Floral Visitor Guilds of Five Allochronic Flowering Asteraceous Species in a Xeric Community in Central Mexico

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ABSTRACT In this research, we determined: 1) the insect guilds visiting the flower heads of five Asteraceae species (*Eupatorium petiolare* Mociño ex De Candolle, *Senecio praecox* [Cavanilles] De Candolle, *Dahlia coccinea* Cavanilles, *Tagetes lunulata* Ortega, and *Verbesina virgata* Cavanilles); 2) the role of floral phenology and floral morphology on species composition and frequency of visits of different insect order; and 3) the diurnal schedules of anthophilous visitors and their relationship to temperature and relative humidity. Collections and observations of floral visitors for each species were made over 24 h per day. The five Asteraceae were visited by 137 Diptera, Hymenoptera, Coleoptera, and Lepidoptera species. *Tagetes lunulata* had the highest species richness of floral visitors (41 species), while *V. virgata* had the lowest (23 species). *Apis mellifera* L. (Hymenoptera) was the only visitor found visiting all five species. Species composition of insect visitors was closely related to plant phenology. Order-level frequency of visits was closely related to floral morphology. Two separate principal component analyses based on frequency of visits and floral morphology showed similar plant species groupings. Two groups of insects (Formicidae and Coleoptera) and two floral traits (ligulae length and presence of a cylindrical-campanulate involucre), respectively, were the variables determining these groupings. The highest frequency of anthophilous visitors coincided with the highest temperatures and the lowest relative humidity levels on flowers of all species, except *S. praecox*. The combination of diurnal activity and guild visitor analyses in this study showed the importance of including both characteristics in pollination studies.

KEY WORDS Asteraceae, floral visitors, similarity indexes, temporal variation, xeric community

ASTERACEAE ARE A GROUP OF PLANTS that have characteristic "head-type" inflorescences, which multiply the attractive functions provided by single flowers (Kevan and Baker 1983). Asteraceae congregate numerous flowers together, enhancing attractiveness for insect visitors, offering a flat surface for them to land, and improving pollination efficiency of insect visitors (Leppik 1977, Richards 1986). Because of their open structure, inflorescences may be visited by a large array of insect species, including ineffective pollinators and floral herbivores (Waser et al. 1996), which in turn may decrease plant reproductive success. It has been discussed that pollination effectiveness is a complex function of floral visitor identities, their relative abundances, and behaviors (Fishbein and Venable 1996).

Insects are the most frequent floral visitors of Asteraceae (Grashoff and Beaman 1970, Leppik 1977). Species of Coleoptera, Diptera, Hymenoptera, and Lepidoptera visit the flowers searching for nectar, pollen, predation sites, sex sites, oviposition sites, gums, fragrances, oils, resins, and floral tissues (Faegri and van der Pijl 1971, Bertin 1989). Pollination efficiency of insects can also be affected by environmental factors such as light, temperature, humidity, and wind (Willmer et al. 1994). These conditions determine both the periods of high insect activity and the quality of the nectar offered by plants (Kevan and Baker 1983).

It has been suggested that Asteraceae species are an important resource for pollen, nectar, and foliage feeders at the 'Pedregal de San Ángel' reserve in Central Mexico (Cano-Santana 1994). Soberón et al. (1991) estimated that *Dahlia coccinea* Cavanilles flower heads are visited by >25 insect species; however, their study was theoretical and no observational data were taken. Another study at the 'Pedregal de San Ángel' describes the importance of butterflies as pollen vectors (Domínguez and Nuñez-Farfán 1994). This study is a general approach to the importance of Lepidoptera to plant pollination, including some examples concerning Asteraceae. Many revisions of Asteraceae neglect any mention of the 'Pedregal de San Ángel' communities (Paray 1949, 1956, 1958; Sorensen 1969; Grashoff and Beaman 1970; Sullivan 1975; Heywood et al. 1977; Jeffrey 1977; Leppik 1977; Nordenstam 1977; Robinson and King 1977; Strother 1977; Stuessy 1977; Schmitt 1980, 1983). In spite of the im-

Table 1. Morphological and ecological features of the five Asteraceae species studied

Features	*E. petiolare*	*S. praecox*	*D. coccinea*	*T. lunulata*	*V. virgata*
Growth form[a]	Shrub	Shrub	Perennial Herb	Annual Herb	Shrub
Plant height (cm)[a]	90–200	100–500	40–200	20–80	100–250
Ligulate flowers[a]	Absent	Yellow	Yellow-Orange	Yellow	Yellow
Disc flowers[a]	White	Yellow	Yellow	Yellow	Yellow
Number of disc flowers by capitulum[a]	35–42	13–22	70–160	20–40	30–60
Flowering period[b,c]	Feb-Mar.	Feb-Apr.	July–Oct.	Oct-Dec.	Nov-Jan
Pollination[c]	Wind or self-compatible	Wind	Diurnal insects	Self-compatible	Self-compatible
Flower fragrance[b]	Sweet	Chocolate	Nonaromatic	Bitter	Nonaromatic

[a] Rzedowski and Rzedowski (1985).
[b] Figueroa-Castro (1997).
[c] Figueroa-Castro et al. (1998)

portance that these plants have for the 'Pedregal de San Ángel' and other terrestrial ecosystems, few studies have been undertaken to describe which insects are their floral visitors and possible pollinators.

Because of the lack of information about the reproductive biology and floral visitors to Asteraceae species and because of the importance of this family at the 'Pedregal de San Ángel' in terms of biomass (Cano-Santana 1994) and number of species (Valiente-Banuet and De Luna 1990), this work will greatly contribute to the knowledge about Asteraceae reproductive biology and ecology. The objectives of the current study are: 1) to identify and compare the guilds of floral visitors in five allochronic Asteraceae of high relative abundance at the Pedregal's reserve: *Eupatorium petiolare* Mociño ex De Candolle, *Senecio praecox* (Cavanilles) De Candolle, *D. coccinea* Cav., *Tagetes lunulata* Ortega, and *Verbesina virgata* Cavanilles; 2) to determine the role of floral phenology and floral morphology on the composition of insect visitor guilds; 3) to determine the diurnal variation in flower visitation by groups of floral visitors to these five Asteraceae species; and 4) to determine the relationship between environmental conditions (temperature and relative humidity) and floral visitor abundance.

Asteraceae flowers present a generalized floral syndrome; then, it is expected to find a high diversity of insects visiting their flower heads. Because of allochronic flowering of the study species, floral phenology should explain much of the variation seen in floral visitor species. At the order level, visitor guilds are expected to respond most strongly to floral traits caused by evolutionary history (Herrera 1996). Furthermore, insect frequency of visits should be correlated with temperature and humidity. It is also expected that insect activity will be different during diurnal and nocturnal hours, mainly because of temperature variation.

