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The importance of ecological costs for the evolution of plant defense against herbivory

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HIGHLIGHTS

- We model evolution of plant defense against specialist or generalist herbivores.
- Costs are direct (growth) or ecological (competition).
- Evolutionary branching can only occur under ecological costs.
- Stable polymorphisms are only possible against generalist herbivores.
- Nutrient availability affects defense against generalists and specialists differently.

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ABSTRACT

Plant defense against herbivory comes at a cost, which can be either direct (reducing resources available for growth and reproduction) or indirect (through reducing ecological performance, for example intraspecific competitiveness). While direct costs have been well studied in theoretical models, ecological costs have received almost no attention. In this study we compare models with a direct trade-off (reduced growth rate) to models with an ecological trade-off (reduced competitive ability), using a combination of adaptive dynamics and simulations. In addition, we study the dependence of the level of defense that can evolve on the type of defense (directly by reducing consumption, or indirectly by inducing herbivore mortality (toxicity)), and on the type of herbivore against which the plant is defending itself (generalists or specialists). We find three major results: First, for both direct and ecological costs, defense only evolves if the benefit to the plant is direct (through reducing consumption). Second, the type of cost has a major effect on the evolutionary dynamics: direct costs always lead to a single optimal strategy against herbivores, but ecological costs can lead to branching and the coexistence of non-defending and defending plants; however, coexistence is only possible when defending against generalist herbivores. Finally, we find that fast-growing plants invest less than slow-growing plants when defending against generalist herbivores, as predicted by the Resource Availability Hypothesis, but invest more than slow-growing plants when defending against specialists. Our results clearly show that assumptions about ecological interactions are crucial for understanding the evolution of defense against herbivores.

1. Introduction

Plant fitness can be greatly reduced by herbivory, and it is no surprise that a wide variety of defensive strategies have evolved to fend off herbivores. These include physical defenses such as thorns or trichomes, indigestible substances such as cellulose or tannin, or compounds that are toxic to herbivores. Despite the obvious advantage of resisting herbivory, defense comes at a cost (Bergelson and Purrington, 1996; Strauss et al., 2002). The most obvious is a cost in allocation: resources invested in defense are unavailable for growth or reproduction (Coley et al., 1985; Coley, 1987; Herms and Mattson, 1992). Costs can take many other forms, however: from reduced attractiveness to mutualists such as mycorrhizal fungi or pollinators (Gehring and Delph, 1999; Strauss et al., 1999; Adler, 2000) to increased susceptibility to pathogens (Felton et al., 1999) and lowered competitive ability (van Dam and Baldwin, 1998; Kempel et al., 2011). These types of

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costs, which are only expressed in the context of ecological interactions, are known as ecological costs, in contrast to direct costs (e.g. lower growth rate). Strauss et al. (2002) found a direct trade-off between defense and growth in 51% of the systems studied, whereas ecological costs were present in 62%.

While the evolution of defense in the face of costs has been the subject of theoretical study (Coley et al., 1985; Fagerstrom et al., 1987; Yamamura and Tsuji, 1995; Poitrineau et al., 2004; Ito and Sakai, 2009), the effect of ecological costs has not received much attention. Most models use a direct trade-off between defense and growth rate (Coley et al., 1985; de Jong, 1995; Loeuille et al., 2002; Loeuille and Loreau, 2004; Ito and Sakai, 2009; Vage et al., 2014) or explicitly allocate resources to various functions including growth and defense (Loreau and de Mazancourt, 1999; Krzysztof Janczur, 2009; DeAngelis et al., 2012), but do not consider any type of ecological costs. We found one study (Weis and Hochberg, 2000) that includes the effect of competitiveness through reduced size, and it reports that including competition has dramatic effects on the outcome of competition between defending and non-defending plants. However, this study only looks at the competitive advantage or disadvantage of defense; it does not study evolutionary dynamics of the defensive trait.

Another commonality of most theoretical studies is that herbivory is often implemented as a constant rate, which is independent of the level of defense, even though there is both theoretical and experimental evidence that defense can affect herbivore population dynamics (Underwood, 1999; Underwood and Rausher, 2002; Agrawal, 2004). Specialist herbivores are especially likely to be affected by the evolution of defense in the plant species they feed on, unlike generalists which may switch to other plant species. This kind of ecological feedback is absent in most models (an exception is DeAngelis et al., 2012), but it may significantly affect evolution.

