Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification

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1. Introduction

Obligate mutualism poses a conundrum for evolutionary biology for two reasons. First, mutualistic interactions are antagonistic interactions in which the fitness benefits outweigh the fitness costs, and the net benefits and costs may shift depending on ecological conditions (Thompson and Pellmyr, 1992; Bronstein, 1994). For example, in mutualisms involving seed-eating pollinators, plants pay a cost in terms of loss of offspring, but this cost is outweighed by a larger fitness gain through increased pollination and seed production. Evolutionary theory predicts that over time natural selection should act on mutualists to maximize fitness benefits and minimize fitness costs (Trivers, 1971; Axelrod and Hamilton, 1981; Murray, 1985; Bull and Rice, 1991; Doebeli and Knowlton, 1998; Herre et al., 1999; Weiblen et al., 2001; Bronstein, 2001; West et al., 2002; Holland et al., 2002), and mutualism is likely to break down without regulatory mechanisms that prevent overexploitation (Sachs and Simms, 2006; Edwards et al., 2010; Jandér and Herre, 2010). In spite of these regulatory mechanisms, cheaters/exploiters have evolved from within mutualistic lineages (Addicott, 1996; Pellmyr et al., 1996; Pellmyr and Leebens-Mack, 2000; Segraves et al., 2008). The second reason is that obligate mutualism usually results in extremely specialized interactions. Although not always true, specialization has been suggested to be an evolutionary dead-end because it increases the likelihood of extinction (Kelley and Farrell, 1998; Tripp and Manos, 2008; Johnson, 2010). For obligate mutualists, extinction of one mutualist leads to the extinction of the other. Despite the results from theoretical models and the assumption that specialization is a dead-end, some obligate mutualisms such as those between yuccas and yucca moths, figs and figs wasps, and attine ants and fungi have persisted for tens of millions of years (Pellmyr and Leebens-Mack, 1999; Mueller et al., 2001; Rønsted et al., 2005). Furthermore, once started, these mutualisms have diversified into species complexes of interacting mutualists whose evolutionary histories and futures are intricately linked (Pellmyr, 2003; Jousselin et al., 2006).

Obligate mutualisms are a small subset of mutualistic interactions, but they provide excellent systems to test ideas about the role of coevolution in mutualism. One of the unanswered questions in mutualism is the degree to which coevolution, reciprocal evolutionary change between mutualists, can be a significant factor in causing reproductive isolation, speciation, and cladogenesis. For
example, once an obligate mutualism is established and coevolution has molded the mutualists, does subsequent diversification of the interacting lineages demonstrate that ongoing coevolution is the driver? Answering this question in a phylogenetic framework is often difficult because there are a number of possible outcomes in phylogenetic patterns that could be generated by coevolution (Thompson, 1994, 2005; Segraves, 2010), and coevolution may have been important in some diversification events but not all lineages within a group. Co-speciation analyses have been widely used as a starting point to assess the potential importance of coevolution in diversification, but co-speciation between interacting lineages does not necessarily imply that reciprocal evolutionary change was the causative agent. Interacting mutualistic species will experience the same biogeographic and climatic events that may cause allopatric divergence in both lineages as a mutualistic interaction spreads across the landscape (Smith et al., 2008a). A pattern of co-speciation, then, can be generated by multiple processes making it imperative to differentiate among them in order to determine the major factor driving diversification.

