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Research Article

Temporal variation in native bee diversity in the tropical sub-deciduous forest of the Yucatan Peninsula, Mexico

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Abstract

Native bee community diversity is known to vary temporally in the Neotropics, but little research has been done to quantify the extent of this variation. We studied monthly variation in native bee diversity in tropical semi-deciduous forest on the Yucatan Peninsula, Mexico, over a twelve-month period in 2007. Hurricane Dean traversed the study area in August of that year, causing some changes in the environment and in the native bee community. A total of 2,335 individual bee specimens were collected, belonging to 102 species from four families. The family Apidae had the highest number of species (46%) and individuals (71%). Species richness, abundance, and diversity varied throughout the study period. Species proportions of lifestyles and nesting behaviors varied from month to month, and absolute numbers changed. Low to moderate similarity values indicated high monthly species turnover, with almost half of species present for only one to two months. Species richness declined after the hurricane, with a loss of 40% of the species present beforehand, but nine new species appeared in September. The hurricane also reduced the number of solitary, parasocial, and social species, mostly those nesting in preexisting cavities and wood. Species composition in August had similarity values nearer to those of months in the dry season than to those in the rainy season. Two months after the hurricane, the native bee community had returned to previous species diversity levels, probably due to the rapid recovery of the vegetation on which the bee community depends. Effective biodiversity conservation programs will need more data on changes in vegetation community structure and how such changes influence Neotropical native bee communities after natural disturbances.

Key words: bee diversity, Hurricane Dean, Yucatan Peninsula, Neotropics, Mexico.

Resumen

Es conocido que la diversidad de la comunidad de abejas nativas en el neotropico varia temporalmente, y poco ha sido hecho para cuantificar la extensión de esta variación. La variación mensual de la diversidad de abejas nativas fue estudiada en la selva mediana subcaducifolia en la Península de Yucatán,

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en México, en un periodo de 12 meses en 2007. El Huracán Dean atravesó el área de estudio en agosto de ese año, causando algunos cambios sobre el ambiente y la comunidad de abejas nativas. En total se recolectaron 2,335 individuos, de 102 especies pertenecientes a cuatro familias. La familia Apidae presentó el mayor número de especies (46%) e individuos (71%). La rigueza, abundancia y diversidad de especies vario a través de los meses. La proporción de especies en términos de estilos de vida y conductas de anidación vario mes a mes y el número de especies cambio. La baja a moderada similitud indico alto recambio de especies mensual y cerca del 50% de las especies estuvieron presentes solo uno o dos meses. La riqueza de especies declino después del paso del huracán, se perdieron el 40% de las especies presentes en agosto aunque nueve especies aparecieron como nuevas en septiembre. Después del huracán decrecieron especies solitarias, parasociales y sociales y principalmente las especies que anidan en cavidades preexistentes y en la madera. Agosto fue más similar en la composición de especies con los meses de secas que con los de lluvias. Dos meses después, presumiblemente la recuperación rápida de la vegetación posiblemente jugo un papel importante para la persistencia de la comunidad de abejas en el área de estudio. Se requieren más investigaciones para determinar los cambios en la estructura de la comunidad vegetal y los efectos en las comunidades de abejas neotropicales que permitan predecir el efecto de estos fenómenos naturales para la planeación de la conservación de la biodiversidad.

Palabras clave: diversidad de abejas, huracán Dean, Neotrópico, Península de Yucatán, México.

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Introduction

Native bee community diversity in the Neotropics is still an open field, since many zones have yet to be studied [1], particularly in Mexico [2]. Little is known about temporal variation in bee community diversity, which has received only occasional attention [*e.g.*, 3, 4]. In addition, no reports exist on the changes that natural phenomena such as hurricanes can cause in these bee communities. Native bee diversity had received minimal attention until the last twenty years, especially on the Yucatan Peninsula [2, 5, 6, 7]. Other studies have focused on bee diversity in some regional agricultural crops [8, 9], or on how habitat fragmentation has affected native bee diversity [10]. Most studies have been done in the northern portion of the Peninsula, and little is known about diversity in its south central portion, where intact remnants of sub-deciduous tropical forest remain, mainly in the area where the states of Yucatan, Campeche and Quintana Roo meet [11, 12].

