EVOLUTIONARY ECOLOGY OF PLANT DEFENCES

Current trends in the evolutionary ecology of plant defence

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Summary

1. In this essay I summarize current trends in the evolutionary ecology of plant defence, while advocating for approaches that integrate community ecology with specific tests of classic evolutionary hypotheses. Several conclusions emerge.

2. The microevolution of defence is perhaps best studied by reciprocal transplant experiments of differentiated plant populations while simultaneously manipulating the presence of the herbivore(s) hypothesized to be the agent(s) of natural selection.

3. Although there is continued interest in the costs of defence, I argue that some empirical approaches to estimating costs (e.g. genetic engineering) may provide limited insight into evolutionary processes.

4. Essentially all plants employ several different lines of defence against herbivory. It is thus time to abandon searching for single silver bullet traits and the simple trade-off model (where traits are arbitrarily expected to negatively covary across genotypes or species). We still know very little about which trait combinations are most effective and have repeatedly evolved together. Thus, some of our prominent theories (e.g. a predicted trade-off between direct and indirect defence) need to be revised.

5. Studies of the macroevolution of plant defence are enjoying renewed interest due to available phylogenies and analytical methods. Although general trends are not currently surmisable, we will soon have strong case studies evaluating both biotic and abiotic drivers of convergent evolution in defence strategies and the role of defence evolution in the adaptive radiation of plant lineages.

6. The evolution of specificity is proposed as a final frontier in understanding complexity in plant–herbivore interactions. Although it is abundantly clear that plants can deploy highly specific defensive responses that are differentially perceived by herbivore species, how such responses evolve and are physiologically regulated remains an important gap. Relatively straightforward methodologies are now available to close the loop between plant perception of herbivory, hormonal responses, and production of defensive end-products across genotype or species.

Key-words: co-evolution, community ecology, costs of defence, macroevolution, phylogenetic ecology, plant defence theory, plant–herbivore interactions, resistance, specificity of induced defence, tolerance
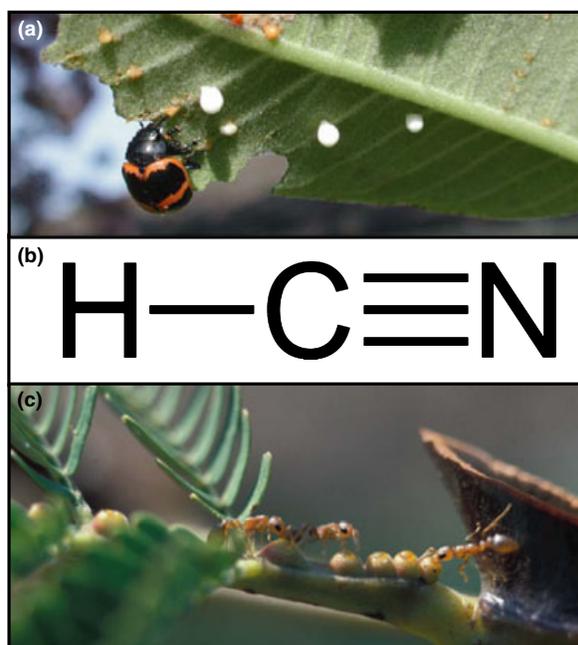
Introduction

As the bulk of energy supporting organisms in food webs comes from the autotrophic action of green plants, it should not be surprising that one of the most prominent sets of adaptations in the history of life is plant defence against natural enemies. On average, across biomes, habitats, natural and managed systems, and including estimates of folivory, sap feeding and root herbivory, herbivores remove >20% of annual net primary productivity (summarized from Schoonhoven, Van Loon & Dicke 2005; Rasmann & Agrawal 2008; Schowalter 2000; Pimentel 2002; Maron 1998; Coley & Aide 1991; Brown & Gange 1989; Coupe & Cahill 2003). The wonderful natural history of plant defence and its importance in mediating community interactions has led to it being a model in evolutionary ecology.
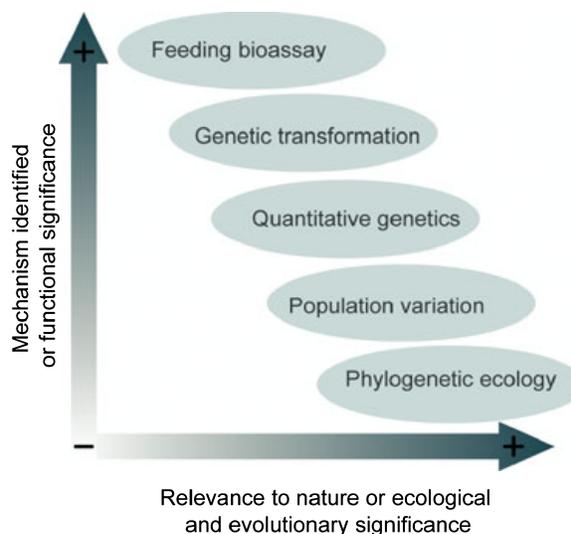
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Perhaps one of the most outstanding aspects of plant defence, and one that makes it highly desirable as a focus of study, is that many defences have convergently evolved (Fig. 1). One interpretation of convergence, especially when traits are associated with particular habitats or interactions, is that the traits are adaptive. Add to this that there are at least some plant traits which are known to exclusively function as defence, and have not been implicated in the primary metabolism of plants (Fig. 1), and you have a strong starting point from which to address important conceptual questions in evolutionary ecology.

In this paper, I summarize current trends in the study of plant defence and advocate for particular approaches that address long-standing theory. Questions in the evolutionary ecology of plant defence are manifold, and addressing them requires a diversity of approaches (Fig. 2). Nonetheless, in

Fig. 2. Various approaches have been used to study the mechanisms, ecology and evolution of plant defence. This scheme shows some of these major approaches and their respective strengths (+). Although there appears to be a trade-off between the extent to which mechanisms can be identified and the ecological and evolutionary relevance among the approaches, a combination of approaches can be particularly insightful. For example, in populations that have different herbivory regimes and that have phenotypically differentiated, field studies of natural selection and molecular differences would have reductionist and holistic appeal. Modified from Rasmann & Agrawal 2009a.

