

Plant–herbivore coevolution and plant speciation

JOHN L. MARON,^{1,5} ANURAG A. AGRAWAL,² AND DOUGLAS W. SCHEMSKE^{3,4}

¹*Division of Biological Sciences, University of Montana, Missoula, Montana 59812 USA*

²*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*

³*Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824 USA*

⁴*W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060 USA*

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Abstract. More than five decades ago, Ehrlich and Raven proposed a revolutionary idea—that the evolution of novel plant defense could spur adaptive radiation in plants. Despite motivating much work on plant–herbivore coevolution and defense theory, Ehrlich and Raven never proposed a mechanism for their "escape and radiate" model. Recent intriguing mechanisms proposed by Marquis et al. include sympatric divergence, pleiotropic effects of plant defense traits on reproductive isolation, and strong postzygotic isolation, but these may not be general features of herbivore-mediated speciation. An alternate view is that herbivores impose strong divergent selection on defenses in allopatric plant populations, with plant–herbivore coevolution driving local adaptation resulting in plant speciation. Building on these ideas, we propose three scenarios that consider the role of herbivores in plant speciation. These include (1) vicariance, subsequent coevolution within populations and adaptive divergence between geographically isolated populations, (2) colonization of a new habitat lacking effective herbivores followed by loss of defense and then re-evolution and coevolution of defense in response to novel herbivores, and (3) evolution of a new defense followed by range expansion, vicariance, and coevolution. We discuss the general role of coevolution in plant speciation and consider outstanding issues related to understanding: (1) the mechanisms behind cospeciation of plants and insects, (2) geographic variation in defense phenotypes, (3) how defensive traits and geography map onto plant phylogenies, and (4) the role of herbivores in driving character displacement in defense phenotypes of related species in sympatry.

Key words: plant defense; plant–herbivore coevolution; plant–insect cospeciation; speciation; vicariance.

INTRODUCTION

In 1964, Ehrlich and Raven published *Butterflies and Plants: A Study in Coevolution*. This now-classic paper fostered a new way of thinking about the ecology and evolution of plant–herbivore interactions. A major assertion of Ehrlich and Raven's paper (hereafter E & R), motivated in part by Fraenkel's (1959) insights, was that plant secondary chemistry was adaptive and contributed to defense against herbivores. This idea laid the foundation for over five decades of research on plant chemistry, anti-herbivore defense and coevolution.

In addition to asserting the primacy of plant secondary chemistry as an adaptive trait, E & R made several other broad assertions that explicitly dealt with the importance of coevolution to both the origin of species and the maintenance of species diversity. In particular, E & R suggested that coevolution between plants and their insect herbivores could drive the adaptive diversification of both groups. Conceptually, E & R's paper continues to raise interesting questions about the role of coevolution in speciation.

E & R's thesis was that the evolution of novel chemistry would reduce herbivore pressure. "Such a plant, protected from the attacks of phytophagous animals, would in a sense have entered a new adaptive zone. Evolutionary radiation of the plants might follow..." (Ehrlich and Raven 1964:602). Thus, the evolution of novel defensive chemistry was thought to result in a starburst

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⁵E-mail: john.maron@mso.umt.edu

phylogenetic pattern of plant speciation, dubbed “escape and radiate” (Thompson 2005). An herbivore that subsequently evolved the ability to circumvent or detoxify novel plant chemistry in turn would speciate and diversify on the newly radiated plants. Although much recent work has addressed the radiation of insects on plants (Winkler et al. 2009, Fordyce 2010, Rainford and Mayhew 2015), the role of plant defense in plant diversification is poorly understood.

The strongest support for a pattern of plant defense corresponding to plant diversification comes from comparative studies of plants that produce latex or extrafloral nectaries, two highly convergent defensive traits (Farrell et al. 1991, Weber and Agrawal 2014). Some evidence for a quantitative association between plant defense and diversification has also been found within plant clades (Agrawal and Fishbein 2008, Agrawal et al. 2009, Becerra et al. 2009, Cacho et al. 2015). Nonetheless, some of these patterns have been non-intuitive (i.e., defense declines associated with diversification) and none linked strongly to causal mechanisms (Yoder and Nuismer 2010). Moreover, it is unclear whether cases of increased plant diversification that coincide with novel defense evolution occur because of how novel defenses influence rates of speciation or extinction. Lineages with more successful defenses might have lower extinction rates, which would lead to greater diversity of those lineages.

E & R did not consider the geography of speciation (i.e., speciation in sympatry/parapatry vs. allopatry), or propose mechanisms whereby the evolution of novel plant chemistry and plant–herbivore coevolution would cause plant speciation. As Futuyma (2000) pointed out: “Ehrlich and Raven thus shared the common presumption that a trait that is advantageous for an individual organism should also promote ‘evolutionary success’ in the form of increased cladogenesis and species diversity. This, however, requires a logical leap that may not be justified. The mechanism connecting the two is seldom specified. . .” In other words, even if a phylogenetic pattern of defense and diversification exists, why does this occur?

