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**1Multidimensionality of plant defenses and herbivore niches: implications for eco-
2evolutionary dynamics**

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8*equal contribution

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

11Abstract

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
32maintenance

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

86 evolution of these two defense types and of the herbivore, affect the functioning and structure
87 of 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**

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

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

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

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

$$\frac{dH}{dt} = H (f\beta P - m)$$

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

| | Name | Definition domain | Dimension |
|-------------------|------------------------------------------------------------------------|-----------------------|----------------------------------------------|
| <i>Variables</i> | | | |
| 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 |
| <i>Functions</i> | | | |
| K | Carrying capacity | | kg.m^{-2} |
| β | Per capita consumption rate | | $\text{m}^2.\text{kg}^{-1}.\text{time}^{-1}$ |
| α | Trait dependent competition scaling | | dimensionless |
| <i>Parameters</i> | | | |
| K_0 | Basal carrying capacity of plant | $]0, +\infty[$ | kg.m^{-2} |
| f | Conversion efficiency | $[0, +\infty[$ | Dimensionless |
| m | Herbivore <i>per capita</i> 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 | $[0, +\infty[$ | $\text{m}^2.\text{kg}^{-1}.\text{time}^{-1}$ |
| 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:

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

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:

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

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

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

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

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

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

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

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

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

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

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

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

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

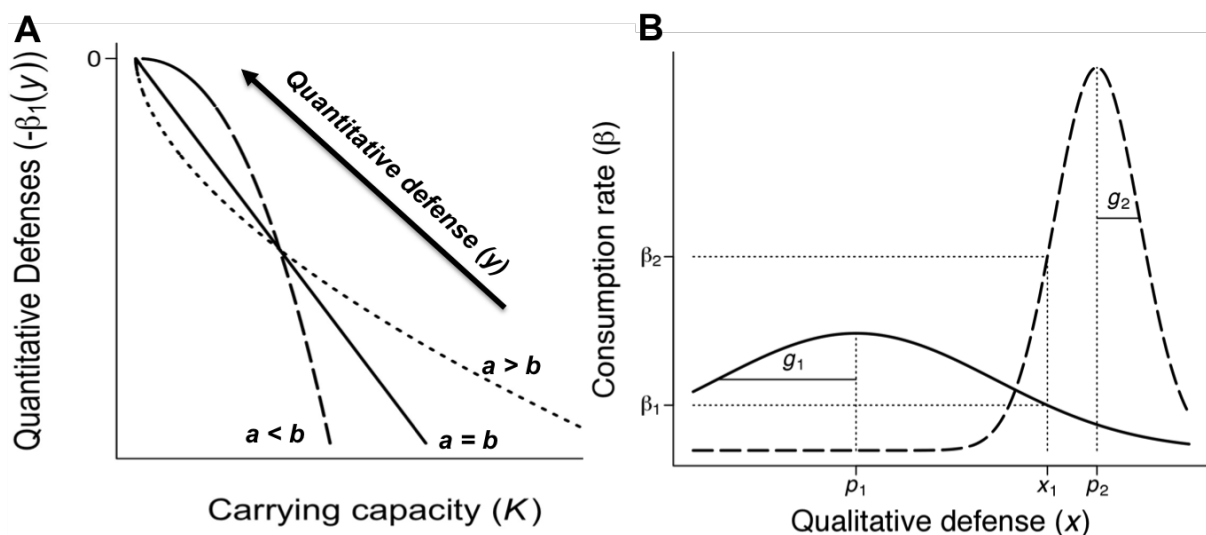
151 costs and no allocation costs (x). We acknowledge that in nature, defense traits are not

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

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

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

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



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

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

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

174 **Evolutionary dynamics**

175 We 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
177 study the evolution of each species and each trait separately, to contrast the implications
178 of the different evolutionary dynamics. Therefore, for each trait, we consider a

179 monomorphic population and determine a fitness of a mutant whose value for the given
180 trait slightly differs.