We address the importance of coevolution to diversification in the obligate pollination mutualism between yuccas and yucca moths (reviewed in Pellmyr, 2003). This mutualism is often considered a classic example of coevolution and diversification (Rose and Mueller, 2006; Ricklefs, 2010). The mutualism has persisted for over 40 million years and has lead to interacting species complexes of plants and moths that are distributed across North America (Pellmyr and Leebens-Mack, 1999). The genus Yucca is the host plant for the yucca moths and consists of three monophyletic sections that differ in fruit type: the capsular-fruited Chaenocarpum, the fleshy-fruited Sarcocarpum, and the spongy-fruited Clustocarpum (McKelvey, 1938, 1947, Clary, 1997; Pellmyr et al., 2007). Yucca species range in size from small rosettes to large, towering plants, but all produce one or more inflorescences that hold ten to several hundreds of flowers, and all are pollinated by yucca moths. There are two genera of pollinator moths, Tegeticula and Parategeticula, in which female moths use unique mouthparts referred to as maxillary tentacles to actively collect and deposit pollen on the yucca flower stigmas (Riley, 1892; Davis, 1967; Pellmyr, 2003). Females lay eggs in the yucca flower, and moth species differ in how they place their eggs in the floral tissues. Among the 20 known species of Tegeticula, some species lay eggs deep into the locule next to developing ovules, and others lay eggs superficially in the outer pistil wall (Pellmyr, 2003). There are also two cheatier species that feed on seeds but do not pollinate (Pellmyr et al., 1996; Pellmyr and Leebens-Mack, 1999, 2000). In contrast, the five Parategeticula species lay eggs in shallow pits excavated in the flower petiole or petal, and after hatching, the larva crawls to the developing fruit to feed on seeds. Because moth larvae of all pollinator species only consume a small fraction of the developing seeds, the interaction is mutualistic for both moths and plants. The complete life cycle of the moth is tied to its host, with mating occurring on the host plant, and larvae and adults feed on no other plants. There are no co-pollinators of yuccas. Plant reproduction is occurring on the host plant, and larvae and adults feed on no other plant species. Plant fitness (Bronstein and Ziv, 1997; Althoff et al., 2004).

The radiations of Tegeticula, Prodoxus, and Yucca provide a comparative template to examine whether the coevolving mutualistic interaction between pollinators and yuccas is responsible for diversification in moth and plant lineages. Although members of the non-pollinating Prodoxus lineage are also extreme specialists on yuccas, they are commensalists. Thus, Prodoxus is unlikely to coevolve with yuccas, unlike the pollinator moths, because there is no reduction in plant fitness due to Prodoxus feeding. Consequently, examining co-speciation of Prodoxus with Yucca provides an ecological contrast to help determine the role of coevolution in co-speciation between Tegeticula and yuccas. These sister lineages of moths have similar levels of intimacy with their hosts, but differ in the type of interaction and propensity to coevolve with yuccas. We use previously published phylogenies of Yucca and Tegeticula, and supplemented a mtDNA phylogeny of Prodoxus to examine patterns of host use and speciation within moth lineages and to compare patterns of speciation between the interacting groups. Given the differences in selection pressures applied by pollinators in the genus Tegeticula relative to commensalistic Prodoxus moths, we predict that Tegeticula would exhibit a stronger pattern of co-speciation with their yucca hosts. Alternatively, if speciation within Tegeticula is largely due to geographic isolation as a result of range expansion and historical biogeography as opposed to coevolution, we would expect both pollinator and non-pollinator lineages to have similar patterns of phylogenetic congruence with yuccas.

2. Methods

Phylogenetic data from Althoff et al. (2006), Pellmyr et al. (2006), Pellmyr et al. (2007) and Pellmyr et al. (2008) were supplemented with new mtDNA cytchrome oxidase I and II sequences of a new species of Prodoxus, P. praedictus, that feeds within the fruit of Y. schidigera (GenBank Accession number GQ981319) (Pellmyr et al., 2009). These data included 4322 AFLP markers for the genus Yucca, and 2105 bp of mtDNA cytchrome oxidase I and II for the moth genera. A single individual was chosen to represent each species with the exception of Tegeticula corruptrix, which is the only moth species that feeds on both fleshy and capsular-fruited yuccas. A more extensive phylogeographic analysis suggests populations of T. corruptrix feeding on fleshy and capsular-fruited yuccas may constitute distinct lineages (Segraves et al., unpublished). We used one individual from each lineage. Methods for sequencing followed those in Althoff et al. (2006).

2.1. Phylogenetic analyses

The Yucca AFLP data were used in a Bayesian analysis implemented in MrBays 3.1.2 (Ronquist and Huelsenbeck, 2003) to estimate the plant phylogeny. Hesperoyucca whipplei was used as the outgroup. We chose one representative individual for each species except for Y. brevigolia, where emerging data suggest that Y. brevigolia may be two species situated along a north–south transect in the Mojave desert region (Pellmyr and Segraves, 2003; Godsoe et al., 2008; Smith et al., 2008a,b). For Y. brevigolia, we used one representative each from the northern and southern lineages. Bayesian analysis parameters included a restriction site model with Iset coding = noabsencesites, two runs with four chains, with relative burnin of 0.25, 4 million generations, and sampling every 1000 generations.