In this article, we study the evolution of constitutive (i.e. always expressed, not induced) defense against herbivory in the face of either direct or ecological costs. Specifically, in the case of ecological costs, we study a trade-off between defense and competitiveness, rather than between defense and growth rate. We look for conditions leading to either evolutionary stability or evolutionary branching points, allowing for both the evolution of suboptimal (but stable) strategies and for the evolution of stable polymorphisms. For these purposes, the adaptive dynamics framework (Geritz et al., 1998; Waxman and Gavrilets, 2005) is ideally suited. We combine this with simulations to confirm the analysis. Our study looks at three major questions: first, does the trait with which defense trades off (growth rate or competitiveness) affect the evolutionary dynamics of defense? Second, does the type of defense and its effect on herbivory (directly through reducing consumption, or indirectly through toxicity-induced herbivore mortality) influence the level of defense that evolves? And finally, given the above-mentioned possible effect of eco-evolutionary feedbacks, does defense evolve differently against generalist or specialist herbivores?

2. General model

We used a set of differential equations to model the ecological dynamics of a single plant and herbivore population. Defense is implemented in two independent traits, each representing a possible effect on the herbivores: x for directly reducing the amount of plant material consumed (for example, by physically interfering with the herbivores), and y for toxicity, causing extra mortality for the herbivores. We used adaptive dynamics to find the ESS solutions for the two traits, and used the differential equations as a basis for a stochastic evolutionary simulation to confirm the results.

2.1. Ecological dynamics

2.1.1. Plant dynamics

The ecological dynamics of plant abundance $P(t)$, expressed as total plant biomass, is given by

$$\frac{dP}{dt} = f(P(t), x(t), y(t)) - h(x(t), H, P(t)). \tag{1}$$

Plant growth is given by the first term, $f(P(t), x(t), y(t))$. Because including or excluding nutrient dynamics can dramatically affect the ecological and evolutionary dynamics (see e.g. Loeuille et al., 2002), we compared two different plant growth functions, logistic growth or nutrient limited growth; the specifics are described in their respective sections below. The second term in Eq. (1) denotes consumption by herbivores (H). This takes the form of a Holling type 2 functional response, modified by the level of defense:

$$h(x(t), H, P(t)) = g(x(t)) \frac{HaP(t)}{1 + t_h aP(t)} \tag{2}$$

with H being herbivore biomass, and a and t_h the attack rate and handling time, respectively. The effect of defense on consumption is determined by $g(x(t))$, which is assumed to be a decreasing function of $x(t)$:

$$g(x(t)) = \frac{1}{1 + x(t)e_x} \tag{3}$$

here, e_x is the efficiency of defense, or the susceptibility of herbivores to the defensive trait.

We assume toxicity (y) does not directly affect consumption, and its only effect on the level of herbivory is through increasing herbivore mortality. The details are described in the following section.

2.1.2. Herbivore dynamics

To study the effect of an eco-evolutionary feedback between evolution of defense and herbivore population dynamics, we studied two different scenarios for all models, corresponding to specialist or generalist herbivores. Because specialists depend on the focal plant species only, their abundance directly responds to the amount of plant biomass available for their consumption. In contrast, the numerical response of generalist herbivores to plant abundance and level of defense should be much weaker, as they consume more than just the focal plant species and can switch to another food source if the focal species becomes unavailable. We assume that generalist herbivores do not respond numerically to their level of consumption of the plants considered in the model at all, allowing us to assume constant herbivore pressure.

In both scenarios, we assume that herbivores are mobile and can move easily between plants, as is the case for larger herbivores, making the herbivore and plant populations well-mixed and all interactions global.

2.1.2.1. Generalist herbivores. In this case, we assume herbivore pressure to be independent of plant abundance or the level of direct defense x. We do assume that the level of toxicity y causes increased mortality for generalist herbivores, decreasing herbivore pressure:

$$H = H_{\max} - d_{\mathrm{tox}} \tag{4}$$

$$d_{\mathrm{tox}} = h(x(t), H, P(t))y(t)e_y \tag{5}$$

where e_y is the parameter determining how toxic any level of secondary compounds is to the herbivores. The total toxicity is determined by the product of the level of toxicity and its