

Coevolution of Joshua trees and their Pollinators: A Short Review

Christopher Irwin Smith¹

The Joshua tree is an endemic yucca characteristic of the Mojave Desert. In this article Chris Smith summarizes recent research on the coevolution of Joshua tree and its pollinating moths.

Understanding how macroevolutionary patterns that take shape over epochs are produced by microevolutionary processes occurring over generations is the principal challenge for modern evolutionary biology. One of the most noticeable macroevolutionary patterns is the diversity of life on earth, and in particular the relatively enormous diversity of some groups compared to the rest of the living world. Flowering plants and herbivorous insects, for example, outnumber nearly all other organisms, both in terms of their sheer biomass and in their species diversity. The beetles (the insect order Coleoptera), for example, account for nearly one quarter of all described species (1), and may include millions more undescribed species (2). (The geneticist J. B. S. Haldane is said to have remarked that the creator has, “An inordinate fondness for beetles” (3)). Similarly, insect-pollinated species account for 90% of all land plants (4), or approximately 20% of all species on Earth. Work my collaborators and I have completed over the last ten years has focused on the pollination biology of the Joshua tree (*Yucca brevifolia*) as a way to understand the factors that have produced the diversity of plants and insects.

A commonly proposed explanation for the startling diversity of plants and insects is that coevolution – reciprocal evolutionary change in two interacting groups of organisms – has generated this diversity (5). There are a number of lines of evidence that support this idea. At a

¹ Willamette University, Department of Biology, 900 State Street Salem, OR 97301.

macroevolutionary level, plants with specialized defenses against insect herbivores - such as sticky sap or toxic compounds - have significantly greater species diversity than their more weakly defended relatives (6), and insect lineages that feed on flowering plants (the most diverse of all land plant lineages) contain more species than their close relatives that feed on less speciose groups of plants (3). Similarly, groups of plants with specialized pollinators are more diverse than those that rely on generalist pollinators (7). So it seems that groups of plants and insects that interact with one another often contain a large number of species. Finally, many plant / insect interactions demonstrate phenotype matching—that is, features of the plant’s and insect’s anatomy that are correlated in shape or sizes—that is suggestive of reciprocal adaptation. For example, Darwin’s Orchid, *Angraecum sesquipedale*, has a nectar spur an astonishing thirty centimeters long, and is pollinated by a hawk moth, *Xanthopan morgani praedicta*, with a proboscis just long enough to reach the nectar at the bottom of the tube (8). Similarly, the seed-eating camellia weevil, *Curculio camelliae*, has a rostrum (i.e., a snout) that is just long enough to penetrate the pericarp (i.e., the fruit) and reach the seeds of its host plant, the Japanese camellia, *Camellia japonica*. In different populations of the camellia, variation in the thickness of the pericarp is correlated with differences in length of the weevil’s rostrum (9).

While these findings are suggestive of coevolution between plants and insects, and indicate some connection between ecological interactions and species diversity, they stop short of showing that reciprocal natural selection is actually responsible for the diversity of plants and insects. To make a truly convincing case

that coevolution has contributed to the diversification of these groups it would be necessary to show that the plants affect the fitness of the insect, that these same insects affect the fitness of the plant, and that together these have caused the formation of new species. Clearly, testing all three of these ideas is a tall order, and finding one system where it is feasible to address each of these questions remains a much sought-after goal for research in coevolution. My collaborators and I are hopeful that we may be getting closer to this goal with our studies of the Joshua tree.

Natural History and Biogeography of Joshua Trees – Joshua trees are one of the most unusual and striking plants that occur in the Mojave National Preserve; their spiny, twisted silhouette and creamy white, musky-scented flowers seem to inspire strong reactions in anyone that sees them. The nineteenth century American explorer John C Frémont, perhaps the first European to ever see a Joshua tree, described them as, “the most repulsive tree in the vegetable kingdom,” whereas legend holds that early Mormon settlers imagined the trees as the prophet Joshua, pointing the way to the promised land (10). The early twentieth century botanist Susan McKelvey wrote of the Joshua tree that, “One would not be surprised to see a huge prehistoric monster standing by and feeding upon the fruit.” McKelvey described the tree’s flowers as, “curious rather than beautiful in appearance” (10), but her predecessor, William Trelease, considered them to be “the most attractive of all the Yuccas.” Trelease did admit however that scent of the flowers was “so oppressive as to render the flowers intolerable in a room,” but added on a more positive note that “the usual designation of fetid is not strictly accurate” (11).