The Yucatan Peninsula (YP) is a biotic province with Neotropical biogeographic affinity. Its climate is largely sub-humid. Because it is highly and uniformly exposed to the sun year round, there are only two clear seasons: a rainy season from late spring to early fall, and a dry season from late fall to early spring (the driest months are usually February to April). The Atlantic hurricane season officially spans from May to November, but the YP is most frequently affected during August and September. A common pattern for hurricanes that affect the YP is for a tropical storm to form east of the West Indies, to become a hurricane as it enters the Caribbean Sea, and then to sweep across the YP and into the Gulf of Mexico [13]. Relatively common in Mexico and Central America, hurricanes can cause dramatic changes in tropical forest structure when they make landfall, including generalized defoliation, loss of branches, trunk breakage, and the toppling of entire trees [14]. The almost complete defoliation caused by hurricanes can disrupt the canopy's role in providing shade and controlling soil microclimates [15], as well as rapidly increase the amount of leaf cover and wood detritus on the forest floor [16, 17]. Studies of this post-hurricane dynamic in the YP have only recently begun [e.g., 18]. Although tropical forests frequently experience hurricanes, only limited attention has been given to the response of insects to such extreme natural disturbances [19]. Exacerbating this lack of data is that only a few tropical forest insect communities have been thoroughly evaluated [e.g. 20]. In contrast, a number of studies have documented the effects of anthropic disturbances on insects, particularly native bee communities [e.g., 21].

Despite their being vital pollinators, no previous reports have been done on native bee communities' responses to high-energy natural phenomena such as hurricanes. To survive, native bee communities require floral resources and nesting sites, normally vegetation and other substrates. The food needs of each bee species in a community vary according to their feeding habits (generalist or specialist), social habits (*e.g.*, solitary, social, cleptoparasitic), nesting behavior, and life cycles [22, 23, 1]. Thus, their highly variable individual biology probably determines how each native bee species responds to large natural disturbances such as hurricanes. We describe monthly variation in the diversity of native bees in semi-deciduous forest on the Yucatan Peninsula before and after a hurricane affected the forest. These data will help to explain the response of the bee fauna to this type of natural phenomenon and its effect on bee ecological services.

Methods

Study area. The study area is located in the southern extreme of the state of Yucatan, in the municipality of Tekax (19°47′04″ and 19°43′03″ N, 89°18′13″ and 89°09′31″ W), very near the point at which the Mexican states of Yucatan, Campeche and Quintana Roo meet, known as the Punto PUT (*i.e.* Punto de Unión Territotial) (Fig. 1). The area's climate is type Awo(i)gw, hot subhumid with summer rains [24], with annual rainfall ranging from 1,000 to 1,229 mm [11]. Mean annual temperature is 24.9 °C; the hottest month is May, and the rainiest is September [25]. Soils in the area are vertisol, gleisol, nitisol, rendzinas, and lithosols [26]. Vegetation type is tropical sub-deciduous forest (TSF), which occurs as a wide band through the center of the state of Yucatan, narrowing to the south. It continues into northern Campeche and occupies only a small area in Quintana Roo, on its border with Yucatan. Trees in the TSF reach an average height of 10 to 20 m, although maximum height can be 25 to 30 m in some areas. During the dry season, typically 50% to 75% of trees in the TSF drop their leaves.

