

Natural History Note

Coevolution and Divergence in the Joshua Tree/Yucca Moth Mutualism

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ABSTRACT: Theory suggests that coevolution drives diversification in obligate pollination mutualism, but it has been difficult to disentangle the effects of coevolution from other factors. We test the hypothesis that differential selection by two sister species of pollinating yucca moths (*Tegeticula* spp.) drove divergence between two varieties of the Joshua tree (*Yucca brevifolia*) by comparing measures of differentiation in floral and vegetative features. We show that floral features associated with pollination evolved more rapidly than vegetative features extrinsic to the interaction and that a key floral feature involved in the mutualism is more differentiated than any other and matches equivalent differences in the morphology of the pollinating moths. A phylogenetically based, ancestral states reconstruction shows that differences in moth morphology arose in the time since they first became associated with Joshua trees. These results suggest that coevolution, rather than extrinsic environmental factors, has driven divergence in this obligate pollination mutualism.

Keywords: coevolution, diversification, mutualism, pollination, *Tegeticula*, *Yucca*.

Coevolution between mutualists, such as plants and their pollinators, is thought to be a fundamental force shaping evolutionary change (Thompson 2005). Biologists have long speculated that coevolutionary interactions between plants and their pollinators might drive divergence and, ultimately, speciation (Darwin 1862). Empirical tests of this idea remain elusive, however, and much of the current

evidence consistent with joint divergence driven by coevolution might also be explained by alternative hypotheses, including biogeographic and ecological factors extrinsic to the interaction. Congruence between plant and pollinator phylogenies on a macroevolutionary scale has provided some support for coevolution as an engine of diversification (Kawakita et al. 2004; Weiblen 2004), although this congruence is sometimes absent at the species level. Similarly, phenotype matching in plant and pollinator traits that mediate these interactions also suggests that reciprocal adaptation may be important in the diversification of obligate pollination mutualism (Molbo et al. 2003; Weiblen 2004). Although this past work has shown that pollination mutualism can result in shared evolutionary histories, cospeciation may arise simply because intimately associated species often have a shared biogeographic history. Likewise, it is often unclear whether matching phenotypes are a product of reciprocal selection (coevolution *sensu stricto*) as opposed to pollinators tracking plant adaptations to the external environment. Indeed, while host plants must deal with a variety of selective pressures apart from the pollination mutualism, obligate pollinators such as fig wasps and yucca moths spend nearly all of their lives in direct association with their hosts and so should be highly susceptible to changes in their host plants. Much of the current evidence therefore might be more consistent with plants driving evolutionary changes in their pollinators rather than coevolution *per se*.

The Joshua tree (*Yucca brevifolia*) presents an unusual opportunity to explore the role of plant-pollinator coevolution in driving codivergence. Joshua trees are pollinated exclusively by yucca moths in the genus *Tegeticula* (Trelease 1893). The female yucca moth oviposits in Joshua tree flowers, cutting through the ovary wall and extending her ovipositor down the stylar canal to lay eggs atop the ovules, before pollinating the flower to ensure the availability of seeds to feed her progeny (Trelease 1893; Pellmyr 2003; fig. 1A). Because the female's ovipositor must be long enough to reach the ovules but not so long as to injure them (Pellmyr and Huth 1994), coevolution acting on the