This distinctive appearance has made the Joshua tree the iconic plant of the Mojave Desert. The trees occur across the Mojave in middle elevations between ~850 and ~1950 meters. Death Valley, the Amargosa Desert, and various low-elevation inland basins therefore create a natural barrier that divides the Joshua tree's range roughly in half, and populations on either side of this barrier differ noticeably in their growth form and foliage (Figure 1). Trees growing in the western half of the range are typically taller, have longer leaves, and do not begin to branch until they have grown to at least a meter in height. In contrast, eastern trees are typically smaller overall, branch closer to the ground, and have much shorter leaves on average (12, 13). Historically, taxonomists have recognized two varieties of Joshua tree on the basis of these differences (*Y. brevifolia brevifolia* in the west, and *Y. b. jaegeriana* in the east (10, 11)), and recently some have advocated splitting *Y. brevifolia* into two species (14).

Perhaps the most interesting thing about Joshua trees, however, is their pollination biology. Like all yuccas, Joshua trees are pollinated exclusively by yucca moths – a group of drab grey moths in the family Prodoxidae. The moths in turn reproduce solely by laying their eggs in the developing flowers. The female yucca moth has a unique set of tentacle-like appendages that grow out of her external mouthparts, and that are not equivalent to structures in any other group of insects. The moths use these 'tentacles' to grasp tiny balls of pollen as they move between flowers on the yucca plant. When the moth reaches an unfertilized flower, she first positions herself on the pistil (the female part of the flower), and then cuts into the pistil with her ovipositor, a specialized, blade-like organ at the tip of her abdomen that delivers her eggs (Figure 2). The moth deposits several eggs directly onto the undeveloped ovules (the part of the flower that will eventually develop into seeds). After

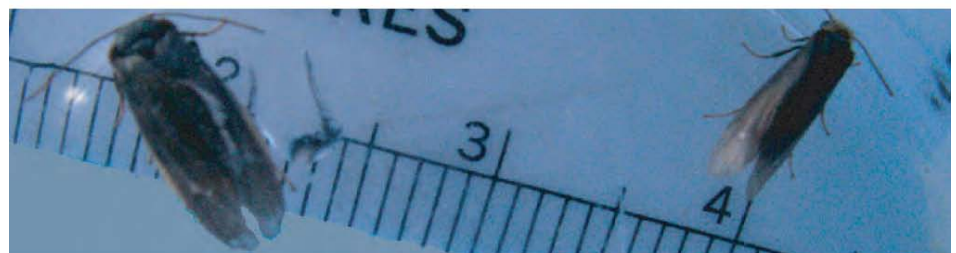
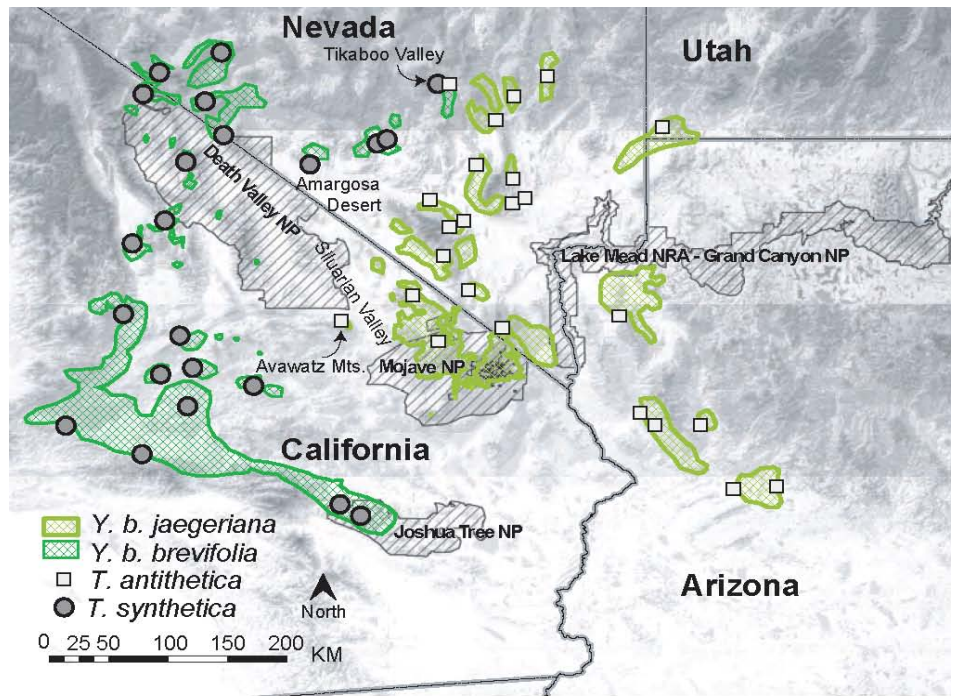