Materials and Methods

Study Area

The research was undertaken at the 'Pedregal de San Ángel' reserve, an area of 176 hectares located within the main campus of the 'Universidad Nacional Autónoma de México,' southwest of Mexico City (19° 20′ N, 99° 08′ W, 2300 m above sea level). This site registers an annual average temperature of 15.5°C and a yearly precipitation of 879 mm differentially distributed across the year, producing two distinctive seasons: a rainy season from June to October and a dry one from November to May (Rzedowski 1954, Valiente-Banuet and De Luna 1990). The reserve is located over a basaltic substratum deposited during the eruption of the volcano Xitle, 2,000 yr ago (Carrillo 1995). Vegetation at the reserve has a xerophilous scrubland aspect (Rzedowski and Rzedowski 1985), with most species showing resistance to drought. Most plant species are herbaceous or shrubby, although it is also possible to find 7-m trees (Rzedowski and Rzedowski 1985).

The 'Pedregal de San Ángel' reserve is located within Mexico City, isolated by at least 4.95 km from the closest natural areas. From the first half of the 20th century, the reserve has been subject to the effect of

Table 2. Approximate dimensions of the collecting areas, dates that insects were collected, and density of plants and flower heads on the patches in which collections were conducted in 1996

Species	Diurnal collection	Nocturnal collection	Site	Mean density of plants (No./m^2)	Mean density of floral heads (No./m^2)
E. petiolare	14 Mar.	15 Mar.	Three patches (20, 32 and 375 m^2)	0.46	635.6
S. praecox	9 Apr.	12 Apr.	Diurnal, one 300-m^2 patch; nocturnal, four patches (16, 45, 102, and 120 m^2)	0.37	18.5
D. coccinea	22 Aug.	6 Sept.	One 750-m^2 patch	13.30	56.9
T. lunulata	16 Oct.	18 Oct.	Two transects (151 and 174 m)	33.25	42.1
V. virgata	15 Nov.	22 Nov.	One 300-m^2 patch	0.79	77.5

street lighting, thermic inversions, high levels of atmospheric pollution, and an important decrease of adjacent natural areas caused by urbanization.

Study System

The flowering plant family Asteraceae is the most important at the reserve in terms of species richness (20%) (Valiente-Banuet and De Luna 1990) and has the greatest above-ground net primary productivity (ANPP) of the ecosystem (>32.6%; Cano-Santana 1994). The study species were selected according to their contribution to ANPP, as follows: *V. virgata* provides 15.1%, *D. coccinea* 9.6%, *S. praecox* 4.8%, and *E. petiolare* 2.5% (Cano-Santana 1994). *T. lunulata* is an herbaceous plant that contributes significantly to the above-ground phytomass of the ecosystem (Z.C.-S., unpublished data). Morphological and ecological features of the five species are described in Table 1.

Methods

Floral Visitor Composition. Insect visitors for each plant species were collected in 1996 during the peak flowering season, 24 h per day (Table 2). Two 12-h collections were made, one during the day and the other at night, no more than 1 wk apart in most cases. However, this was not possible for *D. coccinea,* because it flowers during the rainy season when rain occurs almost every night. Accordingly, the nocturnal collection was made 2 wk after the diurnal collection. Collections were made over plant patches that presented a high density of mature flower heads with flowers in anthesis (Table 2). We tried to make both day and night collections in the same patch of plants, to eliminate diurnal variation in microclimatic conditions, floral density, and reward quantity and quality. However, collections for *S. praecox* were made on various floral patches because flowers sampled in the diurnal collection had advanced anthesis and were no longer available for the nocturnal survey. Collections were made with aerial nets. For nocturnal collections, flashlights were used. Collected insects were put into cyanide-killing bottles, then transferred to paper bags and later pinned, dried, and classified. Voucher specimens of all the floral visitors were deposited in the Colección Entomológica at the Instituto de Biología from the Universidad Nacional Autónoma de México. To compare the composition of insect visitor guilds among Asteraceae species, Sorensen (S) and Czekanowski (C) similarity indexes were calculated (McNaughton and Wolf 1979). Sorensen similarity index considers only species richness. However, Czekanowski similarity index considers species abundance and richness. This index was calculated as: $C = \Sigma\ (2\,m_i)/\Sigma\ (a_i + b_i)$, where a_i is the frequency of visits of insects of order i to plant species a, b_i is the frequency of visits of insect of order i to plant species b, and m_i is the minimum value for the insect order (that is, in either a or b, whichever is smaller). Because pollination syndromes predict visitor guilds at the order level and because it is the level at which evolutionary responses might occur (Herrera 1996), we considered four distinct orders for Czekanowski similarity indexes: Hymenoptera, Lepidoptera, Diptera, and Coleoptera. Besides these four groups, we also included as separate groups some species, genus, or families into these orders that were highly abundant for at least one of the Asteraceae species. In addition, we divided all the groups in diurnal and nocturnal, as these are expected to differ from one another. In total, Czekanowski similarity indexes were conducted considering 12 groups of insect visitors: *Apis mellifera, Bombus* spp., other diurnal Hymenoptera, *Camponotus* sp., other Formicidae, other nocturnal Hymenoptera, diurnal Diptera, nocturnal Diptera, diurnal Lepidoptera, nocturnal Lepidoptera, diurnal Coleoptera, and nocturnal Coleoptera. Dendrograms showing the similarity among the 12 groups were made using methods described by Southwood (1978).

Table 3. List of floral traits examined in the principal components analysis

Floral trait
Minimum number of ligulae flowers
Maximum number of ligulae flowers
Presence of yellow ligulae
Minimum length of ligulae
Maximum length of ligulae
Minimum number of disc flowers
Maximum number of disc flowers
Presence of yellow disc flowers
Presence of white disc flowers
Minimum length of achene
Maximum length of achene
Presence of visible nectar guides
Presence of fertile ligulae flowers
Presence of a turbinate involucre
Presence of a cylindrical-campanulate involucre
Presence of a hemispheric involucre
Minimum length of involucre
Maximum length of involucre

To determine the role of floral traits on floral visitor guilds to the five Asteraceae species, principal component analyses (PCAs) based on floral traits and frequency of visits were conducted. PCA involving floral traits (PCA-FT) was developed considering 20 floral traits of the Asteraceae species taken from Rzedowski and Rzedowski (1985) and Sánchez (1980) (Table 3). PCA based on visitor guild frequency (PCA-VF) was conducted considering the same 12 groups used for *C.* Discrete variables were log transformed (Zar 1999). PCAs were conducted in Statistica, version 6.0. PCA-FT was compared with PCA-VF and also with Sorensen and Czekanowski similarity index-based dendrograms.

To determine the role of floral phenology on insect visitor composition, a floral phenology dendrogram was made. This dendrogram was made based on the number of days (d) between floral peaks of each pair of plant species, using the following equation of similarity index (SI): $SI = 1 - (d/182.5)$. This dendrogram was compared with those obtained through Sorensen and Czekanowski similarity indexes and with PCA-VF.