Moth sequence data were analyzed with both maximum likelihood and Bayesian methodologies. The analyses included Prodoxus (22 species), Parategeticula (5 species) and Tegeticula (20 species) (Supplemental Table 1). Mesepiola speisa (U49022) was used as the outgroup. The model of sequence evolution was determined using DT-ModSel (Minin et al., 2003). GTR + I + G was identified.


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as the most likely model of sequence evolution with the following
model parameter estimates: rate matrix = (4.783, 21.205, 7.854,
6.733, 62.251) base frequencies = (0.329, 0.110, 0.127), proportion
of invariant sites = 0.511, and gamma shape = 0.885. Maximum
likelihood analyses were implemented in PAUP 4.0b10 using a
heuristic search with random sequence addition and TBR branch
swapping. One hundred nonparametric bootstrap replicates were
performed to assess support for the resulting nodes (Felsenstein,
1985). MrBayes3.1.2 was used for the Bayesian analyses. Parame-
ters included a sequence evolution model of Iset nst = 6, rate-
s = invgamma, two runs with four chains, with relative burnin of
0.25, 4 million generations, and sampling every 1000 generations.

2.2. Comparisons of plant and moth phylogenies

Moth host use patterns were collated from Pellmyr (1999), Alth-
off et al. (2006), Pellmyr et al. (2006), and Pellmyr et al. (2007).
We examined the possibility of co-speciation and host switching
in three ways. First, we examined host use in relation to the moth
phylogeny to determine if, in general, there is a pattern of con-
served host associations with groups of closely related moths feed-
ing on group of closely related plants. Second, we performed
ParaFit analyses (Legendre et al., 2002) on the Tegeticula and the
Prodoxus phylogenies obtained from the maximum likelihood and
Bayesian analyses and the phylogeny of Yucca obtained from the
Bayesian analysis. We used the patristic distances as the distance
matrices for the moths and plants and conducted 1000 replicates
for statistical testing. We did not include an analysis for Paratege-
tica because of its limited number of extant species (Supplemen-
table 1; Pellmyr et al., 2008). For Tegeticula and Prodoxus, we
only included the clades in both lineages that feed on Yucca. Third,
we used JANE (Conow et al., 2010), an event–based method, to
examine co-speciation. We performed analyses with 500 genera-
tions and population sizes of 100. We explored how changes in
the cost structure associated with co-speciation, duplications of
parasites, host switches, loss of parasites, and failure to diverge
changed the overall costs of co-speciation between plant and moth
lineages. Although there are several other possible methods to
compare phylogenies of two lineages (summarized in Hughes
et al., 2007), there are two confounding factors that preclude the
use of many of these methods in comparisons of yuccas and their
associates: some moth species use multiple hosts, and parts of
the phylogenies of moths and plants are poorly resolved. Given
these conditions, we chose to compare the phylogenies of plants
and moths using ParaFit and JANE because these are co-speciation
tests that can account for these confounding factors.

2.3. Range overlap analysis in Yucca

We estimated the current range distributions for the Yucca spe-
cies with known Tegeticula pollinator species. Yucca range distribu-
tions were compiled from previously published systematic
revisions of the moths (Pellmyr, 1999; Pellmyr et al., 2006) and
collection notes by each of the authors. These ranges were drawn in
ArcGIS (version 9.2) and range size in hectares was calculated.
The degree of range overlap between all pairs of Yucca species
within the fleshy-fruited and capsular-fruited lineages was calcu-
lated following Berlocher (1998) where degree of overlap equals
the area of overlap divided by the smaller of the two species’
ranges. Mantel tests were used to test for an association between
genetic distance and degree of range overlap. If Yucca speciation
events within the capsular-fruited and fleshy-fruited lineages oc-
curred sympatrically, we expected a negative correlation between
genetic distance and the degree of range overlap (i.e., sibling spe-
cies should have low genetic distances with high degree of range
overlap).

