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Hummingbirds and the plants they visit in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico

Colibríes y las plantas que visitan en la Reseva de la Biosfera Tehuacán-Cuicatlán, México

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Abstract. We describe the relative abundance, plant species visited, and plant communities used by hummingbird species inhabiting the Tehuacán-Cuicatlán Biosphere Reserve, a semiarid area in South-central Mexico. We recorded 14 hummingbird species and 35 plant species distributed in 4 plant communities during our study. We found 86 different hummingbird-plant interactions. *Amazilia violiceps* and *Cynanthus latirostris* were the most common hummingbirds, while *C. latirostris, A. violiceps*, and *Cynanthus sordidus* were the hummingbirds that visited more plant species. Hummingbirds were distributed differentially between plant communities inside the reserve, with 12 species being present in the arboreal plant community of the lowlands, 11 both in cactus forest and perennial spine shrub plants, and 6 in perennial unarmed shrub plants. *Cercidium praecox* (Fabaceae) was the plant species with the highest number of visiting hummingbird species (10 species). Cactus forest and perennial spine shrub plants were the plant communities with largest number of possible interactions (57 and 51, respectively). The mean connectance value of the interaction matrix was similar between plant communities (near to 22%), but lower than those reported previously in other places. In the Tehuacán-Cuicatlán Biosphere Reserve the hummingbird-plant interaction system will be preserved if the hummingbirds *C. latirostris*, *A. violiceps*, *C. sordidus*, and *L. clemenciae*, and the plants *C. praecox*, *I. arborescens*, *E. chiotilla*, and *N. glauca,* are protected.

Key words: hummingbird-plant interaction, Puebla-Oaxaca,Tehuacán-Cuicatlán Biosphere Reserve, ornithophilous flowers.

Resumen. Describimos la abundancia relativa, especies de plantas visitadas y tipos de vegetación utilizados por los colibríes de la Reserva de la Biosfera Tehuacán-Cuicatlán, México. Durante nuestro de estudio registramos 14 especies de colibríes y 35 especies de plantas utilizadas por ellos dentro de cuatro tipos de vegetación, representando 86 diferentes interacciones colibrí-planta. *Amazilia violiceps* y *Cynanthus latirostris* fueron los colibríes más comunes, mientras que *C. latirostris, A. violiceps* y *Cynanthus sordidus* fueron las especies que visitaron a un mayor número de especies de plantas. Los colibríes estuvieron distribuidos diferencialmente entre los tipos de vegetación, con 12 especies presentes en la comunidad de plantas arbóreas de tierras bajas, 11 tanto en los bosques de cactus como en la comunidad de plantas perennes arbustivas espinosas, y seis en la comunidad de plantas arbustivas perennes no espinosas. *Cercidium praecox* (Fabaceae) fue la especie con mayor número de especies de colibríes visitantes (10 especies). Las comunidades de bosque de cactus y plantas perennes arbustivas espinosas tuvieron los números más altos de posibles interacciones (57 y 51, respectivamente). El valor de conectancia de las matrices de interacciones fue similar entre las cuatro comunidades de plantas (cercano al 22%), pero más bajo que lo reportado previamente a nivel mundial. En la Reserva de la Biosfera Tehuacán-Cuicatlán el sistema de interacción colibrí-planta puede ser conservado si se protegen las especies de colibríes *C. latirostris*, *A. violiceps*, *C. sordidus* y *L. clemenciae*, y las de plantas *C. praecox*, *I. arborescens*, *E. chiotilla* y *N. glauca.*

Palabras clave: interacción colibrí-planta, Puebla-Oaxaca, Reserva de la Biosfera Tehuacán-Cuicatlán, flores ornitofílicas.

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Introduction

The distribution and ecology of hummingbird species inhabiting dry habitats are not fully understood (e.g. Ornelas and Arizmendi, 1995). Particularly, there is limited information regarding which plant species are used by these hummingbirds (but see Villada, 1873; Wolf, 1970; Baltosser, 1989; Arizmendi and Ornelas, 1990; Ornelas et al., 2002; Ortiz-Pulido and Vargas-Licona, 2008). A better understanding of hummingbird communities in semiarid zones can be useful in planning conservation strategies to maintain hummingbirds and the ecological services they provide, such as pollination. This is even more important under the conservation problems faced associated with land use change, and the different predictions of global warming scenarios (Sekercioglu et al., 2004; Diáz-Valenzuela and Ortiz-Pulido, 2011), where we expect and increase in aridity in large areas of Mexico.

Currently, hummingbirds, as a group, are not considered endangered. However, changes in food availability and negative human effects, such as destruction of habitat, could threaten their survival (CITES, 2000; Sekercioglu et al., 2004). Data from Sekercioglu et al. (2004) suggests that, if the actual tendencies are maintained, 15% of the current hummingbird species could be extinct in the next century. Since many nectarivorous bird species affect plant populations and community dynamics, a reduction in their abundances could result in an increase in plant extinction risk. Thus, the extinction of nectarivorous birds may eliminate many established mutualisms between plants and birds (Sekercioglu et al., 2004).