Here, we address how plant defense evolution could be associated with plant speciation. Our discussion builds on a recent paper by Marquis et al. (2016), that proposed six different “pathways” whereby the adaptive evolution of plant defense traits indirectly or directly could result in reproductive isolation and plant speciation (*Pathways to the evolution of plant defense driving speciation proposed by Marquis et al. (2016)*). Their first three pathways involve speciation in sympatry. Although sympatric speciation is theoretically possible (Dieckmann and Doebeli 1999), and has some empirical support (e.g., Schliewen et al. 1994, Savolainen et al. 2006, Bolnick and Fitzpatrick 2007), it is generally accepted that speciation in sexual, outcrossing organisms typically occurs in allopatry (except for polyploid speciation), largely as a byproduct of adaptation to local environments

(Coyne and Orr 1998, 2004, Schluter 2009, Schemske 2010). The last three pathways proposed by Marquis et al. (2016; *Pathways to the evolution of plant defense driving speciation proposed by Marquis et al. (2016)*) involve parapatric or allopatric speciation, where the major isolating barrier is extrinsic post-zygotic reproductive isolation caused by the reduced fitness of hybrids that are poorly defended against herbivores. While extrinsic postzygotic isolation is certainly feasible (Schluter 2009), we suggest that herbivore-mediated selection can lead to the evolution of other isolating barriers, and that it is therefore useful to take a broader view of how herbivory might contribute to speciation.

Pathways to the evolution of plant defense driving speciation proposed by Marquis et al. (2016)

Marquis et al. (2016) proposed several pathways that would couple the evolution of novel plant chemistry with reproductive isolation, thereby enabling plant speciation. The first three of these pathways rely on prezygotic isolating mechanisms, whereas pathways 4–6 (below) involve postzygotic isolating mechanisms. These pathways are as follows.

Pathway 1: Coupled herbivore defense and pollinator attraction.—Reproductive isolation evolves in sympatry due to pleiotropic effects of plant defense on traits involved in pollinator attraction such as flower size or nectar traits. Although correlations exist between plant defenses and floral traits (Strauss and Whittall 2006), no evidence indicates pollinator fidelity to different defensive morphs, let alone the potential for reproductive isolation

Pathway 2: Coupled herbivore defense and phenological changes or resource allocation to pollinator attraction.—Reproductive isolation is hypothesized to evolve in sympatry as a consequence of changes in phenology or floral traits that result from reduced herbivore damage following the evolution of enhanced defenses. One scenario is that better defended genotypes flower earlier because reduced herbivory increases resource availability. Another scenario is that better defended plants produce larger flowers than poorly defended plants, and reproductive isolation evolves because pollinators prefer small or large flowers. Given the likely overlap in phenology and floral size associated with defended genotypes, it is difficult to imagine that this mechanism alone could cause complete reproductive isolation.

Pathway 3: Coupled defense and stigma-pollen interactions.—Compounds involved in plant defense pleiotropically affect post-pollination dynamics such as stigma receptivity, pollen germination or pollen-tube growth. Thus, plant defense drives reproductive isolation in sympatry due to reduced fertilization success by pollen from different genotypes. To impose complete reproductive isolation,

pleiotropy between plant defense traits and reproductive isolation would need to be extremely strong, and changes in reproductive traits would need to be of sufficient magnitude to impose non-overlapping use of different plant genotypes by generalist pollinators, which seems unlikely. Although pathways 1–3 are unlikely to operate forcefully enough to enable sympatric speciation, these processes could occur within geographically isolated populations. Thus, they could contribute (along with other unique traits that evolved in allopatry) to reproductive isolation of newly speciated plants that came back into contact.

More plausible pathways proposed by Marquis et al. (2016) involve speciation in parapatry or allopatry.

Pathway 4: Selection against hybrids in hybrid zones.—Geographically isolated populations evolve different plant defenses and in areas of secondary sympatry, hybrids experience greater herbivory than their parents, thereby reducing interspecific gene flow. This is a form of extrinsic postzygotic isolation, where hybrids are unfit because of ecological maladaptation, as opposed to intrinsic postzygotic isolation where the performance of hybrids is independent of environment. There is some evidence that plant hybrids experience greater herbivory than their parents, but mainly owing to changes in phenology (Floate et al. 1993, Orians et al. 1997). Nevertheless, local adaptation to other biotic and abiotic factors could also contribute to poor fitness of hybrids.

