

## Strong Conservation of Floral Scent Composition in Two Allopatric *Yuccas*

Glenn P. Svensson · Olle Pellmyr · Robert A. Raguso

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**Abstract** Floral scent has been suggested to play a key role in the obligate pollination mutualism between yuccas and yucca moths. We analyzed floral fragrance compounds of *Yucca elata* with headspace collection followed by gas chromatography and mass spectrometry, and compared the odor blend with the recently characterized blend of the allopatric *Yucca filamentosa*. A principal component analysis based on 20 scent compounds revealed that the floral odor bouquets of *Y. elata* and *Y. filamentosa* are virtually identical. Although the two plants belong to the same section of capsular-fruited yuccas, they rely on different species of *Tegeticula* moths for pollination and probably have been allopatric for several million years. Yet, their floral odor blends are very similar, which may indicate that strong selection by obligate pollinators counteracts drift or divergence in this trait.

**Keywords** *Yucca elata* · *Y. filamentosa* · Floral scent · Geographic variation · Pollination mutualism

### Introduction

*Yucca* (Agavaceae) consists of perennial plants that grow in arid areas in North and Central America. Yuccas are known to be involved in an obligate mutualism with moths of two genera, *Tegeticula* and *Parategeticula* (Prodoxidae), in which pollination by female moths and provision of seeds for pollinator larvae are traded (Riley, 1872; Powell, 1992; Pellmyr, 2003). This moth–plant association is species-specific, and most yuccas rely on single yucca moth species for pollination (Pellmyr, 1999). *Yucca* is divided into three sections:

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G. P. Svensson · R. A. Raguso  
Department of Biological Sciences, University of South Carolina, Coker Life Sciences Building,  
700 Sumter St., Columbia, SC 29208, USA

G. P. Svensson (✉)  
Department of Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden  
e-mail: glenn.svensson@ekol.lu.se

O. Pellmyr  
Department of Biological Sciences, University of Idaho,  
P.O. Box 443051, Moscow, ID 83844-3051, USA

spongy-fruited *Clistocarpa*, fleshy-fruited *Sarcocarpa*, and capsular-fruited *Chaenocarpa*. Whereas *Clistocarpa* consists of a single species, *Yucca brevifolia* Engelm., the other two sections consist of some 20 species each. Plants produce up to several hundreds of flowers on single or multiple inflorescence stalks, and individual flowers are open and fragrant only after sunset. All reproductive behaviors of yucca moths, i.e., mating within host flowers, oviposition into ovaries, and active pollination, take place at night in all but one species (Powell and Mackie, 1966), and floral volatiles are thus suggested to be important sensory cues for these insects during host and mate search.

In contrast to the fig–fig wasp pollination mutualism, where the floral scents of many *Ficus* species have been chemically identified (Grison et al., 1999; Grison-Pigé et al., 2002a; Song et al., 2001) and where there is behavioral evidence for fig pollinator attraction to host volatiles (Grison-Pigé et al., 2002b; Hossaert-McKey et al., 1994; Song et al., 2001), data on the chemical ecology of the yucca–yucca moth mutualism are scarce. Recently, however, a research program was initiated to elucidate the role of floral scent in this classic insect–plant interaction and to analyze how the floral fragrance chemistry has evolved within the yucca lineage. So far, a detailed chemical analysis of the floral odor has only been conducted on the capsular-fruited *Yucca filamentosa* L. (Svensson et al., 2005). This species is native to southeastern USA, but has been spread by European settlers across eastern USA in modern times (Pammel, 1925). It relies on two distantly related *Tegeticula* species for pollination in different parts of its range: *Tegeticula cassandra* Pellmyr on the Florida peninsula and *Tegeticula yuccasella* Riley elsewhere (Pellmyr, 1999; Althoff et al., 2006). Gas chromatography and mass spectrometry (GC-MS) analyses of the floral headspace of *Y. filamentosa* revealed a complex blend of homoterpenes and long-chain aliphatic hydrocarbons, but also two dioxygenated compounds previously not reported as floral compounds in angiosperms (Svensson et al., 2005).