Floral Visitor Activity. To determine diurnal patterns of floral visitors and how environmental factors

Table 4. Table showing collected insects on the Asteraceae floral heads (U.F. = undetermined family)

Order/Family	Species	*E. petiolare*	*S. praecox*	*D. coccinea*	*T. lunulata*	*V. virgata*
Coleoptera						
Buprestidae	*Aemaeodera flavomarginata* (Gray)			X		
Carabidae	*Platynus* sp.			X		
Cerambycidae	*Trichoxys sulphurifer* Chevrolet					X
Chrysomelidae	Species 1			X	X	X
Coccinellidae	*Hippodamia convergens* Guerin		X			
Curculionidae	Species 1	X				
	Species 2				X	
Melolonthidae	*Diplotaxis* sp.		X			
	Euphoria basais Gory and Percheron			X		
	Phyttophago sp.			X		
U.F.	Species 1			X	X	X
U.F.	Species 2		X			
	Species 3		X			
	Species 4			X		
	Species 5	X				
	Species 6			X	X	
Tenebrionidae	*Cyrtomius plicatus* Champion					X
	Steriphanus mancus Champion					X
Diptera						
Agromyzidae	Species 1		X			
Anthomyiidae	Species 1		X			
Bibionidae	*Dilophus* sp.	X	X			
Bombyliidae	*Aphoebantus* sp.				X	
	Bombylius sp.				X	
	Diochanthrax sp.				X	
	Geron (Geron) sp.		X			
	Ligyra sp.				X	
	Paravilla sp.	X			X	
	Phthiria (Poecilognathus) sp.				X	
Calliphoridae	*Calliphora terraenovae* Macquart	X				
Conopidae	Species 1				X	
Culicidae	*Culiseta particeps* (Adams)	X				
Empididae	*Rhamphomya* sp.					X
Lonchaeidae	Species 1					X
Sarcophagidae	Species 1	X				
	Species 2				X	
	Helicobia sp.					X
	Sarcofahrtia ravinia Parlier	X				
Syrphidae	*Allograpta obliqua* Sail					X
	Cheilosia sp.			X		
	Copestylum meleum (Jeannicke)		X			
	Copestylum sp.		X	X		
	Eristalis (Esoohstalis) circe (Willston)		X	X		X
	Eristalis tenax (Linneaus)			X	X	
	Species 1		X			
	Eupeodes sp.	X	X			
	Lejops (Anasimya) sp. 1	X	X	X	X	
	Lejops (Anasimya) sp. 2		X			X
	Melangyna (Meligramma) sp.				X	
	Palpada sp.				X	
	Paragus (Pandasyopthalmus) haemorrhous Meigen	X	X			
	Platycheirus stegnum (Say)	X				X
	Toxomerus mutuus (Say)				X	
Tachinidae	*Adejeania vexatrix* (Osten Sacken)		X			
	Epalpus sp.		X			
	Species 1		X		X	
	Species 2				X	
	Species 3				X	
	Species 4					X
	Species 5				X	X
	Mochlosoma sp.				X	
	Peleteria sp.	X				
	Xanthophyto sp.					X
Tephritidae	Species 1					X
Tipulidae	*Nephrotoma* sp.					X
Hymenoptera						
Andrenidae	*Andrena* sp.					X
Apidae	*Apis mellifera* Linneaus	X	X	X	X	X
	Bombus ephippiatus Say			X		
	Bombus fervidus sonomae Howard			X		
	Ceratina neomexicana Cockerell	X			X	

Continued on next page

Table 4. Continued

Order/Family	Species	*E. petiolare*	*S. praecox*	*D. coccinea*	*T. lunulata*	*V. virgata*
Braconidae	Species 1				X	
	Species 2				X	
Colletidae	*Colletes* sp.					X
Formicidae	*Camponotus* sp.		X			
	Species 1		X			
Halictidae	*Mexalictus* sp.					X
Ichenumonidae	Species 1	X			X	
Megachilidae	*Paranthidium gabbi* Cresson		X	X		
Pompilidae	Species 1				X	
Scoliidae	*Capsomeris limosa* (Burmeister)			X		X
Sphecidae	*Steniolia* sp.		X			
	Stigmus sp.		X			
Vespidae	*Eumenes consobrinus* Saussure	X				
	Myschocyttarus pallidipectus (Smith)	X				
Lepidoptera						
Rhopalocera						
Hesperiidae	*Atalopedes campestris* (Boisduval)	X				
	Autochton cellus (Boisduval and Leconte)		X			
	Calpodes ethlius (Cramer)		X			
	Erynnis funeralis (Scudder and Burgess)			X		
	Hylephila philaeus (Druce)			X	X	
	Ochlodes librita (Ploetz)	X				
	Panoquina hecebolus (Scudder)			X	X	
	Paratrytone melane (Edwards)				X	
	Pyrgus communis (Grote)				X	
	Urbanus dorantes calafia Williams				X	
Nymphalidae	*Agraulis vanillae incarnat* (Riley)	X		X		
	Anemea ehrenbergii (Geyer)			X		
	Athanassa texana Edwards	X			X	
	Dione juno huascuma (Reakirt)				X	
Pieridae	*Aphrissa statira* Cramer			X		
	Catasticta teutila Dobleday			X		
	Colias philodice Godart				X	
	Euraema daira (Godart)			X		
	Nathalis iole Boisduval				X	
	Pieris protodice Boisduval and Leconte	X				
Rhiodinidae	*Calephelis perditalis* Varnes and MacDunnough	X				
U.F.	Species 1		X			
Heterocera						
Agaristidae	*Alypiodes bimaculata* Herrich-Schaffer			X		
Geometridae	Species 1	X				
	Species 2	X	X			
	Species 3	X				
	Species 4		X			
	Eupithecia sp.		X			
	Hydriomena sp.	X				
	Hygrochroma sp.	X				
	Plataea orsima Druce	X	X			
Noctuidae	Species 1	X				
	Species 2			X		
	Species 3	X				
	Species 4			X		
	Species 5			X		
	Species 6			X		
	Hydroeciodes mendicosa Dyar	X				
	Hydroeciodes sp.	X				
	Lycophotia margaritosa Haworth			X		
	Polia erecta Walker				X	
	Polia eresia Walker	X				
	Polia sp.			X		
	Prothortodes pseudochroma (Dyar)	X				
	Pseudaletia unipuncta Haworth			X		
	Zatrephes philobia Druce			X		
Pterophoridae	Species 1	X				
	Species 2	X				
	Species 3		X			
	Species 4		X			
Tortricidae	Species 1	X				
U.F.	Species 1				X	
	Species 2				X	
	Species 3					X
Total	**137**	**39**	**31**	**37**	**41**	**23**

Table 5. Species richness of the four most abundant insect orders on the heads of the studied Asteraceae at the 'Pedregal de San Ángel' reserve in Mexico City

Species	Coleoptera	Diptera	Hymenoptera	Lepidoptera	Total
E. petiolare	2	11	5	21	39
S. praecox	4	15	5	7	31
D. coccinea	8	5	5	19	37
T. lunulata	4	18	7	12	41
V. virgata	5	12	5	1	23

affect these patterns, insects landing on the heads of each species were observed and counted during 10 min every hour for a single 24-h period. Moreover, from two to five temperature and humidity measurements were made every hour using a hand-held Oakton thermohygrometer, which was <0.5 m from the flowers. Correlations of average temperature and humidity with the number of visitors to flowers of each species were determined on an hourly basis. Counts and humidity values were transformed as $(x + 0.5)^{1/2}$ and arcsine $(x)^{1/2}$, respectively (Zar 1999).