3. Results

3.1. Patterns of host use and speciation in Tegeticula

The Tegeticula clade that uses Yucca contains 19 named species
(Supplemental Table 1). Seven of these species use capsular-fruited
yuccas as hosts, nine moth species use fleshy-fruited yuccas, and
two species use spongy-fruited yuccas (Supplemental Table 1).
The cheater T. corruptrix is the only moth species that uses yuccas
from more than one section, and it may best be viewed as two spe-
cies based on host use and DNA sequence divergence (Segraves
et al., unpublished). Twelve of the 17 pollinator species use a single
yucca species (Fig. 1). Tegeticula yuccasella is the most polyphagous
pollinator species, using seven species of yuccas (Pellmyr, 1999;
Leebens-Mack and Pellmyr, 2004). The non-pollinating cheater
species, T. intermedia and T. corruptrix, are known to use six yucca
species each (Supplemental Table 1).

The mtDNA phylogeny for Tegeticula was well supported at de-
eper nodes, but less so for more recent divergence events (Fig. 2).
There was no support for monophyly of moth species that feed on
the capsular and fleshy-fruited yucca sections. The monophyly
of moths on the spongy-fruited section is a consequence of the fact
that this section contains a single yucca species. There have been at
least two instances of host switches between capsular and fleshy-fruited
yuccas within clades of pollinators. Pollinator species that use multi-
ple yucca species, however, only use yuccas from one section. ParaFit
analysis of Tegeticula and Yucca rejected the hypothesis of indepen-
dence of speciation events (ParaFitGlobal = 0.01368; P < 0.001)
(Fig. 2). Twenty-eight of the 40 host–parasite links were significant.
There was evidence of overall co-speciation, but there are many in-
stances of diversification in one clade without corresponding diver-
sification in the other. JANE analyses corroborated this finding.
There were 22 failure to diverge events, 24 host switching events
and only 8 co-speciation events (Table 1). Changes to the cost struc-
ture for different events demonstrated that limiting the number of
co-speciation events by increasing the cost ten-fold did not change
the overall costs estimates for reconciliation in comparison to
changes in costs for other events (Table 1).

3.2. Patterns of host use and speciation in Prodoxus

The Prodoxus clade that uses Yucca contains 17 identified moth
species. Of these, two species use capsular-fruited yuccas as hosts,
13 species use fleshy-fruited yuccas, and two species use spongy-
fruited yuccas. Approximately half of the moth species are monophagous and many use two yucca species (Pellmyr et al., 2006) (Fig. 1).

The mtDNA-based phylogeny for Prodoxus was well supported (Fig. 2). There were two monophyletic clades, one consisting of the fruit-feeders on fleshy-fruited yuccas (P. y-inversus, P. praedic-tus, P. tamaulipellius, P. carnerosanellus, and P. sonorensis) and the other consisting of the rest of Prodoxus. Fleshy-fruited and spongy-fruited yuccas have fruit-feeding and stalk-feeding moths, whereas capsular-fruited yuccas are only used by stalk-feeding moths.

Fig. 2. Bayesian AFLP phylogeny for the plant genus Yucca and maximum likelihood/Bayesian cytochrome oxidase I and II mtDNA phylogeny for (a) Tegeticula and (b) Prodoxus. Numbers below the branches are Bayesian posterior probabilities and numbers above the branches are non-parametric bootstrap support values for the moth phylogenies. Names in green signify fleshy-fruited yuccas (section Sarcocarpa) and the moths that feed on them, names in brown signify capsular-fruited yuccas (section Chaenocarpa), and names in orange signify spongy-fruited yuccas (section Clistocarpa). The asterisk indicates the burst of speciation in Tegeticula approximately 3 Mya. ParaFit analysis indicated a significant overall level of co-speciation for yuccas and both moth genera. Solid lines represent significant individual co-speciation links between moth species and their hosts and dotted lines are non-significant links.
In contrast to *Tegeticula*, there was little speciation (2 *Prodoxus* vs. 7 *Tegeticula* species) associated with capsular-fruited yuccas. ParaFit analysis of *Prodoxus* and *Yucca* rejected the hypothesis of independence of speciation events (ParaFitGlobal = 0.06366; $P \leq 0.001$) (Fig. 2). Twenty-nine of the 37 host-parasite individual links were significant. There is evidence of overall co-speciation.

