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# Insect visitors to the annual plant community in a xeric environment in Central Mexico

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## Abstract

The interactions between the plant community and their floral visitors might vary through space, causing changes in the structure and composition of the communities of floral visitors. Although numerous studies have addressed the variation in the communities of floral visitors through space, none of them have analyzed how the structure of the community of floral visitors for all the co-flowering annual plant species changes between sites. We describe how the community of floral visitors to annual plants varies through space in a xeric community in central Mexico. We collected all the insects visiting the flowers of the annual plants growing in 2 sites with contrasting plant density (low vs. high). We determined species richness, abundance, and diversity for the insect communities in each site. We established the similarity in the composition of the insect communities and the importance of environmental variables on the dynamics of the communities of floral visitors. Abundance and diversity of floral visitors were significantly higher in the low plant density site. The composition of the insect communities differed between sites (similarity = 32%). Changes in abundance of a few groups of insects seem to be related to environmental factors such as disturbance (*Myrmecocystus mexicanus* Wesmäl [Hymenoptera: Formicidae] and Tiphiidae sp. 1 [Hymenoptera]), humidity (Curculionidae sp. 1 [Coleoptera]), and temperature (*Dorymyrmex grandulus* (Forel) [Hymenoptera: Formicidae]). Our results indicate that vegetation density has a strong effect on the community of floral visitors of annual plants, which in turn, might affect their reproduction and their interactions with other organisms within the ecosystem.

Key Words: abundance; diversity; plant density; Sørensen index of similarity; species richness

## Resumen

Las interacciones entre las comunidades vegetales y sus visitantes florales pueden variar en el espacio, ocasionando diferencias en la estructura y composición de las comunidades de insectos visitantes. Aunque diversos estudios han analizado la variación espacial en las comunidades de visitantes florales, ninguno ha estudiado dicha variación en la estructura de la comunidad de visitantes florales de toda la comunidad de especies anuales coexistentes. En este estudio se describe la variación espacial en la comunidad de visitantes florales de la comunidad de plantas anuales de una zona xérica en la región central de México. Se colectaron los insectos que visitaban las flores de las especies anuales que crecían en 2 sitios con densidad vegetal contrastante (baja vs. alta). Se determinó la riqueza específica, la abundancia, y el índice de diversidad de la comunidad de insectos en cada sitio. Se estimó la similitud en la composición de las comunidades de insectos así como la importancia de variables ambientales sobre la dinámica de las comunidades de visitantes florales. La abundancia y la diversidad de visitantes florales fueron significativamente mayores en el sitio con baja densidad vegetal. La composición de las comunidades de insectos fue distinta entre sitios (similitud = 32%). La abundancia de unos cuantos grupos de insectos parece responder a factores ambientales como el disturbio (*Myrmecocystus mexicanus* Wesmäl [Hymenoptera: Formicidae] y Tiphiidae sp. 1 [Hymenoptera]), la humedad (Curculionidae sp. 1 [Coleoptera]), y la temperatura (*Dorymyrmex grandulus* (Forel) [Hymenoptera: Formicidae]). Los resultados sugieren que la densidad vegetal tiene fuertes efectos sobre la comunidad de visitantes florales de las plantas anuales, lo que a su vez puede afectar su reproducción y las interacciones con otros organismos dentro del ecosistema.

Palabras Clave: abundancia; densidad vegetal; diversidad; índice de similitud de Sørensen; riqueza específica

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Numerous studies have shown spatial variation between interacting species of plants and their floral visitors (Horvitz & Schemske 1990; Gilbert et al. 1996; Fenster & Dudash 2001). These studies have documented the variation in composition (Grombone-Guaratini et al. 2004; Moeller 2005; Gibson et al. 2006), abundance (Traveset & Sáez 1997; Steffan-Dewenter et al. 2001; Moeller 2005), species richness (Gibson et al. 2006), and diversity (Herrera 1988) of floral visitors across space. For example, it has been shown that the abundance of floral visitors increases with the closeness to a source of water or to a semi-natural

habitat, with the presence of a facilitator species, with higher vegetation coverage, and with lower altitude (Traveset & Sáez 1997; Steffan-Dewenter et al. 2001; Moeller 2005). Similarly, Gibson et al. (2006) and Herrera (1988) have documented higher species richness and diversity at sites with agricultural management, and close to a source of water, respectively.

Most studies addressing the spatial variation in the structure of the community of floral visitors are focused on a subset of species within the community. Thus, most studies are focused on the community of

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floral visitors or pollinators to 1 or 2 species of plants (Moeller 2005; Gibson et al. 2006; Campbell & Husband 2007). In addition, some studies are focused on specific groups of visitors (Dupont & Skov 2004; Moeller 2005; Rader et al. 2012). Sampling a sub-set of species within a particular community might limit the scope of the results obtained. Thus, generalizations about the environmental factors driving the distribution and responses of floral visitors should be made with caution.

Although numerous studies have documented the existence of spatial variation in different aspects of the communities of floral visitors (Gilbert et al. 1996; Fenster & Dudash 2001; Gibson et al. 2006), none of them have conducted a thorough analysis of the spatial variation in the structure of the community of floral visitors for all the coexisting plant species with the same growth form. In this study, we analyze the variation in the structure of the community of floral visitors of annual plants in a xeric environment in Central Mexico.

# Material and Methods

## STUDY SITE

This study was conducted within the Tehuacán-Cuicatlán Reserve, in the locality of Zapotitlán Salinas, Puebla, Mexico (18.3333°N, 97.4666°W), at an altitude of 1460–2600 masl (Zavala-Hurtado 1982). Mean annual temperature is 18–22 °C. Precipitation is scarce throughout the year, with mean annual precipitation of 400–450 mm (Zavala-Hurtado 1982). Climate in the locality is arid to semiarid, with a summer rainy season (Arias-Toledo et al. 2000). The predominant vegetation at the study site is xeric scrubland (Rzedowski 1978), with columnar cacti as the most important physiognomic element (Valiente-Banuet et al. 1997).

At this locality, 2 sites with contrasting vegetation density were selected to conduct the study. Plant density was estimated by counting the number of plants within an area of 50 m<sup>2</sup> at each site. Because of the differences in plant density, atmospheric temperature and humidity also are different between sites (Table 1). Temperature and humidity were measured with a digital thermo-hygrometer every h during the d when insects were collected (see the Floral Visitors section below). Maximum temperature was higher at the low than at the high plant density site. Also, on average, temperature at the low plant density site was 2.4 °C higher than at the high plant density site (Table 1). In contrast, minimum RH was higher in the high plant density site than in the low plant density site, and average RH was 9.6% higher in the high than in the low plant density site (Table 1). Moreover, these sites differ in level of disturbance (Table 1). Local people use the low plant

density site as horse racing track and it is also a common trail for livestock. Thus, soil compaction and disturbance were higher at the low plant density site. We acknowledge that conducting the study at only 2 sites with no replication might limit our conclusions; however, replications were logistically impossible. Many other studies analyzing spatial variation on different aspects of floral biology (including floral visitors) have been conducted at only 2 sites (e.g., Steffan-Dewenter et al. 2001; Grombone-Guaratini et al. 2004; Campbell & Husband 2007; Stucky et al. 2012; Czarnecka & Denisow 2014).

