Synthesis

Coevolution and the Diversification of Life

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Abstract: Coevolution, reciprocal adaptation between two or more taxa, is commonly invoked as a primary mechanism responsible for generating much of Earth’s biodiversity. This conceptually appealing hypothesis is incredibly broad in evolutionary scope, encompassing diverse patterns and processes operating over timescales ranging from microbial generations to geological eras. However, we have surprisingly little evidence that large-scale associations between coevolution and diversity reflect a causal relationship at smaller timescales, in which coevolutionary selection is directly responsible for the formation of new species. In this synthesis, we critically evaluate evidence for the often-invoked hypothesis that coevolution is an important process promoting biological diversification. We conclude that the lack of widespread evidence for coevolutionary diversification may be best explained by the fact that coevolution’s importance in diversification varies depending on the type of interaction and the scale of the diversification under consideration.

Keywords: coevolution, diversification, speciation, geographic mosaic theory, natural selection, adaptive radiation.

Introduction

Coevolution between interacting taxa is widely invoked as a major cause of the continuing diversification of life on Earth (Schluter 2000a; Dietl and Kelley 2002; Thompson 2005, 2009, 2013; Jablonski 2008; Futuyma and Agrawal 2009; Janz 2011). The hypothesis that coevolution between lineages influences their diversification dates back at least as far as Darwin’s “struggle for existence” (1859) and received increasing attention in the past half-century following Flor’s pioneering study of infection genetics (1942, 1955), Ehrlich and Raven’s seminal paper on reciprocal diversification of plants and butterflies (1964), and the development of the geographic mosaic theory of coevolution (GMTC) by Thompson (1994, 2005, 2013). However, despite extensive empirical study of coevolution in nature, evidence supporting the claim that coevolution has helped to generate much of the earth’s biodiversity is equivocal.

Some confusion on this topic arises from the fact that, while the term “coevolution” is widely used—even following Janzen’s (1980) strict-sense definition as reciprocal adaptation by interacting species—it describes a number of very different types of biotic interactions that may have different effects on diversification. Conversely, not all kinds of biotic interactions that are important in diversification may create reciprocal adaptation. Furthermore, the hypothesis that coevolution drives diversification is incredibly broad in evolutionary scope, encompassing patterns and processes operating over timescales ranging from microbial generations to geological eras. Many studies have linked increases in diversification rate to interspecific interactions that may be coevolutionary, without demonstrating that coevolution is important in speciation (Farrell et al. 1991; Farrell 1998; Winkler et al. 2009; Lengyel et al. 2009; Gómez and Verdú 2012; Litsios et al. 2012; Joy 2013). We know that coevolution in nature is ubiquitous—all species interact with many other species in nature in a variety of biotic interactions. What we endeavor to define is how variation in the strength and form of coevolution matters for diversification.

In this Synthesis, we critically evaluate evidence for the long-standing hypothesis that coevolution promotes diversification. Althoff et al. (2014) recently proposed a series of tests for this hypothesis, arguing that evidence to date is limited because few empirical systems have been rigorously tested. We agree with this assessment and contend that evidence for coevolutionary diversification is limited by the fact that the importance of coevolution in diversification varies depending on the type of interaction (e.g., competition, antagonism, mutualism) and the scale of diversification (population differentiation, speciation, diversification of clades) being considered. We define coevolutionary diversification as diversification at any level—within populations and species or across clades—that is driven by the reciprocal adaptation of interacting species (sensu Janzen 1980; Thompson 1994, 2005, 2013).
definition is broader than that of Althoff et al. (2014), who defined coevolutionary diversification as those cases in which coevolution promotes an increase in the net speciation rate of one or both interacting lineages. We use a broader definition here because the hypothesis inherent in the definition of Althoff et al. has rarely been tested in empirical systems, as these authors point out. Like that of Althoff et al., our definition does not require diversification to be reciprocal; indeed, many of the putative examples discussed below involve diversification in only one of two interacting lineages.

**How Different Types of Coevolutionary Interactions May Promote Diversification**

Competitive, antagonistic, and mutualistic interactions have been thought to be associated with diversification since the origins of evolutionary ecology, and each type of interaction has also been thought to promote diversification in different ways (Darwin 1859, 1877; Grant 1949; Mode 1958; Ehrlich and Raven 1964). Current evidence supporting coevolutionary diversification is far stronger for some kinds of species interactions than for others. Theory suggests that both competitive and antagonistic coevolution promote diversification, while mutualistic coevolution may or may not (Doebeli and Dieckmann 2000; Kopp and Gavrilets 2006; Yoder and Nuismer 2010). However, it remains difficult to know whether empirical evidence reflects actual, general differences in diversifying effects of the different interactions or simply biases induced by sampling extreme cases. The strongest body of empirical evidence for diversification driven by coevolution is found in cases of competition between species at the same trophic level—and these interactions have been the focus of an extensive literature on adaptive radiation (see reviews in Schluter 2000a; Yoder et al. 2010; Thompson 2013). In contrast, we have disproportionately fewer examples of diversification arising from antagonistic interactions between species at different trophic levels and still fewer for mutualistic interactions.