### Table 1

Results of JANE co-speciation analyses for *Yucca* and *Tegeticula* and *Yucca* and *Prodoxus*. A combination of co-speciation, moth species duplication, host switching, moth species loss, and failure to diverge events were detected for each comparison. Changes to the event cost structure (default = 0, 1, 1, 2, 1) suggest that co-speciation events are not major factors in reconciliation between plant and moth phylogenies.

<table>
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<th>Type of event</th>
<th>Cost scheme</th>
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<th>Duplication</th>
<th>Host switch</th>
<th>Parasite Loss</th>
<th>Failure to diverge</th>
<th>Overall cost</th>
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![Fig. 3.](image)

**Fig. 3.** Geographic distributions and correlations of range overlap with Nei-Li pairwise genetic distances of *Yucca* pollinated by *Tegeticula*. Similarly shaded ranges represent species from the same clade. (a) Ranges of fleshy-fruited yuccas (section Sarcocarpa) in green. Correlation, $r = -0.1565$, $P \leq 0.88$. (b) Ranges of capsular-fruited yuccas (section Chaenocarpa) in brown and spongy-fruited yuccas (section Clustocarpa) in orange. Correlation for capsular-fruited species $r = 0.11$, $P \leq 0.45$. 

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with few instances of independent speciation events. JANE analyses detected 40 failure to diverge events and 6 co-speciation events. As with Tegeticula, increasing the event cost for co-speciation ten-fold did not substantially change the total cost of reconciling the trees.

3.3. Range overlap analysis in Yucca

Within each subclade of the capsular-fruited and fleshy-fruited yuccas, the species ranges of Yucca with known Tegeticula pollinators are mostly allopatric (Fig. 3). For each Yucca section, mantel tests did not detect a significant correlation between genetic distance and percent range overlap (capsular-fruited, $r = 0.11$, $P < 0.45$; fleshy-fruited $r = -0.1565$, $P < 0.88$) (Fig. 3). Yucca species ranges do overlap, but these ranges are from species that are from different subclades within a section or from different sections. Species ranges from the fleshy-fruited and capsular-fruited clades overlap extensively, but within each section there is little range overlap.

4. Discussion

There is no doubt that species interactions have been an integral force in generating biodiversity (Thompson, 2005). Co-speciation analyses are one means to examine how species interactions may influence the patterns of speciation between interacting lineages. The terms co-speciation, co-diversification and coevolution have sometimes been used interchangeably, but there is an important distinction. Co-speciation and co-diversification refer to the pattern of reciprocal cladogenesis between interacting lineages, whereas coevolution is a process of reciprocal evolutionary change in response to selective pressures that interacting species impose on each other (Thompson, 1994). Interacting lineages may co-speciate or co-diversify, such as a parasites and hosts (e.g. Hafner and Page, 1995; Hughes et al., 2007), but not necessarily be coevolving. Host speciation may promote parasite speciation, as limited contact between sibling host species would isolate parasite populations as well. This process can occur in the absence of coevolution of host and parasite traits. A pattern of co-speciation may also arise in less intimately associated taxa, when geographic isolation due to climatic or geological factors affects interacting lineages similarly, resulting in concordant patterns of speciation (Segraves, 2010).

Coevolution between interacting lineages has been suggested as a major process that may lead to diversification and potentially co-speciation. Ehrlich and Raven (1964) envisioned rounds of coevolution of plant defenses and insect counter-defenses leading to bursts of speciation, but not co-speciation. Thompson (1994) termed this connection between coevolution and diversification sensu Ehrlich and Raven (1964) as ‘escape and radiate coevolution’. Thompson (1994) expanded on how coevolution may generate diversification by suggesting that diversifying coevolution is possible when one species controls the mating patterns of another. Diversifying coevolution has the potential to cause co-speciation between interacting lineages due to reciprocal reproductive isolation in both groups. Thompson (1994) envisioned diversifying coevolution as potentially important in plant-pollinator interactions and symbionts such as Wobacula that distort sex ratios or influence mating compatibility among their insect hosts.