In this study, we report on the chemical characterization of the floral fragrance of a second species within *Chaenocarpa*. *Yucca elata* Engelm. occurs in southwestern USA and adjacent Mexico and appears to rely solely on *Tegeticula elatella* Pellmyr for pollination (Pellmyr, 1999). A recent amplified fragment length polymorphism (AFLP) based phylogeny of a subset of closely related *Tegeticula* pollinators has confirmed close relationship between *T. elatella* and *T. cassandra*, whereas *T. yuccasella*, the most abundant pollinator of *Y. filamentosa*, is nested within another species cluster of moths (Althoff et al., 2006). As no robust phylogeny is available for *Chaenocarpa*, the precise phylogenetic relationship between *Y. elata* and *Y. filamentosa* is not known. However, a phylogeographic analysis of the widely distributed, nonmutualistic *Tegeticula intermedia* Riley, which utilizes both yuccas as hosts, has revealed indirect evidence that these plants have probably been allopatric for several million years (Segraves and Pellmyr, 2004). This is also supported by paleoecological data showing an emergent barrier between eastern and western yuccas (Graham, 1999). The combination of a long history of isolation and dependence on distantly related pollinators in most parts of their ranges suggests that these yuccas may have diverged in their floral odor blends, and this hypothesis was tested here.

## Methods and Materials

### The Plants

*Yucca elata* inhabits semidesert grasslands in Arizona, New Mexico, northwestern Texas, and adjacent Mexico (Fig. 1). This 3- to 4-m-tall species produces single or multiple

rosettes on trunks, each with one or several paniculate inflorescence stalks. It flowers from early May to early June. In contrast, *Y. filamentosa* grows in sandy and rocky habitats in eastern USA. From a basal rosette, a single paniculate inflorescence stalk is produced. Plants flower from late April to mid July. Both yuccas produce up to several hundreds of white, bell-shaped flowers per inflorescence.

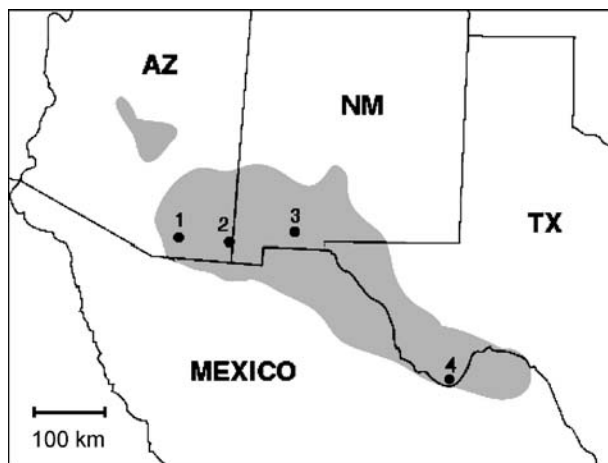
### Floral Scent Collection

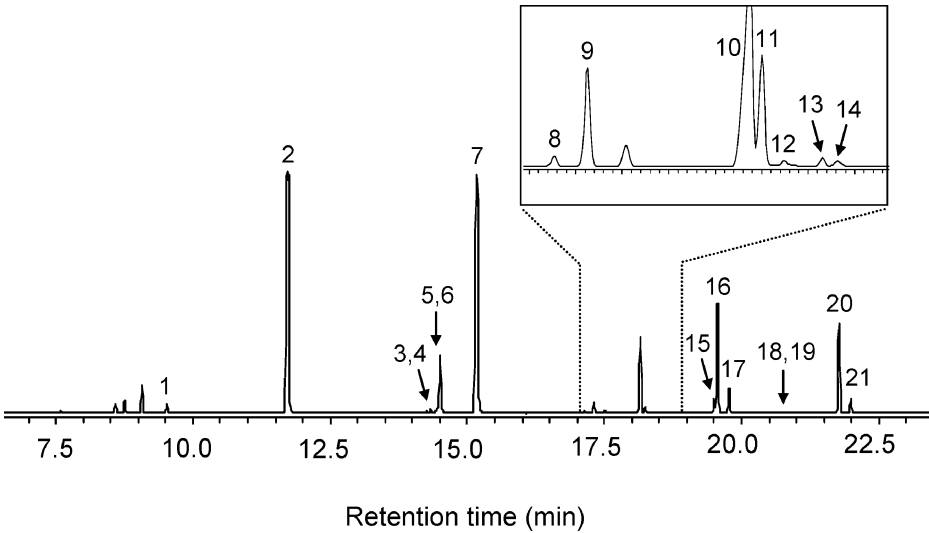
The floral fragrance of *Y. elata* was collected from four populations in 2004 and 2006: Benson (Cochise, Arizona; 31°58'04N, 110°17'40W), Portal (Cochise; 31°52'17N, 109°02'59W), Rock Hound State Park (Luna, New Mexico; 32°11'13N, 107°36'36W), and Big Bend National Park (Brewster, Texas; 29°15'00N, 103°15'00W; Fig. 1). The number of young flowers on each plant was counted before odor sampling to estimate release rates of volatile compounds on a per flower basis. The inflorescence was enclosed with a polyvinylacetate bag (406×444 mm), and a glass cartridge (7 mm i.d.) filled with 100 mg of Super Q absorbent (Alltech Associates, State College, PA, USA) was connected to the bag. Air passed through the filter at a rate of 200 ml/min using a PAS-500 personal air sampler (Supelco, Bellefonte, PA, USA). Odor collection was performed from 2000 to 2400 hours, corresponding to the maximum release of floral scent of *Y. elata* and peak activity of associated yucca moths, and after collection filters were eluted with 3 ml of hexane and extracts were stored at -18°C until analysis. Empty bags were used as ambient controls to check for possible contaminants emitted from a bag itself. Before GC-MS analysis, extracts were concentrated to 75 µl under N<sub>2</sub>, and 5 µl of 0.03% toluene were added as an internal standard to each sample to enable crude estimation of release rates of compounds.