## THE COMMUNITY OF ANNUAL PLANTS

The study was conducted using the complete community of annual plants growing on the study sites, which totaled 11 species. Eight of them were located at both the high and low plant density sites: *Al-lionia incarnata* L. (Nyctaginaceae), *Bouteloua barbata* Lag. (Poaceae), *Eragrostis mexicana* (Hornem) (Poaceae), *Flaveria ramosissima* Klatt. (Asteraceae), *Florestina pedata* (Cav.) (Asteraceae), *Parthenium bipinnatifidum* (Ortega) (Asteraceae), *Zinnia peruviana* L. (Asteraceae), and *Gomphrena decumbens* Jacq. (Amaranthaceae). In addition, 3 other plant species were found in only 1 of the sites: *Dalea humilis* G. Don. (Fabaceae) and *Portulaca pilosa* L. (Portulacaceae) were present only at the high plant density site, whereas *Kallstroemia rosei* Rydb. (Zygophyllaceae) was present only at the low plant density site. Therefore, the community of annual plants at the high and low plant density sites was composed of 9 and 10 species, respectively. Morphological and ecological traits of the annual species are described in Table 2.

## FLORAL VISITORS

We collected all the insects visiting the flowers of the annual plants growing in 2 sites with contrasting plant density. Insects were collected on 20 and 21 Sep 2011 from 7 to 19 h, and on 22 and 23 Sep 2011, from 20 to 23 h. Collections of floral visitors were made on 2 floral patches of 1 m<sup>2</sup> for each plant species at each site (Table 3). Sampling areas were chosen based on the abundance of flowers of each plant species. Collections were conducted simultaneously at both sites for 15 min each h, except in *A. incarnata*, *K. rosei* and *P. pilosa*, which have short periods of anthesis. Therefore, the collection of floral visitors of *A. incarnata* was conducted from 8 to 15 h, whereas in *K. rosei* and *P. pilosa* it was from 10 to 17 h. Thus, total time of insect collection varied among species from 210 min (*A. incarnata*), and 240 min (*K. rosei* and *P. pilosa*), to 510 min (all other plant species) at each site. All flying and crawling floral visitors were collected with insect nets and ethyl acetate-killing chambers, respectively. Nocturnal collections were made using hand lamps

**Table 1.** Environmental characteristics of the 2 sites in which collections of floral visitors were conducted.

Environmental trait	Site	
	High plant density	Low plant density
Plant density	13.7 individuals per m <sup>2</sup>	6.4 individuals per m <sup>2</sup>
Mean (maximum) atmospheric temperature (°C)	24.1 (33.2)	26.5 (37)
Mean (minimum) relative humidity (%)	52.5 (31)	42.1 (17)
Disturbance index <sup>1</sup>	1.04	16.34
Vegetation composition <sup>2</sup>	<i>Yucca</i> (Asparagaceae), <i>Beaucarnea gracilis</i> Lem. (Asparagaceae), <i>Croton ciliatoglandulosus</i> Ort. (Euphorbiaceae), <i>Myrtillocactus geometrizans</i> Console (Cactaceae), <i>Agave kerchovei</i> Lem. (Agavaceae)	<i>Parkinsonia praecox</i> (Ruiz & Pav.), <i>Prosopis laevigata</i> (Humb. & Bonpl.) (Leguminosae), <i>Lantana</i> sp. (Verbenaceae), <i>Agave marmorata</i> Roezl (Agavaceae), <i>Gymnosperma glutinosum</i> Less. (Asteraceae), <i>Cylindropuntia tunnicata</i> (Lehm.), <i>Myrtillocactus geometrizans</i> (Cactaceae)
Geographic coordinates	18.32706° N, 97.49575° W	18.28617° N, 97.52733° W

<sup>1</sup>Rivas-Arancibia, SP. unpublished data obtained following methods from Martorell and Peters 2005.

<sup>2</sup>Zavala-Hurtado 1982.

**Table 2.** Biological traits of the herbaceous plant species that constitute the community of annual plants at the study site.

Plant Trait	<i>Allionia incarnata</i>	<i>Bouteloua barbata</i>	<i>Dalea humilis</i>	<i>Eragrostis mexicana</i>	<i>Flaveria ramosissima</i>	<i>Florestina pedata</i>	<i>Gomphrena decumbens</i>	<i>Kallstroemia rosei</i>	<i>Parthenium bipinnatifidum</i>	<i>Portulaca pilosa</i>	<i>Zinnia peruviana</i>
Plant length (cm) <sup>1,2,9</sup>	20–100	Up to 30	10–40	Up to 60	Up to 100	10–60	10–50	Up to 100	Up to 120	5–25	Up to 100
Flower color <sup>1,2</sup>	Pink – purple	NA	Pink or white	NA	Yellow	White with purple	White or pink	White – light orange	White	Pink, red-purple	Red and yellow
Flowering period <sup>1,2,3,4,5,7,8,9</sup>	Jun–Nov	Jun–Oct	Aug–Nov	Jun–Nov	Jun–Oct	Jun–Nov	Jul–Nov	Jun–Oct	Mar–Nov	Summer	Jul–Nov
Distribution <sup>2,3,4,5,6,7,9,10</sup>	Disturbed sites, grasslands, and xeric shrublands.	Southwestern USA to southern Mexico	Ruderal weed frequent on roads and temporary crops. Nayarit, to Puebla and Guatemala	Ruderal weed found in xeric shrublands and disturbed grasslands. Central USA to Argentina	Endemic to the xeric environment at the Tehuacán – Cuicatlán Reserve; Oaxaca-Puebla, Mexico; 800–1700 masl	Widely distributed in grasslands and xeric shrublands throughout Mexico and Guatemala; up to 2600 masl	Xeric shrublands and Florida and southern Texas to Bolivia and Paraguay. Up to 2400 masl	Ruderal on xeric shrublands and grasslands. Tropical and subtropical America. 2300–2450 masl	Endemic to Mexico; widely distributed throughout the lowlands of Central Mexico; 1500–2650 masl	Grasslands, shrublands, and on sandy soils. Throughout the South of USA to South America; 2500 masl	Shrublands and grasslands. Arizona to Argentina. 2250–2550 masl

<sup>1</sup>Rzedowski and Rzedowski 2005.  
<sup>2</sup>Vibrans 2009.  
<sup>3</sup>Méndez-Larios et al. 2004.  
<sup>4</sup>Villareal-Quintana et al. 2008.  
<sup>5</sup>Spellenberg 2001.  
<sup>6</sup>Turner 1994.  
<sup>7</sup>Ford 1986.  
<sup>8</sup>Hauser 2005.  
<sup>9</sup>Rzedowski and Rzedowski 2004.  
<sup>10</sup>Zepeda and Velázquez 1999.

**Table 3.** Floral density (number of flowers or inflorescences/m<sup>2</sup>) of each annual plant species at 2 sites with contrasting plant density. ND= species not distributed at this site.