Pathway 5: Defense evolution in parapatry.—Habitats differ in resource availability. Following Coley et al. (1985), increased plant defense is favored in resource poor environments, resulting in differences among populations in defense allocation. In this scenario, hybrids produced in areas of secondary sympatry experience reduced fitness because of sub-optimal defense allocation. Although there is broad support for Coley et al.'s (1985) Resource Availability hypothesis (Endara and Coley 2011), there are currently few data relating to herbivory on parapatric species that hybridize (but see Floate et al. 1993, Whitham et al. 1994, Dungey et al. 2000).

Pathway 6: Geographic mosaic selection in allopatry.—Spatial variation in the composition of herbivore communities results in divergent selection for defenses through disruptive selection. Plant populations eventually diverge enough to become reproductively isolated. Several of our scenarios expand on this idea. However, unlike Marquis et al. (2016), we do not stress the importance of inviability of hybrids produced in areas of secondary sympatry as a key mechanism maintaining incipient species.

LOCAL ADAPTATION AND SPECIATION

The emerging perspective of how ecological interactions contribute to speciation is that geographically

isolated populations experience divergent selection owing to differences in local abiotic and biotic environments. Adaptations to these distinct environments contribute directly or indirectly to reproductive isolation and speciation (Schluter 2001, 2009, Schemske 2010, Sobel et al. 2010). In principle, a wide variety of pre- and postzygotic isolating barriers may be involved, but in practice, it is challenging to estimate the magnitude of most barriers, particularly those that involve ecological factors. Thus, we do not yet have a full understanding of the contributions of the many potential isolating barriers to the overall magnitude of reproductive isolation. Particularly neglected is the role of local adaptation in speciation. Due to ecological trade-offs, phenotypes that are adaptive locally often are poorly adapted elsewhere. Thus, traits that contribute to local adaptation are effective isolating barriers in that they reduce the likelihood that a local population can expand beyond its current geographic range. This component of reproductive isolation has been variously described as ecogeographic isolation (Sobel et al. 2010) or immigrant inviability (Nosil et al. 2005), and studies using reciprocal transplants and other approaches suggest that it is typically strong (Lowry et al. 2008, Schemske 2010, Sobel 2014). Thus, it is likely that this prezygotic isolating barrier prevents many species from coming back into sympatry following speciation.

Any trait that contributes to local adaptation has the potential to reduce gene flow between populations that have experienced different abiotic and biotic environments. Historically, researchers have focused on plant adaptation to different abiotic environments and how this could affect population differentiation and speciation. However, just as plants that possess physiological adaptations to wet soils are unlikely to do well in dry soils, and vice versa, plants defended against their local herbivores may become locally adapted to their specific herbivore community. For example, herbivore-mediated divergent selection between isolated populations, either because of differences in herbivore community composition, abundance, or abiotic differences that influence the fitness effects of herbivory, can result in defense divergence across environments (Zangerl and Berenbaum 2003, Toju and Sota 2006, Thompson et al. 2017a,b, Hahn et al. 2018). If these populations subsequently come back into sympatry, the foreign population may suffer reduced fitness because its defenses are not matched to the herbivores in the novel community. This is perhaps easiest to envision if the composition and feeding habits of the dominant herbivores differ in space. For example, plant defenses that are effective against aphids may be ineffective in habitats dominated by folivores (Züst and Agrawal 2016), and plants that rely on ants for defense against herbivores may fail to colonize environments where defensive ant species are missing.

The relative importance of herbivores in relation to all other ecological sources of selection (both biotic and abiotic) is unknown. Plant populations that become

isolated, either from vicariance or colonization, inevitably will experience different abiotic conditions as well as distinct herbivore selective pressures. Differences in the abiotic environment can influence both the abundance of herbivores as well as availability of resources that plants can devote to defense (Coley et al. 1985, Hahn and Maron 2016). This, in concert with differences in herbivore community composition, can result in divergent defenses of plants as well as other adaptive traits. Focusing on traits involved in adaptive divergence to different abiotic and biotic factors provides a means of evaluating the relationship between adaptation and speciation. It is also important to note that local adaptation can contribute to reproductive isolation at several life history stages. Here we emphasize its role in prezygotic isolation by virtue of limiting range expansion, but postzygotic isolation is also possible if the genetic factors that underlie local adaptation interact to reduce hybrid viability and/or fertility (intrinsic postzygotic isolation), or if hybrid phenotypes are ecologically unfit (extrinsic postzygotic isolation). The latter mechanism, the low fitness of hybrids, was one of the allopatric pathways proposed by Marquis et al. (2016).

HOW MIGHT PLANT–HERBIVORE INTERACTIONS CONTRIBUTE TO SPECIATION?