Fig. 1. Quintessential plant defences. (a) Latex from common milkweed *Asclepias syriaca*, exposed following vein cutting sabotage behaviour of a specialist leaf beetle *Labidomera clivicollis*. Just under 10% of all plant species (and 10% of plant families) produce latex, which is typically a physical barrier to feeding and contains high concentrations of defensive chemicals (Agrawal and Konno 2009) (Photo by Pete Van Zandt). (b) Hydrogen cyanide: volatile at room temperature, produces a mild almondy odour and found in just over 10% of plant species, including cherries *Prunus* spp., rice *Oryza sativa* and peanut *Arachis hypogaea* (Jones 1998). The CN⁻ molecule is highly toxic to most organisms by interfering with respiratory enzymes. (c) *Pseudomyrmex peperi* workers consuming extrafloral nectar and serving as an indirect defence of *Acacia collinsii* (Photo by Martin Heil, modified from Heil 2008; with permission of New Phytologist). Although this association is obligate, many plants produce extrafloral nectar (it has evolved in 25% of angiosperm families) in more facultative defensive mutualisms (Koptur 1992). Two aspects make these three traits excellent targets of study: they are highly convergent (i.e. have evolved independently many times in different plant families) and there are no credible hypotheses for functions of these traits other than defence.

this paper I do not address strictly functional questions and approaches. Instead, I focus on micro- and macroevolutionary approaches. As I discussed in a recent paper (Agrawal 2007), the origin of hypotheses explaining differential investment in defence was in comparative biology (i.e. comparison of plant species). A historical lack of methods to make strong inference from the comparison of species (because species vary in many ways other than the traits that a researcher may be interested in) prevented some comparative approaches from making rigorous contributions. The lack of phylogenetic methods and rigorous tests of comparative hypotheses gave way to microevolutionary and functional approaches, which have largely dominated our thinking on plant defence evolution for the past 20 years. Nonetheless, we are currently seeing a resurgence of interest in testing comparative hypotheses of plant defence, in large part due to the availability of molecular phylogenies and novel analytical methods to test phylogenetic hypotheses (Futuyma & Agrawal 2009a). Thus, the time is ripe to make linkages between functional and microevolutionary approaches to macroevolutionary patterns.

Microevolution of resistance

It was nearly 25 years ago that we had our first estimates of natural selection on heritable traits that provide resistance against herbivores (Berenbaum, Zangerl & Nitao 1986; Simms & Rauscher 1987). A decade later, large field experiments convincingly showed the potential for natural selection to act on heritable resistance traits (e.g. Mauricio & Rauscher 1997;

Shonle & Bergelson 2000). Such studies were critical for the advancement of the field. Nonetheless, I believe that three issues limit this classic quantitative genetic approach to studying selection on defence: (i) year-to-year or plot-to-plot variation may be large enough to obscure important findings in short term studies. Short-term common garden studies may not capture the ecological complexity (presence of a full community of interactors) or otherwise important spatial or temporally variable conditions required to detect selection (Hare, Elle & Van Dam 2003; Lau & Strauss 2005). In addition, selection is not likely to be directional year-to-year, especially in relation to the standing genetic variation; (ii) the sample sizes needed to address questions about selection, especially when other major environmental factors are being manipulated, are huge. For example, Lau (2008) needed to employ thousands of plants to demonstrate independent and combined impacts of two invasive species (a plant competitor and an insect herbivore) on selection for resistance and tolerance on a native plant and (iii) employing within population standing variation may be a low-statistical-power approach to studying natural selection because the bulk of genotypes will have phenotypes near the mean. Over even a few generations of artificial selection (or longer periods in separated natural populations), more extreme phenotypes can be studied, which should allow for stronger tests of selection (Ågren & Schemske 1993; Stowe 1998; Valverde, Fornoni & Nunez-Farfan 2001). Even relatively small-scale screens of naturally occurring genotypes may allow for the identification of phenotypic extremes that reduce the required replication and increase statistical power (S. Rasmann, T. L. Bauerle, K. Poveda & R. Vannette, unpublished data).

I believe that quantitative genetic studies demonstrating selection on plant defence, and in particular, demonstrating that the magnitude or direction of selection is altered by the biotic or abiotic environment, will continue to be important contributions. Nonetheless, I advocate the use of natural variation between populations to study how variable selection can result in altered phenotypes. Differentiated populations have presumably experienced repeated bouts of directional selection from their common ancestor and thus are an excellent place to start to study adaptation. It is remarkable that despite several reciprocal transplant studies measuring local plant adaptation to herbivores (usually transplanting two populations), apparently none have conducted the transplants while also manipulating the presence of herbivores (the putative agents of population differentiation) (Nuismer & Gandon 2008). Such experiments have the tremendous advantage of estimating the relative roles of herbivores versus other factors (e.g. abiotic conditions) in the local adaptation of plants over evolutionary time. Although the success of such experiments hinges on consistent population variation in species interactions across years, this is apparently not uncommon (Thompson & Cunningham 2002; Thompson & Fernandez 2006). Applications of such population transplant experiments include studies of variation in defence investment across gradients (such as latitude, stress, resources, etc.) that have a long history as theoretical predictors of investment in plant defence.

Costs and community complexity

Of course there are costs of producing any trait, but these costs may be difficult to detect and may be context dependent (i.e. only evident under some ecological conditions). In this section I focus on three current aspects of costs and their detection: (i) what is the most ecologically relevant approach to studying costs; (ii) the 'general vigour problem' of positive covariance between growth and resistance and (iii) costs measured in ecological currencies.