Plant species	High plant density	Low plant density
<i>Allionia incarnata</i>	30 inflorescences per m <sup>2</sup>	70 inflorescences per m <sup>2</sup>
<i>Bouteloua barbata</i>	9 inflorescences per m <sup>2</sup>	24 inflorescences per m <sup>2</sup>
<i>Dalea humilis</i>	25 inflorescences per m <sup>2</sup>	ND
<i>Eragrostis mexicana</i>	11 inflorescences per m <sup>2</sup>	12 inflorescences per m <sup>2</sup>
<i>Flaveria ramosissima</i>	450 capitula per m <sup>2</sup>	500 capitula per m <sup>2</sup>
<i>Florestina pedata</i>	45 capitula per m <sup>2</sup>	30 capitula per m <sup>2</sup>
<i>Gomphrena decumbens</i>	233 inflorescences per m <sup>2</sup>	152 inflorescences per m <sup>2</sup>
<i>Kallstroemia rosei</i>	ND	23 flowers per m <sup>2</sup>
<i>Parthenium bipinnatifidum</i>	42 inflorescences per m <sup>2</sup>	197 inflorescences per m <sup>2</sup>
<i>Portulaca pilosa</i>	13 flowers per m <sup>2</sup>	ND
<i>Zinnia peruviana</i>	6 capitula per m <sup>2</sup>	119 capitula per m <sup>2</sup>

covered with red translucent paper in order to avoid collecting insects attracted by white lights instead of only those that were attracted by the inflorescences of the studied species. Weather conditions on the sampling dates were mostly sunny (mean temperature: 24.4 °C, mean atmospheric humidity: 50.9%). All insects collected were sacrificed and stored in glassine paper bags or 70% alcohol. Collected insects were identified to the lowest possible taxonomic level.

Total abundance of each insect species, abundance per insect group, total abundance of floral visitors, total species richness, per group-species richness and the Shannon-Wiener diversity index were determined for the communities of annual plants at each site (high versus low plant density). To establish if species richness, per group-species richness, per group-abundance, and total abundance differed between sites,  $\chi^2$  tests were applied (Zar 1999). Abundance tests at the insect species level were conducted only on those cases in which the total number of individuals collected (pooling data from both sites) was equal or higher than 5. Thus, we conducted abundance tests for: Curculionidae sp. 1 (Coleoptera); Dasytinae sp. 1 (Coleoptera: Meloidae); *Exoprosopa* sp. 1, *Lepidophora* sp. (both Diptera); *Nysius* sp. 1, *Lopidea* sp. 1, Miridae sp. 1, *Harmostes* sp. 1 (all Hemiptera); *Apis mellifera* L., *Exomalopsis pueblana* Timberlake, *Dorymyrmex grandulus* (Forel), *D. insanus* (Buckley), *Myrmecocystus mexicanus* Wesmael, Tiphiidae sp. 1 (all Hymenoptera); *Ascia monuste* (L.), and *Nathalis iole* Boisduval (both Lepidoptera). Therefore, a total of 28  $\chi^2$  tests were conducted to compare insect abundance (total, per-group [5], and per-species [16]) and richness (total and per-group [5]) between sites. In order to prevent the increase of the likelihood of committing a type I error, a sequential Bonferroni procedure was conducted on this set of 28 tests of abundance and species richness (Rice 1989).

Relative abundance curves (James & Rathbun 1981) were used to compare the patterns of species abundance between sites with contrasting plant density. Relative abundance was estimated as  $n_i/N$ , where  $n_i$  = number of individuals of the  $i$ th insect species, and  $N$  = total number of individuals from all species including both high and low plant density sites. Then, relative abundance was plotted on a log 10 scale against the rank from the most to the least common species.

Differences in the Shannon-Wiener diversity indices of floral visitors to annual plants in each site were explored by applying Hutcheson  $t$  tests (Hutcheson 1970). Diversity and  $t$  tests analyses were carried out in PAST v. 2.17 (Hammer et al. 2001).

The composition of floral visitors was compared between the communities at each site with the Sørensen similarity index. In addition, a cluster analysis with abundance data was performed using the unweighted pair-group average as grouping method, and the  $r$ -Pearson as distance. The analysis was performed with the software Statistica ver. 7.1 (StatSoft 2006. STATISTICA. Data analysis software system and

computer program manual. Version 7.1. StatSoft Inc., Tulsa, Oklahoma).

Finally, we analyzed the dynamics of the communities of floral visitors in relation to environmental variables. We conducted 2 canonical correspondence analyses, 1 at the order level and the other at the specific level for those species whose abundance was significantly different between sites. Temperature, humidity, and disturbance were the environmental variables considered within each canonical correspondence analysis. Measurements of both temperature and humidity were taken each h during insect collections, then mean values were estimated and used in the analyses. These analyses were conducted in the program PAST v. 2.17 (Hammer et al. 2001).

## Results

### SPECIES RICHNESS

A total of 113 species belonging to the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera were collected visiting the flowers of the annual plants at both sites (Table 4). The communities of floral visitors of annual plants at the high and low plant density sites were composed of 55 and 81 insect species, respectively. Species richness of floral visitors did not differ significantly after the Bonferroni procedure ( $\chi^2 = 4.97$ ;  $df = 1$ ;  $P > 0.05$ ).

The insect groups with the highest species richness were Hemiptera and Diptera at the high and low plant density sites, respectively (Tables 4, 5). In contrast, Hymenoptera and Coleoptera were the groups with the lowest species richness at the high and low plant density sites, respectively (Tables 4, 5). However, there were no significant differences in species richness for any of the insect orders ( $3.52 \leq \chi^2 \leq 0.13$ ;  $df = 1$ ;  $P > 0.05$ ).

### ABUNDANCE

A total of 571 individual insects were collected visiting the flowers of the community of annual plants across the 2 study sites. The number of individual insects visiting the flowers of annual plants at the low plant density site (339) was significantly higher than the number of floral visitors at the high plant density site (232;  $\chi^2 = 20.05$ ;  $df = 1$ ;  $P < 0.001$ ; Tables 4, 5).

Coleoptera and Hymenoptera were the most abundant groups of insects visiting the flowers of annual plants at the high and low plant density sites, respectively (Tables 4, 5). In contrast, Lepidoptera was the least abundant group of floral visitors at both sites (Tables 4, 5). Although the total abundance of floral visitors from each insect group

**Table 4.** Abundance of insects collected visiting the flowers of annual species in 2 sites with contrasting plant density in Zapotitlán Salinas, Puebla, Mexico.