The main tree species in the TSF are Acacia pennatula (Schlech and Benth), Caesalpinia gaumeri Grenm., Caesalpinia platyloba S.Watson., Lysiloma latisiliquum (L.) Benth., Enterolobium cyclocarpum (Jacq.) Griseb., Mimosa bahamensis Benth., Spondias mombin L., Metpium brownie (Jacq.) Urban., Cochlospermum vitifolium (Willd) Spreng., Guazuma ulmifolia Lam., Trema micrantha (L.) Blume., Annona reticulata L., Gyrocarpus americanus Jacq., Piscidia piscipula (L). Sarg., Pithecellobium dulce (Roxb) Benth. and Pithecellobium albicans (Kunth) Benth. Epiphytes in the area include some Areaceae (Anthurium tetragonum Schott), Bromeliaceae (Tillandsia brachycaulos Schltdl) and Orchidaceae (Catasetum integerrimum Hook) [11].

Hurricane Dean reached category 5 on the Saffir-Simpson scale off the southeast coast of the YP on 21 August 2007 (Fig. 1). As it crossed the YP from east to west and moved over the study area, it varied from category 4 to 3 [27, 28, 25].

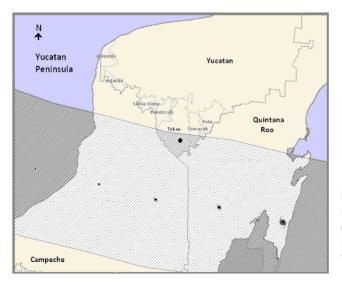


Fig. 1. Sampling area location in Tekax Municipality (black dot ●), Yucatan Peninsula, Mexico. Trajectory of Hurricane Dean is marked with (symbol size indicates relative intensity from 5 to 1)[modified from 28].

Bee sampling. The native bee fauna was sampled monthly from January to December 2007. In August, sampling was done before Hurricane Dean traversed the area. Every month, sampling was done in 100 x 200 m quadrants, each quadrant using 15 McPhail traps [29], baited with 50% honey and placed at 10 m intervals; three Malaise traps placed at 50 m intervals; and three lots (12 traps per lot) of yellow pan traps placed at 50 m intervals. The three types of traps were left to collect specimens for 48 hours a month. During this same time, a research team member surveyed each quadrant for two hours to collect bees with an entomological aerial net. Bees were also collected by one team member along four 1-km-long transects. Collected bees were preserved in 70% ethanol, and later prepared and dried using a conventional treatment for Hymenoptera. Specimen identification was done following Ayala [30] and Michener [1], and corroborated by comparison with bee specimens in the Regional Entomological Collection of the Autonomous University of Yucatan (CER-UADY). Some individual specimens were established as "morphospecies" [*sensu* 31], because a number of bee genera have not been taxonomically reviewed. All collected specimens were deposited in the CER-UADY (Collecting permit-SEMARNAT- authorization code: SGPA/DGVS/ 10220).

Data analysis. We estimated species richness and total abundance by month. Representation of species richness values throughout the year was calculated with the quantitative Chao 2 richness estimator, one of the least biased estimators for small samples [32]. We calculated diversity using the proportional abundance indices classified as evenness indices (Shannon-Wiener). A random test was applied to the Shannon-Wiener index to detect differences among data, and calculations were done with the programs Biodiversity Pro [33] and Species Diversity and Richness [34]. The number of singletons and doubletons (species represented by only one or two bees, respectively, in the sample) was determined using the EstimateS program [35]. Environmental variable data were mean monthly temperature and rainfall during 2007, collected at the federal meteorological station nearest the study area (Nohalal Station, Tekax Municipality) [25]. Any correlations between environmental variables (temperature and rainfall) and bee species richness and abundance were identified with the Statistica program [36]. Native bee richness, abundance and diversity, as well as lifestyles and nesting behavior, were compared among the sampling data sets.