It may not be particularly useful, in terms of ecological and evolutionary insight, to demonstrate costs of particular resistance compounds by genetically engineering their production (Fig. 2). The main issue here is that natural selection does not typically operate as a sledgehammer turning on or off production of major resistance traits (the exception is polymorphic traits which do often exist as present or absent within the same genetic background (e.g. Daday 1965; Hare, Elle & Van Dam 2003; Linhart *et al.* 2005; Loe *et al.* 2007; Schappert & Shore 1995). For quantitative traits, most populations will evolve multiple traits simultaneously (because of strong genetic correlations or because particular trait combinations are favoured). Thus, given that most plants contain tens, if not hundreds, of secondary compounds that contribute to resistance, knowing their individual costs would be an expensive endeavour, and perhaps not that informative. Nonetheless, as a functional tool, or in combination with other methods, genetic manipulation can be especially powerful (e.g. Steppuhn & Baldwin 2007). As a related approach, Schemske pioneered the use of introgression to study selection on specific traits (Schemske & Bradshaw 1999). Although this approach also focuses on isolating specific traits, it employs alternative *natural* copies of the genes of interest. Depending on the experimental designs employed, introgression studies could be useful in studying costs of defence.

To understand costs, and how costs may promote the maintenance of variation, I suspect that quantitative genetic approaches (including artificial selection and reciprocal transplant experiments of differentiated populations) will continue to be useful when used creatively. One annoying reality of such studies is that many traits may covary in plants, making it difficult to detect the costs of specific traits. One must decide then, is the question of interest about the cost of particular traits, or the costs of particular strategies that have evolved in concert? I would argue that the covariation of traits is typically part of plants' resistance strategy, and thus costs are most relevant in a multivariate framework.

A second general issue with detecting costs of traits is the general vigour problem (Fig. 3). That is, it is often the case that larger plants may produce higher levels of traits, including resistance traits. Three scenarios could fit the pattern. First, as Van Noordwijk & Dejong (1986) proposed, variation in resource acquisition could create a positive phenotypic correlation between two traits (say growth rate and defence) even when there is a trade-off between the same two traits for a given level of resource acquisition. For example, in resource
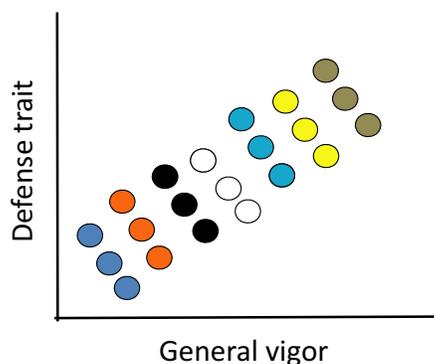
Fig. 3. How a trade-off in the allocation of resources to two traits can be masked across scales by general vigour. For example, larger plants may produce higher level defence, even if a trade-off occurs. In this illustration, colour represents different species with three genotypes shown for each. A trade off is shown within each species, but different species have altered resource acquisition which enhances growth and defence, masking the trade-off. The same logic can be applied across genotypes or environments (see text and Agrawal, Conner & Rasmann 2010).

rich environments, we have found that milkweed plants grow larger and produce more latex than plants in low resource environment (Agrawal & Konno 2009c). The implication of the general vigour problem is that although latex is costly, the resource environment masks this cost. Houle (1991) extended this concept to genetic correlations, showing that if there is more genetic variation in resource acquisition than allocation, genetic correlations between growth and defence could also be positive despite a trade-off. Again, my laboratory has found this relationship, with larger genotypes of *Asclepias syriaca* having greater latex exudation than smaller genotypes (unpublished results); the implication is not that there is no cost of latex production, but rather that some genotypes are simply more vigorous (i.e. greater growth and defence) than others. Another mechanism of this obscuration is that negative covariance between two segregating loci (e.g. linkage disequilibrium) that contribute to resistance may be masked by variation in other loci having effects that are positively correlated across environment (Fry 1992). These genotypic general vigour issues illustrate why it may be difficult to detect costs from quantitative genetic studies and beg the question of why some genotypes may vary more in acquisition than allocation.

Finally, at the species level, a positive species correlation may occur if species vary in their total resource acquisition (or production of a trait) despite genetic trade-offs that occur within species (Agrawal, Conner & Rasmann 2010). The interpretation of such a species correlation is that macroevolution has favoured altered resource allocation that can mask costs (when looking across species). One solution to the issue of the general vigour problem is to statistically correct for relationships between size and other plant traits. For example, Hare *et al.* (Hare, Elle & Van Dam 2003) reported costs of glandular trichome production in *Datura wrightii*, but these costs were only detectable when accounting for seed

production per unit of vegetative biomass. In other words, although some well-defended plants had relatively high fitness (in the absence of herbivores), their efficiency of seed production per unit leaf area was reduced compared to less defended genotypes. As long as genetic variation for resource acquisition and investment in defence are not caused by the same genes, they should be able to respond independently to natural selection.

A final issue relating to costs is that costs come in many flavours, and may only be realized in certain ecological environments. It appears that negative consequences of investing in resistance may come in the form of reduced interactions with mutualists, including pollinators, microbial symbionts, fruit dispersers, and natural enemies of herbivores (Strauss *et al.* 2002). Alternatively, costs of 'resistance' traits may be in the form of benefiting specialist herbivores (Lankau 2007). In either case, although there has been much written about the ecological impacts of particular traits, costs should be measured in terms of fitness impacts and measures of natural selection. In other words, the many rippling consequences of plant traits on the structure of insect communities and diverse species interactions (Whitham *et al.* 2003; Johnson 2008; Mooney & Agrawal 2008; Mooney *et al.* 2010; Schweitzer *et al.* 2005) may be passive consequences of the traits or shaped by a dynamic feedback between resistance and the interactions that resistance modifies (Johnson & Agrawal 2005; Genung *et al.* 2011). This area is wide open, and there is little current consensus as to whether the rippling effects of resistance traits are actually ecological costs (i.e. part of a dynamic evolutionary feedback impacting fitness) or simply ecological legacies of resistance evolution (and not subject to selection).