E & R continues to profoundly influence work on the ecology and evolution of plant–herbivore interactions. With increased sophistication of molecular and phylogenetic methodologies, a growing body of work has evaluated specific predictions that emerged from E & R (Becerra et al. 2009, Fordyce 2010, Janz 2011, Weber and Agrawal 2014). These include: (1) defensive escalation through time within clades of plants, (2) novel defense evolution that is coincident with a “starburst” pattern of plant speciation, and (3) parallel patterns of speciation among clades of plants and insects. More generally, E & R has spurred thinking about the role of coevolution in plant and herbivore speciation. Yet since E & R’s predictions and their general argument linking coevolution with speciation were not based on specific mechanisms (Futuyma 2000, Marquis et al. 2016), empirical patterns such as those described above that seem consistent with E & R’s thesis might be due to other processes.

Although divergent selection on plant defenses may occasionally have pleiotropic effects on traits such as flowering phenology or pollinator specificity (Marquis et al. 2016), we suggest that it is unlikely that plant defense traits provide unique mechanisms to reduce gene flow. Instead, as outlined above, we assert that herbivory is one of many selective factors that may differ among plant populations, and that adaptation to the sum total of unique factors in each environment (including spatial differences in herbivore identity, types of tissues damaged, timing of damage, etc.) can contribute to reproductive isolation and speciation. Where herbivores exert strong selection on plant defenses, plant–herbivore

coevolution could speed the rate of divergence among isolated populations because the optimum phenotypes of herbivores and their host plants are constantly shifting (Box 1).

Below we introduce mechanisms of allopatric speciation where populations become geographically isolated due to *vicariance*, i.e. the emergence of a new barrier that limits gene flow, or *dispersal*, where individuals colonize a new habitat following dispersal across a pre-existing barrier. In each scenario, divergent selection on plant defense traits is caused by differences among populations in the composition and/or impact of herbivores.

SCENARIO 1: GENETICALLY DIFFERENTIATED POPULATIONS AND VICARIANCE

Here we suggest that plant populations have evolved different defense phenotypes in different portions of their ancestral range due to spatial variation in herbivore identity or herbivore pressure. This is analogous to ideas about how spatial variation in interaction strength can yield diverse coevolutionary outcomes (Thompson 2005). If a vicariance event isolates these differentiated populations, further adaptive divergence in response to the unique selection pressures imposed by herbivores may ultimately be large enough to lead to speciation. Initial geographic variation in plant defenses and herbivore counter-defenses (or herbivore species identity) and continued coevolution among interacting plants and herbivores would likely accelerate the rate of divergence among isolated plant and herbivore populations. Insect speciation would also ensue (in cases where isolated populations initially contained the same, but genetically differentiated, insect species).

Physically associated herbivores (e.g., those that pupate in reproductive structures) and those with other highly intimate associations with host plants frequently show a pattern consistent with this scenario (Rønsted et al. 2005, Bracewell et al. 2018). The literature on phenotype matching among interacting species pairs in different populations is concordant with this scenario (Zangerl and Berenbaum 2003, Toju and Sota 2006), although these studies have not considered the consequences for reproductive isolation. Also consistent with this scenario is genetic divergence between subspecies of Ponderosa pine (*Pinus ponderosa*) that are matched with host races of bark beetles (*Dendroctonus brevicornis*; Bracewell et al. 2018). Although scenario 1 could lead to plant and insect cospeciation, and joint vicariance of plants and associated herbivores is sufficient to generate a phylogenetic pattern of cospeciation, such a pattern may not be driven by coevolution per se.

SCENARIO 2: DISPERSAL AND RELEASE FROM HERBIVORES

Plants disperse to a geographically isolated novel habitat (Fig. 1b) where herbivores are absent or not adapted to the plant colonist. Herbivore-free plants reduce

Box 1. Coevolution and speciation.

“The conditions under which coevolution produces reproductive isolation among populations are the least understood aspects of reciprocal evolutionary change.” (Thompson 1989, pg. 181)

It is generally accepted that speciation results primarily from the accumulation of pre- and postzygotic barriers that arise as a byproduct of adaptive divergence among geographically isolated populations (Schluter 2001, Schemske 2010, Sobel et al. 2010). Although the specific mechanisms of how reproductive isolation is achieved will differ for barriers that arise through abiotic vs. biotic selection, the kinds of barriers should not differ appreciably. For example, in the case of intrinsic postzygotic isolation, hybrids between populations that have adapted to their local abiotic conditions and biotic communities may show reduced fitness due to genetic incompatibilities for genes fixed during adaptive divergence to both abiotic and biotic factors. Nevertheless, the strength of selection from abiotic and biotic factors may often differ, and this could markedly affect the rates at which reproductive isolation evolves (Schemske 2009). In particular, coevolutionary adaptation may have unique consequences for the rate of speciation when the traits involved in the interaction directly lead to reproductive isolation (Smith and Benkman 2007, Thompson et al. 2017a,b). Coevolution is undeniably common, but there are few well documented cases in which it directly spurs speciation (Althoff et al. 2014; but some examples given in Hembry et al. 2014, Thompson et al. 2017a,b). More recent theory also suggests that coevolution may promote diversification for only a limited number of interactions (Yoder and Nuismer 2010).