181 The relative fitness of a mutant population in a resident population, denoted W_m ,
182 depends on both the mutant and resident traits. It is defined as the *per capita* growth
183 rate of a rare mutant population in a resident population at equilibrium (P_{eq}, H_{eq}) . For
184 instance, considering the trait y , a mutant plant has a relative fitness:

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

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

189 The evolution of a trait is modeled using the canonical equation of the adaptive
190 dynamics, which assumes that the amplitude of mutation effects, ω , is small. For trait y :

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

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

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

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

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

$$196 \frac{\partial W_m}{\partial y_m} \Bigg|_{y_m \rightarrow y} = 0 \quad (9)$$

197 Evolutionary dynamics around the singular strategies can be analyzed by computing the
198 second derivatives of the fitness function (Dieckmann and Law, 1996; Geritz et al.,
1991998). Singular strategy y^* , cannot be invaded by nearby mutants, provided:

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

201 Moreover, singular strategies satisfy the convergence criteria (ie, selection favors
202 mutant closer to the singularity in its vicinity) provided:

203

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

205 When an evolutionary equilibrium satisfies both the non-invasibility and the
206 convergence criteria, it is called a Convergence Stable Strategy or CSS (Eshel, 1983).

207 When an evolutionary equilibrium satisfies the convergence condition but is invasible,
208 the selection near the equilibrium is disruptive and an evolutionary branching
209 eventually occurs, creating a diversification in the corresponding trait (ie, the
210 coexistence of two or more phenotypes exhibiting different defense levels). Finally, we
211 also encountered singularities that were invasible and non convergent, called repeller.

212 Note that the framework we use here can be extended to account for variations not in
213 one trait at a time, but of multiple traits simultaneously (eg, Loeuille et al. 2002). It can
214 also be extended to follow the evolution of traits along branches passed the first
215 branching point. Our study can then be thought as the first step of a more complete
216 evolutionary analysis. Our analysis of single traits however allows a complete
217 mathematical 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).

221Results

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.

225Ecological dynamics

226The model described by the system of equation (1), has a single equilibrium allowing the
227coexistence of plants and herbivores:

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

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

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

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:

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

237 Thus, when considering only ecological dynamics, as plants limiting factor increases (K
 238 increases), herbivore biomass increases whereas plant biomass remains constant (Fig.
 239 4A), stressing the importance of top-down controls in the ecological model.

240 Evolution of quantitative defenses

241 When the carrying capacity of plants is sufficiently high to maintain herbivores, the
 242 consumption of plants by herbivores depends on the level of quantitative defense of
 243 plants y . Incorporating trait y in equation (13), one gets that herbivore coexist with
 244 plants when