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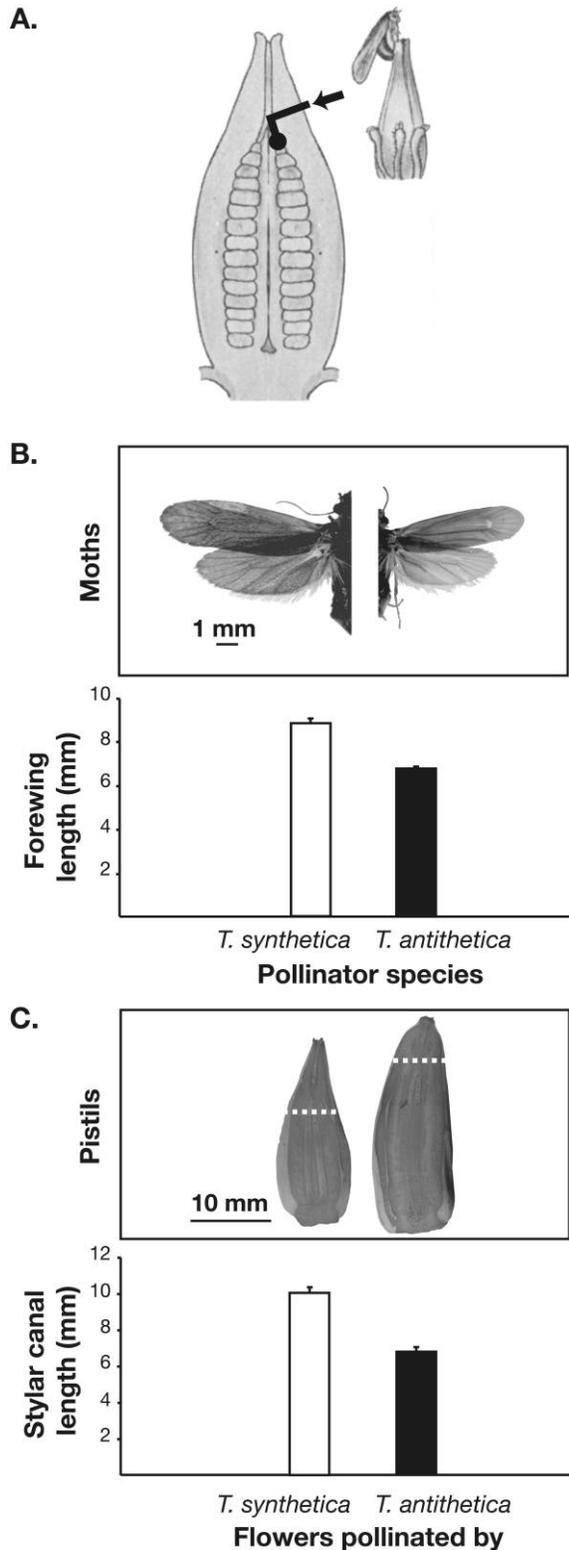


Figure 1: Mechanics of oviposition and phenotype matching in flowers and pollinators of *Yucca brevifolia*. **A.** Oviposition into a Joshua tree flower by a female moth and cross section of floral pistil showing the path taken by the moth's ovipositor, first cutting through the stylar wall and then

partners should favor matching between the length of the moth's ovipositor and the flower's stylar canal.

Theory predicts that reciprocal divergence should be an important promoter of speciation in systems such as the Joshua tree/yucca moth mutualism (Kiestler et al. 1984; Parker 1999). Because of the expected strong selection for phenotypic matching, evolutionary changes in either partner should promote divergence in the other. For example, divergence in a host plant due to drift would encourage divergence in the pollinator, just as divergence due to sexual selection in the moths could drive host plant evolution. In this way, these processes are analogous to models of speciation involving correlated evolutionary changes in males and females (Nei et al. 1983; Hayashi and Masakado 2001).

The Joshua tree is distributed throughout the North American Mojave Desert, occurring in a number of isolated patches of desert scrub (fig. 2; Rowlands 1978; Cole et al. 2003), and previous studies show that Joshua trees exhibit considerable differences in stature and branching architecture between populations in the eastern and western portions of this range (fig. 3; Webber 1953; Rowlands 1978). Recent work also reveals that Joshua tree is pollinated by two parapatrically distributed sister species of moth: *Tegeticula antithetica*, occurring primarily in the eastern portion of the Joshua tree's range, and *Tegeticula syntheticca*, occurring in the western part (Pellmyr and Segraves 2003; fig. 2). These moths differ in body size by about 30% (fig. 1B) and in ovipositor length by about 50% (Pellmyr and Segraves 2003). However, despite these differences in growth form and pollinator species between eastern and western populations, phylogenetic analysis indicates strong support for the monophyly of Joshua trees overall (Pellmyr et al. 2007).

On the basis of their distribution, Pellmyr and Segraves (2003) hypothesized that the two moths may have speciated allopatrically in response to the Bouse Embayment, an estuarine extension of the Sea of Cortez that inundated low-lying areas in the Mojave Desert region approximately

pushing down the stylar canal to the ovules. Modified from Trelease (1893). **B.** Half-images of female *Tegeticula syntheticca* (left) and *Tegeticula antithetica* (right) above a bar chart showing the mean and 95% confidence intervals for female forewing length (a standard index of overall body size) for each species. **C.** Cross-sectioned, stained pistils from Joshua trees in populations pollinated by *T. syntheticca* and *T. antithetica*, respectively, with the lowest extent of their stylar canals (i.e., top of the column of ovules onto which the female moth oviposits) marked by dashed horizontal lines, above a bar chart showing the mean and 95% confidence intervals of stylar canal length for trees pollinated by each moth species. Trees pollinated by the larger *T. syntheticca* have significantly longer stylar canals ($P < .0001$).