A fundamental aspect of reciprocal adaptation is that the optimum phenotype of the interacting species is not fixed. Adaptive evolution in one of the interacting species shifts the optimum for the other. In contrast, if the selective environment is constant, stabilizing selection typically maintains a population near its phenotypic optimum. Hence, in comparison to non-reciprocal adaptation, we expect that traits involved in reciprocal adaptations will continually evolve. This could drive faster divergence between populations and cause a higher rate of accumulation of reproductive isolating barriers in coevolving populations (Schemske et al. 2009). Moreover, because the optimum phenotype of each coevolving taxon depends on the phenotype of the other(s), the traits associated with reciprocal adaptations may encompass a greater range of phenotypic space than those that evolve in response to selection from abiotic or non-reciprocal, biotic factors. This is particularly the case for strong reciprocal selection in highly specialized interactions (e.g. one plant species consumed by a single species of herbivore).

In geographically isolated populations, mutations that underlie coevolving traits will evolve independently, and each population of coevolving taxa may follow a unique evolutionary trajectory (Thompson 2005). In this scenario, reproductive isolation may evolve more rapidly than in cases of non-reciprocal selection, owing to the greater range of phenotypic space that can be explored. Finally, if reciprocal selection results in a moving optimum, then the effect sizes of mutations that contribute to coevolutionary adaptations may be larger than in cases of a fixed optimum (Dittmar et al. 2016). This could increase the rate of phenotypic evolution as well as the rate of accumulation of genetic incompatibilities that might contribute to postzygotic isolating barriers. Although the rate of defense evolution and reproductive isolation might be greatest where a single plant species and a single herbivore species are locked in tight reciprocal coevolution, isolated plant populations could also diverge due to differences in their herbivore communities, and differences in the traits that provide defense to those herbivores.

investment in defense (Fig. 1b) because the ancestral defense is costly. Reduced allocation to costly defense might facilitate rapid adaptation to novel abiotic conditions in the new habitat. This scenario is consistent with the loss of herbivore defense for plants in insular environments (Janzen 1973, Bowen and Van Vuren 1997, Vourc'h et al. 2001), and the geographic scale of colonization and isolation may be quite small (Stenberg et al. 2006). Consistent with this notion, losses of defense have been observed when plant lineages have diversified in new regions lacking their native specialist herbivores (Desurmont et al. 2011).

Over time, host plants are attacked by herbivores, due to either migration of new herbivores or to host shifts

involving local herbivores (Fig. 1b). This either could select for different defenses (Fig. 1b), which in turn could promote the evolution of a novel counter-defense (sensu Wheat et al. 2007), or result in the re-evolution of defense phenotypes using ancestral pathways (Zangerl and Berenbaum 2005; R.J. Marquis, *personal communication*). The colonist plant population evolves along a different trajectory than the ancestral population, due to both different selection pressures imposed by newly associated insect communities as well as changes in plant resource allocation patterns that occur in the new habitat.

In this scenario, liberation from herbivory enables plants to adapt to novel selection pressures imposed in their new abiotic environment. Once undefended plants