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

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

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

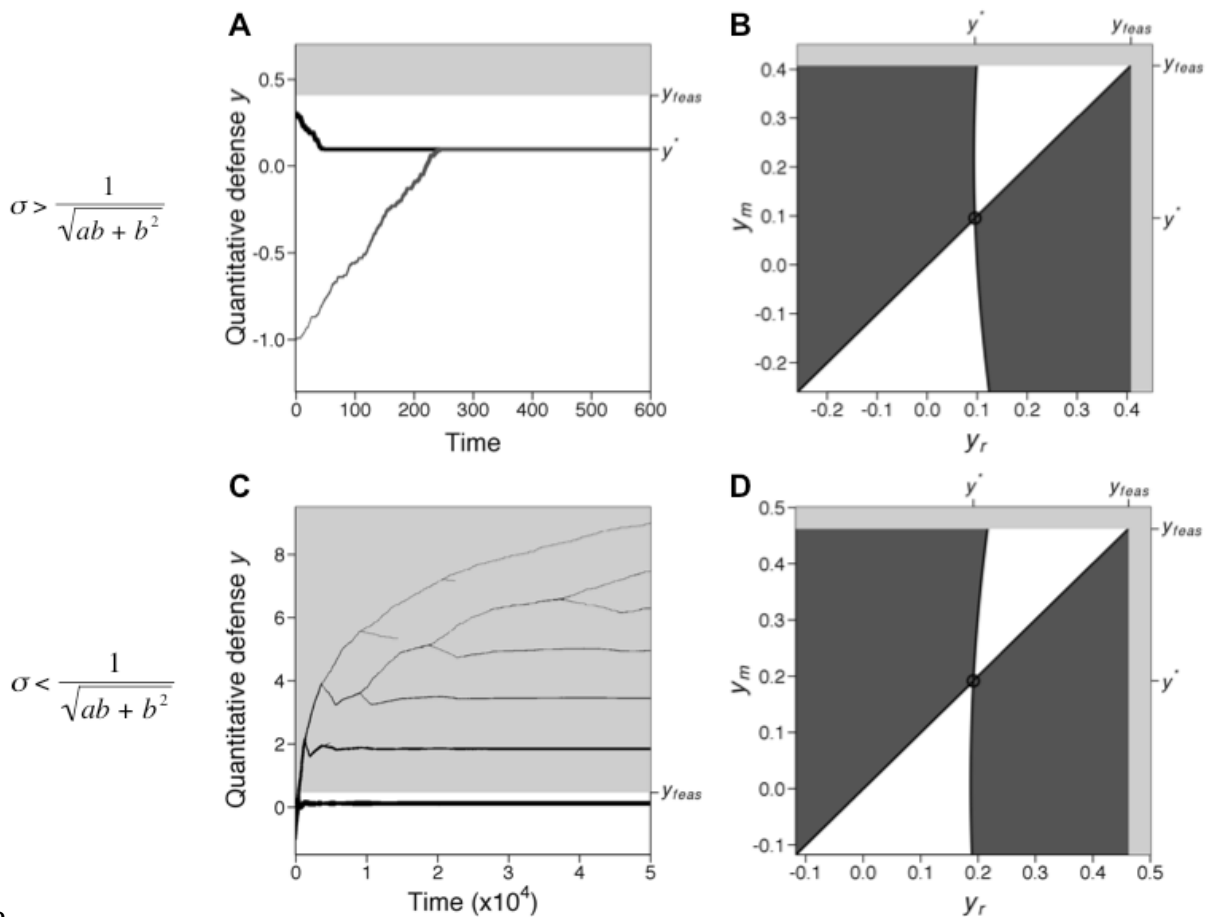
249 The evolutionary dynamics of the quantitative defense y are described by the canonical
 250 equation (8)

251 The associated singular strategy is:

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

253 Comparing (17) and (15) shows that the evolutionary singular strategy is always
 254 feasible ($y^* < y_{feas}$). The properties of this evolutionary equilibrium (invasibility and
 255 convergence criteria) depend on the competition scenario that is considered. When

256 competition does not depend on trait similarity ($\alpha=1$), the singular strategy satisfies
 257 both the convergence (eq 11) and the non-invasibility (eq 10) criteria, being therefore a
 258 Continuously Stable Strategy, or CSS (Marrow et al., 1996). Quantitative defense levels
 259 then evolve to reach y^* at which point the evolutionary dynamics stabilize. Note that the
 260 selected amount of quantitative defenses increases with energetic parameters of the
 261 plant population (eg, K_0) and with herbivore consumption pressures (βf_0).



262

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
 265 H_{eq} if the quantitative defense y is below y_{feas} ($H_{eq} < 0$, light grey background; $H_{eq} > 0$ white
 266 background). When σ is high (A, B), trait difference has small effects on the direct
 267 competition, the quantitative defense y converges to the evolutionary equilibrium y^*

268 which is a CSS. When σ is low (C, D), similar morphs compete very strongly, yielding
 269 disruptive selection and successive evolutionary branchings. On A and C, the thickness
 270 of 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
 272 resident 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): $a=0.5$

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

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

277 • If $\sigma < \frac{1}{\sqrt{ab+b^2}}$, the singular strategy γ^* , while still convergent becomes inviable. 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 than 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).