Order: Family	Species	High Plant Density	Low Plant Density	Total
Coleoptera				
Buprestidae	<i>Acmaeodera</i> sp.	0	2	2
Carabidae	<i>Lebia</i> sp.	2	0	2
Chrysomelidae	<i>Diabrotica balteata</i> (LaConte)	1	3	4
Chrysomelidae: Alticinae	Species 1	1	0	1
Chrysomelidae: Doryphorinae	Species 2	0	1	1
Coccinellidae	<i>Cycloneda emarginata</i> (Mulsant)	0	1	1
	Species 1	1	0	1
	Species 2	0	1	1
Curculionidae: Entiminae	Species 1	0	1	1
Curculionidae	Species 1	1	21	22
Melyridae: Dasytinae	Species 1	70	64	134
	Species 2	1	3	4
Melyridae: Malachiinae	Species 1	0	2	2
	Species 2	1	0	1
Scarabaeidae: Dynastinae	<i>Cyclocephala lunulata</i> Burmeister	0	1	1
Coleoptera: Staphylinidae	Species 1	1	0	1
Coleoptera: Tenebrionidae	Species 1	1	0	1
	Species 2	0	1	1
Diptera				
Anthomyiidae	Species 1	0	1	1
Asilidae	<i>Cophura</i> sp. 1	0	1	1
	<i>Cophura</i> sp. 2	0	1	1
	<i>Efferia</i> sp.	1	1	2
	<i>Taurhynchus</i> sp.	0	1	1
Bombyliidae	<i>Exoprosopa</i> sp. 1	4	1	5
	<i>Exoprosopa</i> sp. 2	1	0	1
	<i>Geron</i> sp.	1	0	1
	<i>Lepidophora</i> sp.	34	16	50
	<i>Ogcodocera</i> sp.	3	0	3
	<i>Paravilla</i> sp.	0	1	1
	<i>Poecilanthrax</i> sp.	0	1	1
	Species 1	0	1	1
Drosophilidae	Species 1	0	1	1
Lauxaniidae	Species 1	0	1	1
Muscidae	Species 1	0	1	1
	Species 2	1	0	1
	Species 3	0	1	1
	Species 4	0	3	3
	Species 5	0	2	2
	Species 6	0	1	1
Sciaridae	Species 1	0	1	1
Scatophagidae	Species 1	0	1	1
Syrphidae	<i>Leucopodella</i> sp. 1	0	1	1
	<i>Leucopodella</i> sp. 2	0	1	1
	<i>Syrphus</i> sp. 1	1	0	1
	<i>Syrphus</i> sp. 2	1	0	1
Tachinidae	<i>Jurinia</i> sp.	1	0	1
	<i>Lespesia</i> sp.	1	0	1
	<i>Madremyia</i> sp.	1	0	1
	Species 1	1	0	1
	Species 2	0	1	1
	Species 3	0	1	1
Unidentified	Species 1	0	1	1
Hemiptera				
Coreidae	<i>Scolopocerus uhleri</i> Distant	1	1	2
Lygaeidae	<i>Crophius</i> sp.	1	1	2
	<i>Nysius</i> sp.	6	2	8
	<i>Phlegyas</i> sp.	1	0	1
Miridae	<i>Lopidea</i> sp.	7	3	10



**Table 4.** (Continued) Abundance of insects collected visiting the flowers of annual species in 2 sites with contrasting plant density in Zapotitlán Salinas, Puebla, Mexico.

Order: Family	Species	High Plant Density	Low Plant Density	Total
Pentatomidae	Species 1	37	29	66
	<i>Mecidea</i> sp.	0	1	1
	Species 1	2	0	2
	Species 2	1	1	2
	Species 3	1	0	1
Reduviidae	<i>Apiomerus</i> sp.	1	0	1
	<i>Sinea</i> sp.	0	2	2
	<i>Zelus</i> sp. 1	0	2	2
	<i>Zelus</i> sp. 2	2	0	2
Rhopalidae	<i>Harmostes</i> sp. 1	6	3	9
	<i>Harmostes</i> sp. 2	1	1	2
Scutelleridae	<i>Homoemus</i> sp. 1	2	0	2
	<i>Homoemus</i> sp. 2	0	2	2
Unidentified	Species 1	1	0	1
	Species 2	1	1	2
	Species 3	0	3	3
Hymenoptera				
Apidae	<i>Anthophora californica</i> Cresson	1	0	1
	<i>Apis mellifera</i> Linnaeus	2	3	5
	<i>Exomalopsis pueblana</i> Timberlake	4	1	5
Andrenidae	<i>Heterosarus (Pterosaurus)</i> sp.	1	2	3
	<i>Macrotera opuntiae</i> (Cockerell)	1	0	1
Braconidae	<i>Chelonus</i> sp.	0	1	1
Formicidae	<i>Dorymyrmex grandulus</i> (Forel)	0	32	32
	<i>Dorymyrmex insanus</i> (Buckley)	0	6	6
	<i>Myrmecocystus mexicanus</i> Wesmael	0	27	27
	<i>Pheidole</i> sp. 1	0	1	1
	<i>Pheidole</i> sp. 2	0	1	1
	<i>Pogonomyrmex barbatus</i> Smith	0	2	2
	<i>Augochlorella</i> sp.	0	2	2
Halictidae	<i>Dianthidium (Dianthidium)</i> sp.	0	1	1
Pompilidae	Species 1	0	2	2
Sphecidae	Species 1	4	0	4
Tiphiidae	Species 1	3	37	40
Vespidae	Species 1	0	1	1
	Species 2	0	1	1
Lepidoptera				
Arctiidae	<i>Cisthene tehuacana</i> Dyar	0	1	1
Geometridae	Species 1	2	0	2
Hesperiidae	<i>Ancyloxypha arene</i> (Edwards)	1	0	1
	<i>Atalopedes campestris</i> (Boisduval)	1	0	1
	<i>Pyrgus orcus</i> (Stoll)	2	0	2
	<i>Pyrgus</i> sp.	1	1	2
	<i>Strymon cestri</i> (Reakirt)	1	0	1
Lycaenidae	Species 1	0	1	1
	Species 2	0	1	1
	Species 3	0	3	3
Noctuidae	Species 1	1	0	1
	Species 2	1	1	2
	Species 3	0	1	1
	Species 4	0	1	1
Nymphalidae	<i>Agraulis vanillae incarnata</i> (Riley)	0	1	1
	<i>Mestra amymone</i> (Menetries)	0	2	2
Pieridae	<i>Ascia monuste</i> (Linnaeus)	0	5	5
	<i>Nathalis iole iole</i> Boisduval	4	2	6
	<i>Pyrisitia proterpia</i> (Fabricius)	0	2	2
	<i>Zerene cesonia cesonia</i> (Stoll)	0	1	1
Pyralidae	Species 1	0	1	1
<b>Total</b>		<b>232</b>	<b>339</b>	<b>571</b>

**Table 5.** Species richness (abundance) per group of insects collected visiting the flowers of the communities of annual plants in 2 sites with contrasting plant density in Central Mexico.

	High plant density site	Low plant density site
Coleoptera	10 (80)	12 (101)
Diptera	13 (51)	24 (42)
Hemiptera	16 (71)	14 (52)
Hymenoptera	7 (16)	16 (120)
Lepidoptera	9 (14)	15 (24)
Total	55 (232)	81 (339)

was different between sites, this difference was only significant for Hymenoptera ( $\chi^2 = 79.53$ ;  $df = 1$ ;  $P < 0.001$ ). There were significantly fewer hymenopterans at the high plant density site (16) than at the low plant density site (120).

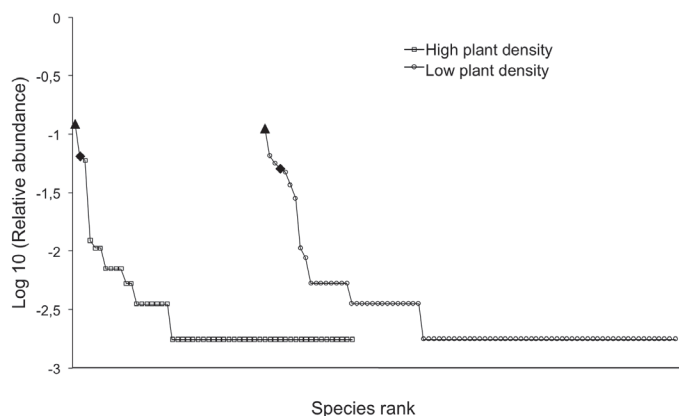
At the specific level, Curculionidae sp. 1 (Coleoptera), and *Dorymyrmex grandulus*, *Myrmecocistus mexicanus*, and Tiphidae sp. 1 (all Hymenoptera) were significantly more abundant at the low than at the high plant density site ( $32.0 \geq \chi^2 \geq 18.18$ ;  $df = 1$ ;  $P < 0.001$ ; Table 4). All other insect species with abundance equal or higher than 5 across both sites did not differ significantly between sites ( $6.48 \geq \chi^2 \geq 0.2$ ;  $df = 1$ ;  $P > 0.05$ ).