A useful way to understand community hummingbird-plant interactions is to study the relationship through connectance and mutualistic networks. Connectance is a measure that helps to determine the relationship established in a community between 2 groups of species (Jordano, 1987). It has been used to describe patterns in several pollination systems around the world (e.g. Jordano, 1987). Mutualist networks are a way to represent, with graphs (drews) or equations, the established relationships between pairs of species in a community (e.g. Bascompte et al., 2006). Even though there are several studies where the connectance has been determined for hummingbird-plant systems, to the best of our knowledge, there is not a single study relating connectance and hummingbird-plant mutualistic networks of several plant communities located within a dry landscape.

The hummingbird species present in the Tehuacán-Cuicatlán Biosphere Reserve (RBTC), Mexico, which is a semiarid region, along with the identity and seasonality of plants used by them throughout the year is only partially known (e.g., Ornelas et al., 2002; Arizmendi and Valiente-Banuet, 2006). Different authors have published information on hummingbird and cactacean pollination from this region (hummingbirds: Arizmendi and Espinosa de los Monteros, 1996; Peterson et al., 2003; Arizmendi and Valiente-Banuet, 2006; Vázquez et al., 2009; cactacean: Valiente-Banuet et al., 1996, 1997; Casas et al., 1999; Ornelas et al., 2002; Otero-Arnaiz et al., 2003; Oaxaca-Villa et al., 2006). These studies report the presence of 9 hummingbird species (*Cynanthus sordidus, C. latirostris, Amazilia violiceps, Lampornis clemenciae*, *Eugenes fulgens*, *Calothorax lucifer, C. pulcher, Archilochus colubris*, and *Atthis eloisa*) in 3 of the 6 plant communities present in the RBTC (called plant groups by Valiente-Banuet et al., 2000). However, a review of the literature of the birds of Mexico and Central America (Howell and Webb, 1995) and the RBTC surrounding areas (Binford, 1989; Forcey, 2002) suggest the existence of 12-14 species in the RBTC. Besides, it is unknown the connectance values that exist for the hummingbird-plant mutualistic networks in this important arid region of Mexico.

In this study, we describe hummingbird species richness and the plants they visit in 4 plant communities of the RBTC. Our objectives are: 1) to describe how hummingbirds use these 4 plant communities, 2) to report the plant species visited by them in this semiarid zone of central Mexico, and (c) to describe the hummingbird-plant mutualist networks of this region, by using the conectance value and mutualistic network graphs.

Material and methods

The RBTC is located in the States of Puebla and Oaxaca in central Mexico (17º48´-18º56´ N, 97º03´-97º43´ W, 545-2 950 m asl; INE, 1999; Fig. 1). It is a large reserve (490 186 ha), that mainly protects semiarid habitats (Gobierno de Mexico, 1998). More than 2 750 plant species had been described in the area and nearly 30% of them are endemic to the RBTC (Villaseñor et al., 1990).

The vegetation diversity present within the RBTC has been systematized into 6 plant communities ("plant groups" *sensu* Valiente-Banuet et al., 2000): cactus forest (CF), arboreal plants of the lowlands (APLL; <2 100 m asl), perennial spine shrub plants (PSSP), perennial non-spiny (unarmed) shrub plants (PUSP), arboreal plants and shrubs associated with perennial rivers (ASPR), and arboreal plants of the highlands (APHL). Details on the plant communities can be reviewed in Arriaga et al. (2000) and Valiente-Banuet et al. (2000). For our study, we only considered plant communities with a climate that can be described mainly as semiarid (CF, APLL, PSSP and PUSP; INEGI, 1998a).

Fieldwork was conducted from February 2001 to February 2002 at 14 sites (Fig. 1). All sites were selected