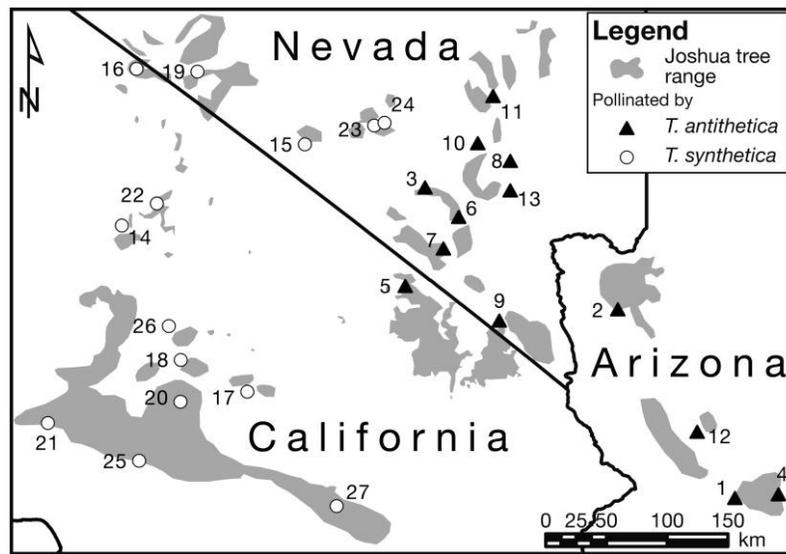


Figure 2: Study sites sampled for the present analysis mapped onto the range of *Yucca brevifolia* (gray). Sites are numbered according to table A1 in the online edition of the *American Naturalist*. We measured trees and their flowers in 27 sites across the range of Joshua trees: 13 populations pollinated by *Tegeticula antithetica* (triangles) and 14 pollinated by *Tegeticula synthetica* (circles). The Joshua tree range map is based on distributions determined by Rowlands (1978) and Cole et al. (2003), with additions and corrections from our own field surveys.

6.5 million years ago (Lucchitta 1972) and that is hypothesized to have promoted speciation in a number of Mojave Desert taxa (Lamb et al. 1995; Mulcahy et al. 2006). This vicariance event would have isolated both the moths and the trees, creating the opportunity for correlated divergence in both partners. Thus, it is likely that both the plants and the insects have been associated throughout their history, and differentiation in both partners probably occurred in concert.

However, distinguishing codiversification due to coevolution from the simple effects of a common biogeographic history requires some means of identifying reciprocal natural selection between both partners. Within antagonistic host-parasite interactions, evidence for natural selection has generally come from experimental work (Clayton et al. 1999; Buckling and Rainey 2002) and reciprocal transplant experiments (Via 1991; Kaltz and Shykoff 1998). Unfortunately, obligate pollination mutualisms like the Joshua tree/yucca moth system typically involve long-lived, highly specialized organisms that do not lend themselves to experimental manipulation to detect reciprocal selection (Janzen 1979; Holland and Fleming 1999; Weiblen 2002; Pellmyr 2003). However, another method for identifying traits under selection is to compare relative rates of divergence between different suites of traits. This approach was used by natural historians before the advent of genetic and statistical approaches to measure selection and is still commonly employed in nonmodel systems where exper-

imental work is difficult or impractical. For example, Darwin (1871) cited the greater differentiation of male secondary sexual characters as evidence for sexual selection, and, more recently, comparisons of the differentiation in male and female traits between closely related species have been used to test alternative models of sexual selection (Eberhard 1985, 1996, 2004). This approach has also been used to infer selection in protein evolution; for example, studies of cryptic sexual selection have compared the rates of evolution in reproductive proteins to those in nonreproductive genes (Wyckoff et al. 2000; Swanson and Vacquier 2002), and rapid evolution at particular loci relative to genome-wide substitution rates has been used to distinguish positive selection acting on specific genes in the human genome from past demographic changes (Nielsen et al. 2005).