286 Variations in biomasses P_{eq} and H_{eq} and in trait γ^* with plant limiting factor can be
 287 studied by differentiating with respect of K_0 (see appendix). Contrary to the pattern
 288 observed for the purely ecological model, when the evolution of the quantitative defense
 289 γ leads to a CSS, the plant biomass P_{eq} , herbivore biomass H_{eq} and the level of defense γ^*
 290 at the evolutionary equilibrium all increase with K_0 (Fig. 4B). Evolution of quantitative

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

293 Evolution of qualitative defenses

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

295 Incorporating 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 ($\alpha = 1$), $A = \frac{\beta_0 f K}{m g \sqrt{2\pi}}$.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

312 Evolution of herbivore preference

313 When the carrying capacity of plants is sufficiently high to maintain herbivores, the
314 consumption of plants by herbivores is constrained by the difference $p-x$. Herbivore

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

316 Only one evolutionary equilibrium then exists, $p^* = x$, which is always convergent and
317 cannot be invaded (CSS). Evolution eventually leads to this value. Thus, herbivore
318 preference p increases or decreases depending on its initial position with respect to x
319 until herbivore preference matches plant qualitative defenses x . As for plants, such
320 simple dynamics would be altered in more complex communities. A herbivore
321 consuming several plants differing in their trait x would face a trade-off between the
322 consumption of one plant and the other.

323 Higher resource availability leads to an increase of herbivore biomass while plant
324 biomass and herbivore preference p^* are unaffected (see appendix & Fig. 4D).

325 Evolution of herbivore generalism

326 Equilibrium value of herbivore biomass as defined by equation (12) can be defined as a
327 function of trait g , and that this function reaches a peak at $|p-x|$. This peak is positive (ie,

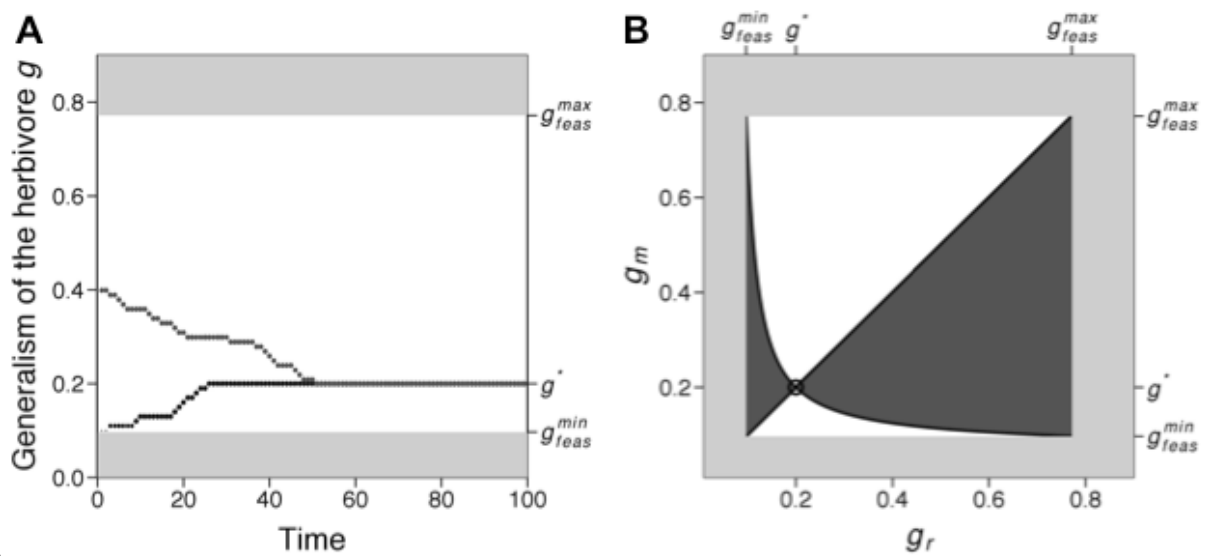
328 herbivore population can be positive), only if $|p-x| < B$ where $B = \frac{\beta_0 f K}{m \sqrt{2\pi} e}$. Therefore, g

329 is constrained to an interval $[g_{feas}^{min}, g_{feas}^{max}]$ that allows both plant and herbivore populations
330 to be positive.