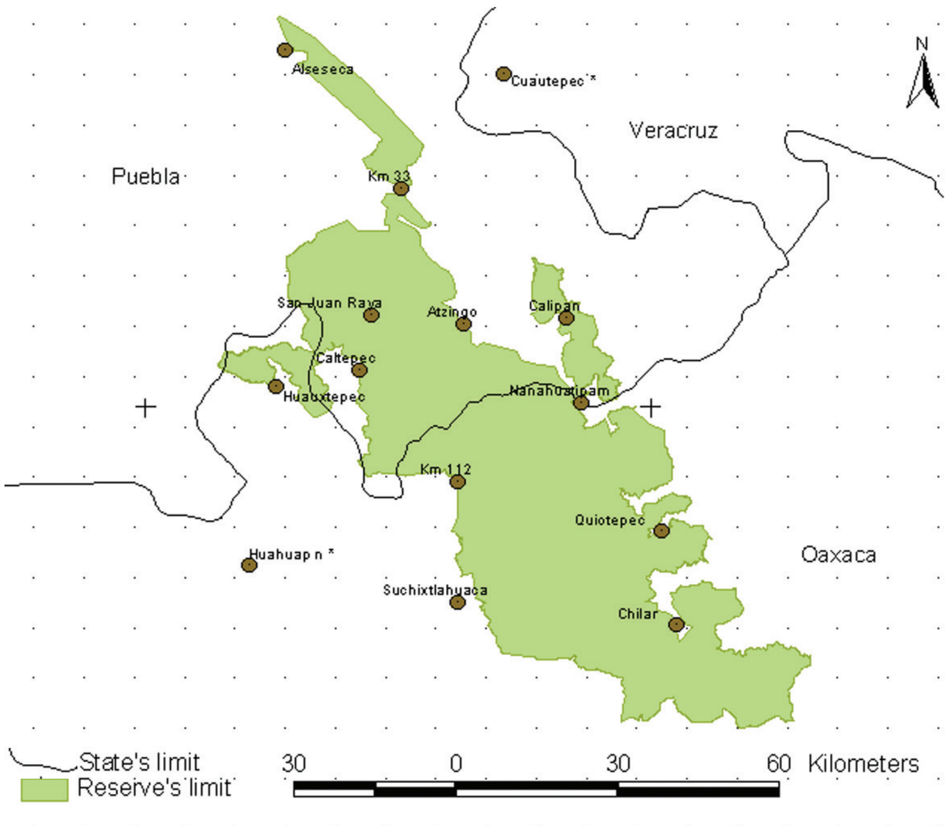

Figure 1. Sites monitored in or near to the Tehuacán-Cuicatlán Biosphere Reserve in Mexico. Small circles mark sites visited during this study.

randomly from a pool of accessible sites of each of the plant communities using a map (scale 1:250,000; INEGI, 1998b) and a table of random numbers. All the sites were ≥15 km apart. Four sites were sampled from each plant community, except for PUSP, which had only 2 sampling sites. It was not possible to reach more sites of this plant community due to inaccessibility problems in the field. The name of each site, location, altitude, and dominant plant association are listed in Table 1. Plant communities and dominant plant species were determined following Valiente-Banuet et al. (2000). Each site was sampled monthly or bimonthly due to weather conditions, combined with rough topography, and lack of roads, affected the access to some of the sites during some seasons or months.

To identify hummingbird species and determine their relative abundances, a technique described by Emlen (1971) was followed, and it was modified by Ortiz-Pulido and Diaz (2001). Briefly, one observer counted hummingbirds along a 2 km x 40 m transect at a rate of 1 km/hr at each site, paying particular attention to flower clusters with ornithophilus characteristics (tube shape and bright colors; Johnsgard, 1997). Transects at each site were established using existing animal or human paths. Three different observers (ROP, OIVI, and ADFL) identified the hummingbirds during this study, recording only visual sightings of hummingbirds that visited flowers or were observed perched inside the transects area. Observers standardized their hummingbird field identification abilities by conducting 3 months of training previous to the study. Due to the difficulties of identifying females in the field, we report only hummingbird species for which males were observed. Transects were sampled within 6 hrs of sunrise. We registered monthly information on hummingbird species and the number of individuals. Occasionally, we used mist nets, to capture secretive species. The names of the species reported follows the American Ornithologists' Union Checklist (1998) and posterior modifications (American Ornithologists' Union, 2009). Hummingbird relative abundance (taking into account only visual records) was estimated following Ortiz-Pulido et al. (2010) methods. Briefly, we adjusted the fieldwork effort (170 hrs of sampling effort in the transects) to a standardized sampling effort (SSE), which takes into account 100 hrs of observation or 400 ha

Table 1. Characteristics of the 14 sites sampled in the RBTC, México

Site	*Altitude (m asl)*	*Plant community*[1]	*Dominant plant association (sensu Valiente-Banuet et al., 2000)*	*Mean annual precipitation (mm)*	*Mean annual temperature (°C)*
Chilar	660	CF	*Escontria chiotilla* Jiotillal	400-500	22-24
Quiotepec	630	CF	*Pachycereus weberi* Cardonal	400-500	22-24
Nanahuatipam	810	PSSP	Shrubs with lateral thorns	300-400	26-28
Calipan	1200	CF	*Pachycereus weberi* Cardonal	400-500	22-24
Atzingo	1260	PSSP	Shrubs with lateral thorns	400-500	20-22
San Juan Raya	1560	PSSP	Shrubs with lateral thorns	600-700	18-20
Km 33	1745	APLL	Izotal[2]	400-500	18-20
Huauxtepec	1800	CF	*Escontria chiotilla* Jiotillal	700-800	16-18
Suchixtlahuaca	2010	PUSP	Perennifolial sclerophilous shrubs (mexical)	600-700	20-22
Km 112	2040	PUSP	Perennifolial sclerophilous shrubs (mexical)	400-500	22-24
Alseseca	2100	APLL	Izotal[2]	400-500	16-18
Caltepec	2190	PSSP	Shrubs with lateral thorns	400-500	18-20
Cuautepec *	1900	APLL	Tropical dry forest	500-600	18-20
Huajuapán *	1600	APLL	Tropical dry forest	600-700	18-20