This approach has potentially useful application in pollination biology, and it can provide a novel test for the role of coevolution in driving divergence. Grant (1949) first noted that plants with specialist pollinators have greater differences in floral characters between species (as measured by the number of floral characters taxonomists used for species delimitation) than do wind-pollinated species or those that rely on generalist pollinators. Similarly, work by Stebbins (1981) and Schluter (2000) predicts that when pollinator-mediated selection (rather than extrinsic factors) drives diversification, floral features will tend to diverge more rapidly than other ecologically important

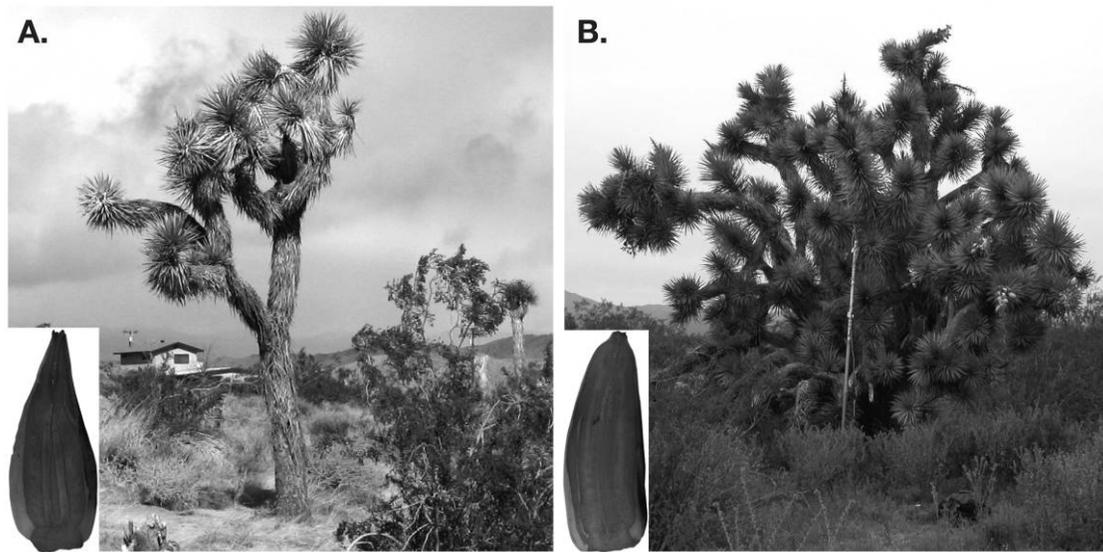


Figure 3: Photographs of *Yucca brevifolia* with high first branching, asymmetric crown, and long narrow pistil (*inset*) typical of trees pollinated by *Tegeticula syntheticca* (A) and with branching near the ground, symmetric crown, and short thick pistil (*inset*) typical of trees pollinated by *Tegeticula antithetica* (B). Photos not to scale.

traits (Stebbins 1970; Schluter 2000; Sargent 2004). A number of empirical studies have also lent support to this prediction, showing that changes in a plant's pollinator community can cause rapid evolution of floral characters (Armbruster 1993; Hapeman and Inoue 1997; Whittall and Hodges 2007). However, despite the theoretical and empirical support for this prediction, it has not previously been used to test coevolution in an obligate pollination mutualism.

The Joshua tree/yucca moth pollination mutualism represents an excellent empirical system in which to use comparisons between suites of characters to test for coevolution, as other workers have done to test the role of sexual selection. As outlined by previous studies, if coevolution with pollinators has been important in the evolution of the Joshua tree, then floral features associated with the mutualism should evolve more rapidly than vegetative characters and thus show greater differentiation. If, however, vegetative features evolve at the same rate as or more rapidly than floral features, we can reject coevolution as a cause of divergence in this system. Indeed, given that plants face selective pressures from many environmental factors apart from pollination, the a priori expectation should be that vegetative features would evolve more rapidly than floral features. Additionally, because the moths interact with the plants in a highly stereotyped manner, it is relatively straightforward to identify features involved in the interaction and make predictions about which features should be under strong selection. If pollinator-

mediated selection and coevolution are important, the stylar canal of Joshua tree flowers should be under particularly strong selection. *Tegeticula syntheticca* has an ovipositor that is 50% longer than that of *T. antithetica* (Pellmyr and Segraves 2003), so there is a strong a priori prediction that plants pollinated by *T. syntheticca* should have longer stylar canals.