**Competitive Coevolutionary Diversification**

The idea that coevolution between competitors leads to speciation received extensive attention during the “modern synthesis” (Simpson 1944, 1953; Mayr 1942; Lack 1947; Brown and Wilson 1956). Competitive coevolution is now a major component of the ecological theory of adaptive radiation (Schluter 2000a; Yoder et al. 2010). This theory has three major component processes: (1) phenotypic divergence among populations is a result of natural selection in different environments, (2) phenotypic divergence among populations results from resource competition, and (3) ecological speciation results from this phenotypic divergence. Empirical evidence from experimental systems supports these ideas, suggesting that coevolution in the form of resource competition plays an important role in adaptive radiation (Rainey and Travisano 1998; Kassen 2009) and that it acts synergistically with other factors, particularly geographic isolation.

Models of competition within trophic levels (e.g., DeVaux and Lande 2009) typically assume that members of each interacting species maximize their fitness when their phenotypes (or, for explicit genetic models, genotypes) are as different from the other species as possible; this creates character displacement (Kopp and Gavrilets 2006), which is characteristic of classical adaptive radiations (Schluter 2000a; Thompson 2013). Such models uniformly predict increased diversity of the two species considered together (DeVaux and Lande 2009) and across metapopulations (Yoder and Nuismer 2010); and even within individual populations (Doebeli and Dieckmann 2000, Kopp and Gavrilets 2006).

Many examples from the literature of competitive character displacement can be considered coevolutionary and support the second component of the ecological theory of adaptive radiation, that resource competition drives divergence between closely related populations and species (see Schluter 2000a, 2000b; Kassen 2009). Here we discuss three examples from natural systems that illustrate this view. One of the best-understood examples of speciation driven by competitive interactions is the case of stickleback (Gasterosteus aculeatus) species pairs in postglacial lakes in British Columbia (Schluter 1994, 2000b, 2003). These result from double colonizations of the lakes by two genetically and temporally separated marine stickleback populations. The first stickleback populations to colonize the lakes evolved to be morphological and trophic generalists, as is seen today in numerous single-stickleback species lakes in the same region (Schluter and McPhail 1992). Several lakes were secondarily colonized by a second wave of marine sticklebacks, and disruptive selection subsequently drove the preexisting population to evolve into limnetic specialists and the invading population to become benthic specialists (Schluter and McPhail 1992; Schluter 2010). In other words, these species pairs are polyphyletic and do not result from in situ speciation within a single preexisting population (Schluter 2000b), although gene flow is believed to have occurred during character displacement (Gow et al. 2006, 2007). In the absence of multiple colonization events, stickleback populations can exhibit within-population competition and concurrent assortative mating, but without proceeding to speciation (Bolnick 2011).

Competitive coevolution is also likely to have played a role in the adaptive diversification of Anolis lizards across
the West Indies (reviewed in Losos 2009). Evidence suggests that anoles tend to speciate in allopatry, either on different islands or within very large islands (Losos and Schluter 2000; Losos 2009). Anoles may diverge phenotypically while undergoing allopatric speciation, but extensive field data suggest that they further diverge ecologically (and may diverge phenotypically) in secondary contact (Schoener 1975; Losos 2009). In addition to competitive displacement in ecological traits, mating signals (dewlap color) also show evidence of character displacement and are thought to play a role in speciation and coexistence of anoles (Jenssen and Gladson 1984; Lambert et al. 2013). Similar processes, namely initial divergence in allopatry followed by subsequent competitive character displacement in sympatry (reinforced by mate choice mediated by beak size) are thought to have been important in the adaptive radiation of Darwin’s finches (Grant and Grant 2006, 2008).

Although competition is a major component of the ecological theory of adaptive radiation, it has also been widely invoked as a process which restricts diversification. In these formulations, competition between clades constrains diversification asymmetrically (i.e., a competitively superior clade inhibits or reduces the diversification of a competitively inferior clade). This hypothesis has received extensive attention in the paleontological literature (Simpson 1944, 1953; Jablonski 2008), despite difficulties in distinguishing the effects of competitors from those of predators (Dietl and Kelley 2002; Stanley 2008). Competition has also been invoked as a factor restricting adaptive radiation as well as governing extinction within adaptive radiations on oceanic islands (Gillespie and Baldwin 2009; Bennett and O’Grady 2013). Finally, experiments with Pseudomonas fluorescens support the hypothesis that the presence of competitors can restrict diversification (Brockhurst et al. 2007).

Antagonistic Coevolutionary Diversification

Antagonistic interactions, in which members of one species benefit at the expense of members of another, received less attention than competitive interactions during the modern synthesis. Coevolutionary diversification in antagonistic interactions received renewed attention following Ehrlich and Raven’s review (1964) and Vermeij’s (1987) work on escalation in the fossil record of marine animals.

