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# Macroevolutionary and geographical intensification of chemical defense in plants driven by insect herbivore selection pressure

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Plants produce an extensive array of secondary chemical compounds that often function as defenses against insect herbivores. In theory, because of steadily herbivore adaptation, lineages of plants have reacted by escalating their chemical arsenals over time. Following this assumption, over the last three decades researchers have searched for potential signs of chemical intensification in plants. Although modern methodologies now allow the inference of macroevolutionary chemical trends with substantial confidence there are still only a handful of studies on this subject. These examples suggest that intensification of plant chemical defenses is the result of lineages progressively incrementing their compounds as well as recruiting an increasing number of biosynthetic pathways to produce more complex chemical mixtures.

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## Introduction

Insects and other arthropods have consumed live plants for more than 350 million years. Soon after plants evolved true roots and leaves they became a food resource indispensable to insect survival. This event marked the beginning of herbivory, a new type of trophic and antagonistic relationship that is now the most frequent interaction on Earth [1].

A crucial aspect of plant and insect herbivore interactions is the presence of a variety of secondary chemical compounds in plants that do not play an essential role in plant physiology and/or metabolism [2]. Thousands of plant secondary chemical structures have been discovered, and with recent advances in analytical chemical technology, this number is only expected to increase.

Half a century ago, a consensus began to emerge that secondary compounds evolved to defend plants from herbivores [3]. This was followed by the now classic theory that postulates that the coevolutionary war between insects and plants is the force that has promoted the incremental elaboration, proliferation, and intricacy of defensive chemistry in plants (Figure 1) [4,5]. While highly intriguing, this escalation paradigm was only sparsely explored until accumulations of DNA sequence data and advances in phylogenetic methods allowed the inference of specific plant evolutionary histories with sufficient confidence. Further advances in statistical modeling of evolution on phylogenetic trees, enabled the reconstruction of ancestral character states of defense profiles as well as estimation of their time of evolution [6–8].

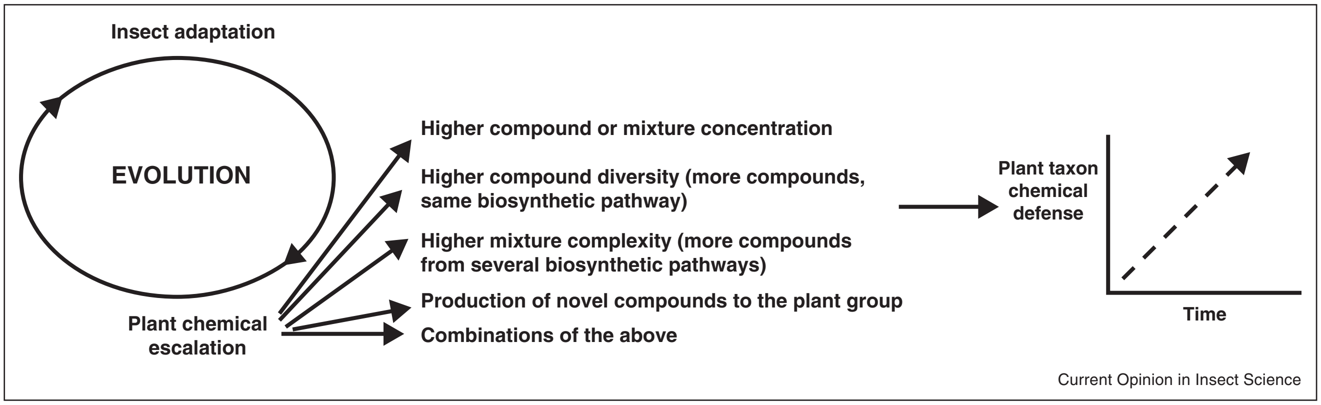
Equipped with these innovations, researchers in the last decade have started to make strong inferences not only on whether there has been intensification of plant chemical defenses through time but also on what forms the intensification can take (e.g., increased concentration or increased number of compounds and metabolic pathways). The questions asked are getting progressively more refined: have plant lineages reacted to continuous herbivore pressure by increasing the concentration of their chemicals over evolutionary time? Is plants' response to the confrontation with the steady adaptation of insect herbivores characterized by evolving novel chemicals to increase the complexity of their chemical arsenal? How do historical patterns of defense play a part in ecological communities throughout the world? In this review I describe recent advances in these topics.