[1]«Plant group» sensu Valiente-Banuet et al. 2000. CF= cactus forest, APLL= arboreal plants of the lowlands, PSSP= perennial spine shrub plants, and PUSP= perennial unarmed shrub plants. *Places visited only one time.
[2]Valiente-Banuet et al. (2000) reported a dominant species in this type of plant community, but the site sampled was located in a perturbed area, so we could not determine a dominant plant species.

sampled. Following this criteria, species where classified as: rare if they were recorded <3.5 times per SSE, common if they were recorded between 3.5 to 21.9 times at SSE, and abundant if they were recorded >22 times at SSE. The limit values between abundance categories used here (i.e. 3.5 and 21.9 records) reflect the common abundance distribution of the species in communities (Tokeshi, 1993; Begon et al., 2006); this distribution appears when the the percentage of rare, common, and abundant species in bird communities is considered (see details in Ortiz-Pulido et al., 2010).

Using the hummingbird records per species per site, the expected RBTC hummingbird richness with the program Estimates (Colwell, 2005) was determined. To do this we used Chao2 and 1st order Jacknife richness index. These indexes had been suggested as good estimators of species richness in several global reviews (Colwell and Coddington, 1994; Walther and Morand, 1998; Walther and Moore, 2005).

Additionally, to document the highest number of hummingbird-plant interactions we conducted focal observations of flowering plants. Focal observations on plants species were done monthly in every site sampled, with at least 1 hr of observation on groups of flowering plants per site (n= 14 sites), so a plant species located in several sites by several months had more time of observation than a plant located in only 1 site 1 month.

The distribution of hummingbirds species in each plant community was assessed by taking into account our data, and literature reports of previous studies conducted in the RBTC (Arizmendi and Espinosa de los Monteros, 1996; Valiente-Banuet et al., 1996, 1997; Casas et al., 1999; Ornelas et al., 2002; Otero-Arnaiz et al., 2003; Peterson et al., 2003; Arizmendi and Valiente-Banuet, 2006; Oaxaca-Villa et al., 2006; Vázquez et al., 2009). We did not consider studies outside the RBTC (e.g. Forcey, 2002; Grosselet and Burcsu, 2005), or those conducted inside the reserve in plant communities not considered in this study (e.g. Binford, 1989).

At each site, we collected herbarium specimens of the flowering plants visited by hummingbirds, and recorded the corolla color, one of the main signals used to select flowers by hummingbirds (Johnsgard, 1997). All the plant specimens were deposited in the herbarium of the Universidad de las Americas-Puebla. Scientific names of plant species follow nomenclature established by the nomenclatural data base VAST (Missouri Botanical Garden, 2005). We only considered plant species in which we registered hummingbird visits. We consider a "visit" when a hummingbird introduced its bill into the flower. Plant visits were recorded both during our visits along the transects, or during focal observations.

Using transect and focal observations we built a qualitative interaction matrix (sensu Jordano, 1987), where, for the entire reserve, the identity of a pair of interacting species was indicated. We extrapolated the information contained in this interaction matrix to every plant community studied. In this way we calculated the connectance value (C) and elaborated the interaction mutualistic network (graphs) by plant community.

Table 2. Relative abundance of hummingbirds per plant community, as defined in Table 1, in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico, at 2001-2002

Species	*Relative abundance*			*Records*		
		Total	*CF*	*APLL*	*PSSP*	*PUSP*
*Colibri thalassinus**	Rare	1				1
Cynanthus sordidus	Common	22	3	#	17	2
Cynanthus latirostris	Common	27	4	4	19	
Hylocharis leucotis	Rare	5	2	2	1	
Amazilia tzacatl	Commom	11	1	3		7
Amazilia violiceps	Abundant	37	6	5	8	18
Amazilia viridifrons	Common	16	2	1	3	10
Eugenes fulgens	Common	15	8	5	#	2
Lampornis clemenciae	Common	15	5	1	9	
Calothorax sp. (*C. lucifer* +*C.pulcher*)	Common	14		4	10	
Calothorax lucifer			#	R	#	
Calothorax pulcher			#	R #	R#	
Archilochus colubris	Rare	3	1	#	2	
Atthis eloisa #				#		
Selasphorus platycercus	Rare	4			4	

*= Species captured in mist nests; R species sighted; #= species reported by other authors (Valiente-Banuet et al., 1996, 1997; Casas et al., 1999; Ornelas et al., 2002; Otero-Arnaiz et al., 2003).

Connectance value is defined as C= 100xI/(AxP), where I is the total number of interactions recorded by plant community, and A and P is the number of animals and plant species recorded by plant community (sensu Jordano, 1987). The graphs were constructed taking into account the hummingbirds and plants species present in each plant community.