Ehrlich and Raven (1964) noted that plants are under intense selection to evolve defenses (primarily chemical) against herbivores, and the herbivores (in their formulation, butterflies) benefit greatly by evolving counterdefenses allowing them to feed on previously inedible plant resources. As a result of this reciprocal selection, plant lineages that evolve defensive compounds are able to radiate in the absence of herbivory; after some time, butterfly lineages which evolve counterdefenses allowing them to digest the tissues of toxic plants are then able to radiate onto previously unexploited plant resources. As evidence, Ehrlich and Raven (1964) cited extensive phylogenetic conservatism of host plant taxa in many large butterfly groups, as well as the observation that butterfly groups that are able to consume chemically defended plants often include species which feed on chemically similar but phylogenetically distant hosts. Their article inspired a great deal of research on the adaptive value of plant defenses and insect counterdefenses (see reviews in Futuyma and Agrawal 2009; Janz 2011), as well as on coevolution in general (see review in Thompson 1994) but rather less testing of the specific original hypothesis. This mechanism, since named “escape and radiate coevolution” (Thompson 1989), has subsequently been invoked to account for the diversification of other insect groups and their host plants (see review in Janz 2011), as well as other antagonistic interactions in the tree of life (see review in Jablonski 2008). One point often ignored in subsequent literature has been that under the escape-and-radiate model, diversification occurs not as a result of coevolutionary selection but rather its absence: lineages evolve a new defense or counterdefense, which creates ecological opportunity in the form of enemy-free space or a novel food resource and spurs adaptive radiation (Yoder et al. 2010; Thompson 2013). Still, in this model coevolution defines the boundaries of new ecological opportunity—the enemies from which a lineage is released or the food resource to which it gains access.

Theory predicts that interactions such as those described in Ehrlich and Raven’s verbal model—in which one species maximizes its fitness when its phenotype differs from the interacting phenotype of the other, which maximizes its fitness by matching the phenotype of the first—can maintain polymorphism and lead to the evolution of greater among-population diversity within one or both species (Gandon 2002; Nuismer et al. 2005; Calcagno et al. 2010). Whether the victim or the exploiter is the species that benefits from closer phenotype matching depends on the specific species interaction considered, but generally, the species that benefits from reduced matching will evolve greater diversity, and this can drive the evolution of greater diversity in the other species as well (Yoder and Nuismer 2010; Nuismer et al. 2008).

In contrast to escape-and-radiate coevolution, Vermeij (1987) described a quantitative increase in defensive traits, which he called escalation, during the diversification of clades. Evidence for escalation comes from increases in defensive traits (shell armor in marine gastropods) and offensive traits (strong claws, crushing mouthparts in
predators of gastropods) over geologic time both in fossil biotas as a whole and within specific groups, both primarily in the marine fossil record. Similarly to escape-and-radiate coevolution, Vermeij proposed that the acquisition of new defensive, competitive, or predatory traits leads to a net increase in diversification (either elevated speciation, or reduced extinction). This argument has been invoked to explain diversification for a number of cases in the fossil record (Jablonski 2008). Vermeij (1987, 1994) drew a distinction between escalation and coevolution on the basis of the argument that in escalation, the strength of selection between predators and prey may be asymmetric, whereas he asserted that for coevolution, the strength of selection should be symmetrical. Nevertheless, the two hypotheses share many attributes and may overlap under many circumstances.

Models of the escalatory interactions Vermeij described assume that each species improves its fitness with increasing value of its interacting phenotype (e.g., Gandon and Day 2009; Bonds 2006). These selective dynamics are not necessarily expected to increase trait variation within an individual population (Yoder and Nuismer 2010) but can promote variation within and among populations, particularly if conditions permit coevolutionary cycling, for example, if trait escalation incurs a fitness cost (Gavriles et al. 1997; Nuismer et al. 2007). Coevolution mediated by the explicit infection genetics equivalent of such escalatory selection, the gene-for-gene model, can sometimes result in assortative mating—but this depends on the model of mate choice applied to hosts (Nuismer et al. 2008).

A number of examples support the role of antagonistic coevolutionary interactions in macroevolutionary diversification and in speciation. These include: evolution of changes in defensive trait investment (Agrawal et al. 2009a, 2009b; Becerra et al. 2009), correlated evolutionary trends in defensive and counterdefensive traits (Li et al. 2003; Wheat et al. 2007), increased diversification of prey lineages following the acquisition of antipredator defenses (Farrell et al. 1991), increased diversification in predators/herbivores following shifts to new prey (Farrell 1998; Winkler et al. 2009; Fordyce 2010), increased diversification in predators or herbivores following the acquisition of counterdefenses (Wheat et al. 2007), and contemporaneous evolution of defensive and counterdefensive traits (Becerra 2003). However, despite numerous tests of particular components of Ehrlich and Raven’s (1964) hypothesis, surprisingly few systems have been examined for all or even most of its components (Futuyma and Agrawal 2009; Althoff et al. 2014). The best-documented examples are milkweeds coevolving in response to specialist herbivores (Agrawal and Fishbein 2008, Agrawal et al. 2009a, 2009b) and pierine butterflies coevolving with chemically defended members of the Brassicaceae (e.g., Wheat et al. 2007). Consequently, although there is a high probability that antagonistic coevolution between angiosperms and herbivorous insects was a major factor in their mutual diversification (Farrell et al. 1991; Farrell 1998; McKenna et al. 2009; Winkler et al. 2009; Fordyce 2010; Strutzenberger and Fiedler 2011), it remains an open question whether and how such antagonistic coevolution accounts for the bulk of the diversification seen in phytophagous insects and angiosperms (Janz 2011). Recent efforts using experimental evolution have documented antagonistic coevolution in driving diversification in the genotype and phenotypes of bacterial and phage partners (Forde et al. 2008; Paterson et al. 2010; Marston et al. 2012), and this approach holds significant promise for testing mechanistic hypotheses (Brockhurst and Koskella 2013).