## Macroevolutionary trends of secondary chemical escalation in plants

### Concentration of chemical compounds

Although few studies have searched for macroevolutionary patterns in concentration of secondary metabolites, the ones that are available indicate either a lack of trend or a negative one. For example, in the Mediterranean genus *Narcissus* concentration of Amarillidaceae toxic alkaloids has not followed a positive or negative historical trend [9,10]. The most recently derived Amarillidaceae section (*Pseudonarcissus*) has the highest level of alkaloid concentrations, whereas species of closely related sections (*Apodanthi*, *Bulbocodium*) produce low concentrations or only traces of alkaloids. Yet, species of its oldest section

Figure 1




Continuous evolutionary steps of insect adaptation and plant defense have resulted in an incremental elaboration and complexity of secondary chemical defense responses in plants over time.

(*Tazettae*) also have high concentration levels of these compounds. Likewise, metabolonic characterization revealed no trend in concentration of total phenolics among *Urtica* species and subspecies [11]. Furthermore, in *Asclepias*, a phylogenetic pattern of decline cardenolide concentration has been shown [12•].

## Chemical diversity and complexity

One of the first plant families used to investigate potential chemical escalation by increasing chemical diversity and complexity was the Apiaceae [13]. In this family, it appeared that production of simple hydroxycoumarins alone is an ancestral trait relative to producing the more chemically elaborate mixture of linear furanocoumarins plus complex angular furanocoumarins. Unfortunately, at the time this analysis was performed, phylogenetic techniques were still in their infancy, and no formal tests for historical trends were performed. Nevertheless, subsequent analyses of other plant groups suggest that phylogenetic trends in chemical diversity and complexity, both positive and negative, may be common in the plant kingdom.

One early example that tested historical intensification of diversity and complexity of chemistry profiles was performed with *Bursera*, a Mexican tropical genus rich in terpenes that also produces alkanes, and other compounds [14]. This study showed that the diversity of secondary metabolites as well as their biosynthetic pathways used to produce these compounds has escalated. As new species emerged over time they tend to be armed not only with more compounds, but also with compounds that could potentially be more difficult for herbivores to adapt to because they belong to an increasing variety of chemical pathways, and may require different detoxificative catalytic activities and enzymes [15].

Analyses of Anacardiaceae, Fabaceae, and Senecioneae have produced similar results. Anacardiaceae are known for their production of highly toxic phenolic compounds including bioflavonoids, alkylcatechols, and alkylresorcinols. However, more recently derived lineages have them all, or combinations of some of them, whereas the most ancestral lineage (Spondiadeae), lacks all of these three kinds of phenols [16].

Legumes produce a high diversity of secondary metabolites, including a variety of phenolic compounds, alkaloids, amines, peptides and cyanogenic glucosides. To test for evolutionary trends in chemistry, I performed an analysis on Fabaceae combining chemical data and a published phylogeny [17•]. Results of this analysis showed that in this large plant family radiation diversity and complexity of chemical profiles has increased over time. In more recently diverging legume lineages there was a higher complexity of compound mixtures (Figure 2). Most plants in ancestral lineages such as *Duparquetia* and Detarieae produce relatively few different kinds of phenolics, such as flavonoids and anthocyanins, and terpene compounds that are widespread within the family. Yet, in more recently derived lineages such as Crotalariae and Phaseolaceae, many species have not only common phenolics and terpenes, but also more complex and distinctive ones such as isoflavones and coumarins, along with nitrogen-containing active compounds such as cyanogenic glucosides, amines, and a variety of alkaloids.

Senecioneae is a tribe of Asteraceae remarkable for its extensive variety of pyrrolizidine alkaloids. Using reported phylogenies [18–21], alkaloid data summarized in [22], and alkaloid biosynthetic classification of [23], I examined whether there was a pattern of chemical escalation in this tribe. The outcome was very similar to