Relative abundance curves showed that Dasytinae sp. 1 (Coleoptera) was the dominant species at both sites (11–12%; Fig. 1). Miridae sp. 1 (Hemiptera) was the second most dominant species at the high plant density site (6%), and it was also a relatively dominant species at the low plant density site (6%; Fig. 1).

## DIVERSITY AND SIMILARITY

The Shannon diversity index at the low plant density site (3.26) was significantly higher than that obtained for the high plant density site (2.75;  $t = 3.705$ ;  $df = 475$ ;  $P < 0.001$ ). The composition of the community of floral visitors was different between sites (Sor sen similarity index = 32.35%). Only 23 insect species (4 Coleoptera, 3 Diptera, 9 Hemiptera, 4 Hymenoptera, and 3 Lepidoptera) were shared between sites (Table 4).

The cluster analysis indicated 2 groups of annual plants (Fig. 2). The first group comprised the communities of floral visitors of *P. bipin-*



**Fig. 1.** Abundance-rank curves of the insect species collected visiting the flowers of annual plants in sites with contrasting plant density. Relative abundance is plotted on a log10 scale, and the abscissa is the rank from the most to the least common species (James & Rathbun 1981). Closed triangles and diamonds indicate the abundance of Dasytinae species 1 (Coleoptera) and Miridae species 1 (Hemiptera), in the low and high plant density sites, respectively.

*natifidum*, *F. ramosissima*, and *F. pedata* from the low plant density site (Fig. 2). A second group consisted of the communities of floral visitors of all other annual species. Within this group, *F. ramosissima*, *P. bipinatifidum* (from the high plant density site) and *B. barbata* (from the low plant density site) clustered together. Likewise, *D. humilis* from the high plant density site and *Z. peruviana* from both sites constitute a second subgroup (Fig. 2). The communities of floral visitors of *P. pilosa* from the high plant density site and *K. rosei* and *A. incarnata* from the low plant density site show the lowest values of linkage distance (Fig. 2).

## ENVIRONMENTAL FACTORS AND THE COMMUNITY OF FLORAL VISITORS

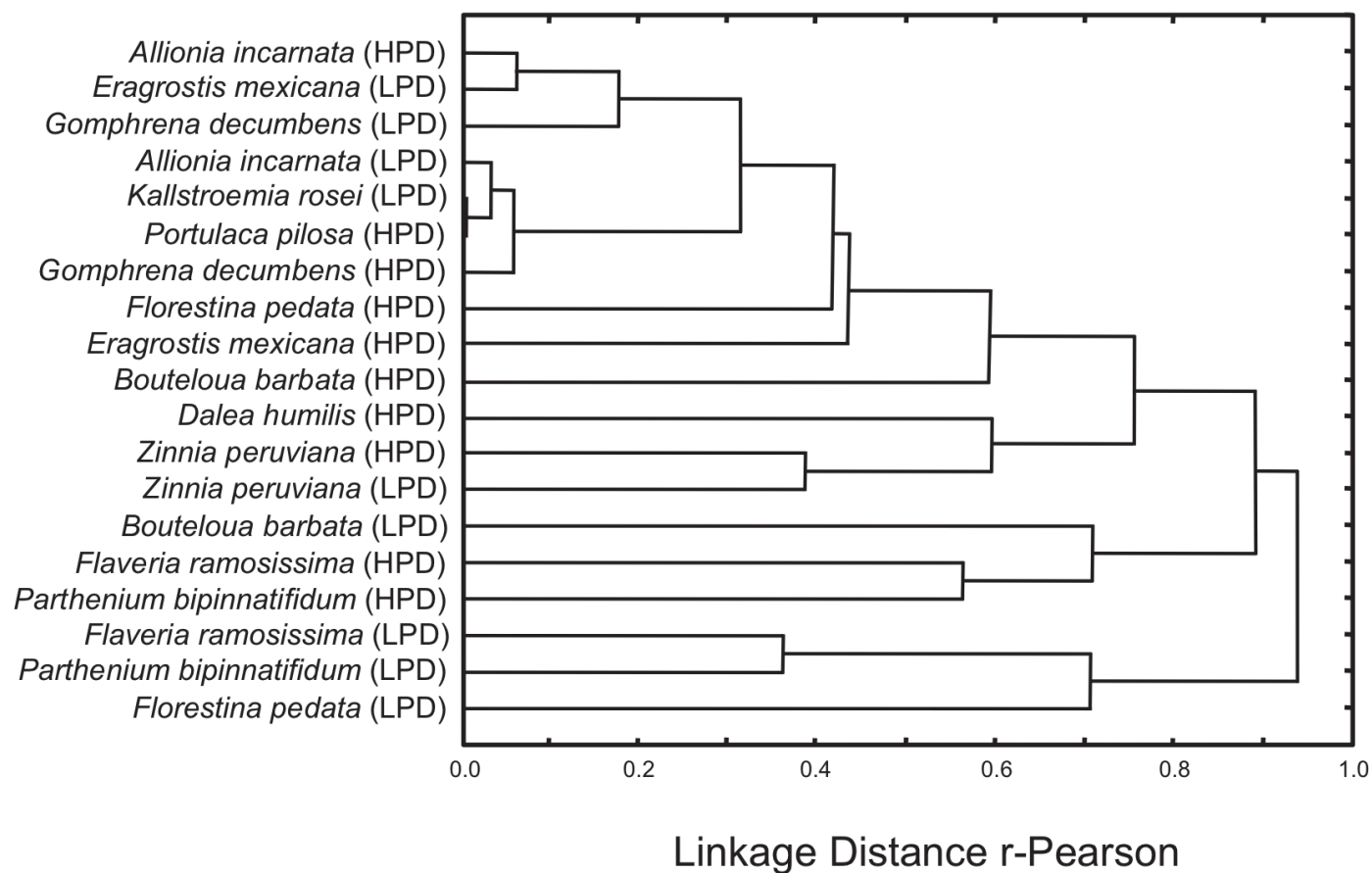
At the order level, the canonical correspondence analysis showed that ordination axes 1 and 2 explain 84.3% and 15.7%, respectively, of the total variation on the abundance of floral visitors (Fig. 3a). Disturbance and temperature were associated with axis 1 (analysis scores: 0.988 and 0.984, respectively). Among the insect groups, Hymenoptera was positively associated with axis 1 (analysis score: 1.641), whereas Diptera was negatively associated with that same axis (analysis score: -0.808; Fig. 3a).