In addition to the macroevolutionary examples described above, many of the best-supported cases of speciation promoted by coevolution are antagonistic. The best-studied are the speciation of red crossbills (Loxia curvirostra complex) coevolving with lodgepole pine (Pinus contorta) in western North America (Benkman 1999; Benkman et al. 2001; Edelaar and Benkman 2006; Smith and Benkman 2007), and red crossbills coevolving with black spruce (Picea mariana) on Newfoundland (Parchman and Benkman 2002). Speciation of Satsuma land snails coevolving with predatory Pareas iwasakii snakes (Hoso et al. 2010) is another example. However, it is also clear that many cases of antagonistic coevolution have not resulted in speciation. These include brood parasitic birds coevolving with their hosts (Gibbs et al. 2000; Yang et al. 2010), Thamnophis sirtalis garter snakes coevolving with toxic Taricha newt prey in western North America (Brodie et al. 2002; Ridenhour et al. 2007), and seed-predatory Curculio camelliae weevils coevolving with their Camellia japonica hosts in Japan (Toju and Sota 2006b). Close examination of particular arms races in the fossil record over million-year timescales (such as that between Sinistrofugur weevils and their Mercenaria bivalve prey in the Plio-Pleistocene of North Carolina; Dietl 2003) provide evidence for coevolution but do not demonstrate diversification in either prey or predators. Similarly, at the vertebrate major histocompatibility complex loci, which mediate immune response, diversity is promoted and maintained by selection from parasites and pathogens (e.g., Froeschke and Sommer 2005; Westerdahl 2007), but this increased diversity is not necessarily accompanied by an increased likelihood of speciation (Nuismer et al. 2008; but see Eizaguire et al. 2009).

Mutualistic Coevolutionary Diversification

In contrast to competitive and antagonistic coevolution, whether and how mutualistic coevolution can promote
diversification (instead of simply promoting the maintenance of diversity) has been a major recent problem in evolutionary ecology. Theory suggests in most cases that mutualistic coevolution should hinder diversification, whereas empirical evidence that mutualisms can promote diversification is primarily restricted to two categories: resource symbioses that facilitate radiation into novel adaptive zones, and pollinator-plant coevolution that promotes reproductive isolation (Thompson 2005; Godsoe et al. 2010; Thompson et al. 2013; Heath and Stinchcombe 2014; Raimundo et al. 2014).

Models of mutualistic coevolution usually assume that interacting species maximize fitness when their phenotypes match those of the other species (e.g., Kiester et al. 1984; McGill 2005; but see Zhang et al. 2013). This effectively creates stabilizing selection acting on both species, reducing diversity within populations (Kopp and Gavrilets 2006; Yoder and Nuismer 2010), but it may also help to create or maintain isolation between populations interacting with phenotypically different partners (Kiester et al. 1984), and it can allow polymorphism in which one group of mutualists relies primarily on the resource benefits of the mutualism (e.g., nectar rewards) while another group mainly uses an external resource (Doebeli and Dieckmann 2000). Both high- and low-intimacy mutualisms may constrain diversification under most conditions, with the possible exception of nonobligate, high-intimacy interactions in which each partner can survive without the other (Raimundo et al. 2014).

In multiple mutualistic symbioses, the symbionts and their hosts have coradiated into novel adaptive zones. Such symbioses are now dominant components of major ecosystems, including the endosymbiosis of plastids and mitochondria with early eukaryotes (Margulis 1970; Maynard Smith and Szathmary 1995); symbioses between mycorrhizal fungi and land plants (Hoeksema 2010); the nitrogen-fixation mutualism between rhizobial bacteria and legumes (Doyle and Luckow 2003); symbioses between reef-building marine invertebrates, particularly scleractinian corals, and their symbiotic algae (Wood 1998); and nutritional symbioses between insects and bacteria which allow exploitation of novel resources such as plant sap (Moran 2007). These symbioses were almost certainly established through reciprocal evolutionary change in both partners; but this coevolutionary selection is not directly implicated in speciation. Mechanistically, diversification following the establishment of such symbioses is explained as mutualism facilitating increased niche width and/or population sizes (Lengyel et al. 2009; Gómez and Verdú 2012; Joy 2013), or the invasion of novel adaptive zones (Doyle and Luckow 2003; Yoder et al. 2010; Litsios et al. 2012). It is also possible that ongoing coevolution within mutualistic symbioses (such as mycorrhizal plant-fungi interactions) may promote trait diversification in a manner that also promotes speciation, though necessary evidence is lacking (Hoeksema 2010). Finally, evidence exists that plastome-genome incompatibility (Greiner et al. 2011) or host-microbiota incompatibility (Brucker and Bordenstein 2013) can serve as reproductive isolation mechanisms and promote speciation.