Which traits mediate resistance?

There have been two utter failures of plant resistance research (and my own work has been part of these failings): there is still the widely held belief that plant resistance traits (i) act singularly, and many researchers continue to search for or measure single plant traits and (ii) should trade-off against each other. But, it is highly unusual that a single plant trait is the key to resistance. And trade-offs rarely occur between arbitrarily selected resistance traits (e.g. genotypes that produce more physical defence do not typically show a trade-off producing lower chemical defence, Koricheva, Nykanen & Gianoli 2004). The lack of support for these paradigms likely lies in a common cause. Multiple plant resistance traits in the same species are not likely redundant or wasteful; on the contrary there is reason to expect multiple resistance traits may evolve together (Rasmann & Agrawal 2009a; Carmona, Lajeunesse & Johnson 2011).

There is an accumulating evidence for multiple trait combinations repeatedly evolving across species, a characteristic of the plant defence syndromes hypothesis (Futuyma & Agrawal 2009b; Armbruster, Lee & Baldwin 2009; Heil *et al.* 2009; Kursar *et al.* 2009; Fine *et al.* 2006). For example, based on community-wide surveys, Kursar & Coley (2003) concluded

that tropical rain forest tree species have defence syndromes of young leaves based on contrasting investment in leaf expansion rate, nitrogen content and chemical defence. Taking an approach based on a clade of plants (the new world genus *Asclepias*), Agrawal & Fishbein (2006a) found trait syndromes associated with either low nutritional quality for herbivores or a balance of higher nutritional quality coupled with physical or chemical defences. It is still unclear, however, whether these initial approaches to studying syndromes represent discrete classifications with a real correspondence to resistance against particular herbivores.

Why might multiple traits convergently evolve as a suite? I briefly highlight three major hypotheses: (i) a diversity of plant attackers requires diverse defences; (ii) the need for a safety net (adaptive redundancy) and (iii) synergistic impacts. First, most plants have many herbivores, several of which usually have some negative fitness impact. Nonetheless, there is typically specificity in the impacts of various resistance traits on the herbivores. From my own work on milkweed, it appears that 4 of the 10 or so common herbivores of milkweed likely have some fitness impact on the plant, yet there is trait specificity in terms of which traits impact which herbivores (Agrawal 2004b, 2005b; Agrawal & Van Zandt 2003; Van Zandt & Agrawal 2004b). Trichomes have divergent effects on chewing (negative) vs. sucking (positive) insects (Agrawal 2004a; Agrawal & Fishbein 2006a). Latex is generally effective against chewing herbivores, but suckers are unaffected as their probing and subsequent feeding does not pierce the laticifers. Thus, a diversity of fitness-impacting attackers likely favours multiple plant resistance strategies. Nonetheless, I cannot think of a study which has directly addressed how multiple herbivores differentially impact selection on multiple traits.

Secondly, some level of redundancy may be adaptive as a safety net for when resistance traits fail (Rasmann & Agrawal 2009a). For some of our best studied and iconic resistance traits, experiments sometimes show negative effects on herbivores, while others do not. Although this is frustrating for scientists, it is a reality. For example, proteinase inhibitors and nicotine, which typically correlate well with resistance in wild tobacco, were not associated with reduced caterpillar performance in some experiments (Mitra *et al.* 2008). Similarly, cardenolides and latex, which typically correlate with resistance to caterpillars, do not always show this effect (Agrawal 2005b; Agrawal & Fishbein 2006a). One reason to believe that these inconsistencies represent ecological reality is that other traits were predictive of resistance to caterpillars in the studies cited above. Thus, an interpretation of the results is that under varying ecological conditions, multiple resistance traits may be adaptive because some may fail to provide resistance, even against a single herbivore species. In other words, there is at least intermittent natural selection for several resistance traits. Currently, we have little understanding of the specific conditions where this redundancy may be beneficial.

Thirdly, there is some evidence that multiple resistance traits may provide a higher level of resistance than could be predicted from their independent action (Romeo, Saunders &

Barbosa 1996). Evidence for this defensive synergism hypothesis comes from *Nicotiana attenuata*, where the presence of toxic nicotine increases the negative impact of digestibility reducing proteinase inhibitors by preventing compensatory feeding (Steppuhn & Baldwin 2007). Although there are a few other good examples of defence compound synergism (Dyer *et al.* 2003; Berenbaum & Neal 1985; Fig. 4), much work is needed on identifying such synergisms and placing them in an evolutionary context by employing genetic variation, population differentiation, or related species.

But really, how strong is the evidence for joint selection or evolution of combinations of defence traits? Scant. As suggested above, digestibility reducers may evolve with toxins to pack a one–two-punch. Alternatively, digestibility reducers may evolve with low nitrogen content, which could essentially starve an herbivore (Broadway & Duffey 1988). Finally, multiple, related toxins may evolve as synergists (Berenbaum & Zangerl 1996). In all cases, the opposite of a trade-off is predicted. There are likely many secondary compounds which similarly act synergistically, but these have not been well-identified (Carmona, Lajeunesse & Johnson 2011). Although some physiological work has long-suggested that multiple resistance traits are important (e.g. Duffey & Stout 1996), this point is just emerging in evolutionary studies.