### GC-MS Analysis of Floral Scent

Floral volatiles of *Y. elata* were analyzed using a Shimadzu GC-17A gas chromatograph, equipped with a DB-5 column (30 m×0.32 mm i.d., and 1-mm film thickness), and linked to a Shimadzu QP5000 mass spectrometer (EI: ionization energy=0.70 kV). Helium was used as carrier gas at a velocity of 43 cm/sec, and injector temperature was 270°C. Oven temperature was programmed for 50°C for 2 min after injection and then increased at 10°C/

**Fig. 1** Distribution of *Y. elata*. Dots indicate sites of odor collection: (1) Benson, (2) Portal, (3) Rock Hound State Park, and (4) Big Bend National Park





**Fig. 2** Gas chromatogram of the floral headspace of *Y. elata*. Peak numbers correspond to compounds in Table 1

min to 275°C. Compounds in extracts were identified by comparing mass spectra and retention times with those of available reference compounds and by mass spectral matches to library spectra.

#### Analysis of Geographic Variation in Floral Scent

For each population, the relative abundance of individual compounds in the fragrance blend was calculated. Also, the coefficient of variation ( $CV = \text{standard deviation} \times 100 / \text{mean}$ ) for each compound was calculated, using arcsine square-root-transformed ratios to better approximate a normal distribution. Two principal components analyses (PCA) were performed on arcsine square-root-transformed proportions of scent compounds. The first analysis included scent data from the four populations of *Y. elata* to screen for geographic variation in the odor blend. The second analysis also incorporated scent data from 10 populations of *Y. filamentosa* (Svensson et al., 2005) to test whether the floral odor blends of these two species differ. Before analysis, each variable was scaled to unit variance. The total release of floral compounds from *Y. elata* was quantified by the formula:

$$\text{Emission rate} = \frac{\left( \sum \frac{\text{peak area of compound}_x}{\text{peak area of IS}} \right) \times \text{amount of IS}}{\frac{\# \text{ flowers on plant}}{\text{h of sampling}}}$$

× extract volume after addition of IS

Total release rates of compounds were compared between populations using one-way analysis of variance. All statistics were performed using JMP 3.2.1 (SAS Institute, 1998). Leaves and flowers of *Y. elata* from each population were kept as vouchers and deposited at the A. C. Moore Herbarium at University of South Carolina.

## Results

Analyses of floral headspace extracts of *Y. elata* revealed that this species produces a blend of homoterpenes and aliphatic hydrocarbons virtually identical to that of *Y. filamentosa* (Fig. 2). The same 21 compounds recently identified from *Y. filamentosa* were also found in all *Y. elata* individuals, with the exception of the six plants from Big Bend NP, which lacked  $\beta$ -myrcene. The same two dioxygenated compounds with a prominent peak at  $m/z$  66 in the mass spectrum found in *Y. filamentosa* were also present in all *Y. elata* extracts (Fig. 2). Additional compounds, like  $\beta$ -pinene and *trans*- $\beta$ -ocimene (not found in *Y. filamentosa*), were detected only in trace amounts in a few samples. Few compounds in small amounts were found in ambient controls.