In contrast, interactions between plants and pollinators are thought to be extremely likely cases of mutualistic coevolutionary speciation, because animal pollinators control the gametes of the plants whose flowers they visit (Thompson 1994). Accordingly, pollinator-mediated speciation has long attracted the interest of botanists (Grant 1949; Stebbins 1970). There is an extensive literature, focusing on a number of model systems (e.g., Mimulus; Bradshaw and Schemske 2003; Ramsey et al. 2003; Ag-Iulégia: Hodges and Arnold 1994a, 1994b), and several recent reviews (Kay and Sargent 2009; van der Niet and Johnson 2012; also see Coyne and Orr 2004; Armbruster and Muchhala 2007) on the role of animal pollinators in angiosperm speciation. A number of examples in which pollinator shifts are implicated in plant speciation have been documented (Bradshaw et al. 1998; Hodges and Arnold 1994a; Kay et al. 2005; Muchhala 2007; Okuyama et al. 2008); according to one estimate, roughly one-quarter of plant speciation events examined may involve pollinators (van der Niet and Johnson 2012). Finally, a number of macroevolutionary studies suggest pollinating mechanisms can lead to increases in diversification rate (Sargent 2004; Ree 2005; but see Bolmgren et al. 2003). However, the literature suggests that pollinator-mediated isolation rarely acts alone and rather promotes speciation in connection with other isolating mechanisms (chief among these is geographic isolation; Kay and Sargent 2009). It is also unclear whether many of the cases examined represent truly coevolutionary diversification. Microevolutionary studies usually fail to test whether pollinators are evolving in response to the plants they visit, and recent phylogenetic studies suggest that reciprocally associated plant and pollinator clades may undergo asynchronous diversification consistent with a model of plants diversifying in response to sensory biases of their pollinators (e.g., Ramírez et al. 2011). As with antagonistic coevolution, diversification in these systems may be structured by competitive coevolution among plants competing for pollinators, rather than mutualistic coevolution between plant and pollinator (Gilbert 1979; Armbruster and Muchhala 2007).

Finally, one portion of the plant-pollinator literature that has often been considered separately focuses on obligate pollinating seed-predation mutualisms—notably those between figs and fig wasps (Cook and Rasplus 2003), yuccas and yucca moths (Pellmyr 2003), leafflowers and leafflower moths (Kawakita 2010), and senita cacti and...
senita moths (Holland and Fleming 1999). In these mutualisms, specialized insects actively pollinate the flowers of their hosts, and their larvae consume a subset of the hosts’ developing seeds. The plants in such interactions have no alternative pollinators, and the insect pollinators have no alternative hosts; furthermore, species-level specificity is typically very high, with most plant species pollinated by one or a few insect species locally and vice versa—all circumstantial evidence that these mutualisms have coevolved (Janzen 1979; Cook and Rasplus 2003; Pellmyr 2003; Herre et al. 2008; Kawakita and Kato 2009; Okamoto et al. 2013). However, almost nothing is known about how speciation and diversification occurs in either figs and fig wasps (but see Yokoyama 2003) or leafflowers and leafflower moths, although both show evidence for pollinator host shifts, which may be a mechanism through which coevolution promotes diversification (Cook and Segar 2010; Hembry et al. 2013). Recent work has demonstrated strong pollinator isolation among sympatric fig species—but at the same time found that while wasps suffer reduced fitness on nonnative host figs, figs seem to tolerate such small reductions in fitness regardless of pollinator species (Moe and Weiblen 2012). Thus, reproductive isolation in the figs may have arisen from a fig-wasp interaction that does not generate truly coevolutionary selection. Research on similar, but not strictly obligate, coevolving mutualisms between woodland stars (Lithophragma spp.) and Greya moths in western North America suggest a role for allopatric isolation in Greya diversification (Rich et al. 2008); a role for coevolution in plant or moth diversification is likely but has not been explicitly investigated (Thompson et al. 2013).

The only pollinating seed-predation mutualism where mechanisms of diversification and coevolution’s role in that process have been explicitly examined is that between yuccas and yucca moths (Godsoe et al. 2008, 2009, 2010; Smith et al. 2008a, 2008b, 2009; Althoff et al. 2012; Yoder et al. 2013). Detailed examination of recently diverged varieties of Joshua tree (Yucca brevifolia) and its pollinator moths (Tegeticula synthetica and T. antithetica) in the Mojave Desert indicate that coevolution is ongoing between each variety of Joshua tree and its associated pollinator (Smith et al. 2009); but the initial divergence in this system is due at least in part to geographic isolation, possibly due to a Pliocene marine invasion in the Mojave (Smith et al. 2008a). Furthermore, phylogenetic analysis of Yucca, pollinating Tegeticula, and closely related commensalistic (nonpollinating) Prodoxus moths indicate that closely related species in all three clades have primarily allopatric distributions, and that both Tegeticula and Prodoxus similarly show phylogenetic congruence with their Yucca hosts (Althoff et al. 2012). Finally, the genus Yucca is not more species rich than its non-moth-pollinated sister group (Smith et al. 2008b). Taken together, these results suggest that geographic isolation plays a predominant role in speciation for both Yucca and Tegeticula, with coevolution between yuccas and yucca moths acting primarily to create codivergence after one partner or the other begins to diverge for other reasons (Kiester et al. 1984; Yoder et al. 2013). The fact that even in this highly specialized, obligate mutualism, coevolution is not solely responsible for diversification suggests that truly coevolutionary speciation may be rare indeed.