Finally, I predict that sublethal resistance traits (which seem to be the most common form of plant resistance), may frequently evolve in concert with indirect resistance. Remarkably, because we typically assume high costs of production for any resistance trait, and because we assume redundancy among resistance traits, the dominant prediction for the rela-
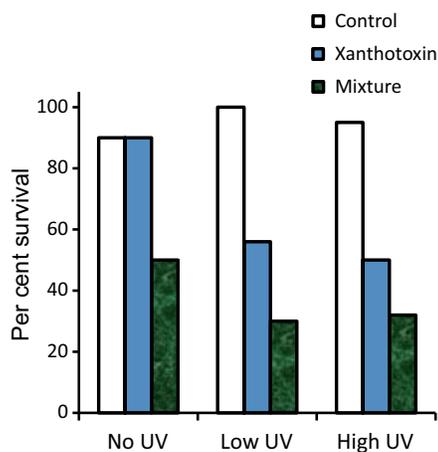
Fig. 4. Phytochemical mixtures can provide higher levels of resistance than individual compounds. Shown here is the per cent survival of *Heliothis zea* caterpillars after 6 days on control diets containing no furanocoumarins, a highly toxic UV-light-activated furanocoumarin (xanthotoxin), and a mixture of six furanocoumarins (in equimolar concentration to the xanthotoxin treatment) at three levels of UV-light. Wild parsnip fruit naturally contain the six furanocoumarins, including xanthotoxin. Redrawn from Berenbaum, Zangerl & Nitao (1991). Very few studies have controlled the concentrations in a substitutive design as was done here, yet this is critical to determine the significance of phytochemical diversity *per se* over simply increased concentrations.

tionship between direct and indirect resistance has been a trade-off (Agrawal *et al*. 2002b; Steward & Keeler 1988; Dicke & Van Loon 2000; Ballhorn *et al*. 2008). However, one well-supported hypothesis for sublethal plant defences is that slow growth of insect herbivores may be coupled with high mortality via enemies, which take advantage of the expanded opportunity for predation (Benrey & Denno 1997). Thus, should we not predict that direct resistance (i.e. secondary metabolites, or physical barriers that slow herbivore growth) and indirect resistance (traits such as parasitoid-attracting volatiles) should evolve in concert? After all, these traits are often co-regulated at the physiological level (Thaler *et al*. 2002). Further study of their co-regulation and their co-expression across genotypes, populations, and species will likely be fruitful. Indeed, some single compounds even serve as both a direct and indirect defence (e.g. linalool: Kessler & Baldwin 2001; alpha-pinene: Kenis, Wermelinger & Grégoire 2004; Wallin & Raffa 2004; and isothiocyanate: Bradburne & Mithen 2000; Agrawal & Kurashige 2003).

We are in desperate need of creative (but also well-motivated) hypotheses about why plants vary in their investment in indirect defence. Within a single plant genus, one may easily find tremendous variation in leaf domatia (that house plant-beneficial mites) (Brouwer & Clifford 1990; Karban *et al*. 1995), extrafloral nectaries (Koptur 1992; Heil *et al*. 2004), and herbivore induced volatiles (Degen *et al*. 2004; Gouinguené, Degen & Turlings 2001). Is this variation predictable? Does it correspond to defensive syndromes? It may be time to revisit Price *et al*.'s (1980) seminal review in a modern evolutionary framework to better develop hypotheses about the evolution of indirect resistance. Over the last decade there have been some evolutionary predictions made, but most surround the specific costs and benefits of indirect defence, and are less focused on explaining variation in indirect defence investment (Agrawal & Karban 1999; Dicke, Van Loon & Soler 2009; Zangerl 2003; Dicke 1999).

Macroevolution of defence

Comparative phylogenetic analyses have recently yielded novel insights into previously untested hypotheses about the evolution of plant defence. For example, recent work has suggested (i) evolutionary trends in the production of secondary metabolites (Agrawal & Fishbein 2008; Agrawal *et al*. 2009a; Wink 2003; Aguilar-Ortigoza & Sosa 2004; Becerra, Noge & Venable 2009); (ii) evolution of plant defence is associated with adaptive radiation (Agrawal *et al*. 2009a; Farrell, Dussourd & Mitter 1991); (iii) macroevolutionary constraints on diversification in biochemical pathways (Rausher 2006; Armbruster 2002; Agrawal *et al*. 2009b; Armbruster, Lee & Baldwin 2009); (iv) habitat affiliation has convergently been associated with the evolution of divergent defences (Agrawal *et al*. 2009b; Fine, Mesones & Coley 2004; Fine *et al*. 2006; Kursar & Coley 2003; Van Zandt 2007) and (v) how and why plant reproductive strategy shapes the evolution of defence (Johnson, Smith & Rausher 2009). Progress on these hypotheses is summarized below.

Classic hypotheses predicted that secondary metabolite production was associated with the degree of phylogenetic nesting, with an 'escalation of defence' associated with increasingly derived taxa (Vermeij 1994). Here, escalation is defined as a directional trend for increased anti-herbivore traits during the diversification of a plant lineage. This prediction was made explicitly by Vermeij and is a special case of Ehrlich and Raven's 'escape and radiate' hypothesis, where the evolution of novel traits that promote speciation are incremental and directional through the diversification process (Ehrlich & Raven 1964; Agrawal 2007). Whether such trends are causal (i.e. does defence trait variation cause speciation, or does defence trait variation follow speciation?) is unclear and currently subject to debate (Agrawal, Salminen & Fishbein 2009d).

Two different approaches have suggested that changes in defence allocation do indeed contribute to the diversification process. First, Farrell, Dussourd & Mitter (1991) showed that latex-bearing plant clades were significantly more species-rich than sister clades lacking latex (13 of 16 pairs showed this pattern). At this deep phylogenetic scale, evolution of latex appears to be associated with either reduced extinction or greater speciation rates. Secondly, within the genus *Asclepias*, species-rich lineages underwent a proportionately greater change (in this case a decline) relative to species-poor lineages, and the rate of trait change was most rapid early in the radiation (Fig. 5) (Agrawal *et al*. 2009a). Because a likely signature of adaptive radiation is a high level of trait change during the diversification process, and a plateau towards the end of the radiation, an interpretation of the result in Fig. 5 is that reduced investment in defensive traits accelerated diversification (Pagel 1999; Schluter 2000; Freckleton, Pagel & Harvey 2003).