**Table 1** Mean percentage and CV of 21 floral volatiles from four populations of *Y. elata*

Compound	Site								Range of all populations (%)
	Benson (N=8)		Portal (N=11)		Rock Hound (N=9)		Big Bend (N=6)		
	%	CV	%	CV	%	CV	%	CV	
<b>Monoterpenes</b>									
1. $\beta$ -Myrcene <sup>a</sup>	0.7	55.7	0.6	45.7	0.4	71.8	0	–	0–1.8
<b>Homoterpenes</b>									
2. ( <i>E</i> )-4,8-Dimethyl-1,3,7-nonatriene <sup>a</sup>	35.4	20.1	31.8	18.8	35.9	29.9	28.0	13.8	15.4–71.0
4. Unknown homoterpene 1	0.5	28.8	0.8	25.7	0.4	45.2	0.2	4.1	tr.–1.2
6. Unknown homoterpene 2	6.1	17.6	8.4	17.9	5.9	29.8	2.4	4.9	1.0–11.3
7. C <sub>11</sub> -alcohol	25.1	12.5	25.4	5.6	26.7	12.8	23.8	14.8	19.4–35.9
11. Nerolidol <sup>a</sup>	2.5	43.2	2.4	42.3	1.6	51.6	3.2	42.7	0.1–5.3
<b>Unknowns</b>									
3. Unknown $m/z$ 67 1 (C <sub>11</sub> H <sub>18</sub> O)	0.4	18.1	0.5	35.5	0.4	51.7	0.2	12.0	tr.–0.9
5. Unknown $m/z$ 67 2 (C <sub>11</sub> H <sub>18</sub> O)	1.5	17.2	2.1	15.3	1.3	31.0	0.3	20.1	0.2–2.7
10. Unknown $m/z$ 66 1 (C <sub>11</sub> H <sub>14</sub> O <sub>2</sub> )	6.5	28.1	7.8	18.9	7.7	35.7	3.4	21.8	1.1–17.9
14. Unknown $m/z$ 66 2 (C <sub>11</sub> H <sub>14</sub> O <sub>2</sub> )	0.1	118.6	0.1	20.8	0.1	40.1	0.1	105.3	tr.–0.4
<b>Aliphatic hydrocarbons</b>									
8. Pentadecane	0.3	63.4	0.4	23.0	0.1	28.4	0.3	55.0	tr.–0.8
9. Pentadecane	1.6	43.2	1.9	32.5	1.4	24.0	2.0	16.0	0.4–4.9
12. Hexadecene	0.2	34.9	0.1	33.7	0.1	48.4	0.3	9.8	tr.–0.3
13. Hexadecane	0.1	35.7	0.1	22.0	0.1	28.7	0.3	26.7	tr.–0.2
15. Heptadecadiene	1.8	35.1	1.8	24.2	1.3	28.1	2.7	5.5	0.2–3.8
16. 1-heptadecene <sup>a</sup>	9.8	14.3	8.5	9.5	9.1	18.4	15.7	11.7	5.2–23.2
17. Heptadecane <sup>a</sup>	2.4	26.4	1.5	17.9	1.8	26.8	4.8	7.7	0.5–5.7
18. Octadecene <sup>a</sup>	0.3	45.5	0.2	57.0	0.2	56.6	0.8	9.6	tr.–0.7
19. Octadecane <sup>a</sup>	0.1	34.5	0.1	29.7	0.1	48.0	0.3	18.1	tr.–0.3
20. Nonadecene <sup>a</sup>	4.2	19.7	5.3	11.0	4.9	25.5	10.5	8.2	0.5–12.5
21. Nonadecane <sup>a</sup>	0.3	25.1	0.3	16.4	0.4	33.2	0.8	18.7	0.1–1.1

Compound numbers are the same as in Fig. 2. Trace (tr.) indicates amounts less than 0.1% of total.

<sup>a</sup>Compounds in which mass spectra and retention times were compared with that of reference compounds.