**Role of Coevolution in Diversification at Different Scales**

Theory rarely distinguishes between coevolution promoting polymorphism within species and promoting phylogenetic diversity, but empirical evidence for coevolution promoting diversification varies depending on the temporal and spatial scale examined. For example, research on anoles in the Greater Antilles suggests that competitive coevolution may both promote and constrict diversification at different evolutionary timescales. Despite strong evidence that coevolution has driven phenotypic diversification and thus probably also promoted speciation in anoles (Losos 2009), macroevolutionary analyses suggest that the rate of net lineage diversification has declined to equilibrium conditions on three of four major islands in the Greater Antilles (Jamaica, Puerto Rico, and Hispaniola; Rabosky and Glor 2010) and that the rate of phenotypic diversification has decreased over the course of this radiation (Mahler et al. 2010). Competition is invoked to explain both of these decreases (Mahler et al. 2010; Rabosky and Glor 2010), suggesting competitive coevolution may have different effects on diversification over different timescales.

Some of the strongest evidence for a role of coevolution in diversification comes at the level of diversification among populations—tests of the geographic mosaic theory of coevolution (Thompson 1994, 2005, 2013). The GMTC postulates that spatially variable coevolution across a metapopulation promotes genotypic and phenotypic differentiation among populations. Spatial variation in coevolution, and thereby differentiation among populations, can arise due to abiotic selection gradients, differential gene flow between populations, coevolution with different species (or differentiated populations of the same species) across the metapopulation, or some combination of these three processes. Extensive empirical data have confirmed these theoretical predictions (e.g., Nuismer et al. 2000) that among-population differentiation in traits (Brodie et al. 2002; Thompson and Cunningham 2002; Toju and Sota 2006a, 2006b; Thompson and Fernandez 2006; Hanifin et al. 2008; Toju 2008; see review in Thompson 2013) and
in some cases, genes (Parchman et al. 2006) can arise from coevolutionary interactions in a broad range of taxa and across spatial scales.

The GMTC may also provide a “bottom-up” mechanism by which coevolution occurring at ecological timescales can set the stage for speciation and diversification over longer periods: by promoting allopatric or parapatric speciation across a metapopulation (Thompson 2005). The genotype by environment interactions (GxE speciation across a metapopulation (Thompson 2005). The scales can set the stage for speciation and diversification mechanism by which coevolution occurring at ecological time-scales.

Coevolutionary Speciation

Althoff et al. (2014) lay out a series of direct and indirect mechanisms by which coevolution may contribute to reproductive isolation and thus speciation. Coevolution may act directly on traits which are important in determining reproductive isolation: such traits could directly determine mate choice (e.g., magic traits; Gavrilets 2004), they could be genetically correlated with other traits which determine mate choice, or else intermediate hybrid phenotypes could suffer reduced fitness. Alternately, coevolution may act on traits that indirectly increase the probability of speciation but without directly causing reproductive isolation—for example, by promoting the evolution of specialization, a key innovation, the use of new environments, or other functional traits that make geographic isolation more probable.

We are aware of only five well-documented examples of speciation promoted by coevolution. Three of these are antagonistic interactions: speciation of red crossbills co-evolving with lodgepole pine (Benkman 1999; Benkman et al. 2001; Edelaar and Benkman 2006; Smith and Benkman 2007) and with black spruce (Parchman and Benkman 2002) and speciation of Satsuma land snails coevolving with Pareas iwasakii snakes (Hoso et al. 2010). In crossbills, speciation results from selection for trait matching (i.e., of pine cone morphology), whereas in Satsuma it results from selection for trait mismatching (i.e., evasion of predator approach). Speciation also seems to have resulted from competitive coevolution between stickleback species pairs in postglacial lakes in British Columbia (Schluter 2010)—a classic example of ecological adaptive radiation, in which speciation results from selection favoring an ecological habit that minimizes competitive interaction. Finally, coevolution with pollinating yucca moths appears to be contributing to reproductive isolation between two subspecies of Joshua tree in the Mojave Desert (Godsoe et al. 2008, 2009, 2010; Smith et al. 2008a, 2008b, 2009; Yoder et al. 2013); in this case coevolutionary selection is thought to favor plant-pollinator trait matching.