The Jackard index was used to evaluate shared species month to month; we used a cluster analysis to identify gathered species. The Jackard measures of beta diversity (month-to-month species turnover) were done using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) with the MVSP program [37]. Species lifestyle was defined based on several studies [23, 22, 38, 1]: solitary; parasocial (*sensu lato:* quasisocial, semisocial, subsocial, primitively eusocial), eusocial and cleptoparasitic. Nesting behavior was similarly defined [23, 1, 22]: preexisting cavities (nests in holes in rocks, banks of soil, dead tree limbs, etc.); nests excavated in soil; and nests excavated in hard or soft wood. For many native bee species, no data are available on their lifestyles and nesting behavior; when necessary, these parameters were deduced by considering taxonomic relationships at the genus and subgenus levels. The honeybee, *Apis mellifera* L. was not sampled because its presence, abundance and distribution depend more on the location of beehives than on environmental factors [39].

Results

Collected specimens totaled 2,335 bees, from 102 species belonging to four families. The family Apidae had the highest number of species and individuals (~45% were stingless bees), followed by the Megachilidae, Halictidae and Colletidae families (Table 1). Estimated richness for the study area was 122 species, meaning our sample accounted for 85% of estimated richness, and was therefore highly representative.

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Family	Number of species	%	Number of individuals	%
Apidae	46	45.1	1660	71.0
Colletidae	6	6.0	37	1.6
Halictidae	23	22.5	466	20.0
Megachilidae	27	26.4	172	7.4
Total	102	100	2355	100

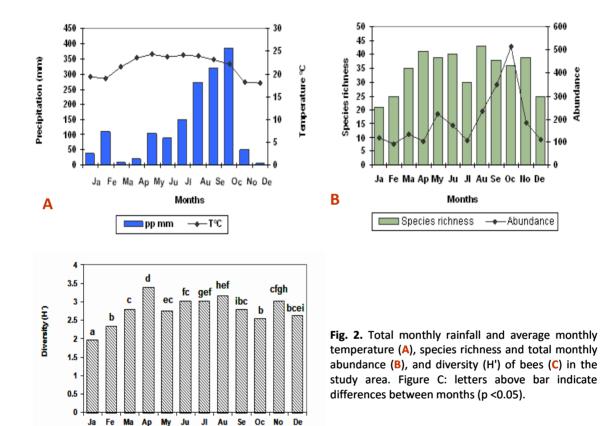
Table 1. Number of species and total abundance by family of the native bee community in tropical semi-deciduous forest, Yucatan Peninsula, Mexico.

Rainfall was highest in the months following Hurricane Dean (September and October) (Fig. 2A). Species richness and total abundance were variable across months. The highest richness was in April and August, while the strongest declines were from June to July, and from November to December. The strongest decline in abundance was from October to November, during the rainy season. The number of individuals increased from August to September, and then again in October, two months after the hurricane (Fig. 2B). Forty-three species were documented in August, of which 17 (40%) were not found in September. However, nine species appeared in September that had not been recorded in August (26% of September's species). Twelve species present in August did not return in the months after the hurricane (Appendix 1). Diversity (H') was highest in April and August, declined in September and October, and then rose again in November (Fig. 2C). Values differed between August and September, were moderately variable in other months, and were lowest in January. Overall, 22 singleton species and 12 doubleton species were identified.

Lifestyles in the sampled native bee community were mostly solitary (50%), followed by parasocial (30%), eusocial (14%) and cleptoparasitic (6%) (Fig. 3A). Nesting in preexisting cavities was the most common strategy, followed by nesting in the ground, in wood, and the cleptoparasites (Fig. 3B). The number of species in each functional group changed from month to month, but the proportions remained constant (Fig. 3C and D). The number of solitary species was highest in April, and decreased steadily in later months, particularly in September and October. The lowest number of solitary species occurred in the months of January and February. Parasocial species were most frequent in August, declined notably in number from August to September, and remained constant from November to December. Present every month, eusocial species were most frequent in March and July, and declined from March to April.

Cleptoparasite species were most numerous in April, very much like the solitary species, but were not recorded in June and August. They reappeared after the hurricane (Fig. 3C).

Species nesting in cavities were most numerous in April and August, and then declined notably from June to July and again from August to September. Ground nesting species exhibited the highest numbers in November, and then declined to December. Those nesting in wood reached their maximum numbers in August, with declines in September and from June to July; their lowest numbers were in January (Fig. 3D).