Figure 1. Distribution and morphology of Joshua trees (*Yucca brevifolia*) and their pollinators (*Tegeticula* spp). Top Panel: Range map of the Joshua tree. Dark green shows the range of the western variety (*Y. brevifolia brevifolia*), lighter green the range of the eastern variety (*Y. brevifolia jaegeriana*). Collection localities for the pollinating moths are shown as grey circles (*T. synthetica*) and white squares (*T. antithetica*). Location of particular populations and geographic features mentioned in the text are indicated. Center panel: The Joshua tree's pollinators, *T. synthetica* (left) and *T. antithetica* (right). Scale is in centimeters. Photo: J. B. Yoder. Bottom panel: The two Joshua tree varieties, *Y. b. brevifolia* (left) and *Y. b. jaegeriana* (right) growing side-by-side in Tikaboo Valley, NV. For consistency of presentation, the image is reversed from its original orientation. Photo: J. B. Yoder.

laying her eggs, in order to ensure that the ovules will develop into the mature seeds that her caterpillars will feed on, she climbs to the top of the pistil and pollinates the flower using her tentacles to spread pollen directly onto the stigma. Needless to say, this deliberate, purposeful pollination is a far-cry from the almost accidental nature by which honey bees pollinate flowers, so much so that Charles Darwin described the yucca-yucca moth interaction as, “The most remarkable fertilization system ever described” (15).

It was recently discovered that the Joshua tree is –in fact– pollinated by two different species of yucca moth, *Tegeticula synthetica*, and *T. antithetica* (16). These two species are genetically distinct (16-18), and differ in overall body size and the in length of the female moths’ ovipositors (16) (Figure 3). Intriguingly, the distribution of the two moth species also shows an east-west split, with Death Valley and the Amargosa Desert forming the primary dividing line (17) (Figure 1). Furthermore, the distribution of the two moth species matches exactly the distribution of the two tree varieties described by previous taxonomic studies (12, 17) (Figure 1).

Over the past seven years, my colleagues and I have visited every publicly accessible population of Joshua trees to collect moths and flowers and to make measurements of the trees. All populations of *Y. b. brevifolia* are pollinated by *T. synthetica*, and all populations of *Y. b. jaegeriana* are pollinated by *T. antithetica*. Our surveys of the moth and tree populations also revealed two exceptions to the general rule that Death Valley and the Amargosa Desert separate the two varieties. The two tree varieties come into contact north of the Amargosa Desert in Tikaboo Valley – an 80 km long basin between the Pahranaagat and Groom Mountains – and both moth species co-occur in a narrow contact zone within this valley. There is