The macroevolution of integration within and between biosynthetic pathways is a novel approach, complementary to
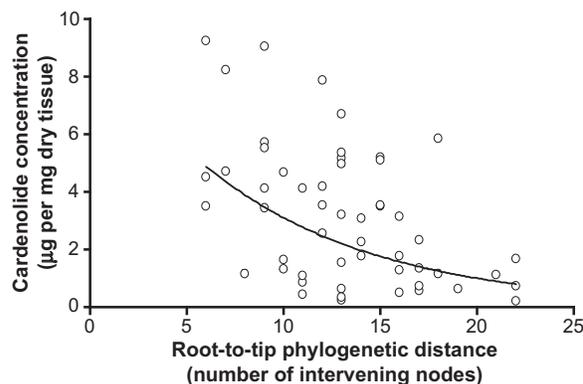
Fig. 5. Phylogenetic deceleration of declining investment in cardenolides across 53 milkweeds. The *x*-axis shows the number of intervening nodes between the root and each taxon calculated from a comprehensive phylogeny. Note that the decline is not linear, but is best fit by an exponential decrease in the rate of trait evolution during the radiation. The reduction of investment in cardenolides occurred disproportionately early in the diversification of the milkweeds suggesting a role in adaptive radiation. Redrawn from Agrawal *et al*. 2009a.

more typical functional (genetic or physiological) studies of secondary metabolism. In particular, correlated evolution (i.e. correlations that persist after accounting for evolutionary non-independence) of defensive traits suggests either (i) a strong physiological constraint exists that is unbreakable, even over speciational time-scales, or (ii) the relationship is adaptive and has been maintained by natural selection. For milkweed species, various phenolic subclasses showed correlated evolution consistent both with trade-offs and synergism in biochemical pathway evolution (Agrawal, Salminen & Fishbein 2009d). For example, coumaric acid derivatives showed negatively correlated evolution with caffeic acid derivatives, probably driven by the fact that the former are used as precursors for the latter. Additionally, cardenolides and flavonoids, which are linked via the acetate-malonate pathway, showed positively correlated evolution (Agrawal, Salminen & Fishbein 2009d). The fact that each of these relationships was upheld after accounting for the evolutionary history of *Asclepias* demonstrates that the associations have either evolved repeatedly or that they could not be broken during the speciational history of the lineage.

Habitat affiliation may shape the evolution of plant defence strategies in at least a few different ways. First, as has long been predicted, slow growing species, which typically evolve in low resource environments, will invest relatively more in resistance than related species that evolve in high resource environments. This prediction has recently been well-supported in phylogenetically controlled analyses from tropical rain forest trees as well as temperate herbaceous species (Fine, Mesones & Coley 2004; Fine *et al.* 2006; Mooney *et al.* 2010; M.-J. Endara & P.D. Coley, unpublished data, Van Zandt 2007; Kursar & Coley 2003). Additionally, habitat may influence plant phenotypic characteristics that only indirectly impact herbivores. For example, in North American milkweeds, it appears that the primary driver of trichome evolution is habitat (species in drier habitats have higher trichome densities) not herbivores, but trichomes nonetheless provide resistance to some herbivores (Agrawal *et al.* 2009b).

Finally, plant reproductive strategy may influence the macroevolution of plant defence. For example, Johnson, Smith & Rausher (2009) recently tested the hypothesis that transitions to asexuality in the Onagraceae limited the evolution of plant defence (due to limited recombination). Indeed, across 15 independent transitions to asexuality, several traits and bioassays showed reduced investment in defence against generalist herbivores. Other hypotheses about variation in defence investment based on plant mating system (i.e. inbreeding vs. outcrossing species) and interactions with pollinators await testing (Kessler & Halitschke 2009).

Specificity of induced resistance

Although the study of induced resistance has exploded in the past 20 years, many unanswered questions remain (Karban 2011). Here, I focus on specificity of induction. In particular, there has been little exploration of how specificity of induction could evolve by natural selection and whether it should

be considered adaptive (Agrawal 2005a). Many studies have identified a heritable basis for constitutive and induced resistance traits to one herbivore (Agrawal 1999; Agrawal *et al.* 2002a; Havill & Raffa 1999; Underwood *et al.* 2000; Stevens & Lindroth 2005). In general, these studies report significant levels of genetic variation in both constitutive and induced responses, with as much as 30-fold variation among plant genotypes in the induced effects on herbivores (Underwood *et al.* 2000). Similarly, heritability of herbivore-specific induced responses is an important prerequisite for pairwise co-evolution and specific defensive responses to evolve, yet the heritability of such response specificity has not been investigated.

To address how specific plant responses could evolve, it is essential to study genetic correlations between responses to different herbivores and different traits of the plant when attacked by different herbivores (Fig. 6) (Bingham & Agrawal 2010). For example, where negative genetic correlations exist between responses to different herbivores, evolution of optimal levels of defence for a particular herbivore may be constrained. Where responses are positively associated, a plant's response to one herbivore will tend to reinforce its response to another, resulting in generalized elicitation. Con-
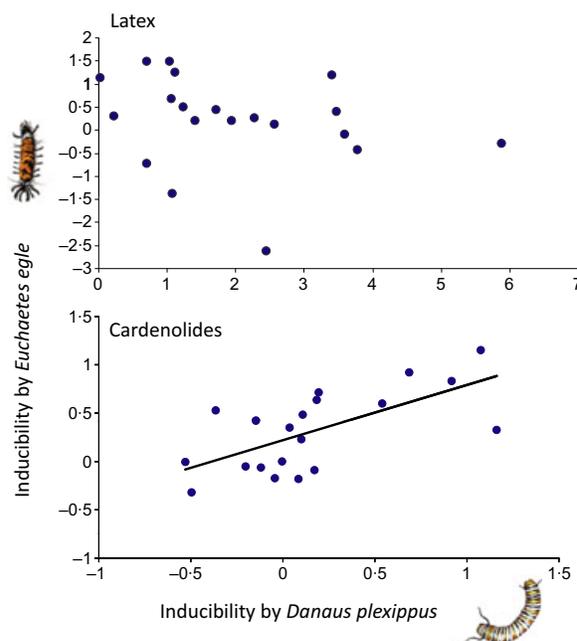
Fig. 6. Genetic correlations between induction (induced minus constitutive values) of latex and cardenolides for 20 full-sib families of common milkweed *Asclepias syriaca* damaged by *Euchaetes egle* or *Danaus plexippus* in a field common garden. There was substantial genetic variation for induction in both traits. Inducibility of latex shows the potential to evolve specificity, as responses to the two herbivores were not genetically correlated. Note also that the mean latex response to *D. plexippus* was fivefold higher than to *E. egle*. On the contrary, there was no evidence that specificity of induction would evolve in cardenolide responses, as both herbivores induced similar responses across the 20 genetic families. Redrawn from Bingham & Agrawal 2010.

versely, plant defence traits that are genetically independent allow for response specificity to evolve, especially where there is a history of strong pair-wise interactions between a plant and a specific herbivore.