Material and Methods

We determined the host plant for the common ancestor of *Tegeticula syntheticca* and *Tegeticula antithetica* using a maximum likelihood ancestral state reconstruction executed in Mesquite (ver. 1.11; <http://mesquiteproject.org>). We surveyed Joshua trees in every accessible population of the species in 2005 and 2006 and collected morphological data from all sites where flowers could be collected and where pollinator species could be definitively determined by collecting adult moths. A total of 27 sites were included in this analysis (see fig. 1; site descriptions and geographic coordinates are listed in table A1 in the online edition of the *American Naturalist*). We analyzed 12 floral and vegetative features selected on the basis of previous accounts of phenotypic variation within *Yucca brevifolia* (Rowlands 1978) and the mechanics of pollination in this system (Trelease 1893). For each tree, we took the following vegetative measurements: total height, height to first branching, total number of branches, crown diameter, and the average length and width of five haphazardly selected

mature leaves from up to five different branches. Flowers were collected and stored in ethanol for subsequent dissection and measurement of the following floral traits: length and width of one petal, exterior length and width of the pistil, length of the styler canal, and midpoint width of the style.

To compare the degree of divergence between character suites, we performed logistic regression of pollinator identity on the top three principal components derived from the raw floral data set and from the raw vegetative data sets, respectively. The top three principal components captured ~80% of the total variation from each data set. We then measured the cross-validated accuracy of models on the basis of these two trait classes and compared their Akaike Information Criterion (AIC) scores. The latter comparison determines which trait class produces the best model to distinguish trees associated with each pollinator.

To compare differentiation in individual traits, we derived univariate ANOVA statistics for each trait and compared their R^2 values (table 1). Stepwise discriminant analysis provided another comparison of the explanatory powers of individual traits (table A2; for further information on our statistical methods, see appendix).

Results

We confirmed that *Tegeticula synthetica* and *Tegeticula antithetica* were associated with the Joshua tree at the time of their speciation using a maximum likelihood ancestral state reconstruction to determine the host of the common ancestor. *Yucca brevifolia* was identified as the most likely host of the moths' common ancestor; this reconstruction had a marginal probability of 0.8929. Its maximum likelihood score exceeded the next most likely reconstruction by >2 log likelihood units, so this difference is significant ($-\ln = 18.1677$ for the ancestor being *Y. brevifolia* vs. 21.0077 for a *Yucca* in the section *Sarcocarpa*). This result was robust to variations in branch length produced by alternative models of sequence evolution; enforcing a molecular clock had no effect on the maximum likelihood reconstruction of the ancestral state and minimal effect on the marginal probability of this state ($P = .8941$ when a molecular clock is enforced; $P = .8929$ when not enforced). The two moth species that pollinate Joshua tree thus most likely diverged while using the same host plant and were always monophagous on Joshua tree. Although host shifts are common in some obligate pollination mutualisms (Machado et al. 2005), the results of this ancestral state reconstruction suggest that observed differences in morphology between the two moths species are not attributable to a recent host shift but are in fact likely to have arisen in concert with correlated changes in the plants.

Table 1: Univariate ANOVA statistics comparing floral and vegetative traits for Joshua trees associated with different pollinator species

Trait	R^2	F	Pr > F
Floral traits:			
Stylar canal length	.5563	259.56	<.0001
Petal width	.2433	66.56	<.0001
Pistil exterior width	.2197	58.30	<.0001
Petal length	.1339	32.02	<.0001
Style basal width	.1257	29.75	<.0001
Style midpoint width	.0853	19.29	<.0001
Pistil exterior length	.0222	4.70	.0313
Vegetative traits:			
Height at first branching	.4094	143.46	<.0001
Mean leaf width	.3825	128.21	<.0001
Mean leaf length	.3499	111.39	<.0001
Number of branches	.1971	50.82	<.0001
Tree height	.0434	9.39	.0025
Crown diameter	.0090	1.87	.1726

Note: All F values have $g - 1 = 1$ and $N - g = 207$ df.

Trees pollinated by different moth species differed significantly in overall morphology (MANOVA $P < .0001$). Logistic regression showed greater accuracy of assignment for the floral model (96.6% for floral traits vs. 87.1% for vegetative) and demonstrated with a very high level of statistical support that floral characters are much more differentiated than are vegetative characters ($\Delta\text{AIC} = 96.048$).