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

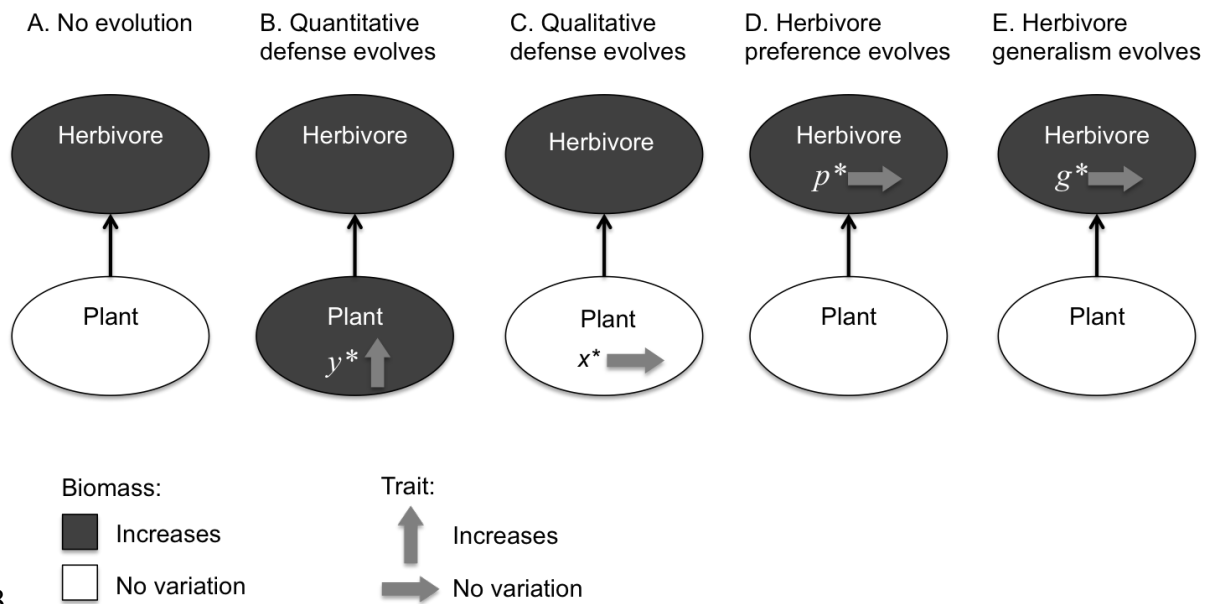
332 singularity is by definition feasible (see the argument above). This equilibrium satisfies

333 non-invasibility and convergence criteria and is thus a CSS (Fig.3B). Evolution of
 334 herbivore generalism g therefore converges toward g^* (Fig.3A). Selection acts to match
 335 the degree of the generalism of the herbivore with the difference that exists between its
 336 preference and the trait of the available plant population. Differentiating with respect of
 337 K , it may be shown that any increase in K leads to an increase in herbivore biomass
 338 while plant biomass and herbivore generalism g^* are not affected by resource
 339 availability (appendix & Fig. 4E).