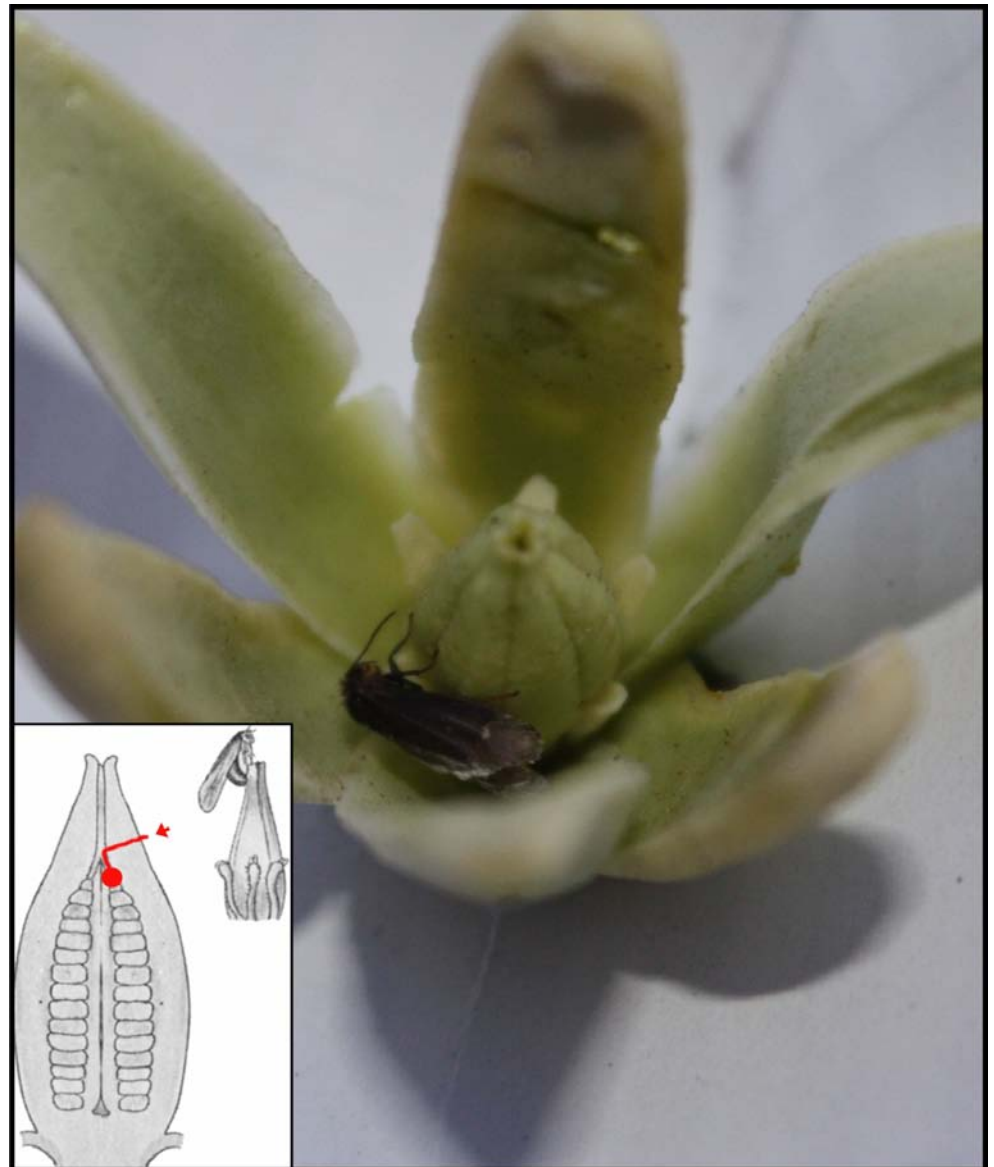


Figure 2. *T. antithetica* on a flower of *Y. b. jaegeriana*. (Photo: C. I. Smith). Inset: Schematic of oviposition behavior by yucca moths on *Y. brevifolia* (11). Moths perch with their forelegs on the stigma, and force the ovipositor through the styler wall, and down the styler canal. Cross section of the pistil shows the path of oviposition.

also a population of *Y. b. jaegeriana* and *T. antithetica* along the ridgeline of the Avawatz Mountains, just west of Silurian Valley at the southern end of Death Valley (Figure 1). This population probably was established by dispersal from the nearby Kingston Mountains.