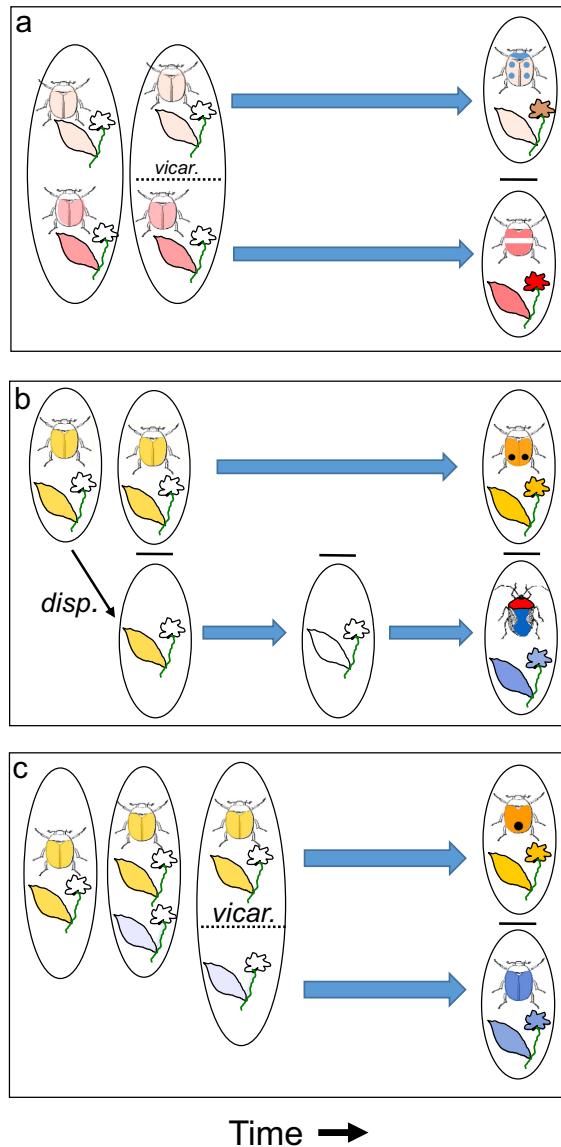


FIG. 1. Scenarios illustrating allopatric speciation of plants and insects and the evolution of plant defense. In each scenario, different leaf colors on plants denote distinct defense phenotypes. Different colors on insects represent insect counter-defenses that correspond to plant defenses. Leaf colors that are somewhat similar to each other, such as in scenario a, denote broadly similar, although differentiated, defense profiles. Wholly different leaf colors, as depicted in scenarios b and c, indicate more extreme divergence between ancestral defense phenotypes and those of colonists or plants isolated by vicariance (vicar.). Wholly different insects in scenario b represent a case in which plants are colonized by unique herbivores in a recipient habitat, although an alternative would be that an herbivore related to the ancestral one colonizes the plant. Another alternative could involve plants re-evolving ancestral defenses. Different colored flowers represent plant speciation, and different patterned insects represent insect speciation. In scenarios a and c, dashed line represents when vicariance divides populations. In scenario b, the arrow refers to the dispersal (disp.) of a plant into a new locale. Circles at extreme right of the figure represent the end-points of vicariance/colonization, coevolution, and speciation.

are discovered, plant defense evolution would be influenced both by herbivores and by the favorability of the new abiotic environment (sensu Coley et al. 1985). For example, variation among habitats in resource availability might affect the cost of particular types of defense, and thus their propensity to evolve under different conditions. Defense divergence has been found in closely related species inhabiting distinct habitats (Fine et al. 2006). As well, variation in resource environments can influence the number of herbivores that attack plants (Louthan et al. 2013, Strauss and Cacho 2013, Rasmann et al. 2014), thereby indirectly affecting selection on herbivore defense.

This scenario could produce a pattern of phylogenetic reductions of particular types of defense (Agrawal and Fishbein 2008, Agrawal et al. 2009, Cacho et al. 2015). In fact, such defense “de-escalation” across a plant phylogeny appears more common than escalation (Livshultz et al. 2018). An association between the evolution of novel defensive traits, such as latex and extrafloral nectaries, and high net diversification rates (Farrell et al. 1991, Weber and Agrawal 2014), may be associated with colonization of habitats with radically different ecologies that modify the costs of supporting these traits, as predicted by scenario 2. This scenario also could result in the predicted starburst pattern of plant radiation that has been a central tenant of the escape and radiate model. In this case, however, escape is geographical in nature (not due to the evolution of novel defense), and speciation is due to a combination of adaptation to novel abiotic and biotic conditions.

SCENARIO 3: DEFENSE EVOLUTION, RANGE EXPANSION AND VICARIANCE

An adaptive mutation for a new defense (Fig. 1c) leads to an increase in population size, range expansion, and increases the probability that a subsequent vicariance or colonization event leads to geographic isolation. Differences in the identity of the attacking herbivore between the ancestral and newly isolated plant population spur further defense divergence and may contribute to local adaptation and reproductive isolation. This scenario predicts plant speciation *following* the evolution of a novel defense in the ancestral range as envisioned by E & R (perhaps what they referred to as plants entering a new adaptive zone). Althoff et al. (2014) explicitly discuss this scenario as a case in which coevolution indirectly influences diversification because “coevolution sets the stage for geographic isolation and subsequent divergence rather than coevolutionary selection directly favoring divergence” (Althoff et al. 2014 pg. 87). In other words, adaptive evolution in response to abiotic and biotic conditions contribute to divergence (Box 1).

This scenario could also produce a “starburst” pattern of speciation if herbivores prevented plants with ancestral defenses from colonizing certain habitats (D. J. Futuyma, *personal communication*). The evolution of a

novel defense against those herbivores allows expansion into different habitats than those occupied by ancestral plants. This could ultimately result in multiple speciation events.