Results

Floral Visitor Composition

The floral heads of the five Asteraceae were visited by 137 insect species: 54 Lepidoptera species, 46 Diptera, 19 Hymenoptera, and 18 Coleoptera, all of them belonging to at least 46 families and 106 genera (Table 4). Species richness of anthophilous insects varied from 23 for *V. virgata* to 41 species for *T. lunulata* (Tables 4 and 5). Only one species, *A. mellifera,* was seen on all five Asteraceae, and only one other species, *Lejops* (*Anasimya*) sp. 1 (Diptera: Syrphidae), was seen on four species. Only three insect species were shared among three Asteraceae species: two unknown species of Coleoptera and the hover-fly *Eristalis* (*Esoohstalis*) *circe* (Willston). Based on the contribution to the species richness, Lepidoptera was the richest order visiting *E. petiolare* and *D. coccinea,* while Diptera was for *E. petiolare, S. praecox, T. lunulata,* and *V. virgata* (Table 5). In contrast, a low species richness of Lepidoptera on *V. virgata* flowers (only one nocturnal species) was found. This was also the case for Coleoptera on *E. petiolare* flowers, in which only two species were recorded (Table 5).

With the exception of *T. lunulata* (Fig. 1), *A. mellifera* was one of the most abundant diurnal visitors to all species. *A. mellifera* was the most frequent species of floral visitors on *V. virgata, D. coccinea,* and *E. petiolare.* Other frequently observed visitors to flowers of *D. coccinea* include bumblebees (*Bombus* spp.) and Diptera (*Cheilosia* sp.) (Fig. 1c). The most frequent visitors to *S. praecox* flowers were the Formicidae *Camponotus* sp. and other unidentified ant species (Fig. 1b), which foraged on the flowers at night. The most frequent insects found on *T. lunulata* flowers were Diptera and Hymenoptera (excluding *A. mellifera*) (Fig. 1d).

In both Sorensen and Czekanowski similarity indexes, the highest similarity was between *D. coccinea* and *V. virgata* (S = 23.1%, sharing 9 of 78 visitor species; C = 68.5%) (Fig. 2). The second highest Sorensen similarity index was for *E. petiolare* and *S. praecox* visitor guilds (20.0%), sharing 7 of 70 insect visitor species. Guilds of visitors to *V. virgata* and *E. petiolare* and to *E. petiolare* and *D. coccinea* were the most dissimilar (6.4 and 7.9%, respectively), sharing only 2 of 62 and 3 of 76 visitor species, respectively (Fig. 2a). According to these indexes, two plant groups can be distinguished, the first one formed by species flowering during the dry season (*E. petiolare* and *S. praecox;* Table 1), and the second one by species flowering during the rainy season or at the beginning of the dry season (*D. coccinea, T. lunulata,* and *V. virgata;* Fig. 2a; Table 1). The second highest Czekanowski similarity index was for *E. petiolare* and *V. virgata* visitor guilds (57.5%). The third highest percentage of similarity was between *T. lunulata* and *E. petiolare* (45.5%). The lowest similarity index was observed between *S. praecox* and *V. virgata* (29.1%) (Fig. 2b).

Similar plant groupings were found with both principal component analyses (Fig. 3). In principal component analysis based on floral visitor frequency, the first component explained 49.30% of the variance, while the second component explained 21.47%. The first component was closely related to *Camponotus* sp. frequency of visits ($r = -0.93$) and other Formicidae ($r = -0.87$), whereas the second component was significantly correlated with frequency of visits of nocturnal Coleoptera ($r = 0.94$), *Camponotus* sp. ($r = 0.89$), and other Formicidae ($r = 0.94$). *S. praecox* had a strong positive relationship with the second component, while the other four plant species had a less positive relationship. *T. lunulata* had the most negative relationship with the second component. Furthermore, while *S. praecox* had a weak positive relationship with the first component, the other four plant species were more strongly positive (Fig. 3a). Similar results were found in PCA-FT. In this analysis, the first component explained most of the variance (89.80%). Similarly to the other analysis, *S. praecox* was at an opposite side from the other four plant species. *S. praecox* showed a strong negative relationship with the second component and less positive than the other species with the first component. *T. lunulata* was also slightly separated from the other three plant species. The first component did not show any significant correlation with any of the floral traits evaluated. However, the second component was significantly correlated to maximum length of ligulae and presence of a cylindrical-campanulate involucre ($r = -0.87$ and -0.86, respectively) (Fig. 3b).

Floral phenology dendrogram showed two groups, one formed by those species flowering during the dry season (*E. petiolare* and *S. praecox*) and the other formed by *D. coccinea, T. lunulata,* and *V. virgata,* which flower during the rainy season (Fig. 2c).

Comparing both phenology dendrogram and PCA-FT with visitor guild dendrogram based on Sorensen similarity index, phenology dendrogram showed the same pattern found in the visitor guild

