

NEWS AND VIEWS

PERSPECTIVE

Host specificity, phenotype matching and the evolution of reproductive isolation in a coevolved plant–pollinator mutualism

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Coevolutionary interactions between plants and their associated pollinators and seed dispersers are thought to have promoted the diversification of flowering plants (Raven 1977; Regal 1977; Stebbins 1981). The actual mechanisms by which pollinators could drive species diversification in plants are not fully understood. However, it is thought that pollinator host specialization can influence the evolution of reproductive isolation among plant populations because the pollinator's choice of host is what determines patterns of gene flow in its host plant, and host choice may also have important consequences on pollinator and host fitness (Grant 1949; Bawa 1992). In this issue of *Molecular Ecology*, Smith *et al.* (2009) present a very interesting study that addresses how host specialization affects pollinator fitness and patterns of gene flow in a plant host. Several aspects of this study match elements of a seminal mathematical model of plant–pollinator codivergence (Kiestler *et al.* 1984) suggesting that reciprocal selection for matched plant and pollinator reproductive traits may lead to speciation in the host and its pollinator when there is strong host specialization and a pattern of geographic subdivision. Smith *et al.*'s study represents an important step to fill the gap in our understanding of how reciprocal selection may lead to speciation in coevolved plant–pollinator mutualisms.

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Laying the foundations for a thorough understanding of the process of codiversification in highly specific coevolved plant pollinator mutualisms requires knowing how plant and pollinator fitnesses are affected by pollinator host

choice, and how that host choice affects reproductive isolation in the pollinator as well as pollen flow and thus reproductive isolation in the plant. Although Smith *et al.*'s study does not address all the required aspects mentioned above, it does provide evidence of the fitness effects of host choice on pollinators and combines this information with previous inferences of host gene flow. In doing so, Smith *et al.* go well beyond what has been done in previous studies in coevolved mutualisms.

Smith *et al.* study the remarkable obligate plant–pollinator mutualism between the Joshua tree (*Yucca brevifolia*) and their yucca moth pollinators (*Tegeticula* spp.). Joshua trees require female moths to pollinate its flowers, and in return lose some seeds that are eaten by the moth larvae as they develop (Pellmyr 2003). The authors report that in a narrow, 4-km wide zone of sympatry, two morphologically different populations of Joshua trees overlap, and their two moth pollinator species show different degrees of (incomplete) host specificity (Fig. 1). To the east of the zone of sympatry grow the shorter form of Joshua trees, *Yucca brevifolia* var. *jaegeriana*, pollinated by the smaller moth species, *Tegeticula antithetica*. To the west of the zone of sympatry grow the taller Joshua trees *Yucca brevifolia* var. *brevifolia*, pollinated by *Tegeticula synthetica*, the larger western moth species. While the two pollinator species are reproductively isolated (Pellmyr & Segraves 2003; Godsoe *et al.* 2008; Smith *et al.* 2009), chloroplast (cpDNA) data suggest significant levels of asymmetric gene flow between western and eastern tree types (Smith *et al.* 2008). Interestingly, the difference in host specificity shown by each moth species matches the inferred pattern of chloroplast DNA introgression (see below).

The authors examined the fidelity of moth pollinators to their plant hosts in the zone of sympatry and the fitness consequences of host choice using a suite of methods: (i) sticky card glue traps documented moth visits to both plant types to determine host fidelity; (ii) genotyping of larvae with mitochondrial DNA and microsatellite markers allowed them to compare larval emergence rates of both pollinator species in the two varieties of host to determine fitness consequences of host choice in the moth; and (iii) genotypic data was also used to establish sibling relationships and matrilineal relationships of moth larvae within and between Joshua trees, allowing estimates of moth maternal clutch sizes per seed and per tree, therefore measuring fitness costs of oviposition in the alternate host.