SYNTHESIS

The scenarios we present are speculative and do not include all biological possibilities. Nevertheless, they highlight possible mechanisms by which allopatric speciation via vicariance or dispersal, combined with novel abiotic and biotic conditions (i.e., herbivore identity and the selection pressures herbivores impose), might together lead to defense evolution and plant speciation. Unlike E & R's original proposition, in which defense and freedom from herbivory was by itself thought to lead to speciation, we focus on the *interaction* between the abiotic and biotic environment in driving adaptive differentiation and speciation. The abiotic environment can critically influence the abundance and composition of the herbivore community, which can influence the strength of selection on plant defense. The abiotic environment (particularly as it influences resource availability) can also directly influence plant defense evolution (Coley et al. 1985, Hahn and Maron 2016).

In scenarios 1 and 3, speciation occurs because of adaptive divergence between isolated populations in response to different selective pressures imposed by herbivores. Differences among isolated populations in the identity of attacking herbivores, and/or the selection they impose, influence the rate and direction of plant defense evolution, and ultimately reproductive isolation. In scenario 2, the initial loss of defense facilitates adaptation to a novel abiotic environment, and subsequent herbivory produces further adaptive differentiation. We recognize that plants and herbivores could experience more than one of the proposed scenarios over deep phylogenetic time scales, which would erase any consistent directional pattern and phylogenetic signal that any one scenario might produce.

In each of our scenarios, strong coevolutionary interactions could result in the escalation of defense, as originally proposed by E & R. However, escalation of defenses through time is not a necessary step to speciation. Evidence for defense escalation appears mixed (Berenbaum and Feeny 1981, Farrell et al. 1991, Agrawal et al. 2009, Becerra et al. 2009). It may be that rather than driving defense escalation, herbivores simply select for the independent evolution of different types of defenses, or novel compounds that use similar biochemical pathways as predecessor defenses (Coley et al. 2018).

Although E & R's original notion was that coevolution spurred diversification in both insect and plant lineages, studies during this era were primarily focused on the natural history of trait matching (e.g., Williams and Gilbert 1981). Over the next 20 yr, a quantitative genetics approach to coevolution emerged, and many studies focused on reciprocal natural selection and adaptation

within pairs of interacting species (Berenbaum et al. 1986, Fritz and Simms 1992). Presently, phylogenetic approaches have reignited study of the role of reciprocal adaptation in speciation and diversification (Fordyce 2010, Janz 2011, Strauss and Cacho 2013, Weber and Agrawal 2014, Volf et al. 2018). From the insect perspective, it is clear that herbivore clades have indeed radiated on similarly defended host plants, which sometimes but not always, are closely related groups of plants (Becerra 1997, Futuyma and Agrawal 2009, Nyman 2010, Volf et al. 2018).

FUTURE DIRECTIONS

First, we encourage evaluation of the proposed scenarios, initially for their potential to result in plant speciation, and ultimately in terms of how common they may be. Second, given that phylogenetic patterns in defense evolution do indeed occur, we are in need of additional hypotheses for how such patterns may arise. For example, an anagenetic hypothesis (Futuyma 1987, Vermeij 1994) is that selection by enemies over long periods of time is directional, but that it takes reproductive isolation (speciation) for traits to phenotypically shift. This explanation has been previously discussed as an interpretation for patterns found in the milkweed genus *Asclepias* (Agrawal et al. 2009). In this scenario, coevolution is not necessarily invoked at any level.

Empirically, the extent to which plant–herbivore coevolution contributes to plant or insect speciation remains unclear (Althoff et al. 2014, Hembry et al. 2014). Unique insect species are found on almost every plant species, but this could be the result of insect diversification following plant diversification or host shifts rather than cospeciation (Janz 2011). Phylogenetic conservatism of host plant taxa used by herbivorous insects is common and was originally highlighted by E & R. Insect herbivores also switch hosts to plant species that might have been fed upon by ancestral species (the “oscillation hypothesis”; Janz et al. 2006, Janz and Nylin 2008) or via “chemical bridges” to novel species (Becerra 1997, Murphy and Feeny 2006). But the mechanism driving these patterns remains unclear. The role of reciprocal evolution between plants and their herbivores for both plant and herbivore speciation can only be determined through studies of the full range of potential barriers and the underlying ecological and genetic factors that cause reproductive isolation.

In closing, we hope that a renewed focus on explicitly linking plant–herbivore coevolution to mechanisms of speciation will lead to further insights into the issues that E & R highlighted over five decades ago. Moving forward, we see the following questions as particularly fruitful for future study:

- 1) How often does local reciprocal selection result in phenotype matching between plants and herbivores, and does this process ultimately result in speciation?

We currently have a few case studies of phenotype matching (e.g., Zangerl and Berenbaum 2003, Toju and Sota 2006), but these have not considered reproductive isolation. Do intrinsic barriers to gene flow exist, and if so, are these geographically structured? New techniques such as population genetic models that incorporate continuous and discrete predictors of genetic structure could be useful in linking phenotypic data to an understanding of population differentiation (Bradburd et al. 2018). Among known closely related species, studies linking biogeographical history with phenotypes and species interactions could be suggestive of Scenario 1.