Obligate seed-eating pollination mutualisms are systems that seem to be likely candidates for diversifying coevolution; pollinators control the movement of male plant gametes and these systems exhibit a high degree of specificity between interacting lineages. Reproductive isolation generated by ecological or evolutionary factors in one lineage would by necessity also influence the other lineage. Co-speciation in figs and fig wasps (Jackson, 2004; Ransted et al., 2005; Herre et al., 2008) and Epicephala moths and the tree genus Glochidion (Kato et al., 2003; Kawakita et al., 2004; Kawakita and Kato, 2006, 2009) demonstrate that there can be co-speciation in obligate seed-eating pollination mutualisms; however, determining whether coevolution has been important in determining the patterns of speciation is more challenging. In figs and fig wasps, coevolution occurred at some point in the evolutionary history of the interacting lineages, but that does not imply that contemporary coevolution is responsible for causing speciation (Weiblen and Bush, 2002; Machado et al., 2005; Marrussich and Machado, 2007; Jackson et al., 2008; Jousselin et al., 2008; Cook and Segar, 2010).

For yuccas and pollinator yucca moths there are a number of traits that are indicative of coevolution (Pellmyr, 2003). The pollinator moths have evolved specialized mouthparts for collecting and depositing yucca pollen, and moth larval feed exclusively on yucca species. Yuccas are solely pollinated by yucca moths and they have effectively lost the ability to produce nectar as a reward for pollinators. The presence of coevolved traits and the high degree of specificity between yuccas and their pollinator moths suggest the potential for diversifying coevolution in this interaction. In the current co-speciation analysis we can reject the null hypothesis of independent speciation. Although there are examples of host-switching and failure to diverge events in the moths, the yucca and yucca moth phylogenies exhibit concordance. Such concordance, however, does not necessarily imply the type of diversifying coevolution envisioned by Thompson (1994).

As in any co-speciation analysis, we are left with the overarching pattern, yet there remains a need to infer the process to gain a more accurate picture of the cause of diversification. Contrary to assumptions about the importance of coevolution in yuccas and yucca moths, there are multiple lines of evidence that suggest diversifying coevolution has at best, only weakly influenced speciation. For instance, one expectation of co-speciation and, in particular, of diversifying coevolution is that speciation events in interacting lineages should be nearly synchronous (Huelsenbeck et al., 2002). Molecular clock estimates for diversification events in the pollinator moths and yuccas suggest that the observed pattern of co-speciation is likely asynchronous. Estimates for the origin of Yucca suggest that the genus arose 18 to 9 Mybp, with the diversification of the capsular-fruited and fleshy-fruited lineages occurring 6 to 4 Mybp (Good-Avila et al., 2006; Smith et al., 2008a,b). Pellmyr and Leebens-Mack (1999) estimated Tegeticula had a burst of speciation (11 species) onto capsular-fruited and fleshy-fruited Yucca lineages 3.2 ± 1.8 Mybp. The results of these molecular clock analyses suggest that Yucca diversified approximately 2–3 My prior to the radiation of Tegeticula, although the error estimates indicate the possibility of contemporary speciation. Comparison of yucca and yucca moth tree shapes, however, does not support the hypothesis of diversifying coevolution. Whereas capsular-fruited and fleshy-fruited yuccas diverged early in the history of the genus (Smith et al., 2008a,b), all moth species currently pollinating capsular-fruited yuccas and several fleshy-fruited species arose relatively late in the history of Tegeticula in association with the burst of speciation mentioned above (Pellmyr and Leebens-Mack, 1999). This radiation in Tegeticula some three million years ago has been linked to shifts in oviposition behavior and the origin of cheating rather than coevolutionary diversification (Pellmyr and Leebens-Mack, 2000; Althoff et al., 2006). If we assume that the molecular clock estimates are accurate, it appears that pollinator moths have phylogenetically tracked yucca lineages rather than diversifying simultaneously.