Sticky card data showed that the larger western moth species (*T. synthetica*) visited eastern Joshua trees less frequently than its western type host, while the smaller eastern moth (*T. antithetica*) visited both Joshua trees types, so that western trees were visited equally by both moth species. However, when Smith *et al.* analysed the genotypes of moth larvae collected from yucca seeds of

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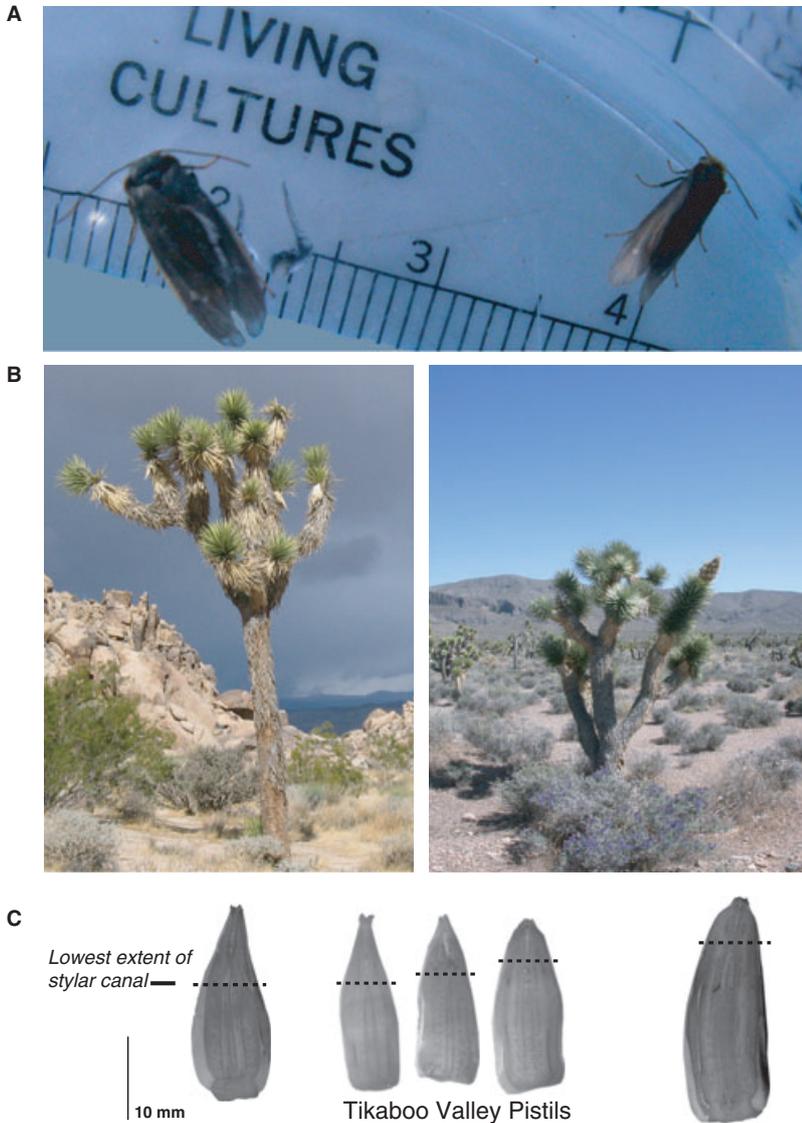


Fig. 1 (A) Live specimens of the western moth *Tegeticula synthetica* (left) and the eastern species *Tegeticula antithetica* (right). (B) Archetypical western Joshua tree (*Yucca brevifolia brevifolia*) in Joshua Tree National Park, California (left), and an archetypical eastern Joshua tree (*Y. brevifolia jaegeriana*) (right) in Desert National Wildlife Refuge, Nevada. (C) Cross-sectioned and stained pistils from the western (left) and eastern (right) varieties of Joshua tree, and variation in style length within the Tikaboo Valley contact zone (center). Dotted lines indicate the lowest extent of the stylar canal; the point which female moths must reach in order to access the ovules. (Photos: A. Christopher Smith; B. William Godsoe; C. Jeremy Yoder.)

eastern and western Joshua trees, they revealed starkly different rates of success in larval emergence. While eastern moths were less selective than western moths in their visitation of nonnative Joshua trees (i.e. western trees), larval success was significantly biased toward their native host, with 378 eastern moth larvae produced from eastern trees, and only 12 eastern larvae from western trees (Smith *et al.* 2009; Table 1B). Differences in larval emergence rates were even more pronounced for the western moth, which visited eastern trees rarely: no larvae of this species were reared from its nonnative eastern host. Therefore, western moths produced significantly less larvae on eastern trees than could be explained by chance or by the low rate of adult visits. Comparison of clutch sizes for each moth between native and nonnative host plants provided evidence of the fitness costs of host switching in the smaller eastern moth, *T. antithetica*. In this species the average clutch size on western nonnative trees was significantly smaller than on eastern native host trees (1.71 vs. 3.51 larvae per female

per fruit). In contrast, since no *T. synthetica* larvae were produced on non-native eastern trees, no comparison could be made between its relative clutch sizes on native vs. non-native host trees (Smith *et al.* 2009, Fig. 5).