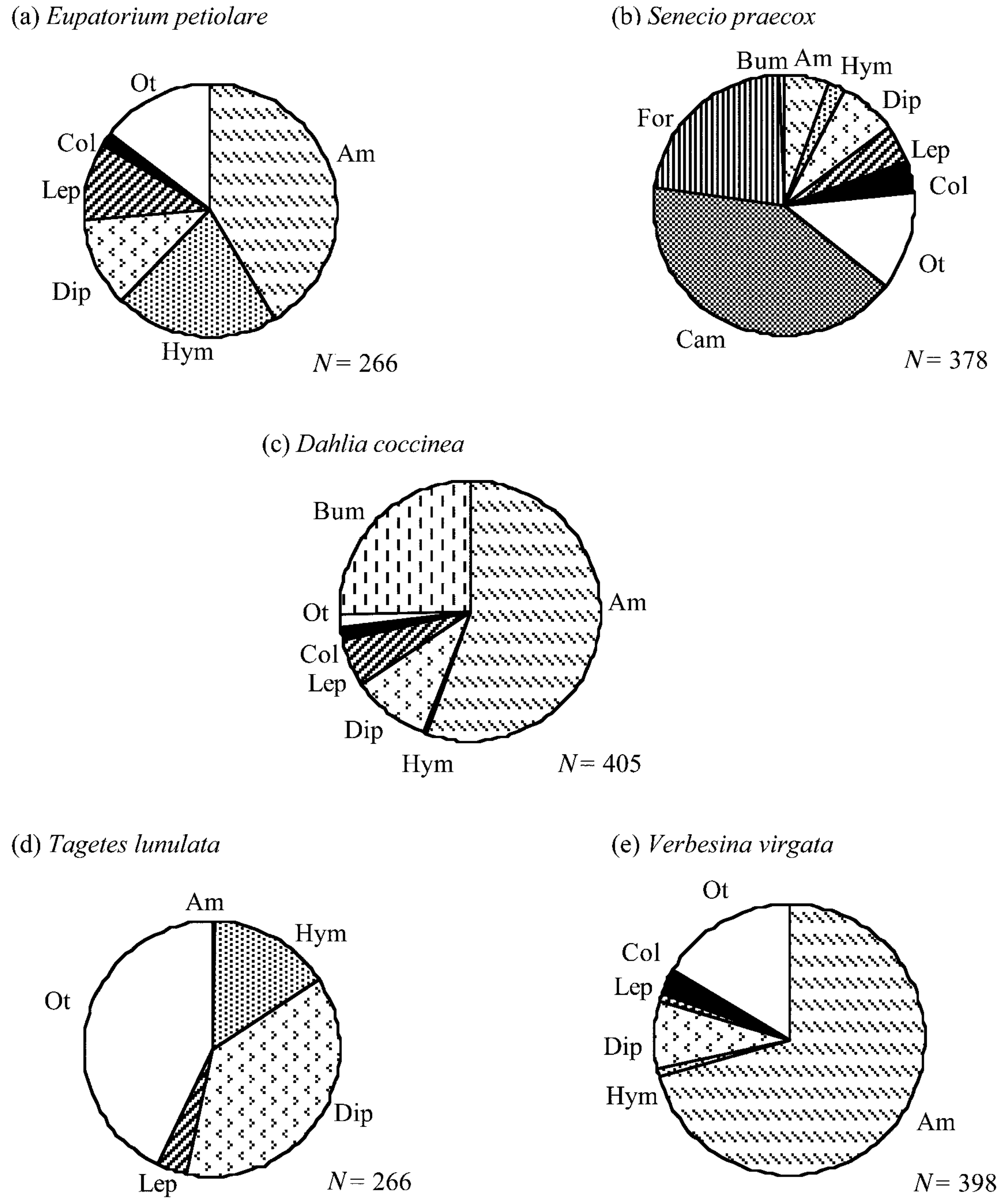
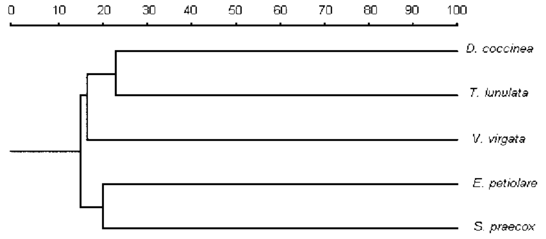


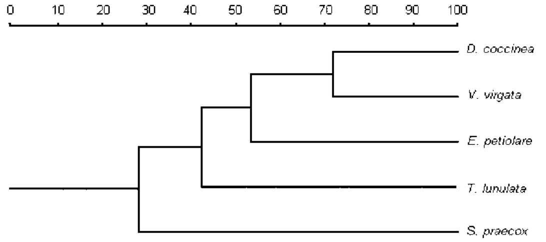
Fig. 1. Relative frequency of the various floral visitor groups that were observed foraging on the heads of the five Asteraceae species at 'Pedregal de San Ángel' reserve, Mexico. Bum, bumblebees; Am, *A. mellifera*; Cam, *Camponotus* sp.; Col, Coleoptera; Dip, Diptera; For, Formicidae; Hym, Other Hymenoptera; Lep, Lepidoptera; Ot, Other.

dendrogram. *S. praecox* and *E. petiolare* were members of the same group, while *D. coccinea, T. lunulata,* and *V. virgata* were members of the other one (Figs. 2c and 3). In contrast, the ordination of plants based on floral traits (Fig. 3b) was dissimilar to dendrogram based on species composition (Fig. 2a), but it was very similar to the pattern obtained with Czekanowski similarity index and to the ordination based on floral visitor frequency. *E. petiolare, D. coccinea, T. lunulata,* and *V. virgata* are close to each other, while *S. praecox* is

a) Sorensen similarity index



b) Czekanowski similarity index



c) Floral phenology

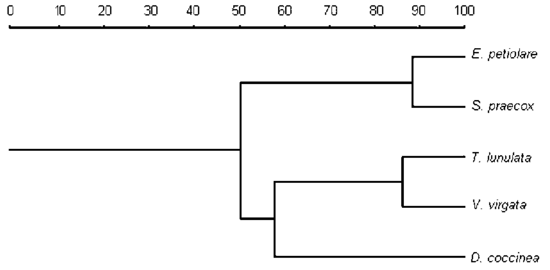


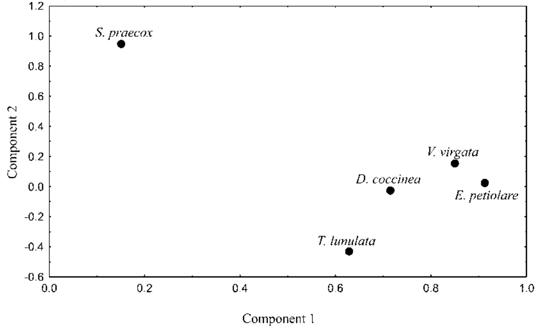
Fig. 2. Dendrograms showing (a) Sorensen similarity indexes (*S*) obtained from species composition of floral visitors shared by the studied Asteraceae, (b) Czekanowski similarity indexes (*C*) obtained from frequency of visits of each insect order, and (c) similarity indexes among the five Asteraceae species based on floral phenology. For details, see *Methods.*

far apart from all of the other Asteraceae (Figs. 2b and 3a).

Floral Visitor Activity

S. praecox received the largest number of nocturnal floral visitors, particularly between 2245 and 0445, when the highest abundance of ants was observed. The flower heads of the other four species had a higher frequency of visitors during the day (Figs. 4 and 5). Nocturnal floral visitors for *D. coccinea, T. lunulata,* and *V. virgata* were almost nonexistent, except for Lepidoptera, whose abundance was almost always highest during and just after sunset, especially on *E. petiolare* heads (Figs. 4 and 5). Visitation frequency to *E. petiolare, D. coccinea, T. lunulata,* and *V. virgata* decreased drastically from 1645 h and on. The lowest frequency of visitors for the five species was observed between 0445 and 0745 h, when virtually no visits occurred (Fig. 5).

a) Floral visitors



b) Floral traits

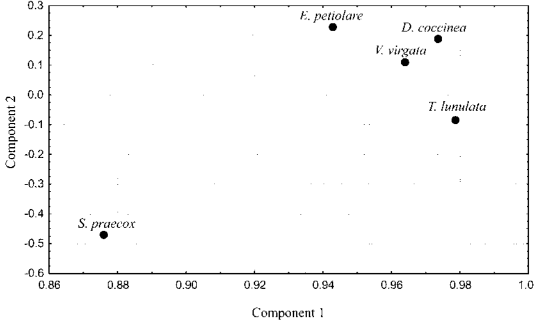


Fig. 3. Bivariate plot of the first two principal components from analyses in variation in (a) floral visitors, and (b) floral traits of the five Asteraceae species studied.