340

341 **Figure 3: Evolution of herbivore generalism g .** The herbivore maintains a positive
 342 biomass H^* if its generalism g is between g_{feas}^{min} and g_{feas}^{max} ($H^* < 0$, light grey area; $H^* > 0$ white
 343 area). Generalism converges to an evolutionary equilibrium $g^* = |p - x|$ that is a CSS. (A)
 344 Two examples of evolutionary dynamics for two initial values of g ($g_0 = 0.1$; $g_0 = 0.4$). (B)
 345 Pairwise Invasibility Plots near represent the sign (+: dark grey area; -: white area) of
 346 mutant fitness as a function of the trait of the resident g_r and of the mutant g_m .
 347 Parameter values (A, B): $r = 1$, $K = 10$, $\alpha_0 = 1$, $\sigma = 0.4$, $\beta_0 = 1$, $f = 0.1$, $m = 0.5$, $p = 0.3$, $x = 0.5$.



348

349 **Figure 4. Effects of increases in resource availability, depending on the eco-**

350 **evolutionary scenario.** Without evolution, enrichment has a positive effect on the
 351 density of herbivores (A). This pattern remains when the herbivore evolves (D, E) or
 352 when qualitative defenses evolve (C). Quantitative defenses (B) are increased when
 353 resource levels are higher, allowing for an increase in plant biomass.

354 Discussion

355 The aim of the present work is to understand how the evolution of various types of plant
 356 defenses and of herbivore consumption strategies alters the structure and the functioning of
 357 plant-herbivore systems. The two types of defenses we consider have been proposed based on
 358 reviews of many different empirical systems (Müller-Schärer et al., 2004; Strauss et al., 2002)
 359 that distinguish quantitative defenses (efficient against all herbivores, but having allocative
 360 costs that reduce growth or productivity) and qualitative defenses (whose costs are not
 361 allocative, but happens through the modifications of other interactions). Most theoretical
 362 works on plant defenses focus on the former type (de Mazancourt et al., 2001; Levin et al.,
 363 1990; Loeuille and Loreau, 2004; Loeuille et al., 2002; Loreau and Mazancourt, 1999), while
 364 the evolution of qualitative defenses has received far less attention (but see Loeuille and
 365 Leibold, 2008).

366 Concerning the structure of the community, evolution of quantitative defenses tends to
367 increase the complexity of the system. First, contrary to our prediction, coexistence of
368 the plant-herbivore system is warranted at the evolutionary equilibrium. Evolution of
369 quantitative defenses indeed decreases the herbivore population. At some point,
370 herbivore population becomes too low and selection of higher levels of defense incurs
371 too 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
373 evolution of quantitative defenses also increases the plant phenotypic diversity, when
374 disruptive selection allows the coexistence of plant phenotypes that have contrasted
375 levels of defenses. Such a diversification within the plant compartment however
376 requires that plant competition is partly linked to trait similarity. These results are
377 consistent with other models that predict branching in defense strategies (Costa et al.,
378 2016; Ito and Ikegami, 2006), but also, from an empirical point of view, with the
379 widespread coexistence of contrasted investment in defenses within natural ecosystems
380 (Züst et al., 2012).

381 Evolution of qualitative defenses, on the contrary, leads the system to simpler structures. Our
382 results suggest that, *per se*, the evolution of such defenses should lead to strategies that ever
383 diverge from the herbivore preference. Because evolution away from the herbivore does not
384 involve costs in itself, evolution eventually allows the existence of plants that will be too little
385 consumed to compensate the herbivore intrinsic mortality rate. Evolution of plant then kills
386 the herbivore (evolutionary murder *sensu* *Dercole et al., 2006*) thereby constraining the
387 maintenance of diversity within the community. Also, we note that, in the case of qualitative
388 defenses, diversification of defense strategies is never observed, even when similar plants
389 compete more strongly. We therefore suggest that, intrinsically (ie, under our assumption of a
390 simple one plant-one predator community), evolution of qualitative defenses may limit
391 diversity (both in terms of species coexistence and in terms of phenotypic variability) while