Smith *et al.* provide one major explanation for the large difference between the observed adult moth visitation rates and the low larval emergence rates on nonnative hosts. They suggest that the difference is due to discrepancies in phenotype matching between each moth species and the Joshua tree types (also see Godsoe *et al.* 2008). The two Joshua tree varieties differ not only in size but also in floral characteristics; the length of the floral stylar canal, where the moth ovipositor is inserted, is longer in the western tree type and shorter in the eastern tree type (Fig. 1C). Those differences match differences in the length of the ovipositor between moth species: the western moth species' ovipositor is 70% larger than the ovipositor of the eastern moth species (Pellmyr & Segraves 2003). Successful egg laying depends upon the length of the moth's ovipositor,

which penetrates down the floral style to the seed ovules. Given that in other yucca species oviposition damage can cause floral abscission (Pellmyr & Huth 1994), it is not unlikely that oviposition by the larger western moth species on the smaller eastern Joshua tree flowers may inflict enough damage to induce abscission. Although this would explain why zero western larvae emerged from eastern trees, the evidence supporting this hypothesis is indirect. Direct observation of western moths laying eggs in flowers of eastern Joshua trees and follow up on the fate of those flowers is required to fully support that hypothesis. The pattern in eastern moths is consistent with the prediction that moths with short ovipositors will not have access to all ovules of long styled flowers and thus will produce less offspring than in their native host. Although the hypothesis of phenotype matching of ovipositor-style length may partially explain the observed differences in larval emergence linked to host specificity, alternative and yet to be explored plausible hypotheses do exist (e.g. differences in volatile attractants, nutritional differences, differences in plant defense mechanisms that inhibit larval growth).

With this clear picture of patterns of host fidelity and fitness costs of oviposition in alternate hosts, it is possible to make predictions about patterns of reproductive isolation between the two tree varieties. The fact that eastern moths visit and produce offspring in the western host although at a significantly lower rate than in their native host, while western moths only do so in their own host, suggests that nuclear gene flow should be observed, and should be higher, from eastern to western trees than from western to eastern trees. Genetic work characterizing and quantifying nuclear gene flow between Joshua tree varieties is yet to be conducted, although the authors have developed nuclear markers to address the issue. However, the authors have shown evidence of cpDNA introgression from *western to eastern trees* (Smith *et al.* 2008). This is a puzzling observation explained as a case of chloroplast capture (Rieseberg & Soltis 1991) due to pollinator mediated nuclear gene flow from *eastern to western trees*. A proper test of that hypothesis will require collecting population genetic data from multiple nuclear markers.

Smith *et al.*'s work nicely connects empirical data to elements of a mathematical model of plant–pollinator codivergence proposed by Kiestler *et al.* (1984). That model is appropriate for explaining cases of plant–pollinator codiversification when some level of geographic isolation has existed during divergence, which seems to be the case in the Joshua tree–Yucca moth system. However, no convincing theoretical model has yet been proposed to explain codiversification in sympatry, when host and pollinator divergence still happen despite the presence of gene flow between diverging populations, as may be the case in the fig–fig wasp system (Machado *et al.* 2005). The presence of pollinator-mediated gene flow between plant hosts during divergence in sympatry or after secondary contact of formerly allopatric populations provides exciting prospects of future genetic work on plant–pollinator mutualisms. Those prospects are particularly exciting in the Joshua tree–Yucca

moth system given the presence of the natural hybridization experiment and the rich ecological and morphological data already in place. Patterns of introgression across the host nuclear genome should be influenced by the genetic architecture of differentially adaptive traits in both Joshua tree types. Therefore, areas of the genome carrying loci under divergent selection (e.g. loci affecting floral style length) are expected to be more differentiated than areas of the genome carrying neutral loci, and multilocus or genomic scans of divergence ('divergence mapping') may lead to the identification of those heterogeneously diverged regions (Machado *et al.* 2002; Nosil *et al.* 2009).

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