Overall, the month-to-month bee community species profile had generally low to moderate similarity (20 to 54%) (Fig. 4). Two groups had 20% similarity (or 80% dissimilarity): the first was present in January-December, and the second in the remaining months, including post-hurricane. Similarity was moderate from August to September and highest from September to October. Indeed, species composition in August (rainy season) had more similarity to compositions in the dry months of June and March than to other months in the rainy season (September and October) (Fig. 4).

Months

С

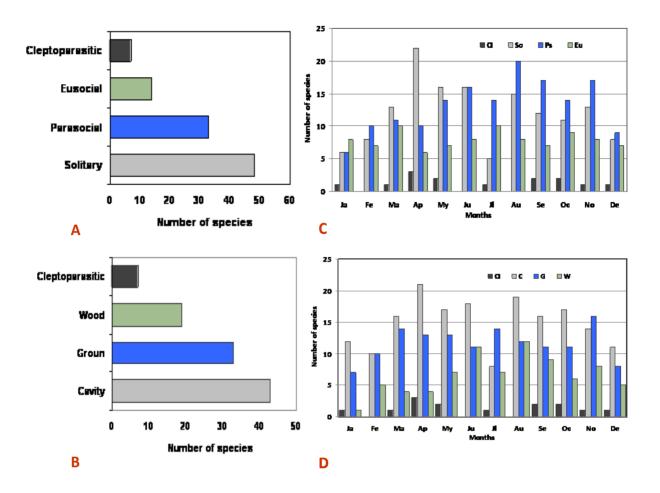


Fig. 3. Lifestyles (A) and nesting behavior (B) in total native bee community; Lifestyles (C) and nesting behavior (D) over time. Figure C: So=Solitary, Ps=Parasocial, Eu= Eusocial and Cl= Cleptoparasitic and figure D: Cl= Cleptoparasitic, C= Preexisting cavity, G= Ground and W=Wood.

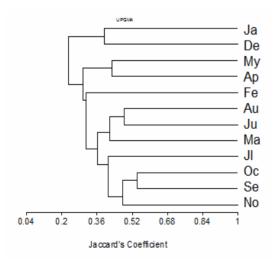


Fig. 4. Similarity dendrogram of native bee species activity in the months of 2007.

Positive correlations were identified between abundance and monthly rainfall (r= 0.71, p<0.5), and between richness and monthly temperature (r=0.68, p<0.5). Bee species exhibited different activity periods throughout the year. Forty-nine species (48%) were caught in only one or two months, 29 species (28.5%) were present during three to six months, and the remaining 24 species (23.5%) were recorded during seven to twelve months (Fig. 5).

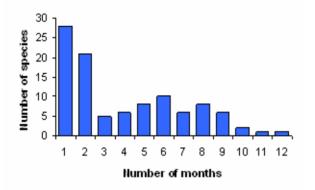


Fig. 5. Number of native bee species and number of months they were present during 2007.

Discussion

Apidae family species were the main components of the native bee community in the studied TSF, and had the highest number of recorded individuals (mainly eusocial stingless bees). This corresponds with reports for bee communities in the Neotropics [22, 40] and in other zones of the YP [5, 6, 7]. The number of recorded species represented 85% of the estimated number of species in the studied community, meaning approximately twenty more species have yet to be recorded. Complementary sampling would be needed to record the less common species that fill out bee community diversity in the Neotropics [40, 41]. Nearly 30% of the recorded species were rare (singletons and doubletons), a trend observed in other areas of the YP [5].

Weather in the YP area in 2007 was highly unusual. Rainfall in February was atypically high (this month is normally quite dry), and Hurricane Dean crossed the study area in August. The latter was an extremely high-energy event, a category 5 hurricane (wind speed: \geq 252 km/h) when it made landfall [27], and the zone it affected was declared a disaster area [28]. When it crossed the study area, Hurricane Dean varied from category 3 to 4 (wind speed: \geq 178-249 km/h), and clearly impacted the TSF.