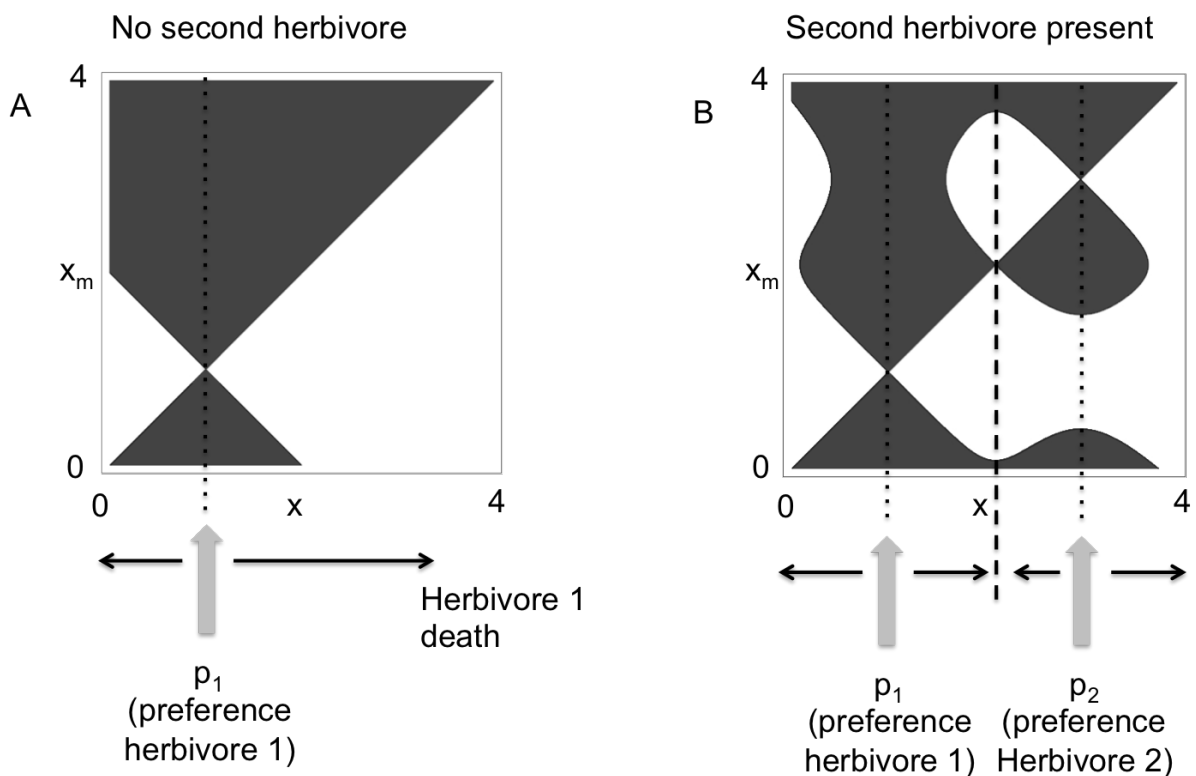
392the evolution of quantitative defenses ultimately favors diversity. Finally, note that, herbivore
393evolution in response to qualitative defenses, either through variations in its preference or
394through variations in its generalism, always allows the coexistence of the plant-herbivore
395community. 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.

421 While the two types of defenses have contrasted effects on coexistence, one may wonder how
422 their evolutions affect system stability. As explained in the result section, in the case of our
423 linear model, coexistence of the two species insures that the equilibrium is asymptotically
424 stable. However, it is still possible to assess the return time to the equilibrium (assuming a
425 small disturbance on the equilibrium), through the changes in the eigenvalues of the
426 associated jacobian matrix (eg, Rip & McCann 2011). Earlier works have shown that the
427 resilience of the system will increase when the consumer (here herbivore) death rate increases
428 relative to the its attack rate (Rip & McCann 2011). Therefore, when evolution favors higher
429 defenses, the system is stabilized (see appendix 2, fig S1, S2). This leads to interesting
430 outcomes if one considers the effects of enrichment in our model (figure 4). Ignoring
431 evolution, enrichment (eg, higher K) is destabilizing (appendix 2), as expected from the
432 paradox of enrichment (Rosenzweig 1971). Now consider the evolution of quantitative
433 defenses. Enrichment then leads to more defenses (Fig 4B), thus a lower attack rate, so that
434 this evolutionary effect of enrichment is stabilizing. Interestingly, the direct (destabilizing)
435 effect of enrichment is exactly compensated by the (stabilizing) effect of selecting higher
436 defenses, so that enrichment is actually neutral for system stability (appendix 2). Conversely,
437 in the case of qualitative defenses, enrichment does not lead to any change in evolved
438 defenses (figure 4), so it remains destabilizing.