At the specific level, ordination axes 1 and 2 explained 53.7% and 46.3% of the variation in the abundance of floral visitors, respectively (Fig. 3b). Disturbance was negatively associated with axis 1 (analysis score: -0.742), whereas temperature and humidity were associated with axis 2 (analysis scores: -0.798 and 0.709, respectively). *Myrmecocistus mexicanus* (Hymenoptera: Formicidae) and Tiphidae sp. 1 were associated with axis 1; however, whereas *M. mexicanus* appears to be associated with disturbance (analysis score: -1.017), Tiphidae sp. 1 seems to avoid it (analysis score: 1.384; Fig. 3b). Curculionidae sp. 1 and *D. grandulus* were associated with axis 2, but to different environmental variables. Curculionidae sp. 1 was associated with humidity (analysis score: 1.784), whereas *D. grandulus* with temperature (analysis score: -1.231; Fig. 3b).

## Discussion

Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera are the groups of insects that compose the insect community visiting the flowers of annual plants at the sites studied. In general, those same groups of floral visitors have been recorded previously for the annual species studied or other species belonging to the same plant families (Zimmerman 1977; Adams et al. 1981; Townsend 1993; Osorio-Beristain et al. 1997; Nore et al. 2013; Bizecki 2014; Moore 2014). In addition, we found that abundance, diversity, and composition of the community of floral visitors of annual plants vary through space. Likewise, other studies have recorded spatial variation in species richness, abundance, diversity, and composition of the community of floral visitors of different plant species (Herrera 1988; Steffan-Dewenter et al. 2001; Moeller 2005; Gibson et al. 2006; Czarnecka & Denisow 2014). Because of these differences, the similarity of the communities was relatively low, as was shown by both S rensen similarity indexes and cluster analysis. The communities of floral visitors to the annual plants do not seem to be grouped by site, floral color, or plant family. According to the cluster analysis, the most similar communities of floral visitors were those of *P. pilosa* (high plant density site), *K. rosei*, and *A. incarnata* (both low plant density site). These species have similar growth form (i.e., creeping plants), and short periods of flower anthesis. In addition, *P. pilosa* and *A. incarnata* flowers are similar in color (Turner 1994; Spellenberg 2001; Rzedowski & Rzedowski 2005).





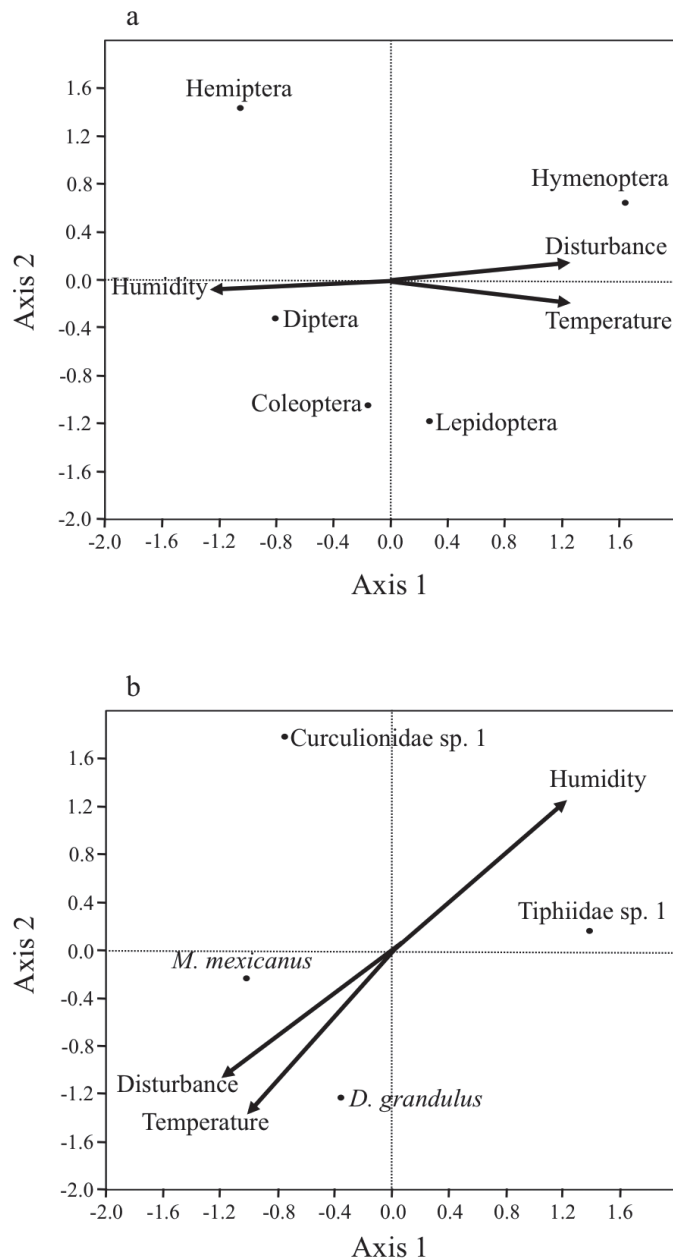
**Fig. 2.** Dendrogram showing similarity indexes obtained from species composition of floral visitors shared by the annual plants distributed at the low (LPD) and high (HPD) plant density sites.

The differences observed in the structure of the community of floral visitors between sites were caused by significant changes in the abundance of 4 insect species: Curculionidae sp. 1 (Coleoptera), *Dorymyrmex grandulus*, *Myrmecocystus mexicanus* (both Hymenoptera: Formicidae), and Tiphidae sp. 1 (Hymenoptera). All of these species were significantly more abundant at the low plant density site than at the high plant density site. However, it seems that their distribution is being determined by different environmental traits. Our results showed that the ants *D. grandulus* and *M. mexicanus* seem to be associated with high temperature and disturbance, respectively (Fig. 3). Both of these species have been recorded at sites with low plant cover (Cole 1966; Chew 1987, 1995; Graham et al. 2008). Moreover, colonies of *M. mexicanus* usually are located at unshaded sites (Cole 1966; Chew 1987, 1995), because low plant cover favors the decrease in temperature needed for these ants to forage at dusk (Chew 1987, 1995). In addition, the canonical correspondence analyses indicate that Curculionidae sp. 1 prefers sites with high humidity (Fig. 3b). Other studies have recorded longer survival, higher reproductive success (eggs laid and eggs hatched) as well as lower mortality at medium to high levels of humidity (Weissling & Giblin-Davis 1993; Al-Ayedh & Rasool 2010). Finally, our results showed that Tiphidae sp. 1 was negatively associated with disturbance (Fig. 3b). Likewise, it has been shown that this group of wasps is more abundant at undisturbed habitats (Quinn 2004). Thus, it seems that the higher temperature (average temperature: 27.3 °C; maximum temperature: 37 °C) and level of disturbance found at the low plant density site favor the occurrence of *D. grandulus* and *M. mexicanus*, but not that of Curculionidae sp. 1 and Tiphidae sp.

1. Instead, the higher abundance of these 2 insect species at the low plant density site must be determined by other factors that were not evaluated in this study.

Dasytinae sp. 1 (Coleoptera: Melyridae) and Miridae sp. 1 (Hemiptera) were the 2 dominant species of floral visitors to the community of annual plants, and their abundance did not differ between sites. Dasytinae is a group of beetles commonly associated with flowers, where they feed on nectar and pollen (Mawdsley 2003; Hoebeke & Wheeler 2013). Miridae is a group of bugs that lives on plants, feeding on their foliage, seeds, and pollen, and laying their eggs within the stems and petioles of their hosts (Eubanks et al. 2003; Cassis & Schuh 2012). It seems that these 2 insect species have a wide niche, because they were able to survive and be relatively abundant under a range of conditions. Moreover, it seems that although annual plants are available for a short period of time, they are an important resource for these 2 insect species. This might be particularly true at disturbed sites where annual plants might be very abundant (Whittaker 1975; Bazzaz & Morse 1991), providing sufficient nectar, pollen, foliage, and seeds to insects that search for these resources, and favoring their population growth and dominance within the communities.