Results

We recorded 12 species of hummingbirds (*Cynanthus sordidus*, *C. latirostris*, *Hylocharis leucotis*, *Amazilia tzacatl, A. violiceps, A. viridifrons, Lampornis clemenciae, Eugenes fulgens, Calothorax lucifer, C. pulcher, Archilocus colubris*, and *Selasphorus platycercus*) in a total of 170 hummingbird sightings within the transects. One more species (*Colibri thalassinus*) was captured using mist-nets, and another one (*Atthis eloisa*) was reported by another study (Table 2). Using the data from the transects, the total expected number of hummingbirds species for the RBTC was 12.5±1.2 (mean±1 sd; Chao2 index) or 13.8±1.2 (Jacknife index). This indicates that our study represents a good sampling effort of the study area. The species with the highest number of records were *A. violiceps* (37) and *C. latirostris* (27) (Table 2); and the ones with the least number of observations were *A. colubris*, *S. platycercus*, and *H. leucotis*.

When we added literature records to our dataset (Table 3) we detected that 12 hummingbird species are reported for the APLL, 11 both in both CF and PSSP communities, and 6 in the PUSP community (Table 2). *Cynanthus sordidus, A. violiceps, A. viridifrons*, and *E. fulgens* are distributed in the 4 plant communities studied, while *C. thalassinus, A. eloisa,* and *S. platycercus* were present in only one of them (Table 3).

We recorded 32 plant species visited by hummingbirds; additionally 3 other plant species were reported by other authors (Table 4). These species represented 21 genera, distributed in 14 families. The family with the highest number of species recorded was Cactaceae (16 species); 9 families were represented by only 1 species (Table 4). The predominant color among flowers was yellow (11 species), followed by white and pink (8 each), purple and red (3 each), and orange (2; table 4). After adding literature records to our results we had a total of 25 plant species to be visited by hummingbirds in CF, 24 in PSSP, 10 in APLL, and 5 in PUSP (Table 4). We recorded 2 species (*Tecoma stans* and *Opuntia hyptiacantha*) distributed in the 4 plant communities studied, and 7 species (*Prosopis juliflora, Ipomoea arborescens, Salvia* sp. 1, *Nicotina glauca, Opuntia huajuapensis, O. pilifera,* and *Stenocereus stellatus*) distributed in 3 plant communities (Table 4).

We registered 62 different hummingbird-plant species interactions for which we could identify both species, 10 more interactions where only identified to the plant species, and 14 more interactions were from the literature (Table 5). The hummingbird species that visited the most plant species were *C. latirostris* (18 plant species visited), *A. violiceps* (15), and *C. sordidus* (11). The hummingbird species that were recorded visiting the smallest number of plant species were *Archilochus colubris* and *C. lucifer* (one each; Table 5). We did not record *C. thalassinus* and *A.*

Table 3. Hummingbird records per plant community and vegetation type. Data are from studies done in the Tehuacán-Cuicatlán Biosphere Reserve, Oaxaca-Puebla, Mexico, reported from 1996 to 2010

Reference		*Vegetation studied **		*Hummingbird species recorded* [#]														
		Plant community	*Vegetation type (or name used in each study)*	*C. thalassinus*	*C. sordidus*	*C. latirostris*	*H. leucotis*	*A. tzacatl*	*A. violiceps*	*A. viridifrons*	*L. clemenciae*	*E. fulgens*	*Calothorax* sp.	*C. lucifer*	*C. pulcher*	*A. colubris*	*A. eloisa*	*S. platycercus*
Arizmendi and Espinosa de los Monteros	1996	Cactus forest	*N. tetetzo* Tetechera		x	x			x					x	x	x		
			C. hoppenstedtii Cardonal															
			N. mezcalaensis y *N. macrocephala* Tetechera		x	x			x					x	x	x		
		Arboreal plants of the lowlands	*Y. periculosa* Izotal		x	x			x					x	x			
Valiente-Banuet et al.	1996	Cactus forest	*N. tetetzo* Tetechera		x				x									
Valiente-Banuet et al.	1997	Cactus forest	*P. weberi* Cardonal			x												
		Perennial spine shrub plants?**	Xerophile shrubs			x												
Casas et al.	1999	Cactus forest	*S. stellatus* Cardonal		x	x			x									
Ornelas et al.	2002	Perennial spine shrub plants?**	Xerophile shrubs		x	x			x		x	x		x				
Peterson et al.	2003	Cactus forest	In a community called "El Venado"		x	x			x									
		Arboreal plants of the lowlands	In a place called "La cañada"		x	x			x									
Otero-Arnaiz et al.	2003	Cactus forest	P. *chichipe* Chichipera		x	x			x									
Oaxaca-Villa et al.	2006	Cactus forest	*E. chiotilla* Jiotillal		x	x			x									
Arizmendi and Valiente-Banuet	2006	Cactus forest	Cactus forest			x									x	x		
		Arboreal plants of the lowlands	Izotal		x	x								x	x			
			Dry forest		x	x												
			Perennial thorned dry forest		x	x									x			
		Perennial spine shrub plants	Perennifolial sclerophilous shrubs (Mexical)			x						x			x			
Vázquez et al. (sensu Apéndice 1)	2009	Arboreal plants of the lowlands	Tropical dry forest		x	x			x		x		x			x	x	
Current study	2012	Cactus forest	*E. chiotilla* Jiotillal		x	x	x		x	x	x	x						
			P. weberi Cardonal		x	x		x	x		x	x				x		
		Arboreal plants of the lowlands	Izotal		?	x	x	x	x	x	x	x	x	x	x			
		Perennial spine shrub plants	Shrubs with lateral thorns		x	x	x		x	x	x	?	x		x	x		x
			Tropical dry forest			x	x	?	x	x		?	x					
		Perennial unarmed shrub plants	Perennifolial sclerophilous shrubs (Mexical)	x	x			x	x	x		x						

