451herbivores. Now imagine a fast variation in qualitative defenses (as they are involve little
452direct costs) in response to increase in a herbivore population. Such fast evolutionary
453dynamics will negatively impact the herbivore population, thereby decreasing the selective
454pressures for quantitative defenses. We therefore expect that quantitative and qualitative
455defenses create evolutionary feedbacks on one another, so that the study of their coevolution
456is especially interesting and an exciting perspective for future works.

457A second important simplification lies in the ecological system we use for our analysis. We
458have considered one single plant and herbivore population, to allow for a more thorough and
459tractable analysis of the consequences of the evolution of the different traits. An important
460perspective is to consider the diffuse coevolution of plants and herbivores within diverse
461communities. Consider for instance the implications of qualitative defenses for diversity. As
462mentioned at the beginning of this discussion part, the evolution of such defenses ultimately
463constrains the diversity in our system, the plant eventually "killing" the herbivore through its
464evolutionary dynamics. We expect this conclusion to differ when a diversity of herbivores is
465considered.

466

467**Figure 5: Effect of herbivore diversity on the evolution of qualitative defenses**.

468Here, herbivore populations are considered constant (eg, herbivore populations vary on

469a much longer timescale). Thick grey arrows show the herbivore preferences. Black thin

470arrows show the direction of evolutionary dynamics of qualitative defenses. Dotted lines

471show the positions of the repellers and dashed line the position of the CSS. A) No second

472herbivore ($H_2=0$). Plants evolve away from preference p_1, decreasing the herbivore 1

473feeding rate eventually threatening its maintenance. B) The second herbivore is present

474($H_2=0.05$). Due to its preference p_2, evolution of the plant may settle between the two

475preferences, facilitating the coexistence of the two herbivores.

476Consider that, next to the herbivore we modeled in the result part (that has a preference p_1),

477we now consider also a second herbivore, whose preference is p_2. Note that, under such

478conditions, we expect that the most efficient herbivore will win the competition and

479eventually exclude the other herbivore (R* rule, Tilman, 1982). For the sake of the argument,

480suppose that ecological and evolutionary dynamics of the plant is however faster than the

481herbivore dynamics (*e.g.*, because the generation time of herbivores and plants may be vastly

482different), so that, on a first approximation, we may consider the herbivore population fixed

483and study the evolution of qualitative defenses x in this context. In the one herbivore context,

484as earlier, selected defenses diverge from the herbivore preference p_1 (hence an expected

485evolutionary murder of this herbivore, figure 5A). The presence of the second herbivore

486however halts this runaway evolution (figure 5B) by creating a selective force constraining the

487evolution of qualitative defenses. It thereby allows the first herbivore to remain in the system

488(at least on this timescale). Similarly, the evolution of the plant due to the first herbivore

489facilitates the maintenance of the second herbivore (as the plant trait becomes more similar to

490its preference p_2). Because this evolution actually leads to an equivalent consumption of the

491plant by the two herbivores, a neutral coexistence is then possible, so that the two herbivores

492eventually remain in the system. Though the herbivores compete for the plant from an

493ecological point of view, indirect effects due to the plant evolution from one herbivore to the

494other are positive, a situation we call "evolutionary facilitation". Such positive effects due to

495evolution have already been shown in other contexts. For instance, Abrams and Matsuda

496(2005) show that adaptation in the prey can facilitate the persistence of its predator. Such

497indirect interactions between herbivores through plant defenses have been also been suggested

498in empirical works. Expression of plant defenses following herbivore consumption has been

499shown to facilitate some other herbivores, while deterring others, so that defenses strongly

500affect herbivore diversity maintenance (Poelman et al., 2008). The extension of the model we

501present here, in a more complex network context, would allow a better understanding

502regarding the role of plant defenses and of herbivore consumption traits in the maintenance of

503diversity within natural communities. It may also help the management of biological control

504in an agricultural context (Loeuille et al., 2013).

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