Activity periods of diurnal insects varied among plant species (Figs. 4 and 5). For *E. petiolare,* the highest period of activity was between 0845 and 1645 h, mainly because of the intense foraging activity of Hymenoptera (Fig. 4). For *S. praecox* and *T. lunulata,* the highest activity of visitors was between 0945 and 1545 h, while for *D. coccinea* between 0845 and 1745 h. Guild visitors that determined such activity peaks were Hymenoptera and Diptera for *S. praecox,* and Hymenoptera, Diptera, and Lepidoptera for *D. coccinea* and *T. lunulata.* Finally, the period of highest activity for *V. virgata* was between 0745 and 1645 hours, mainly because of Hymenoptera, Diptera, and Coleoptera activities (Fig. 4).

Environment was significantly correlated with visitor frequency (Fig. 5). Apart from *S. praecox,* frequency of visitors was positively correlated with temperature and negatively correlated with humidity (Table 6). Most visits occurred during the morning and at noon, at times of the highest temperatures and lowest levels of humidity (Fig. 5). Visitation frequency on *S. praecox* was positively correlated with humidity (Table 6), because the largest number of ants visited at night, when the highest level of humidity was recorded (Fig. 5).

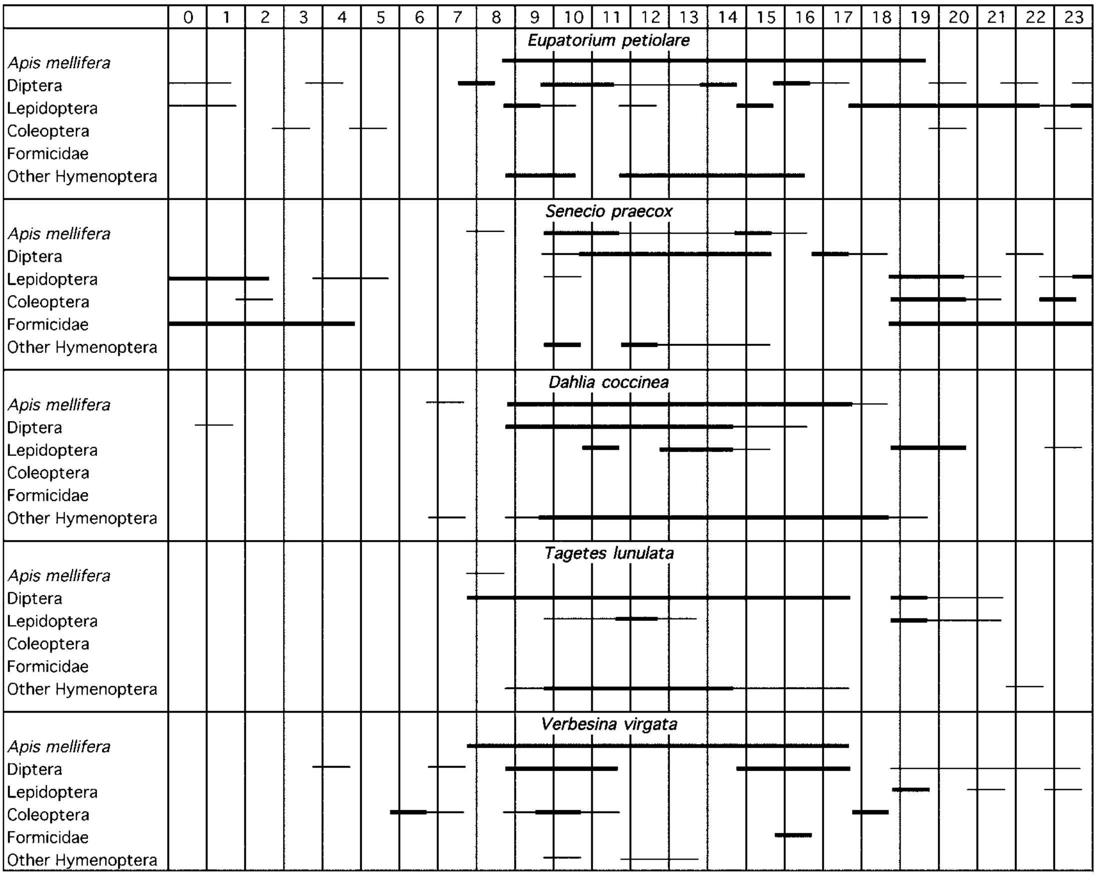


Fig. 4. Periods of activity for floral visitor guilds of five Asteraceae species at the 'Pedregal de San Ángel' reserve in Mexico City. Thick lines represent periods in which two or more individuals were recorded. Thin lines represent periods in which just one individual was recorded.

Discussion

The species of Asteraceae studied are visited by a large diversity of floral visitors. Boldt and Robbins (1987) found similar insect diversity on flowers of *Baccharis neglecta* Britt, which was visited by 46 species of anthophilous insects.

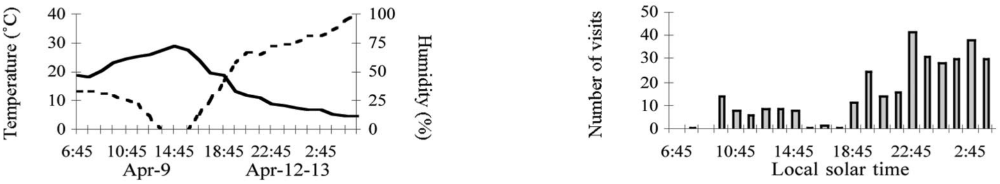
Many surveys suggest that plants of the *Eupatorium* genus are pollinated by wind (Grashoff and Beaman 1970, Sullivan 1975). This has been corroborated for *E. petiolare* at the 'Pedregal de San Ángel' reserve (Figueroa-Castro 1997); however, this species presents floral features that indicate an important entomophilic relationship. Some of those features are white capitula producing a fresh and sweet fragance, which possibly make flowers more visible and attractive at night.

Members of the Formicidae family, particularly the *Camponotus* genus, were found only on *S. praecox*, and therefore these ants could be their pollinators. Regarding this point, many authors have discussed ant ineffectiveness as pollinators primarily because the secretions of the metapleural gland inhibit pollen germination (Faegri and van der Pijl 1971) leading to a decreased seed production (Beattie et al. 1985, Hull and Beattie 1988). However, some authors suggest that ants are effective pollinators (Peakall and Beattie 1989, Peakall et al. 1990, Gómez and Zamora 1992, García et al. 1995, Ramsey 1995, Gómez et al. 1996), particularly those species inhabiting dry and warm sites (Hickman 1974). Some other studies reveal that ants that do not present metapleural glands like *Camponotus* spp. (Beattie et al. 1985), as well as those species having a high relative abundance (with and without metapleural glands) can be effective pollinators (Peakall and Beattie 1989, Gómez and Zamora 1992, García et al. 1995, Gómez et al. 1996). From this, we can infer that the ants observed on *S. praecox* may have some role as pollinators. However, this idea requires more research to be confirmed.