Phenotype Matching and Coevolution Between Joshua Trees and their Pollinators – The intimacy of the relationship between Joshua trees and their pollinators would seem to offer an ideal opportunity for reciprocal evolutionary change. Since the moths

spend most of their time on the flowers of the Joshua tree, and considering how different the two tree varieties are in their overall growth form, it seems reasonable to wonder whether the trees might have different flowers as well. Work I completed with William Godsoe and Jeremy Yoder, two graduate students at the University of Idaho, suggests that, indeed, the flowers are quite different. In fact, statistically the two tree varieties differ much more in floral anatomy than in growth form (12). This difference is particularly noticeable in the pistils – the female part of the flower. Flowers of the

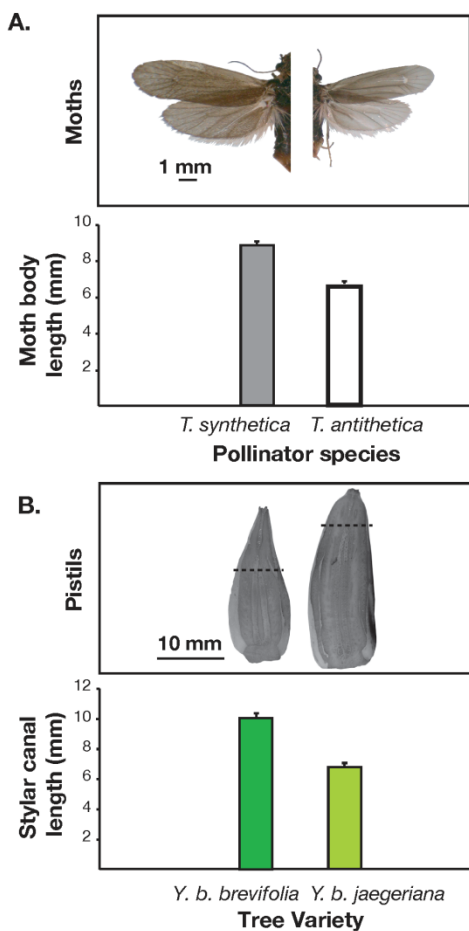


Figure 3. Phenotype matching in Joshua trees and their pollinators. A: Pinned and spread specimens of *T. synthetica* (left) and *T. antithetica* (right), and average body size in each species. **B:** Floral pistils from *Y. b. brevifolia* (left) and *Y. b. jaegeriana* (right), and average length of the stylar canal in each variety. Dotted lines on each pistil represent the lowest extent of the stylar canal. Error bars represent 95% confidence intervals; differences in stylar canal length and moth body size are statistically significant ($P < 0.001$). Figure modified from (12).

western variety, *Y. b. brevifolia*, have relatively slender pistils with a long narrow style, giving them a shape something like a wine bottle. On the other hand, the pistils of the eastern tree variety, *Y. b. jaegeriana*, are thicker, with a very short style, so that they look something like a milk bottle (Figure 3). Preliminary work also seems to indicate that the flowers of each variety also differ in their scent profiles, containing different mixtures of aromatic compounds that have been described as “mushroomy” and “like a fine blue cheese,” respectively (19). Whether or not these odors are

actually ‘fetid’ remains a matter of personal opinion.

Interestingly, the biggest difference of all between the two tree varieties turns out to be the length of the stylar canal, a hollow tube through which germinated pollen grains grow to reach the unfertilized egg (12). The eastern trees have a relatively short stylar canal, whereas that of the western trees is significantly longer. This tube is also the path through which the female yucca moth inserts her ovipositor (Figure 2) (11), and –amazingly– the length of the stylar canal in each tree variety matches exactly the body length of their respective pollinators (12) (Figure 3).