One might expect that the dominant insect species associated with the flowers are important pollinators for the annual plants. Both Miridae and Melyridae have been recorded as common floral visitors of diverse plant species (Mawdsley 2003; Ishida et al. 2009; Fiala et al. 2011; Pendleton et al. 2011). Actually, Melyridae is considered an important group of pollinators of flowering plants (Mawdsley 2003). However, although it has been proved that mirids can transfer pollen successfully



**Fig. 3.** Canonical correspondence analyses of the abundance of floral visitors in response to environmental variables (disturbance index, temperature, and humidity). (a) Effect of environmental variables on the abundance of each insect order of floral visitors. (b) Effect of environmental variables on the abundance of insect species displaying abundance that was significantly different between sites.

(Ishida et al. 2009; Fiala et al. 2011), some studies have shown that these bugs do not always carry pollen on their bodies (Nagamitsu & Inoue 1997); thus, their importance as pollinators is ambiguous.

Similarly, one might wonder if changes in the abundance of Curculionidae sp. 1 (Coleoptera), *D. grandulus*, *M. mexicanus* (Hymenoptera: Formicidae), and Tiphidae sp. 1 (Hymenoptera) might affect the reproductive success of the annual plants studied. Curculionids, ants, and tiphiids have been recorded as floral visitors and important pollinators of diverse plant species (Brown 1998; Ratnayake et al. 2007; Jones et al. 2010; Ibarra-Isassi & Sendoya 2016). Therefore, they might be important pollinators for the plant species studied, especially for the self-incompatible *F. ramosissima*

(Asteraceae), *E. mexicana*, and *B. barbata* (Poaceae) (Powell 1978; de Nettancourt 2001; McKown et al. 2005). In addition, these insect species might be important pollinators for all the other annual species studied, and changes in their abundance through space might have important effects on the reproductive success of annual plants. Thus, studies focused on how changes in the structure of the community of floral visitors across space affect the reproductive success of annual plants are necessary.

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## References Cited

- Adams DE, Perkins WE, Estes JR. 1981. Pollination systems in *Paspalum dilatatum* Poir. (Poaceae): an example of insect pollination in a temperate grass. *American Journal of Botany* 68: 389–394.
- Al-Ayedh HY, Rasool KG. 2010. Sex ratio and the role of mild relative humidity in mating behaviour of red date palm weevil *Rhynchophorus ferrugineus* Oliv. (Coleoptera: Curculionidae) gamma-irradiated adults. *Journal of Applied Entomology* 134: 157–162.
- Arias-Toledo A, Valverde-Valdés MT, Reyes-Santiago J. 2000. Las plantas de la región de Zapotitlán Salinas, Puebla. CONABIO, Mexico.
- Bazzaz FA, Morse SR. 1991. Annual plants: potential responses to multiple stresses, pp. 283–305. In Mooney HA, Winner WE, Pell EJ [Eds.], *Response of Plants to Multiple Stresses*. Academic Press Inc., San Diego, California, USA.
- Bizecki RD. 2014. Mutualistic and antagonistic networks involving the rare silky prairie-clover (*Dalea villosa* var. *villosa*) and its coflowering plants and insect visitors. *Botany* 92: 47–58.
- Brown GR. 1998. Revision of the *Neozeleboria cryptoides* species group of thynnine wasps (Hymenoptera: Tiphidae): pollinators of native orchids. *Australian Journal of Entomology* 37: 193–205.
- Campbell LG, Husband BC. 2007. Small populations are mate-poor but pollinator-rich in a rare, self-incompatible plant, *Hymenoxys herbacea* (Asteraceae). *New Phytologist* 174: 915–925.
- Cassidy G, Schuh RT. 2012. Systematics, biodiversity, biogeography, and host associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha). *Annual Review of Entomology* 57: 377–404.
- Chew R. 1987. Population dynamics of colonies of three species of ants in desertified grassland, Southeastern Arizona, 1958–1981. *American Midland Naturalist* 118: 177–188.
- Chew RM. 1995. Aspects of the ecology of three species of ants (*Myrmecocystus* spp., *Aphaenogaster* sp.) in desertified grassland in Southeastern Arizona, 1958–1993. *American Midland Naturalist* 134: 75–83.
- Cole AC. 1966. Ants of the Nevada test site. *Brigham Young University Science Bulletin. Biological Series* 7: 1–27.
- Czarnecka B, Denisow B. 2014. Floral biology of *Senecio macrophyllus* M. Bieb. (Asteraceae), a rare Central European steppe plant. *Acta Societatis Botanicorum Poloniae* 83: 17–27.
- de Nettancourt D. 2001. *Incompatibility and Incongruity in Wild and Cultivated Plants*. Springer, New York, New York, USA.
- Dupont YL, Skov C. 2004. Influence of geographical distribution and floral traits on species richness of bees (Hymenoptera: Apoidea) visiting *Echium* species (Boraginaceae) of the Canary Islands. *International Journal of Plant Science* 165: 377–386.
- Eubanks MD, Styrsky JD, Denno RF. 2003. The evolution of omnivory in heteropteran insects. *Ecology* 84: 2549–2556.
- Fenster CB, Dudash MR. 2001. Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*. *Ecology* 82: 844–851.
- Fiala B, Meyer U, Hashim R, Maschwitz U. 2011. Pollination systems in pioneer trees of the genus *Macaranga* (Euphorbiaceae) in Malaysian rainforests. *Biological Journal of the Linnean Society* 103: 935–953.
- Ford D. 1986. *Flora de Veracruz*. Portulacaceae. Fascículo 51. Instituto Nacional de Investigaciones sobre Recursos Bióticos, Mexico.