These cases suggest that coevolution promotes speciation through direct mechanisms of the type hypothesized by Althoff et al. (2014), although in several cases speciation has occurred in only one partner, and in all cases the direct mechanism of coevolution operates in concert with other evolutionary processes. Coevolution directly promotes reproductive isolation in crossbills by selecting for bill morphology, which also mediates reproductive isolation via habitat choice (Smith and Benkman 2007). However, additional factors not directly related to coevolution—namely the evolution of call differences—provide reproductive isolation concurrently with the coevolutionary selection gradient (Smith and Benkman 2007). Coevolution directly promotes reproductive isolation in Satsuma by promoting the evolution of changes in shell chirality (Hoso et al. 2010). Sticklebacks mate assortatively by body size, a trait under competitive coevolutionary selection (Nagel and Schluter 1998) and hybrid sticklebacks are at a selective disadvantage (Gow et al. 2007), both direct mechanisms. The two varieties of Yucca brevifolia are likely to have initially diverged during a past period of allopatry (Smith et al. 2008a) and are not completely reproductively isolated, but where they co-occur, reproductive isolation is promoted by pollinator host fidelity (Smith et al. 2009; Starr et al. 2013) and, apparently, selection by pollinators on floral morphology (Yoder et al. 2013), both direct mechanisms.

The paucity of examples of speciation arising from geographic mosaics of coevolution may be due to the limited number of geographic mosaics that have been examined explicitly for evidence of speciation (Thompson 2013). Perhaps more importantly, research into the phylogeography or population genetics of geographic mosaics has tended to take the opposite approach, either asking how vicariance events or population differentiation influences the geographic mosaic of coevolution (Janzen et al. 2002; Thompson and Calsbeek 2005; Ridenhour et al. 2007; Rich
et al. 2008; Parchman et al. 2011) or searching for phylogeographic differentiation in order to test the hypothesis that trait differences result from coevolution (Toju and Sota 2006b).

Another possibility is that, while geographic mosaic dynamics may be stable from year to year (Thompson and Cunningham 2002), they are transient over the longer-term scale of speciation and phylogenetic diversification. This is again analogous to the gradualism versus punctation debate in twentieth-century evolutionary biology; in fact, a similar explanation for the dynamics of trait evolution based on metapopulation evolution has been proposed for lineage evolution and diversification in general (Eldredge et al. 2005; Thompson 2013), and the suggestion that speciation may only occasionally “lock in” otherwise transient adaptive changes (Futuyma 1987). It thus remains possible that coevolution creates and maintains polymorphism (Gibbs et al. 2000; Froeschke and Sommer 2005; Westerdahl 2007; Yang et al. 2010) and drives diversification among populations (Ridenhour et al. 2007) in geographic mosaics, but this among-population diversification rarely progresses to speciation or diversification at higher taxonomic scales. Moreover, it is unclear how often coevolution across a geographic mosaic increases variation and among-population divergence beyond what would otherwise evolve via noncoevolutionary metapopulation dynamics—it may be that the cases where coevolution contributes significantly are so extreme as to be unrepresentative (fig. 1; Yoder and Nuismer 2010). Consequently, broader testing of the hypothesis that coevolution can arise in geographic mosaics of coevolution is of prime importance in our understanding of coevolutionary diversification.

**Coevolutionary Diversification without Coevolutionary Speciation**

Coevolution clearly has the potential to play a role in speciation but does not need to do so in order to promote or constrain diversification at a macroevolutionary level. Antagonistic coevolution may depress population sizes of species in a host clade, with the effect of decreasing net diversification rates (Ricklefs 2010); alternately, mutualistic coevolution between two clades may create ecological opportunity that permits an increase in population sizes and the net diversification rate of one or both clades (Gómez and Verdú 2012). Although some interpretations of escape-and-radiate coevolution (Ehrlich and Raven 1964; Thompson 1989) could conceivably include a role for coevolution in speciation, this process could certainly occur even if coevolution is dissociated from mechanisms of speciation. Some of these proposed mechanisms may overlap with Althoff et al.’s (2014) “indirect mechanisms” by which coevolution promotes reproductive isolation.

Approaches that seek to examine not only diversification rates but the evolution of functional traits presumably under selection are promising (e.g., Wheat et al. 2007; Mahler et al. 2010), although the mechanisms linking diversification and trait evolution often remain vague (Agrawal et al. 2008; Althoff et al. 2014). Complementary studies of both ongoing population divergence and macroevolutionary patterns of diversification, as in *Yucca* and *Tegeticula* (Godsoe et al. 2008; Smith et al. 2008; Althoff et al. 2012; Yoder et al. 2013) or in West Indian *Anolis* (Losos 2009; Mahler et al. 2010; Rabosky and Glor 2010) may provide the best opportunities to link the potential role

![Figure 1: Coevolutionary selection does not necessarily promote greater-than-expected diversity. The among-population variance in hosts’ phenotypes after 1,000 generations of genetic drift, abiotic selection, and coevolution in 1,000 individual-based computational simulations of host-parasite interaction, as a function of the strength of coevolutionary selection (scatterplot points); compared to the “null” of phenotypic variances in 1,000 simulations with genetic drift and abiotic selection but no coevolutionary selection (light gray area, full range of null results; darker gray area, 95% confidence interval of null; white line, median of null). Host phenotype variation is greater when coevolutionary selection is stronger (scatterplot points; solid black regression line, adjusted $R^2$ for regression $= 0.2353, P < 2.2 \times 10^{-16}$), and the mean variation is greater in the coevolutionary simulations ($t$-test $P < 2.2 \times 10^{-16}$). However, even simulations with the strongest coevolutionary selection can result in variation within the range expected from the null, and only 40% of coevolutionary simulations end with host phenotype variation greater than null expectation. Figure produced from the results of simulations presented in Yoder and Nuismer (2010).](image-url)
of coevolution in speciation to its effects at macroevolutionary scales.