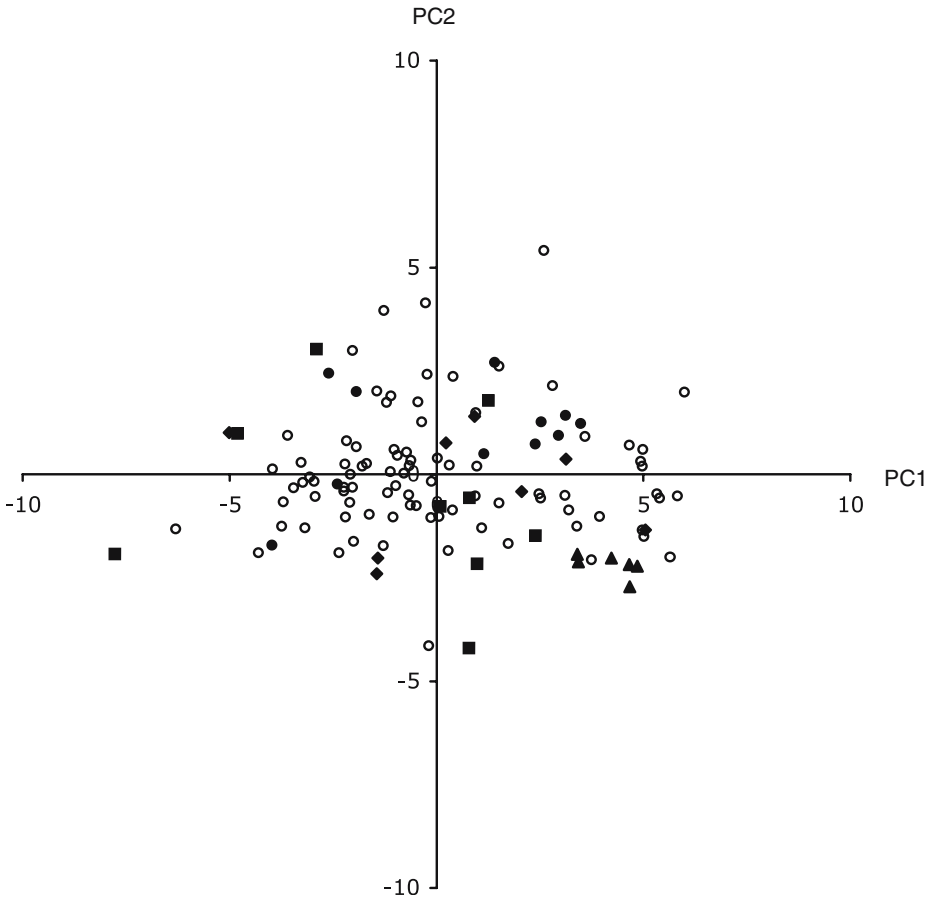
The relative ratios of 21 floral volatiles identified for *Y. filamentosa*, and also present in *Y. elata*, are shown in Table 1. Because of the absence of  $\beta$ -myrcene in Big Bend samples, this compound was excluded from the PCA. In the first PCA, four principal components with eigenvalues  $>1$  explained 85.2% of the total variation found in floral fragrance data. On PC1, (*E*)-4,8-dimethyl-1,3,7-nonatriene was the only compound with strong negative loading, whereas all aliphatic hydrocarbons had similar positive loadings (Table 2). On PC2, the  $C_{11}$ -alcohol and the first eluting dioxygenated compound loaded positively, whereas (*E*)-4,8-dimethyl-1,3,7-nonatriene and a majority of the aliphatic hydrocarbons loaded negatively.

A score plot of the first two principal components in the initial PCA revealed little geographic variation of the odor blend in *Y. elata*. Considerable overlap in the fragrance blend was observed across populations, with the exception of samples from Big Bend, which formed a distinct cluster in odor space. However, in a second PCA including fragrance data also from *Y. filamentosa* (Svensson et al., 2005), the floral odor blends of the two yuccas largely overlapped (Fig. 3), and *Y. elata* from Big Bend was nested within *Y. filamentosa*. The total emission of floral volatiles in *Y. elata* did not differ between populations (Benson:  $1.08 \pm 0.20 \mu\text{l flower}^{-1} \text{hr}^{-1}$ ; Portal:  $1.16 \pm 0.21 \mu\text{l flower}^{-1} \text{hr}^{-1}$ ; Rock Hound:  $1.03 \pm 0.17 \mu\text{l flower}^{-1} \text{hr}^{-1}$ ; Big Bend:  $1.56 \pm 0.23 \mu\text{l flower}^{-1} \text{hr}^{-1}$ ;  $F=1.12$ ,  $df=3$ ,  $P>0.10$ ).