**Sensu* Valiente-Banuet et al. (2000). We did not take into account man-made vegetation types (e.g., cultivations, urban areas), riparian o aquatic vegetation; as those described in Arizmendi and Valiente-Banuet (2006).

**It is not very clear to which plant community the authors refer.

[#] x= recorded in the plant community and vegetation type, ?= doubts about the record.

Table 4. Plant species whose flowers are visited by hummingbirds in the RBTC, México

Family	*Species*	*Corolla color*	*Plant community*			
			CF	*APLL*	*PSSP*	*PUSP*
Acanthaceae	Acanthaceae sp. 1	Red			X	
	Acanthaceae sp. 2	Orange			X	
Agavaceae	*Agave marmorata*[#]	Yellow			#	
	Agave sp. 1	Yellow			X	
	Agave sp. 2	Yellow			X	
Bignoniaceae	*Tecoma stans*	Yellow	X	X	X	X
Bombacaceae	*Ceiba parvifolia*	White	X			
Bromeliaceae	*Tillandsia dugesii*	Pink			X	
Cactaceae	*Escontria chiotilla*	Yellow	X		X	
	Myrtillocactus geometrizans	White	X		X	
	Neobuxbaumia tetetzo[#]	White	#			
	Opuntia decumbens	Yellow		X	X	
	Opuntia depressa	Pink	X		X	
	Opuntia huajuapensis	Yellow	X	X	X	
	Opuntia hyptiacantha	Orange-Yellow	X	X	X	X
	Opuntia kleiniae	Yellow			X	
	Opuntia pilifera	Pink	X	X	X	
	Opuntia tehuacana	Pink	X		X	
	Opuntia velutina	Yellow	X			
	Pachycereus weberi	White	X			
	Pilosocereus chrysacanthus[#]	Pink	#			
	Polaskia chichipe	White		X		
	Stenocereus pruinosus	Pink	X		X	
	Stenocereus stellatus	Pink	X	X	X	
Convolvulaceae	*Ipomoea arborescens*	White	X	X	X	
	Ipomoea sp. 1	Pink	X		X	
Euphorbiaceae	*Cnidoscolus multilobus*	Yellow	X			
Fabaceae	*Cercidium praecox*	White	X		X	
Fouquieriaceae	*Fouquieria formosa*	Red	X		X	
Hydrophyllaceae	*Wigandia urens*	Purple	X			
Lamiaceae	*Salvia* sp. 1	Purple	X		X	X
	Salvia sp. 2	Purple				X
	Labiada sp. 1	Red	X			
Mimosaceae	*Prosopis juliflora*	White	X	X	X	
Solanaceae	*Nicotiana glauca*	Yellow	X	X		X

"#" indicates species reported by other authors (i.e., Valiente-Banuet et al., 1996, 1997; Ornelas et al., 2002).

eloisa visiting any plants. *Cercidium praecox* (Fabaceae) was the plant species that received the most visits from more hummingbird species (10 hummingbird species visiting; Table 5), while 8 plant species were only visited by 1 hummingbird species: *Ipomoea* sp. 1 (Convolvulaceae), *Pachycereus weberi, Pilosocereus chrysacanthus, Opuntia tehuacana, O. velutina* (all Cactaceae), *Tecoma stans* (Bignoniaceae), *Salvia* sp. 2 and *Ceiba parvifolia* (Bombacaceae).

CF and PSSP were the plant communities with largest number of possible interactions (57 and 51, respectively), followed for APLL (28) and PUSP (7) (Fig. 2). The more complex interaction graphs are those from CF and PSSP and the lesser from PUSP. The connectance value is similar between plant communities, with 19.1% for PSSP, 20.7% for CF, 21.2% for APLL, and 26.7% for APLL.