The length of the stylar canal, the feature most closely associated with moth oviposition, is the variable that best discriminates between tree types ($R^2 = 0.556$), and floral characters are the top three variables selected in the stepwise discriminant analysis (tables 1, A2). Additionally, as was predicted on the basis of the differences in body size and ovipositor length between the two moth species, trees pollinated by *T. synthetica* have stylar canals that are significantly longer than those pollinated by *T. antithetica* ($P < .0001$; fig. 1C; table 1). All three of the analyses presented here (logistic regression, univariate ANOVA, and stepwise discriminant analysis) therefore agree, suggesting that floral features are more divergent than vegetative features and that the specific feature predicted to be most intimately associated with the interaction is the most divergent between trees.

Discussion

The principal results of these analyses—that the differences between trees pollinated by different moths are greater in floral traits than in vegetative traits, are greatest in style length, and are matched to pollinator morphology—are precisely what would be expected if pollinator-mediated

selection drove the divergence in Joshua trees. These findings also suggest that pollinator-mediated selection in obligate pollination mutualism may exert selection on particular features of plant and pollinator morphologies, equivalent to the rapid divergence in genitalic morphology and reproductive proteins seen under sexual selection. It is noteworthy that both in the present system and in cases of sexual selection, features involved in reproduction appear to evolve more rapidly than other characters expected to be under strong selection, such as those associated with adaptations to the extrinsic environment. Additionally, because the two pollinators are sister species and have been associated with Joshua trees throughout their history, and because Joshua trees are strongly supported as monophyletic, it is likely that the morphological differences in both partners arose concomitantly through codivergence.

The method used here is a novel approach to studying the role of coevolution in the diversification of pollination interactions. If floral characters appear to be evolving more rapidly than vegetative features (as found here), then pollinator-mediated selection could be driving divergence. However, if floral characters show equivalent, or lower, levels of divergence than vegetative characters, pollinator interactions are not likely to be an important source of divergent natural selection. While it is beyond the scope of this note to study divergence in the pollinators and so to directly examine the role of reciprocal natural selection in this system, it is worth noting that the two moth species show proportionally greater differences in ovipositor length—the pollinator trait most directly associated with the mutualism—than in overall body size (Pellmyr and Segraves 2003).

It is tempting to conclude on the basis of these observations that concurrent, reciprocal adaptations in both the moths and the plants drove morphological divergence in this system. However, as with other studies that compare rates of evolution in different suites of characters, it is difficult to completely rule out alternative hypotheses, such as relaxed constraints on floral traits or genetic drift (see discussion in Eberhard 1996; Wyckoff et al. 2000; Swanson and Vacquier 2002). It is particularly challenging to distinguish coevolution in the strict sense from evolutionary tracking by one partner of changes in the other, since this generally requires knowledge about the relative timing of evolutionary changes in both lineages. Studies of the biogeography of species formation in these two organisms could help in distinguishing among the remaining alternative hypotheses.

Nevertheless, our analysis does offer evidence against one of these alternative hypotheses—that plant adaptations to the abiotic environment drove subsequent changes in the moths. If changes in the trees were driven by adaptation to differing climate rather than pollinator-

mediated selection, then we would expect vegetative features to be more distinct than floral features, which they demonstrably are not.

Adaptations facilitating pollination are among the most important forces shaping the evolution of angiosperms (Grant 1949; Schluter 2000; Coyne and Orr 2004), and recent phylogenetic studies have demonstrated an association between specialized pollination and increased rates of diversification (Hodges and Arnold 1995; Sargent 2004). Although there are a number of mechanisms by which pollination might lead to reproductive isolation in plants, thereby giving rise to increased rates of speciation (Moore and Lewis 1965; Nilsson 1983; Schemske and Bradshaw 1999), it has been unclear whether strict-sense coevolution is an important factor (Coyne and Orr 2004; Fenster et al. 2004). The work presented here suggests that coevolutionary divergence through reciprocal adaptation between plants and pollinators may indeed be an important mechanism driving divergence.

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Top, Tikaboo Valley, Nevada (photograph by Olle Pellmyr). *Bottom*, William Godsoe on a ladder measuring plants near Palmdale, California (photograph by Olle Pellmyr).