- Gibson RH, Nelson IL, Hopkins GW, Hamlett BJ, Memmott J. 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. *Journal of Applied Ecology* 43: 246–257.
- Gilbert F, Willmer P, Semida F, Ghazoul J, Zalut S. 1996. Spatial variation in selection in a plant-pollinator system in the wadis of Sinai, Egypt. *Oecologia* 108: 479–487.
- Graham JH, Krzysik AJ, Kovacic DA, Duda JJ, Freeman DC, Emlen JM, Zak JC, Long WR, Wallace MP, Chamberlin-Graham C, Nutter JP, Balbach HE. 2008. Ant community composition across a gradient of disturbed military landscapes at Fort Benning, Georgia. *Southeastern Naturalist* 7: 429–448.
- Grombone-Guaratini MT, Solferini VN, Semir J. 2004. Reproductive biology in species of *Bidens* L. (Asteraceae). *Scientia Agricola* 61: 185–189.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Paleontologia Electronica* 4: 1–9.
- Hauser AS. 2005. *Bouteloua barbata*. In *Fire Effects Information System*, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.feis-crs.org/feis/> [last accessed Dec 2016].
- Herrera CM. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* 35: 95–125.
- Hoebeker ER, Wheeler AG Jr. 2013. *Dasytes plumbeus* (Müller) (Coleoptera: Melyridae: Dasytinae), a Palearctic soft-winged flower beetle new to North America. *Zootaxa* 3717: 377–382.
- Horvitz CC, Schemske DW. 1990. Spatiotemporal variation in insect mutualists of a neotropical herb. *Ecology* 71: 1085–1097.
- Hutcheson K. 1970. A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology* 29: 151–154.
- Ibarra-Isassi J, Sendoya SF. 2016. Ants as floral visitors of *Blutaparon portulacoides* (A. St-Hil.) Mears (Amaranthaceae): an ant pollination system in the Atlantic rainforest. *Arthropod-Plant Interactions* 10: 221–227.
- Ishida C, Kono M, Sakai S. 2009. A new pollination system: brood-site pollination by flower bugs in *Macaranga* (Euphorbiaceae). *Annals of Botany* 103: 39–44.
- James FC, Rathbun S. 1981. Rarefaction, relative abundance, and diversity of avian communities. *Auk* 98: 785–800.
- Jones CE, Atallah YC, Shropshire FM, Luttrell J, Walker SE, Sandquist DR, Allen RL, Burk JH, Song LC Jr. 2010. Do native ants play a significant role in the reproductive success of the rare San Fernando Valley spineflower *Chorizanthe parryi* var. *fernandina* (Polygonaceae)? *Madroño* 57: 161–169.
- Martorell C, Peters EM. 2005. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. *Biological Conservation* 124: 199–207.
- Mawdsley JR. 2003. The importance of species of Dasytinae (Coleoptera: Melyridae) as pollinators in Western North America. *The Coleopterists Bulletin* 57: 154–160.
- McKown AD, Moncalvo J-M, Dengler NG. 2005. Phylogeny of *Flaveria* (Asteraceae) and inference of C4 photosynthesis evolution. *American Journal of Botany* 92: 1911–1928.
- Méndez-Larios I, Ortiz E, Villaseñor JL. 2004. Las Magnoliophyta endémicas de la porción xerofítica de la provincia florística del Valle de Tehuacán-Cuicatlán, México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Botánica* 75: 87–104.
- Moeller DA. 2005. Pollinator community structure and sources of spatial variation in plant-pollinator interactions in *Clarkia xantiana* ssp. *Xantiana*. *Oecologia* 142: 28–37.
- Moore PH. 2014. Evaluating pollination ecology of the endangered *Pityopsis ruthii* (Small) Small (Asteraceae). M.S. thesis, University of Tennessee, Knoxville, Tennessee.
- Nagamitsu T, Inoue T. 1997. Cockroach pollination and breeding system of *Uvaria elmeri* (Annonaceae) in a lowland mixed-dipterocarp forest in Sarawak. *American Journal of Botany* 84: 208–213.
- Nores MJ, López HA, Rudall PJ, Anton AM, Galetto L. 2013. Four o'clock pollination biology; nectaries, nectar and flower visitors in Nyctaginaceae from southern South America. *Botanical Journal of the Linnean Society* 171: 551–567.
- Osorio-Beristain M, Domínguez CA, Eguiarte LE, Benrey B. 1997. Pollination efficiency of native and invading African bees in the tropical dry forest annual plant, *Kallstroemia grandiflora* Torr ex Gray. *Apidologie* 28: 11–16.
- Pendleton RL, Pendleton BK, Finch D. 2011. Displacement of native riparian shrubs by woody exotics: effects on arthropod and pollinator community composition. *Natural Resources and Environmental Issues* 16: 1–11.
- Powell AM. 1978. Systematics of *Flaveria* (Flaveriinae-Asteraceae). *Annals of the Missouri Botanical Garden* 65: 590–636.
- Quinn MA. 2004. Influence of habitat fragmentation and crop system on Columbia basin shrubsteppe communities. *Ecological Applications* 14: 1634–1655.
- Rader R, Howlett BG, Cunningham SA, Westcott DA, Edwards W. 2012. Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? *Journal of Applied Ecology* 49: 126–134.
- Ratnayake RMCS, Gunatilleke IAUN, Wijesundara DSA, Saunders RMK. 2007. Pollination ecology and breeding system of *Xylopia championii* (Annonaceae): curculionid beetle pollination, promoted by floral scents and elevated floral temperatures. *International Journal of Plant Science* 168: 1255–1268.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Rzedowski GC de, Rzedowski J. 2004. Manual de malezas de la región de Salva-tierra, Guanajuato. Fascículo complementario XX. Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.
- Rzedowski GC de, Rzedowski J. 2005. Flora fanerogámica del Valle de México. Instituto de Ecología A.C. and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro, Michoacán, Mexico.
- Rzedowski J. 1978. Vegetación de México. Limusa, México.
- Spellenberg R. 2001. Nyctaginaceae. Flora del bajo y de regiones adyacentes. Fascículo 93. Instituto de Ecología A.C. and CONABIO, Mexico.
- StatSoft Inc. 1995. Statistical User Guide. Complete Statistical System Statsoft, Tulsa, Oklahoma.
- Steffan-Dewenter I, Münzenberg U, Tschardt T. 2001. Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 1685–1690.
- Stucky JM, Gadd LE, Arellano C. 2012. Pollination biology and seed production of a federally endangered perennial, *Echinacea laevigata* (Asteraceae: Heliantheae). *American Midland Naturalist* 168: 93–111.
- Townsend CC. 1993. Amaranthaceae, pp. 70–91 In Kubitzki K, Rohrer JG, Bittrich V [Eds.], *The Families and Genera of Vascular Plants. II. Flowering Plants: Dicotyledons. Magnoliid, Hamamelid and Caryophyllid*. Springer-Verlag, Berlin, Germany.
- Traveset A, Sáez E. 1997. Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. *Oecologia* 111: 241–248.
- Turner BL. 1994. Revisionary study of the genus *Allionia* (Nyctaginaceae). *Phytologia* 77: 45–55.
- Valiente-Banuet A, Rojas-Martínez A, Arizmendi MC, Dávila P. 1997. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. *American Journal of Botany* 84: 452–455.
- Vibrans H. [Ed.]. 2009. Malezas de México. URL: <http://www.conabio.gob.mx/malezasdemexico/2inicio/home-malezas-mexico.htm> (last accessed 5 Sep 2016).
- Villareal-Quintana JA, Villaseñor-Ríos JL, Medina LR. 2008. Flora de Veracruz: Familia Compositae Tribu Helenieae. Fascículo 143. Instituto de Ecología A.C. Xalapa, Veracruz, Mexico.
- Weissling TJ, Giblin-Davis RM. 1993. Water loss dynamics and humidity preference of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae) adults. *Environmental Entomology* 22: 93–98.
- Whittaker RH. 1975. Communities and ecosystems. McMillan, New York, New York, USA.
- Zar JH. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Zavala-Hurtado JA. 1982. Estudios ecológicos en el Valle semiárido de Zapotitlán, Puebla. I. Clasificación numérica de la vegetación basada en atributos binarios de presencia o ausencia de las especies. *Biotica* 7: 99–120.
- Zepeda GC, Velázquez E. 1999. El bosque tropical caducifolio de la vertiente sur de la sierra de Nanchititla, Estado de México: la composición y la afinidad geográfica de su flora. *Acta Botánica Mexicana* 46: 29–55.
- Zimmerman CA. 1977. A comparison of breeding systems and seed physiologies in three species of *Portulaca* L. *Ecology* 58: 860–868.