Specificity occurs at various scales. At a more mechanistic level, how does specificity evolve, especially when key plant hormones appear to have highly conserved function? It appears that specificity can be achieved through hormonal ratios and interactions between the timing and up- and down-regulation of various plant hormones (Farmer, Almeras & Krishnamurthy 2003; Pieterse *et al.* 2009; Howe & Jander 2008). However, one pattern which appears abundantly clear is that jasmonic acid has evolved as a master regulator of sundry defensive mechanisms (Table 1, Fig. 7). What we are currently lacking is an evolutionary approach to disentangling the web of plant hormonal signalling.

To date, few studies have identified the genetic basis for hormonal signalling and interactions between pathways (Kliebenstein, Figuth & Mitchell-Olds 2002). Here, I am explicitly excluding the many excellent studies of gene expression (where the relationship between various jasmonate-dependent and jasmonate-independent genes are mapped in networks, De Vos *et al.* 2005) or gene identification (Thines *et al.* 2007; Li *et al.* 2004), because these provide little insight into the process of jasmonate evolution. I believe that we now have the tools to close the loop between plant perception of herbivores, hormonal signalling, and the production of defensive end-products. A research programme that made these linkages across plant genotypes within a species, or between plant species in a phylogenetic context, could make substantial progress on understanding the evolution of how plants perceive and respond to specific herbivores.

Finally, the community ecological consequences of specific induced plant responses have just begun to be elucidated in the past decade. Specificity of elicitation (the differential response of plants to attack by different herbivores) and specificity of effect (the differential response of arthropods to a given plant phenotype), both provide mechanisms for induced responses to shape arthropod community structure. Because herbivores, omnivores, predators and parasitoids all show variation in their responses to plant induction (i.e. some respond positively, some negatively and some not at all), the influence of induction on the community is likely strong, but complex. A few studies have implicated induced responses to herbivory *per se* in shaping arthropod community structure (i.e. more than a few arthropod species) (Bernasconi Ockroy *et al.* 2001; Thaler *et al.* 2001; Van Zandt & Agrawal 2004a; Viswanathan, Narwani & Thaler 2005; Wold & Marquis 1997; Kessler, Halitschke & Baldwin 2004; Poelman *et al.* 2008), yet more work is needed to understand how important induction is in shaping arthropod communities.

Tolerance

Although most of this article focused on the evolutionary ecology of plant resistance to herbivory, plant tolerance of herbivory is an additional major defensive strategy (J. Fornoni, unpublished data). Two classic predictions about tolerance have yet to be tested rigorously. Not surprisingly, both predictions are from the 1980s and were rooted in inter-specific comparisons. These hypotheses are ripe for testing, especially in a phylogenetic context. First, as predicted by Coley, Bryant & Chapin (1985), plant growth rate should show correlated evolution with tolerance to herbivory. As discussed above, this prediction is based on the following logic: plants evolve slow growth in low resource environments and slower growing plants suffer disproportionally more for a given amount of herbivory than faster growing plants. Thus, slow growing plants (especially those that evolve in low resource environments), are predicted to be less tolerant of herbivory than faster growing species. Although intuitively pleasing, data addressing this hypothesis is limited, and such relationships should be evaluated in concert with other plant responses to herbivory (e.g. induced chemical defence).

The second classic comparative prediction about tolerance stems from a study by Van Der Meijden, Wijn & Verkaar (1988), suggesting that resistance and tolerance should trade-off, especially among coexisting species. Although I have down-played trade-offs above, there are some theoretical grounds for specifically predicting a trade-off between resistance and tolerance. At least under some conditions, these two strategies may truly be redundant. Organisms with a high level of tolerance should not experience selection for resistance, because attack does not reduce fitness (i.e. the organisms are tolerant). Conversely, evolution of resistance should thwart selection for tolerance (because resistant plants are not receiving attack should not benefit from the ability to withstand attack). This prediction, that resistance and tolerance trade-off because they are redundant, should be reinforced by any costs of these traits. In the study by Van Der Meijden, Wijn & Verkaar (1988), *Verbascum thapsus* was heavily attacked but regrew, whereas coexisting *Senecio jacobaea* was largely resistant, but had very poor ability to regrow when damaged. Such studies are needed in the context of several coexisting species, evaluated using community phylogenies (Cavender-Bares *et al.* 2009). The benefit of addressing this relationship among coexisting species is that one can truly tests whether resistance and tolerance are alternatives, given a common set of ecological conditions. Within clades of species that do not necessarily coexist, there is some phylogenetic evidence for a resistance–tolerance trade-off (Agrawal & Fishbein 2008), but this has not been widely tested.