Discussion

Our study shows that in the semiarid plant communities of the RBTC: (a), there are 14 hummingbird species; (b) 35, plant species are visited by hummingbirds; (c), both species groups have a differential distribution across plant communities; (d), we detected nearly 86 different hummingbird-plant interactions; (e), the interactions are distributed differentially between plant communities,

Table 5. Interaction matrix between hummingbird and plant species in the RBTC, México. "X" indicates that we registered the interaction between the hummingbird (column) and the plant species (row). "*" indicates that we registered hummingbirds visiting these plant species, but we did not identify the visiting species. "#" indicates species or interaction reported by other authors (Valiente-Banuet et al., 1996, 1997; Casas et al., 1999; Ornelas et al., 2002; Otero-Arnaiz et al., 2003)

Plants	*Colibri thalassinus*	*Cynanthus sordidus*	*Cynanthus latirostris*	*Hylocharis leucotis*	*Ama zilia tzacatl*	*Amazilia violiceps*	*Amazilia viridifrons*	*Eugenes fulgens*	*Lampornis clemenciae*	*Calothorax lucifer*	*Calothorax pulcher*	*Calothorax* sp.	*Archilochus colubris*	*Atthis eloisa* [#]	*Selasphorus platycercus*	*Total*
Acanthaceae sp. 1			X						X							2
Acanthaceae sp. 2			X						X							2
Agave marmorata [#]			#			#		#	#		#					5
Agave sp. 1						X						X				2
Agave sp. 2																*
Ceiba parvifolia						X										1
Cercidium praecox		X	X	X	X	X		X	X		X	X			X	10
Cnidoscolus multilobus		X	X													2
Escontria chiotilla		X	X	X		X	X									5
Fouquieria formosa																*
Ipomoea arborescens		X	X					X	X	X	X					6
Ipomoea sp1			X													1
Labiada sp. 1							X	X	X							3
Myrtillocactus geometrizans		X									X					2
Neobuxbaumia tetetzo [#]		#				#										2
Nicotiana glauca		X			X	X	X	X							X	6
Pachycereus weberi			#													1*
Pilosocereus chrysacanthus [#]			#													1
Prosopis juliflora			X									X				2
Opuntia pilifera		X	X			X										3
Opuntia hyptiacantha		X	X			X										3
Opuntia depressa																*
Opuntia velutina						X										1
Opuntia huajuapensis			X			X										2
Opuntia kleiniae																*
Opuntia tehuacana						X										1
Opuntia decumbens																*
Polaskia chichipe [#]		#	#			#										3*
Tecoma stans			X													1
Tillandsia dugessi																*
Salvia sp. 1																*
Salvia sp. 2							X									1
Stenocereus pruinosus			X			X		X	X				X			5
Stenocereus stellatus		X	#			#										3
Wigandia urens																*
Total	0	11	18	2	2	15	4	6	7	1	4	3	1	0	2	