Impacts of this degree could have had negative effects on the area's native bee community. However, identifying which effects are specifically due to the hurricane is difficult, since native bee species' richness, diversity, and abundance exhibit wide monthly variation in response to several factors (*e.g.*, environmental conditions and availability of resources)[22]. Abundance increased after Hurricane Dean due to the presence of several species of stingless bees and other species (Appendix 1) that were apparently unaffected by the disturbance. Abundance peaked in October, two months after Dean, possibly indicating that vegetation (particularly

herbaceous species) quickly recovered after the event [14], and those trees and bushes that flower at this time [45] continued to do so. In addition to variations in response to resource availability [22, 39], native bee abundance patterns can also vary within and between years due to changes in environmental conditions [46, 22]. This was corroborated in the present study, as species richness was correlated to temperature, and abundance to rainfall, highlighting these factors' role in Neotropical bee activity.

Floral resources and nesting site availability are the two factors that most influence bee species' seasonal activity [42]. Bee abundance and frequency on flowers of specific plants are known to vary in response to annual flowering patterns [43]. Temporal variation in habitats occurs because important resources become available at different times [44]. Monthly variation in bee community species profiles in the studied TSF was high, with many species active for only a few months. This may be a common pattern in neotropical forests, since the same trend was reported in a study done in Chamela (Jalisco, Mexico) [4]. In our study, we observed seasonal changes in bee species composition and numbers; many were active during a few months and this activity was associated with flowering in the plants on which they feed. The presence of Cleptoparasite species is closely related to the activity of their hosts [22]. Our results confirm this, as their presence coincided with the activity of their host species (*e.g. Coelioxys* and *Megachile* species) (Appendix 1). Eusocial species are active year round [1], but they were not observed every month, except *Trigona fulviventris*, which was present in all twelve months (Appendix 1). These species are the most abundant in tropical bee communities, and are these communities' main components [22].

Since local and regional environmental conditions and biotic interactions influence native bee community composition, community structure and function exhibit marked spatial changes among locations in different zones worldwide [47]. However, only infrequent analyses have been done of temporal variation in bee communities, and this limited data can lead to erroneous conclusions about diversity in different kinds of habitat [44], and in response to natural disturbances such as hurricanes. In the TSF studied here, species composition in the native bee community varied notably throughout the year, mainly in response to the rainy and dry seasons. The dry season begins in November [13], and the lower temperature and rainfall in this season reduced bee numbers, consequently lowering bee abundance; indeed these two parameters were correlated. Richness remained relatively high in November, suggesting that species turnover exhibited marked changes between seasons. July had the lowest species richness and very low abundance, marking the transition from the dry to the rainy season. The rainy season commonly begins in May, but in 2007, both May and June were unusually dry. August saw increased rainfall, leading to the appearance of several species and the highest species numbers.

Diversity (H') varied throughout the year, but was highest in April. Similar levels can normally be expected during the rainy season, but the hurricane's impact reduced diversity in September and October. It did not fully recover until November. Hurricane Dean apparently altered the normal annual diversity pattern by displacing 17 of the species present before its impact, and introducing nine species afterwards, perhaps due to physical movement by high winds.

Community species composition also changed, losing species in the rainy season (*i.e.*, August had low similarity compared to September and October). Some of these lost species had been present in samples for months beforehand (12 species, *e.g.*, the solitary species *Megachile azteca*) (Appendix 1), but they did not reappear afterwards.