It is clearly tempting to conclude that the differences in the body size and ovipositor length of the two moth species must be adaptations to their respective host species. Perhaps a larger body and longer ovipositor helps *T. synthetica* reach the ovules of its long-styled host? The evidence for this is intriguing, but so far it is incomplete. In Tikaboo Valley, the one site where both tree types co-occur, the female moths of each species visit both tree types more or less indiscriminately (18). So, it is possible to track the success of female moths from both species when they visit trees of each variety. By collecting caterpillars from the fruit of each tree type, and then using DNA fingerprinting techniques to genotype them, we have been able to determine how often *T. synthetica* caterpillars emerge from *Y. b. jaegeriana* trees, how often *T. antithetica* caterpillars emerge from *Y. b. brevifolia* trees, and how many offspring each female moth produces from each flower. The results show that although both moths visit both tree types in the contact zone, *T. synthetica* never successfully produces offspring from flowers of its non native host, and that *T. antithetica* produces many fewer larvae when laying eggs on *Y. b. brevifolia* than on its native host (18) (Figure 4).

These results are compelling, but it is not clear that the lower success of each moth species when visiting a foreign host is due to mismatches between the moth’s ovipositor and the floral style. Differences between the two tree varieties other than the length of the styles –differences in plant secondary chemistry, for example– could also explain the fewer number of larvae produced when moths visit foreign hosts. This spring I will be setting up some additional experiments, and looking specifically at how variation in style length within tree varieties affects moth oviposition success.

Can coevolution cause the formation of new species?

Ultimately, if we want to understand whether coevolution between species is responsible for the diversity of plants and insects, we need to understand how it affects the rate at which new species are formed. On the one hand, considering that the behavior of the moths completely determines whether cross-pollination occurs, it seems to make sense that the

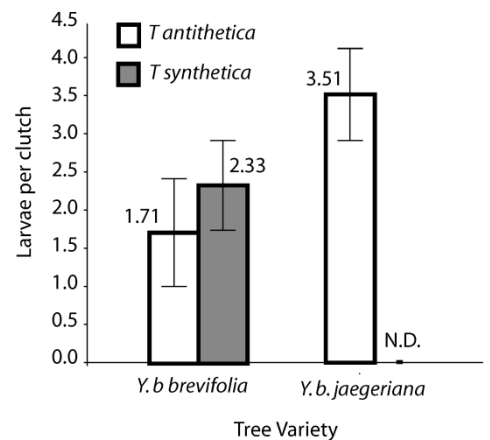


Figure 4. Average clutch sizes of female yucca moths ovipositing onto each variety of Joshua tree. Clutch size data are based on caterpillars reared from fruits collected in the Tikaboo Valley contact zone. Average clutch sizes were estimated using mitochondrial DNA sequences and microsatellite DNA to assign individual larvae to matriline and determine the number of offspring produced by each female on each fruit. Error bars represent 95% confidence intervals; *T. antithetica* females produce significantly fewer larvae on *Y. b. brevifolia* than on *Y. b. jaegeriana* ($p = 0.0014$). *T. synthetica* larvae were never reared from eastern trees. Figure modified from (18).

moths could cause reproductive isolation between yucca species. Indeed, the different rates at which the two moth species oviposit on the two tree types described above mirrors patterns of gene flow between the two tree varieties (18). On the other hand, understanding what caused the two tree types to become differentiated in the first place is not easy. Adaptation to different environments could also have caused the trees to develop different growth patterns and floral shapes, and simple geographic isolation is probably the most common means by which new species originate.

In the case of the Joshua tree, we can say that the climate that the two tree varieties experience are not meaningfully different (20). Similarly although populations of Joshua tree in the eastern and western Mojave have been geographically separated for several million years, the differences between the pollinators associated with these populations evolved much more recently (17). Having eliminated these two alternative hypotheses, coevolution remains a plausible explanation.