- 2) To what extent is phylogenetic cospeciation due to joint vicariance and independent adaptation of plants and herbivores to unique abiotic factors vs. reciprocal selection and coevolution? The two critical approaches to tease these apart will involve: (1) addressing whether traits associated with the species interaction (in both partners) are evolving more rapidly (or diverging more strongly) than traits not associated with the interaction and (2) whether the timing and geography of plant and herbivore divergence is concordant with reciprocal selection or isolation (and speciation) by the plant first, followed by colonization of insects (the latter suggesting no role for coevolution). The best work addressing trait divergence and timing of isolation vs. reciprocal adaptation comes from research on yucca moths and yuccas, where broad scale patterns and closely related species pairs are being studied. Nonetheless, no clear answer has yet emerged (Godsoe et al. 2008, Althoff et al. 2012).
- 3) How do multiple defensive traits together with geography map onto plant phylogenies? An explicit prediction of our Scenario 2 and the Coley et al. (1985) model for plant defense is that an interaction between herbivory and adaptation to the abiotic environment shapes plant defense evolution. By phylogenetically mapping habitat affiliation and multiple defensive traits that may form “defense syndromes,” hypotheses can be generated about the importance of this association (Kursar and Coley 2003, Agrawal and Fishbein 2006, Pearse and Hipp 2012). Nonetheless, in addition to these associations, which have only been addressed in a few systems, tests are needed of how escape from herbivory influences defense evolution and adaptation to different habitats. We suggest that these latter analyses linking the mechanisms of Scenario 2 to phylogenetic patterns would best be studied at the population level, perhaps on islands or high elevations, where plants may escape from herbivory and adapt to changing abiotic conditions (Rasmann et al. 2014, Defossez et al. 2018).
- 4) To what extent does herbivore pressure contribute to establishing range limits? With regard to Scenario 3, it is important to identify defensive traits and their

distribution in range centers and edges. Do novel or extreme defensive phenotypes exist at range edges, and is there selection on these traits, potentially facilitating range expansion? Such evidence would support the first step proposed in Scenario 3, while subsequent isolation and genetic differentiation (and speciation) would still only be inferred (Vourc’h et al. 2001, Rasmann et al. 2014, Defossez et al. 2018). Nonetheless, the role of novel trait evolution (gains or losses in defense) in facilitating population expansion has received remarkably little attention (Farrell 1993).

Relatedly, and of special interest to the study of coevolution and plant speciation, would be a focus on sister species that have parapatric distributions (Fine et al. 2006). In such pairs, understanding divergence in defensive traits, species interactions, and adaptation to the biotic environment could be informative to the processes that led to divergence. In particular, studies of shared vs. distinct interaction partners (herbivores) could be informative as to the role of species interactions in divergence.

- 5) Do defense profiles of related species that come back into sympatry after speciation shift in a manner suggestive of character displacement? Several species-rich groups of tropical trees have defense profiles more divergent than expected by chance (Becerra 2007, Kursar et al. 2009, Salazar et al. 2016, Coley et al. 2018). This pattern of defense overdispersion is thought to be caused by strong selection by shared herbivores that drive defense divergence among closely related trees that have come together in secondary sympatry. This mechanism of divergence could operate following any of the speciation scenarios described above. It implies that coevolutionary interactions between plants and their insect herbivores can influence community-level patterns because herbivores highly adapted to one host species can potentially select against similar defenses in related host species. In other words, herbivores may drive defense divergence in a manner reminiscent of character displacement, thereby further reinforcing differences among species that evolved in allopatry. Although this idea has not been widely tested, one approach to testing this experimentally would be to plant closely related species that occur in allopatry (but occupy similar habitats) together, and quantify levels of herbivory on pairs of species that have similar or dissimilar defense profiles. Such an approach could provide a link between divergence and speciation in allopatry and the potential community consequences when species reunite in sympatry.
- 6) How does the contribution of herbivore-mediated selection to plant speciation compare to that of abiotic factors, and to other biotic agents of selection? E & R proposed that selection by herbivores was a major driver plant speciation, yet it is unclear

whether this form of antagonistic, biotic interaction is more important than competition, or than mutualistic interactions involved in plant reproduction such as pollination and seed dispersal, or mutualisms involved in resource acquisition such as plant–microbe interactions in the rhizosphere. One possible approach to addressing this question is to map traits associated with different abiotic and biotic factors onto a phylogeny, and compare rates of divergence and speciation. To our knowledge, such comprehensive studies are not currently available. There is evidence that mutualistic interactions involved in pollinator-mediated selection foster plant speciation (Kay and Sargent 2009, Van der Niet et al. 2014), but it is not clear how the importance of this or other biotic interactions compare to herbivory.

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