439 We however stress that the model we use here is deliberately simple as its goal is mostly to
440 contrast eco-evolutionary dynamics linked to various plant-herbivore traits. We expect that
441 two levels of complexity, not considered here, will indeed matter much for most empirical
442 situations. First, it seems likely that most plants do not use quantitative defenses or qualitative
443 defenses, but actually use the two types of defenses simultaneously. Also, while the
444 quantitative/qualitative dichotomy is useful as a first approximation, costs and effects are
445 likely to vary in a more continuous fashion so that defenses actually follow a continuum
446 between the two extremes (qualitative/quantitative) used to structure the present work. When
447 considering the coevolution of quantitative and qualitative defenses, we expect strong
448 interactions between their evolutionary dynamics. Consider for instance that the cost of
449 qualitative defenses is to attract another herbivore. A plant having high levels of quantitative

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

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



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

468 Here, herbivore populations are considered constant (eg, herbivore populations vary on
469a much longer timescale). Thick grey arrows show the herbivore preferences. Black thin
470 arrows show the direction of evolutionary dynamics of qualitative defenses. Dotted lines
471 show the positions of the repellors and dashed line the position of the CSS. A) No second
472 herbivore ($H_2=0$). Plants evolve away from preference p_1 , decreasing the herbivore 1
473 feeding 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
475 preferences, facilitating the coexistence of the two herbivores.

476 Consider that, next to the herbivore we modeled in the result part (that has a preference p_1),
477 we now consider also a second herbivore, whose preference is p_2 . Note that, under such
478 conditions, we expect that the most efficient herbivore will win the competition and
479 eventually exclude the other herbivore (R* rule, Tilman, 1982). For the sake of the argument,
480 suppose that ecological and evolutionary dynamics of the plant is however faster than the
481 herbivore dynamics (e.g., because the generation time of herbivores and plants may be vastly
482 different), so that, on a first approximation, we may consider the herbivore population fixed
483 and study the evolution of qualitative defenses x in this context. In the one herbivore context,
484 as earlier, selected defenses diverge from the herbivore preference p_1 (hence an expected
485 evolutionary murder of this herbivore, figure 5A). The presence of the second herbivore
486 however halts this runaway evolution (figure 5B) by creating a selective force constraining the
487 evolution 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
489 facilitates the maintenance of the second herbivore (as the plant trait becomes more similar to
490 its preference p_2). Because this evolution actually leads to an equivalent consumption of the
491 plant by the two herbivores, a neutral coexistence is then possible, so that the two herbivores
492 eventually remain in the system. Though the herbivores compete for the plant from an
493 ecological point of view, indirect effects due to the plant evolution from one herbivore to the

494 other are positive, a situation we call “evolutionary facilitation”. Such positive effects due to
495 evolution 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
497 indirect interactions between herbivores through plant defenses have been also been suggested
498 in empirical works. Expression of plant defenses following herbivore consumption has been
499 shown to facilitate some other herbivores, while deterring others, so that defenses strongly
500 affect herbivore diversity maintenance (Poelman et al., 2008). The extension of the model we
501 present here, in a more complex network context, would allow a better understanding
502 regarding the role of plant defenses and of herbivore consumption traits in the maintenance of
503 diversity within natural communities. It may also help the management of biological control
504 in an agricultural context (Loeuille et al., 2013).

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