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 often have little allocation costs. However, while deterrent to some herbivores, they often incur costs through other interactions within the community (e.g., 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 assess the effects of such evolutionary dynamics for the maintenance of diversity within the plant-herbivore system, and for the functioning of such systems under various levels of resource availability. We show that the two types of defenses have different implications. Evolution of quantitative defenses often helps 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, increased resource availability selects for higher levels of quantitative defenses, which reduces top-down controls exerted by herbivores. Resource availability does not affect qualitative defenses, nor the evolution of the herbivore niche. The growing evidence that plant defenses are diverse in types, benefits and costs has large implications not only for the evolution of these traits, but also for their impacts on community diversity and ecosystem functioning.

1. 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 pollinator assemblages (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), proposing 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, these defenses constrain the proportion of productivity transmitted up the food chains. Second, these defenses reduce the productivity, because of direct 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 ultimately modify 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 pro-

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	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

duced by the plant (for chemical defenses) or for the quantity of protective structures (e.g., hair, spines), several studies failed to detect such allocation costs (Häring et al., 2008; Koricheva et al., 2004). A possibility is that allocation costs exist but were not properly detected, these defenses may also be constrained by alternative costs, for instance through other ecological interactions (ecological costs: Müller-Schärer et al., 2004; Strauss et al., 2002). A higher investment in such defenses can be efficient against some enemies, but incurs costs by attracting other enemies or by rendering the plant less attractive to mutualists (e.g., Adler et al., 2012; Xiao et al., 2012). Ecological costs 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 efficient only against a given herbivore specialist (Becerra, 2003). Many closely related volatile organic compounds exist (Courtois, 2010), involving similar chemical structures and enzymatic pathways. 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. They can also play a crucial role in the diversification of herbivore and plant clades (Becerra, 2007, 2003).

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 (in the sense that efficiency against one herbivore will come at a cost given another herbivore), and a quantitative defense that reduces any herbivore 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 structure of the community. More specifically, we ask:

1. Whether the evolution of each defense type alter the persistence of the herbivore in different ways. According to observations detailed earlier, we hypothesize that qualitative defenses may allow the herbivore persistence 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 (i.e., the coexistence of different defensive strategies).

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 and its changes with resource availability. We hypothesize that investment in quantitative defenses, by reducing overall vulnerability, will lower top-down controls therefore allowing plant biomass increase (and low response of herbivore biomass).

1.1. Ecological model

We model the dynamics of plant and herbivore biomass (P and H respectively) within an isolated ecosystem. In the 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).

The intrinsic growth rate of plants is noted r. Herbivores consume plants at a rate β and converts a proportion f of consumed plant biomass 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.

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

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

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

1.2. 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