Conclusions and Future Directions

Both theory and empirical evidence suggest that the importance of coevolution in diversification varies depending on the type of ecological interaction within which it occurs. In particular, the majority of evidence exists for competitive coevolution promoting diversification, particularly as a result of tests of the ecological theory of adaptive radiation. Some compelling examples exist of antagonistic coevolutionary diversification, whereas despite a great deal of interest in mutualistic coevolution, evidence for diversification driven by mutualisms is limited. Whether this pattern reflects coevolution’s relative importance across these categories of diversification, or simply reflects a strong historic interest by evolutionary biologists in adaptive radiation, is unclear. Even if coevolution is important in promoting divergence only through competitive interactions, it may still play an important role in promoting diversification within trophic levels that are engaged in mutualistic and antagonistic interactions with other taxa, as suggested by some hypotheses of plant-herbivore and plant-pollinator diversification.

Empirical evidence suggests also that whereas among-population coevolutionary diversification may be common, the importance of coevolution in speciation and diversification at higher levels, and the mechanisms by which it promotes diversification, remain unclear. Models comparing coevolution to a “null” expectation of diversification due to genetic drift and spatially variable abiotic selection suggest that coevolutionary selection may be strong and significant in the ecological dynamics of interacting species without necessarily increasing their diversity beyond what would occur in the absence of coevolution (fig. 1). In spite of some compelling individual examples, evidence that coevolution often contributes to speciation is surprisingly sparse. Available data suggest that coevolution may promote speciation directly via selection on traits that mediate reproductive isolation, but it may also do so via indirect mechanisms, although fewer examples of the latter are known. It is not clear whether the relative absence of evidence for coevolutionary speciation is evidence of its absence, but ongoing research must be prepared for this possibility. We must ultimately consider whether the handful of cases in which coevolution is directly implicated in establishing reproductive isolation—such as crossbills and pine trees, or yuccas and yucca moths—are representative of broader patterns, or simply rare, extreme cases. Finally, even if coevolution is rarely the sole, direct cause of speciation, it is still possible that it may play a role in macroevolutionary diversification.

Evidence for such macroevolutionary processes is limited, but largely consistent with the patterns of trait and clade diversification seen in the history of life.

We identify four major research areas that are necessary for improving our understanding of the importance and mechanisms of coevolutionary diversification. (1) Additional empirical examples of speciation in coevolving interactions, and cases in which ecologically significant coevolutionary selection is clearly not responsible for speciation. Currently, we are aware of only five examples of speciation driven by coevolution, and very few studies have investigated the converse—that is, how speciation occurs in coevolving taxa and whether or not coevolution is implicated in this speciation. Empirical field research should focus on (a) whether we find additional examples of coevolutionary speciation if we look for it and (b) whether coevolution promotes reproductive isolation in such cases via direct mechanisms, indirect mechanisms, or both. (2) Theory, field studies, and experiments to address under what circumstances polymorphism and divergent selection promoted by coevolution actually proceed to reproductive isolation. We have ample evidence that coevolution promotes these processes, and circumstantial evidence suggests that it may rarely succeed in proceeding to speciation; however, we have almost no understanding of what factors may be responsible for this pattern, even if it is true. (3) Multilevel studies of coevolution and diversification within the same system. The diversification of many clades has been attributed to coevolutionary processes that may or may not be implicated in mechanisms of diversification. We need to determine at what scale coevolutionary processes are acting and at what scale other processes are acting, in coevolving and diversifying clades. Prior research on Yucca and Tegeticula, and West Indian Anolis, provide examples of the sorts of insights achievable via this approach. (4) Theory and experimental evolution to test the hypothesis that particular kinds of interaction promote or constrain diversification. Although field systems have been important in this area, experimental (e.g., with microbial or other similar systems) and theoretical approaches provide greater capacity to control for the many factors that vary amongst field systems, and to further test hypotheses about the mechanisms responsible for these patterns.

Although evidence that coevolution is an important process promoting diversification is limited, a surprisingly small number of interactions have been explicitly examined for evidence that coevolution plays a role in their diversification. There is, however, compelling evidence that coevolution promotes diversification under certain circumstances. The equivocal evidence for widespread coevolutionary diversification may be due not only to a lack of rigorous testing of this hypothesis but also to the fact
that coevolution’s role in generating much of the Earth’s spectacular biodiversity varies depending on the type of coevolutionary interaction and the scale of diversification being considered.

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A female yucca moth (Tegeticula synthetica) oviposits into the pistil of a Joshua tree (Yucca brevifolia) flower prior to pollinating it. Image copyright 2013, Christopher I. Smith.