A second line of evidence that suggests diversifying coevolution was weak between yuccas and yucca moths is the lack of sympathy of sibling species of plants with sibling species of pollinator moths.
Such a pattern would control for speciation caused by geographic isolation rather than by reproductive isolation driven by coevolution. A comparison of geographic range overlap and genetic distance revealed no association between relatedness and range overlap within the capsular-fruited or fleshy-fruited yucca lineages, suggesting that closely related species do not co-occur (Fig. 3). Furthermore, examination of sympatric populations indicates that there are no cases where both pollinator and yucca species are sibling species. In instances where multiple pollinator species and multiple yucca species do co-occur, the species within each group are not sibling species. In the Mojave desert, for example, the spongy-fruited Y. brevifolia co-occurs with the fleshy-fruited Y. schidigera and Y. baccata. Although Y. schidigera and Y. baccata are members of the same clade and it is possible that they could be sibling species, the pollinator moths that use them, T. mojavella and T. baccatella, are not sibling species and are distantly related. Similarly, Althoff et al. (2006) demonstrated that in cases where multiple capsular-fruited yucca species and their pollinators co-occur, the pollinator species are from distantly related lineages and differ in oviposition behavior.

A third line of evidence that suggests a minor role of diversifying coevolution in yuccas and yucca moths is the similar pattern of co-speciation between Tegeticula pollinator moths and yuccas and the non-pollinating Prodoxus moths and yuccas. These two equally diverse moth genera differ in the propensity for coevolution with yuccas. Prodoxus species do not pollinate nor do they feed on seeds. Instead they feed on other tissues and do not appear to have a significant impact on plant reproductive success (Bronstein and Ziv, 1997; Althoff et al., 2004). Even so, Prodoxus and Yucca have co-speciated. This result suggests that prodoxid moths in general are likely to phylogenetically track their host plant lineages even in the absence of strong coevolution (e.g., Percy et al., 2004). If host plant traits that are important to moths were phylogenetically conserved among closely related Yucca species, then a moth species could colonize closely related Yucca species as is evident for some Prodoxus species. For Prodoxus, mating on the host plant and selection on ovipositor morphology for using different yucca species are important components for causing population differentiation at microevolutionary scales (Groman and Pellmyr, 2000; Svensson et al., 2005), which may help fuel the macroevolutionary pattern of extreme specialization in host use among moth species. In the yucca moth lineage, Prodoxus is more ancestral than Tegeticula, suggesting that Tegeticula may have characteristics that promote phylogenetic tracking even in the absence of coevolution.

What then is the best explanation of the non-independence of speciation between yucca moths and yuccas? The asynchrony in diversification times and the current geographical distributions of yucca and moth species suggest that much of the concordant speciation patterns may be the result of moth lineages tracking yucca lineages through time and space. If current range distributions are indicative of past ranges, then allopatric/parapatric speciation is a likely mechanism for speciation in yuccas, and, subsequently, the moths. Within the capsular-fruited yuccas, only five of the 13 species have overlapping distributions and patterns of species relatedness correspond well with biogeographic divisions (Fig. 3). For example, the clade containing Y. glauca, Y. intermedia, Y. harrimanae, Y. angustissima, and Y. elata represent Yucca speciation in a region spanning the Colorado Plateau, the Great Plains, and the desert regions of the southwestern United States and northern Mexico. Similarly, within the fleshy-fruited yuccas that are pollinated by Tegeticula, there are few overlapping ranges. The range of Y. camerosana is within the range of Y. recurvula, but these are distantly related taxa and the pollinators that use them are also distantly related (Fig. 3). The geographic template of Yucca species distribution served as the foundation for moth speciation events. Thus, yuccas exhibit a pattern of speciation that is consistent with biogeographic separation as do the Tegeticula and Prodoxus species that use them (Althoff et al., 2006; Pellmyr et al., 2006).

The issue of using current range distributions to infer speciation patterns has a long history in evolutionary biology (e.g., Mayr, 1942; Brooks and McLennan, 1991; Morrone, 2009). Relatively recently however, Losos and Glor (2003) raise valid concerns about interpreting the geographical mode of speciation in a phylogenetic context based on current distributions. In particular they argue that species distributions can change drastically over evolutionary timescales and that it is difficult to infer species ranges at the time of speciation event. Given the large geographic range of Yucca and the complex historical biogeography of North America (Graham 1999) attempting to infer the historical range distribution of each Yucca species is problematic at best. We suggest, however, that the alternative scenario of coevolution between pollinators and yuccas causing repeated sympatric speciation events followed by numerous range contractions is highly improbable given the number of times that this would have had to occur to generate the present patterns. A simpler and more probable scenario is that moth lineages have phylogenetically tracked Yucca lineages through time and space. Moths are able fliers and have a much greater dispersal capacity than Yucca, allowing them to colonize new species of plants in different biogeographic regions (Leebens-Mack and Pellmyr, 2004). Coevolution is ongoing between some yuccas and pollinator moths at local scales (Smith et al., 2008a,b; Godsoe et al., 2008; Smith et al., 2009), but coevolution is unlikely to have caused the observed large-scale patterns of co-speciation.