**Table 2** Loading of the first two principal components of the 20 compounds used in the PCA

Compound	PC1	PC2
Total variation explained by each factor (%)	39.9	25.6
Homoterpenes		
2. ( <i>E</i> )-4,8-Dimethyl-1,3,7-nonatriene	-0.24	-0.23
4. Unknown homoterpene 1	0.00	0.42
6. Unknown homoterpene 2	-0.06	0.42
7. $C_{11}$ -alcohol	-0.02	0.14
11. Nerolidol	0.02	0.09
Unknowns		
3. Unknown $m/z$ 67 1 ( $C_{11}H_{18}O$ )	0.02	0.41
5. Unknown $m/z$ 67 2 ( $C_{11}H_{18}O$ )	-0.12	0.40
10. Unknown $m/z$ 66 1 ( $C_{11}H_{14}O_2$ )	0.02	0.27
14. Unknown $m/z$ 66 2	0.13	0.02
Aliphatic hydrocarbons		
8. Pentadecene	0.18	0.13
9. Pentadecane	0.21	0.22
12. Hexadecene	0.32	0.10
13. Hexadecane	0.29	0.01
15. Heptadecadiene	0.27	0.17
16. 1-heptadecene	0.31	-0.10
17. Heptadecane	0.34	-0.07
18. Octadecene	0.34	-0.02
19. Octadecane	0.31	-0.09
20. Nonadecene	0.31	-0.07
21. Nonadecane	0.24	-0.15

Compound numbers are the same as in Fig. 2.



**Fig. 3** Score plot of the first two principal components based on 20 compounds found in the floral headspace from four populations of *Y. elata* (■: Benson,  $N=8$ ; ♦: Portal,  $N=11$ ; ●: Rock Hound,  $N=9$ ; ▲: Big Bend NP,  $N=6$ ) and 10 populations of *Y. filamentosa* (from Svensson et al., 2005; ○,  $N=87$ )

## Discussion

Contrary to our prediction of divergent scent composition with different pollinators, GC-MS analyses of the floral headspace of *Y. elata* revealed that this yucca produces a blend of floral volatiles virtually identical to the related, allopatric species, *Y. filamentosa*. The same 21 compounds identified in the floral scent of *Y. filamentosa* (Svensson et al., 2005) were also found in *Y. elata*. Furthermore, the relative ratios of these compounds within the odor blends of the two yuccas are very similar, as shown in the score plot in Fig. 3. Low variation in the fragrance blend was observed both within and among populations of *Y. elata*, similar to the pattern observed in *Y. filamentosa*, where no difference in the floral scent composition was observed between populations with different pollinators (Svensson et al., 2005). Whether low variation in the fragrance blend and the use of unique compounds reflect mechanisms for selective attraction of exclusive pollinators to host

flowers has yet to be tested. In fact, little is known about the adaptive significance of low variation in the floral odor blends in plants. Few studies have analyzed how this trait varies between populations (e.g., Azuma et al., 2001; Knudsen, 2002; Dötterl et al., 2005), and direct comparisons of the variation of floral compounds that are electrophysiologically active in pollinators with that of nonactive ones have only been conducted in sexually deceptive *Ophrys* orchids (Ayasse et al., 2000; Mant et al., 2005).

Although earlier studies suggested monophyly for the section *Chaenocarpa* (McKelvey, 1947), the phylogenetic relationships among capsular-fruited taxa have not been fully resolved. Available AFLP data support rapid diversification of this group (Pellmyr et al., unpublished data), and at this point, the hypothesis of a close relationship, or even sister species status, of *Y. elata* and *Y. filamentosa* cannot be tested. On the other hand, the phylogeographic work on *T. intermedia* by Segraves and Pellmyr (2004) indicates that the two yuccas may have been allopatric for a long time. Western populations of this yucca moth feed on several capsular-fruited yuccas, including *Y. elata* (Pellmyr, 1999; Segraves and Pellmyr, 2004), whereas eastern populations only use *Y. filamentosa* as host (Pellmyr, 1999). Both mtDNA and AFLP data suggest that this moth arose in the west and later spread eastward. There was a deep genetic split between populations east and west of the Mississippi River basin, corresponding to a divergence time of about three million years (Segraves and Pellmyr, 2004). Although their ancestral ranges are unknown, it is reasonable to assume that *Y. elata* and *Y. filamentosa* have been allopatric for a similar period of time. Still, their fragrance blends are similar, and such lack of divergence in a potential key trait mediating attraction of exclusive pollinators may indicate that strong stabilizing or purifying selection has been imposed on the fragrance blend. Floral traits under strong selection (e.g., tube length in hummingbird-pollinated flowers) are expected to show relatively little variation (Fenster, 1991). If scent is irrelevant to the obligate interactions between yuccas and yucca moths, we would expect measurable divergence in chemistry between isolated populations of *Y. filamentosa* and *Y. elata* simply because of genetic drift. The identification and synthesis of floral scent compounds and their attractiveness to obligate pollinators in the field will be critical steps toward a better understanding of how selection acts on both emitters and receivers in this pollination mutualism.

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