Although *T. lunulata* is self-compatible and can set seeds in absence of floral visitors (Figueroa-Castro 1997), it has the largest number of floral visitors, mainly Diptera, perhaps because of its colored ligules, the presence of nectar guides, and the bitter perfume

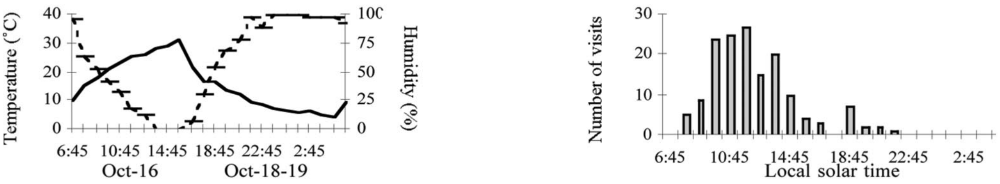
a) *Eupatorium petiolare*

b) *Senecio praecox*



c) *Dahlia coccinea*

d) *Tagetes lunulata*



e) *Verbesina virgata*

Fig. 5. Diurnal variation of floral visitors (bar graphs), temperature (solid line), and relative humidity (dashed line) in 1996, during the collecting days on the five Asteraceae species at 'Pedregal de San Ángel' reserve.

that emanates from its heads. It is also possible that Diptera are visiting the heads of this species not only in search of food, but also in search of oviposition sites, as has been demonstrated by parallel studies correlating the number of achenes per head and the number of Diptera larvae found (Figueroa-Castro 2001).

Diurnal Lepidoptera were not found visiting the heads of *V. virgata*, which suggests its flowers are not

Table 6. Correlation coefficients between floral visitor abundance for each plant species with temperature and humidity

Species	Temperature (°C)		Humidity (%)	
	r	P	r	P
E. petiolare	0.819	<0.05	-0.787	<0.05
S. praecox	-0.462	n.s.	0.566	<0.05
D. coccinea	0.920	<0.05	-0.854	<0.05
T. lunulata	0.797	<0.05	-0.739	<0.05
V. virgata	0.932	<0.05	-0.813	<0.05

In every case df = 22.
n.s. = not significant

offering a good reward (either in quantity or quality) to this group of insects. This study cannot directly assess this possibility; however, in this study, we recorded that diurnal Lepidoptera cross over *V. virgata* to visit *Lagascea rubra* Kunth, another Asteraceae species that flowers in the same season as *V. virgata.*

It is probable that the floral heads of the study species are not only being visited in search of food, but also in search of other kind of rewards, such as warmth and oviposition sites, or even refuge (Faegri and van der Pijl 1971, Kevan and Baker 1983, Richards 1986, Bertin 1989). As an example, some Coleoptera and Thysanoptera may be using floral heads of *D. coccinea* and *T. lunulata* as refuge (Figueroa-Castro 1997). Similarly, some Hymenoptera use *D. coccinea* heads as a "comfort place" (to rest at night) (D.M.F.-C., unpublished data); some Lepidoptera, Coleoptera, and Diptera use them as oviposition sites, allowing their larvae to feed on nonmature fruits, while *Sphenarium purpurascens* Charpentier (Orthoptera: Pyrgomorphidae) and *Euphoria basalis* Gory and Percheron (Coleoptera: Melolonthidae) obtain their food from floral capitula (Figueroa-Castro 2001).

Results obtained with Sorensen and Czekanowski similarity indexes and PCAs provided different and valuable information. According to Sorensen similarity index, seasonality is the factor determining how similar are the insect visitor guilds of the Asteraceae species. However, Czekanowski similarity index and PCA-VF showed that diurnal patterns of insect activity are grouping the Asteraceae species. Sorensen similarity index is an approach to the specific level, whereas Czekanowski similarity index is an approach at the order level. At order level is expected that insects will respond most strongly to floral traits because of their evolutionary histories (Herrera 1996). The results obtained through the Sorensen similarity index showed that seasons strongly determine what kinds of insects visit the Asteraceous flowers. This index showed that those species flowering in the same season are more similar than those flowering at a different time (Fig. 3; Table 1). This was corroborated by phenology dendrogram, which demonstrated a similar pattern to the one showed by floral visitor dendrogram based on Sorensen similarity index. These results suggest that only those insect species having a long life cycle are shared by different plant species, allowing a better exploitation of various resources across the year. A representative case is *A. mellifera,* whose populations obtain food from flowers of various species throughout the year. This phenomenon may suggest the existence of a sequential mutualism (Waser and Real 1979) among the study species, i.e., a facilitation mechanism through pollinators support by which those species flowering chronologically first support the initial populations of pollinators, enabling insect survival and reproduction, therefore facilitating pollinator availability for those species flowering later. Although *A. mellifera* has been considered a very reliable pollen vector (Faegri and van der Pijl 1971), it is probable that it is not acting as an efficient pollinator at the 'Pedregal de San Ángel' because it visits various plant species flowering during the same season (D.M.F.-C., unpublished data).

The order-level frequency of visits obtained through Czekanowski similarity index and plant grouping derived from PCA-VF were more related to floral morphology than floral phenology (Figs. 2 and 3). The floral traits closely related to principal component axis were achene length (possibly related to disc flower length), number of disc flowers, ligulae length, and presence of a cylindrical-campanulate involucre. The groups of anthophilous insects that were correlated to principal component axis were *Camponotus* sp., other Formicidae, and nocturnal Coleoptera. Clearly, *S. praecox* flowers were highly visited by Formicidae during the night (Figs. 2 and 3), while the other Asteraceae plants were more visited by nocturnal Coleoptera at that time of the day.

The abundance of the observed insects had a positive correlation with temperature and a negative one with humidity (Fig. 5). Four of the five Asteraceae had a higher frequency of floral visitors during the day (Figs. 4 and 5). This pattern is even more distinctive for *D. coccinea,* probably because this plant is strongly related with diurnal pollinators, using its ligules to close its floral heads at night (Figueroa-Castro 1997).

S. praecox was the only species with a high frequency of nocturnal visitors, mainly ants (Figs. 4 and 5). Formicidae presented a different behavior in comparison with most of the observed insects. The largest number of ants was observed at low temperature conditions and high levels of humidity, which suggests that ants have a distinctive physiology that allows them to withstand cool temperatures and high humidity. Heinrich (1975) and Kevan and Baker (1983) suggest that there should be a positive trade-off for these insects between the energy invested to reach the top of the plants and the reward received. However, our results are not enough to confirm it, requiring further studies.

The large variety of anthophilous insects observed over the heads of the studied plants confirms that Asteraceae are an important resource and also that they may be the source of food and other resources for many organisms, not only floral visitors, but also herbivores, such as it was suggested by Soberón et al. (1991) and Cano-Santana (1994). Indeed, this makes them a significant element for this ecosystem.

From this study, it is evident the necessity of doing more complete surveys of floral visitors. In this sense, we strongly suggest that studies concerning plant-floral visitor interactions should involve all the groups of insect visitors occurring along the day, but also during the night. Failing in doing so, we will continue missing valuable information about plant-floral visitor interactions.

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References Cited

Beattie, A. J., D. Turnbull, T. Hough, S. Jobson, and R. B. Knox. 1985. The vulnerability of pollen and fungal spores to ant secretions: evidence and some evolutionary implications. Am. J. Bot. 72: 606–614.

Bertin, R. I. 1989. Pollination biology, pp. 23–83. *In* W. G. Abrahamson (ed.), Plant-Animal interactions. McGraw Hill, New York.