Because of the high degree of allopatri in closely related yuccas, the interpretation of host use patterns of Tegeticula and Prodoxus in relation to plant phylogeny is confounded by geography as well. That is, current levels of host specificity may be an artifact of biogeography rather than (co-) evolutionary specialization to a particular Yucca species. This is supported by the fact that some pollinator species are capable of using multiple yucca species within a given area and moth ranges are less constrained than plant ranges. Tegeticula alitiplanella and T. superficiella both use the capsular-fruited yucca species that occur in the Colorado Plateau region (Althoff et al., 2006). The most polyphagous pollinator species, T. yuccasella, uses yucca species across eastern North America and the Edwards Plateau in central Texas (Pellmyr, 2003; Leebens-Mack and Pellmyr, 2004). In Prodoxus, the two species that use capsular-fruited species, P. decipiens and P. quinquepunctellus, are quite polyphagous and have host ranges that segregate into eastern yucca species and western yucca species, respectively (Althoff et al., 2001). Prodoxus mapimiensis appears to have incorporated many yucca species that are circumscribed by the range of Y. treculeana (Pellmyr et al., 2006). There is a high degree of monophagy for both moth groups, but much of this may be driven by ecological opportunity rather than differential selection pressures associated with different species of Yucca. Many of the geographic ranges of closely related yucca species do not overlap so there is no opportunity for moths to encounter additional phylogenetically-similar host plant species.

Given that there is little support for diversifying coevolution between yuccas and their pollinators, the question remains as to the underlying forces driving speciation in yuccas. If yuccas must have a moth pollinator that moves pollen, how were yuccas able to diversify in allopatri without corresponding diversification in the pollinators? This diversification is particularly puzzling since plant reproductive isolation implies that moth dispersal patterns were restricted as well. The lack of concordance of plant and moth diversification timing suggest that yuccas diversified first, followed by a later radiation of Tegeticula pollinators that replaced or complemented existing pollinators. Since yuccas require the pollination services of moths, another group of moths that could have initially
filled this role is *Parategeticula*. *Parategeticula* is the only other genus known to pollinate yuccas (Davis, 1967; Powell, 1984; Pellmyr et al., 2008). There are only five recognized species of *Parategeticula*, all of which occur only in the southern portion of the extant range of *Yucca*, which is the area suggested to be the origin of the genus *Yucca* (Clary, 1997). A possible hypothesis consistent with available phylogenetic data and molecular clock estimates is that *Parategeticula* preceded *Tegeticula* as specialized pollinators of yuccas (Pellmyr and Leebens-Mack, 1999). *Parategeticula* are poor fliers compared to *Tegeticula*, having lost the wing-locking mechanism that facilitates strong flight in lepidopterans. Their reduced flying ability may have facilitated reproductive isolation among yucca populations, and also made the moths more susceptible to extinction especially during glacial cycles. As yucca ranges expanded and contracted, some *Parategeticula* may have become extinct in parts of the host plant range and were replaced by *Tegeticula*.

In conclusion, it may be impossible to fully reconstruct the evolutionary reasons for the pattern of speciation in the yucca–yucca moth obligate mutualism, but currently available data strongly suggest that diversification in both lineages was not driven primarily by coevolution. The large degree of allopatric speciation in closely related plant and moth taxa, the incongruence of timing of speciation events in each lineage, and similar levels of co-speciation in non-pollinating yucca moths and yuccas indicate that other factors were more important. Pollinators in the genus *Tegeticula* likely radiated onto an already existing template of yucca diversification that was delimited by biogeography.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.11.024.

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