Understanding whether and how interactions between species may promote species diversity remains a central question for evolutionary biologists. Although our understanding of the interaction between Joshua trees and their pollinators is still incomplete, a pattern seems to be emerging that suggests reciprocal adaptation has played a direct role in promoting reproductive isolation. We may soon have a very clear idea of how this system has evolved, and the specific factors that have played the largest role in their evolutionary history.

References and Notes

1. D. R. Strong, J. H. Lawton, S. R. Southwood, *Insects on Plants* (Harvard University Press, Cambridge, MA, 1984).
2. T.L Erwin, *Tropical Forests: Their Richness in Coleoptera and Other Arthropod*
3. *jaegeriana* as a distinct species. *Aliso* **24**, 97-104 (2007).
4. C. Darwin, Letter to J. D. Hooker, April 7, 1874, in *A Calendar of the Correspondence of Charles Darwin, 1821-1882*, F. Burkhardt, S. Smith Eds. (Cambridge Univ. Press, Cambridge 1874).
5. O. Pellmyr, K. A. Segraves Species. *Coleopterist's Bull.* **36**, 74-75 (1982).
6. B. D. Farrell, Inordinate fondness explained: why are there so many beetles? *Science* **281**, 555-559. 1998.
7. C. A. Kearns, D. W. Inouye DW, N. M. Waser, Endangered mutualisms: The conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.* **29**, 83-112 (1998).
8. P. Ehrlich, P. Raven, Butterflies and plants: a study in coevolution. *Evolution* **18**, 586-608 (1964).
9. B. D. Farrell, D. E. Dussourd, C. Mitter, Escalation of plant defense: Do latex and resin canals spur plant diversification? *Am. Nat.* **138**, 881-900 (1991).
10. R. D. Sargent, Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. London Ser. B* **271**, 603-608 (2004).
11. L. A. Nilsson, The evolution of flowers with deep corolla tubes. *Nature* **334**, 147-149 (1988).
12. H. Toju, T. Sota, Adaptive divergence of scaling relationships mediates the arms race between a weevil and its host plant. *Biology Letters* **2**, 539-542 (2006).
13. S. D. McKelvey, *Yuccas of the Southwestern United States* (Arnold Arboretum, Harvard University, Jamaica Plain, MA., 1938).
14. W. Trelease, Further studies of yuccas and their pollinators. *Annual Reports of the Missouri Botanical Garden* **4**, 181-226 (1893).
15. W. K. W. Godsoe, J. B. Yoder, C. I. Smith, O. Pellmyr, Coevolution and divergence in the Joshua tree/yucca moth mutualism. *Am. Nat.* **171**, 816-823 (2008).
16. P. G. Rowlands, *The vegetation dynamics of the Joshua Tree (Yucca brevifolia Engelm.) in the southwestern United States of America* (University of California, 1978).
17. L. W. Lenz, Reassessment of *Y. brevifolia* and recognition of *Y.*, Pollinator divergence within an obligate mutualism: two yucca moth species (Lepidoptera; Prodoxidae: *Tegeticula*) on the Joshua Tree (*Yucca brevifolia*; Agavaceae). *Ann. Entomol. Soc. Am.* **96**, 716-722 (2003).
18. C. I. Smith, W. K. W. Godsoe, S. Tank, J. B. Yoder, O. Pellmyr, Distinguishing coevolution from covariance in an obligate pollination mutualism: Asynchronous divergence in Joshua tree and its pollinators. *Evolution* **62**, 2676-2687 (2008).
19. C. I. Smith, J. B. Yoder, W. K. W. Godsoe, O. Pellmyr, Host specificity and reproductive success of yucca moths (*Tegeticula* spp. Lepidoptera: Prodoxidae) mirror patterns of gene flow between host plant varieties of Joshua tree (*Yucca brevifolia*; Agavaceae). *Mol. Ecol.* **18**, 5218-5229 (2009).
20. R. Raguso, personal communication.
21. W. Godsoe, E. Strand, C. I. Smith, J. B. Yoder, T. C. Esque, O. Pellmyr, Divergence in an obligate mutualism is not explained by divergent climatic factors. *New Phytol.* **183**, 589-599 (2009).