Boldt, P. E., and T. O. Robbins. 1987. Phytophagous and pollinating insect fauna of *Baccharis neglecta* (Compositae) in Texas. Environ. Entomol. 16: 887–895.

Cano-Santana, Z. 1994. Flujo de energía a través de *Sphenarium purpurascens* (Orthoptera: Acrididae) y productividad primaria neta aérea en una comunidad xerófita. Ph.D. dissertation, Universidad Nacional Autónoma de México, México City, México.

Carrillo, C. 1995. El Pedregal de San Ángel. U.N.A.M., México.

Domínguez, C., and J. Nuñez-Farfán. 1994. Las mariposas diurnas del Pedregal de San Ángel como vectores de polen, pp. 313–322. *In* A. Rojo (ed.), Reseva Ecológica el Pedregal de San Ángel: ecología, historia natural y manejo. U.N.A.M., México.

Faegri, K., and L. van der Pijl. 1971. The principles of pollination ecology. Pergamon, Oxford, UK.

Figueroa-Castro, D. M. 1997. Análisis comparativo de la biología floral de cinco especies de compuestas del Pedregal de San Ángel, D. F. (México). BSc thesis, U.N.A.M., México.

Figueroa-Castro, D. M. 2001. Efecto de la herbivoría floral sobre el éxito reproductivo de *Dahlia coccinea* (Asteraceae) en el Pedregal de San Ángel. M.S. thesis, U.N.A.M., México.

Figueroa-Castro, D. M., Z. Cano-Santana, and E. Camacho-Castillo. 1998. Producción de estructuras reproductivas y fenología reproductiva de cinco especies de compuestas en una comunidad xerófita. Bol. Soc. Bot. Mex. 63: 67–74.

Fishbein, M., and D. L. Venable. 1996. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa.* Ecology 77: 1061–1073.

García, M. B., R. J. Antor, and X. Espadaler. 1995. Ant pollination of the palaeoendemic dioecious *Borderea pyrenaica* (Dioscoreaceae). Plant Syst. Evol. 198: 17–27.

Gómez, J. M., and R. Zamora. 1992. Pollination by ants: consequences of the quantitative affects on a mutualistic system. Oecología 91: 410–418.

Gómez, J. M., R. Zamora, J. A. Hódar, and D. García. 1996. Experimental study of pollination by ants in Mediterranean High Mountain and arid habitats. Oecología 105: 236–242.

Grashoff, J. L., and J. H. Beaman. 1970. Studies in *Eupatorium* (Compositae). III. Apparent wind pollination. Brittonia 22: 77–84.

Heinrich, B. 1975. Energetics of pollination. Annu. Rev. Ecol. Syst. 6: 139–170.

Herrera, C. M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach, pp. 65–87. *In* D. G. Lloyd and S.C.H. Barret (eds.), Floral biology. Chapman & Hall, New York.

Heywood, V. H., J. B. Harborne, and B. L. Turner. 1977. An overture to the Compositae, pp. 1–20. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. I. Academic, London, England.

Hickman, J. 1974. Pollination by ants: a low energy system. Science 184: 1290–1292.

Hull, D. A., and A. J. Beattie. 1988. Adverse effects on pollen exposed to *Atta texana* and other North American ants: implications for ant pollination. Oecología 75: 153–155.

Jeffrey, C. 1977. Corolla forms in Compositae: some evolutionary and taxonomic speculations, pp. 11–118. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. I. Academic, London, England.

Kevan, P. G., and H. G. Baker. 1983. Insects as flower visitors and pollinators. Annu. Rev. Entomol. 28: 407–453.

Leppik, E. E. 1977. The evolution of capitulum types of the Compositae in the light of insect-flower interaction, pp. 61–89. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. I. Academic, London, England.

McNaughton, S. J., and L. L. Wolf. 1979. General ecology. Holt Rinehart and Winston, New York.

Nordenstam, B. 1977. Senecioneae and Liebeae: systematic review, pp. 799–830. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. II. Academic, London, England.

Paray, L. 1949. El género *Senecio* en el Valle de México. Bol. Soc. Bot. Mex. 9: 20–31.

Paray, L. 1956. El género *Eupatorium* en el Valle Central de México. Bol. Soc. Bot. Mex. 19: 1–15.

Paray, L. 1958. Las compuestas del Valle Central de México. Bol. Soc. Bot. Mex. 22: 41–52.

Peakall, R., and A. J. Beattie. 1989. Pollination of the orchid *Microtis parviflora* R. Br. by flightless worker ants. Funct. Ecol. 3: 515–522.

Peakall, R., C. J. Angus, and A. J. Beattie. 1990. The significance of ant and plant traits for ant pollination in *Leporella fimbriata.* Oecología 84: 457–460.

Ramsey, M. 1995. Ant pollination of the perennial herb *Blandfordia grandiflora* (Liliaceae). Oikos 74: 265–272.

Richards, A. J. 1986. Plant breeding systems. Unwin Hyman, London, England.

Robinson, H., and R. M. King. 1977. Eupatorieae: systematic review, pp. 437–485. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. I. Academic, London, England.

Rzedowski, J. 1954. Vegetación del Pedregal de San Ángel. An. E.N.C.B., I.P.N., México, D. F. 8: 59–129.

Rzedowski, J., and G. C. Rzedowski. 1985. Flora Fanerogámica del Valle de México, vol. II. Instituto de Ecología y Escuela Nacional de Ciencias Biológicas, México.

Sánchez, S. O. 1980. La flora del Valle de México. Herrero, México.

Schmitt, J. 1980. Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). Evolution 34: 934–943.

Schmitt, J. 1983. Flowering plant density and pollinator visitation in *Senecio.* Oecología 60: 97–102.

Soberón, J. M., M. De la Cruz, and G. Jiménez. 1991. Ecología hipotética de la Reserva del Pedregal de San Ángel. Ciencia y Desarrollo 17: 25–38.

Sorensen, P. D. 1969. Revision of the genus *Dahlia* (Compositae, Heliantheae-Coreopsidinae). Rhodora 71: 309–416.

Southwood, T.R.E. 1978. Ecological methods. Chapman & Hall, London, England.

Strother, J. L. 1977. Tageteae: systematic review, pp. 769–797. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. II. Academic, London, England.

Stuessy, T. 1977. Heliantheae: systematic review, pp. 621–671. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), The biology and chemistry of the Compositae, vol. II. Academic, London, England.

Sullivan, V. I. 1975. Pollen and pollination in the genus *Eupatorium* (Compositae). Can. J. Bot. 53: 582–589.

Valiente-Banuet, A., and E. De Luna. 1990. Una lista florística para la Reserva del Pedregal de San Ángel. Acta Bot. Mex. 9: 13–30.

Waser, N. M., and L. A. Real. 1979. Effective mutualism between sequentially flowering plant species. Nature 281: 670–672.

Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. Ecology 77: 1043–1060.

Willmer, P. G., A. M. Bataw, and J. P. Hughes. 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecol. Entomol. 19: 271–284.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ.

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