There are apparently species in the study area that occur for one generation annually in which adult bee activity occurs during two months or less. Examples of these species include *Gaesischia exul* and *Megachile texensis*, both active in March and April, or *Tetrapedia maura*, *Triepeolus cameroni* and *Heriades variolosus*, all active in April and May (Appendix 1). More research needs to be done on each of these species to confirm their phenology. Of the species active for seven or more months, most were eusocial [*e.g. Auglochlora aurífera*, *A. nigrocyanea* and *A. smaradigma* (Halictidae), *Frieseomelitta nigra*, *Melipona yucatanica*, *Nannotrigona perilampoides* and *Trigona fulviventris* (Apidae), some were parasocial (*e.g., Ceratina eximia*, *C. nautlana*, *Euglossa viridissima* and *Eulaema polychroma*), and a few were solitary (*e.g., Anthidiellum apicale* [Halictidae] and *Centris analis* [Apidae]).

When Hurricane Dean impacted the YP in August, its strong winds caused severe damage, including downed trees and branches, almost complete defoliation, almost total destruction of bush and herbaceous species, and removal of any floral resources present at the time [14]. As suggested in other studies [e.q., 48], it may also have displaced some bee species, particularly those small in size, to other areas. However, the hurricane's effects were not catastrophic for the overall bee community, since two months later it had regained much of its lost activity. Although Hurricane Dean was a category 5 and had degraded to a category 3/4 over the study area, it differed from other category 5 hurricanes that have impacted the YP (e.g., Gilbert and Wilma) in that it brought much less precipitation, and its force was exercised mainly as wind. It did cause almost complete defoliation, but within a month leaf cover had reached 70 to 80% of normal, indicating rapid vegetation recovery [14]. This may have allowed a commensurately rapid recovery in native bee activity, since species diversity had recovered (increased) notably within two months after the impact. The hurricane's impact on the native bee community in the study area was apparently temporary. Two possible reasons are that its winds may have had only moderate effects on the bee community, and/or Neotropical bee faunas have the capacity to recover rapidly from natural disturbances as long as the flowering plant community is resilient and adequate nesting sites and floral resources are available.

Implications for conservation

Disturbances from natural phenomena such as hurricanes could be much greater under circumstances different from those documented here; for instance, if strong winds are accompanied by copious rainfall, and/or if an area is already affected by anthropic activities. In tandem, these factors could seriously damage bee populations by altering their phenologic cycles and reducing the number of available nesting sites. This could be especially acute for eusocial species, which nest in cavities in trees, and solitary species, whose nesting sites can be destroyed by flooding, landslides, and soil churning. Further study and a more thorough understanding of pollinator species like native bees are vital because they play vital roles in maintaining vegetation communities and aiding in their recovery after disturbances.

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F	Native bee Species	Jn	Fe	Ma	Ар	May	Ju	JI	Ag	Se	Oc	No	Dc	LS	Nb
Meg	Anthidiellum (Loyolanthidium) apicale (Cresson, 1878)													So	С
Hal	Augochloropsis metallica (Fabricius, 1793)						•			•	•			Ps	W
Hal	Augochlora (Augochlora) nigrocyanea Cockerell, 1897		-						•	-		-		Ps	W
Hal	Augochlora (Augochlora) smaragdina Friese, 1917			-	-	-			-	-	-	-		Ps	W
Hal	Augochlora (Oxystoglossella) aurifera Cockerell, 1897		-	-	-	-			-	-	-			Eu	G
Hal	Augochlora sp 2		-	-		-			-	-	-	-	-	Ps	W
Hal	Augochlora sp 4									-			-	Ps	W
Hal	Augochlora sp 5									-			-	Ps	W
Hal	Augochlora sp 6											-		Ps	W
Hal	Augochlora sp 7													Ps	W
Hal	Augochlorella neglectula (Cockerell, 1897)													Eu	G
Hal	Augochloropsis sp 1	•	-	-					-	-	-	-	-	Ps	G
Hal	Augochloropsis sp 2	•								-	-	-	-	Ps	G
Hal	Augochloropsis sp 3	•							-	-			-	Ps	G
Hal	Caenaugochlora (Caenaugochlora) gemmella (Cockerell, 1912)											-		Ps	G
Hal	Caenaugochlora sp 1													Ps	G
Hal	Caenaugochlora sp 2													Ps	G
Api	Centris (Heterocentris) analis (Fabricius, 1804)				•				•	-	-	-	-	So	С
Api	Centris (Heterocentris) nitida Smith, 1874				-		•		•	-				So	С
Api	Centris (Heterocentris) trigonoides Lepeletier, 1841								•	-		-	-	So	С
Api	Centris (Trachina) eurypatana Snelling, 1984			•										So	G
Api	Centris (Xanthemisia) lutea Friese, 1899									-				So	С
Api	Cephalotrigona zexmeniae (Cockerell, 1912)	•							•			-	-	Eu	G
Api	Ceratina (Calloceratina) eximia Smith, 1862	•	-		-				-	-	-	-	-	Ps	W
Api	Ceratina (Calloceratina) itzarum Cockerell, 1931								•	-				Ps	W
Api	Ceratina (Ceratinula) sp1													Ps	W
Api	Ceratina (Ceratinula) sp2													Ps	W
Api	Ceratina (Zadontomerus) cf. nautlana Cockerell, 1897						•	•			•	•	-	Ps	W
Api	Ceratina (Zadontomerus) sp1						•		•					Ps	W
Api	Ceratina sp 7								-					Ps	W
Meg	Coelioxys (Acrocoelioxys)	•												Cl	
Meg	Coelioxys (Cyrtocoelioxys) sp 1													Cl	
Meg	Coelioxys (Glyptocoelioxys) sp 2										•			Cl	
Meg	Coelioxys vituperabilis Holmberg, 1903													Cl	
Coll	Colletes arizonensis Stephen, 1954						•							So	G
•		•													