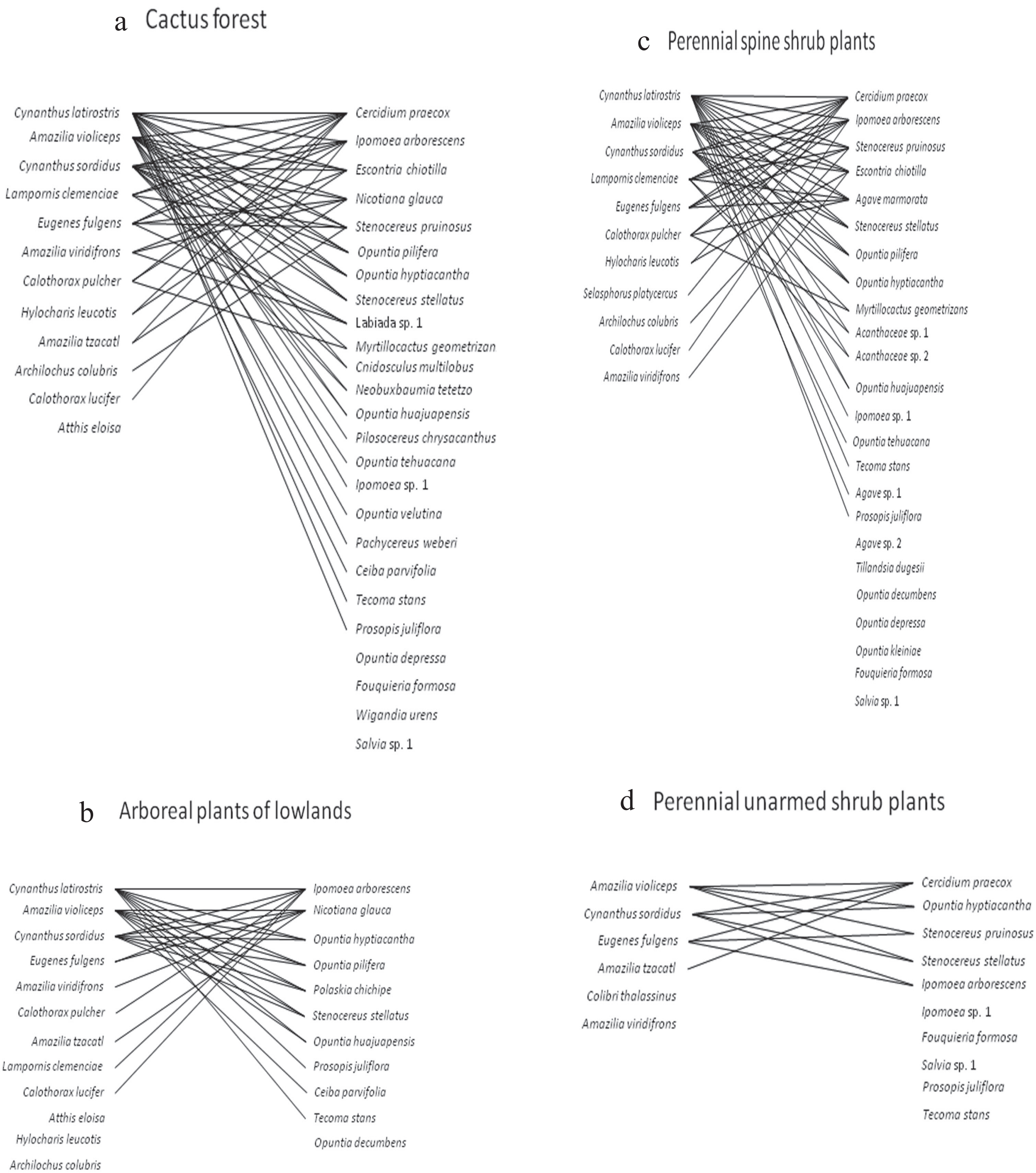

Figure 2. Mutualistic hummingbird-plant networks recorded at 4 plant communities located in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. In each graph, hummingbirds are on the left side and plants on the right side. Lines between 2 species indicate a relationship registered between both species.

and (f), the connectance value is similar between plant communities.

The RBTC is a large area representing several climates and vegetation associations (INEGI, 1998a; Valiente-Banuet et al., 2000). Thus, hummingbirds, ornithophilous plants, and their interactions are expected to be differentially distributed between plant communities in the RBTC. Our results show that CF had the highest numbers of hummingbird species, plant species, and interactions, while PUSP is the plant community with the lowest numbers for the same variables. Hummingbird richness could be influenced by the diversity of plants which act as food resource, which in turn determines the nectar availability, and along with this also determine the interaction richness. At community level several studies have found a possitive significant relationship between nectar availability and hummingbird relative density (see review of Ortiz-Pulido and Lara, 2011), but few of them show a relationship between plant and hummingbird richness (e.g. Stiles, 1985; Cotton, 2007). However, other variables, such as flower number, nectar-energy availability, or hummingbird inter and intraspecific segregation, affect this relationship (e.g., Ortiz-Pulido and Vargas-Licona, 2008; Ortiz-Pulido and Lara, 2011).

In spite of the difference in species and interactions recorded, the RBTC plant communities are similar in their connectance value (i.e. near to 22%; ranking from 19 to 27%). This value is lower than that reported for other sites with hummingbird-plant interaction systems (mean= 42%), but similar to honeyeaters-plant (21%) and insect-plant (24%) systems (Jordano, 1987). The connectance values that we obtained for the RBTC plant communities could have been affected by factors, such as the environment aridness or the conservation level of the study site. From the results of Jordano (1987) it is not clear if the connectance is influenced by aridity or humidy of the environment, precluding any further exploration of the idea. However our results suggest that this is a possibility, with more arid sites having smaller connectance values.

While the connection between connectance values and aridity is not clear, there are some preliminary data related to the relationship between connectance and conservation level. In Costa Rica, data from Wolf et al. (1976) suggest that hummingbird-plant systems located in preserved oak forest have lower connectance value (30%) than unconserved oak forest sites (64%) (Jordano 1987). The results of Wolf et al. (1976) agree with theoretical predictions. It has been suggested that network systems that are broken by hazardous conditions will show increasing connectance between the remaining nodes (in this case, species; Montoya et al., 2001). In general, RBTC plant communities are well preserved, with perhaps the exception that the PUSP that showed some degree of grazing presure. Curiously, this is the plant community that showed the highest conectance value in the RBTC. Unfortunately, there are not enough data to determine if the conservation level of a RBTC plant community is related to its connectance.

Our results suggest the existence of certain conservation priorities in terms of hummingbird-plant interaction systems in the RBTC. The main species that should be protected are, for hummingbirds, *C. latirostris*, *A. violiceps*, *C. sordidus*, and *L. clemenciae*, and, for plants, *C. praecox*, *I. arborescens*, *E. chiotilla*, and *N. glauca,* even when not all these species are endemic to Tehuacán-Cuicatlán. Independently of which plant community we consider, these are the more connected species. According to our results, they control the flow of energy, and can be considered as key species in the hummingbird-plant RBTC systems.

In conclusion, RBTC plant communities differ in species richness and number of interactions, but their connectance values are very similar. These values are similar to those reported in other hummingbird-plant interaction systems. A deeper assessment of the hummingbird-plant interactions indicates that in the RBTC plant communities there are key species. To conserve these plant-pollinator interactions, additional work is needed to further understand the biology of these hummingbirds and plants, and to establish the mechanisms that determine the connectance value between hummingbird and plant communities.

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