Concluding speculation

Plant defence is only one half of the co-evolutionary picture, and most of this essay has focused on a bitrophic view of the evolution of defence (Karban & Agrawal 2002; Singer & Stireman 2005). Nonetheless, certain generalities have emerged that are likely applicable to study of various aspects of the evolutionary ecology of species interactions. I have argued here and elsewhere that a community perspective may be critical to understanding costs of defence, plant defence syndromes, and specificity in induced plant defence (Agrawal & Fishbein

Table 1. Triumph of jasmonic acid as a master regulator of plant defensive responses to herbivores. This non-exhaustive table shows the diversity of plant defensive traits regulated by jasmonate signalling. Methods employed span stimulation, usually by foliar application of jasmonates, endogenous quantitative correlations between jasmonates and defensive end-products, and genetic manipulation of the octadecanoid pathway which mediates jasmonate signalling. Endogenous quantitative correlations (i.e. between individuals or genotypes within a treatment group), especially when assessed across treatments and genotypes may be particularly important for understanding the evolution jasmonate-mediated defence. Interestingly, in many plant species, jasmonate signalling co-regulates several of the responses listed below

Defence type	Methods	Notes	References
Alkaloids	Stimulation, endogenous quantitative correlation, genetic manipulation	A complete story. Most well known from nicotine in *Nicotiana* spp., but other types, including pyrrolizidine alkaloids are regulated	(Abd El-Mawla 2010; Halitschke and Baldwin 2003; Baldwin *et al.* 1997; Baldwin 1996)
Phenolics	Stimulation, endogenous quantitative correlation, genetic manipulation	Phenolics are very diverse, occur in most plants, and have many functions outside of defence; nonetheless jasmonate is a strong regulator	(Cooper & Rieske 2008; Erb *et al.* 2009; Miller *et al.* 2005; Peters & Constabel 2002; Paschold, Halitschke & Baldwin 2007)
Oxidative and anti-digestive enzymes	Stimulation, genetic manipulation	Very common, but not well-studied outside of a few model systems	(Thaler *et al.* 1996; Li *et al.* 2004; Cipollini *et al.* 2005)
Glucosinolates/cyanides	Stimulation, genetic manipulation	Much work to be done disentangling the impact of jasmonates on these two-part systems: is the substrate, enzyme, or the interaction affected?	(Bodnaryk 1994; Kliebenstein, Figuth & Mitchell-Olds 2002; Mikkelsen *et al.* 2003; Cipollini *et al.* 2005; Ballhorn, Heil & Lieberei 2006; Agerbirk *et al.* 2009)
Cardenolides	Stimulation	Provides an excellent example of how defence induction may evolve with specialist herbivores that sequester the compounds	(Rasmann, Johnson & Agrawal 2009b)
Volatiles (terpenoids and other biochemical pathways)	Stimulation, genetic manipulation, endogenous quantitative correlation	Appears to be a universal plant response, but the role of jasmonate should be better established, especially in endogenous quantitative correlations	(Boland, Hopke & Piel 1998; Thaler *et al.* 2002; Kessler, Halitschke & Baldwin 2004; Schuman *et al.* 2009)
Trichomes/glandular and non-glandular	Stimulation, genetic manipulation	Trichomes are nearly universal in plants, but may not be generally regulated by jasmonate as they have many important ecophysiological functions	(Traw & Bergelson 2003; Boughton, Hoover & Felton 2005; Hare & Walling 2006; Li *et al.* 2004)
Latex/resins	Stimulation, endogenous quantitative correlation	Typically is a combination of physical and chemical defence, stored under pressure and exuded upon damage. Jasmonate can alter both the amount of exudation and chemical composition	(Fig, 7, Agrawal & Konno 2009c; Rasmann, Johnson & Agrawal 2009b; Hudgins, Christiansen & Franceschi 2004)
Extrafloral nectar	Stimulation, endogenous quantitative correlation	Jasmonate signalling appears to play a role in both obligate and facultative ant-plant associations. Impacts may be on the number of extrafloral nectaries, nectar quantity and perhaps nectar quality	(Heil *et al.* 2004; Heil 2004)
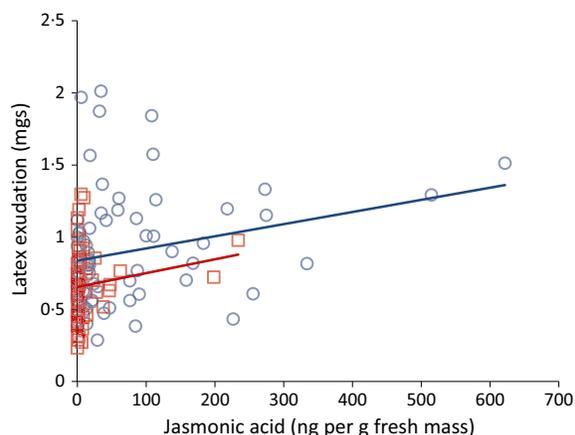
Fig. 7. Relationship between endogenous jasmonic acid (JA) and latex exudation in common milkweed *Asclepias syriaca* in undamaged plants (red squares) and plants damaged by monarch butterfly caterpillars *Danaus plexippus* (blue circles). Although monarchs induce increases in both JA (over a fivefold effect, $F_{1,131} = 14{\cdot}4$, $P < 0{\cdot}001$) and latex (35% increase, $F_{1,131} = 16{\cdot}2$, $P < 0{\cdot}001$) after 3 days of feeding, the relationship (i.e. the slope) between the two remains constant (interaction term between monarch treatment and JA for predicting latex, $F_{1,129} = 0{\cdot}01$, $P = 0{\cdot}914$). Little is currently known about genetic variation and selection on hormonal production, perception, and signal interactions (Agrawal *et al*. unpublished data).

2006a; Agrawal, Lau & Hambäck 2006b). A renewed interest in macroevolutionary hypotheses is finally allowing for the rigorous testing of some of the classic theories of plant defence (Ehrlich & Raven 1964; Fraenkel 1959; Whittaker & Feeny 1971). Although the phylogenetic approach leaves much to be desired because it is largely a descriptive endeavour, it is a strong component of the toolbox to address big historical questions in evolutionary biology. A clear frontier in the study of plant defence is the combination of phylogenetic history and pattern with manipulative field experiments that explicitly test hypotheses (Fine, Mesones & Coley 2004; Mooney *et al*. 2010). Other combinations of approaches represented in Fig. 2 will also contribute to this ongoing synthesis.

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