Appendix 1. Bee species in the Tropical Subdeciduous Forest of the Yucatan Peninsula, Mexico.

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Coll	Colletes rugicollis Friese, 1900		 									So	G
Meg	Epanthidium (Carloticola) cf boharti Stange, 1983		 	-		 						So	С
Api	Eufriesea mexicana (Mocsáry, 1897)		 			 			-			So	С
Api	Euglossa (Euglossa) viridissima Friese, 1899	-					•		•			Ps	С
Api	Eulaema (Apeulaema) polychroma (Mocsáry, 1899)	-	 	-			-		-			Ps	С
Api	Exaerete smaragdina (Guérin-Méneville, 1845)		 -	-				-				Cl	
Api	Exomalopsis (Exomalopsis) boharti Timberlake, 1980	-	-						-			So	G
Api	Exomalopsis (Exomalopsis) mellipes Cresson, 1878		-						-			So	G
Api	Frieseomelitta nigra (Cresson, 1878)	-	-				-		-		-	Eu	С
Api	Gaesischia exul Michener, LaBerge y Moure, 1955		 -	-		 						So	G
Hal	Halictus (Odontalictus) ligatus Say, 1837		 									Eu	G
Meg	Heriades (Neotrypetes) variolosus (Cresson, 1872)			-	-	 						So	С
Coll	Hylaeus (Hylaeopsis) sp1		 									So	С
Coll	Hylaeus sp 4		 			 			-			So	С
Meg	Hypanthidium (Hypanthidium) yucatanicum Cockerell, 1931		 						-			So	С
Hal	Lasioglossum (Dialictus) sp 1		 			 					•	Ps	G
Hal	Lasioglossum (Dialictus) sp 2		-						-			Ps	G
Hal	Lasioglossum (Dialictus) sp 3			-			-		-			Ps	G
Hal	Lasioglossum (Dialictus) sp 4			-								Ps	G
Hal	Lasioglossum (Dialictus) sp 5		-	-				-				Ps	G
Meg	Megachile (Leptorachis) sp 1		 						-			So	С
Meg	Megachile (Acentron) sp 1		 	-		 						So	С
Meg	Megachile (Acentron) albitarsis Cresson, 1872	-	 	-		 					-	So	С
Meg	Megachile (Acentron) sp 2		 	-		 			-			So	С
Meg	Megachile (Austromegachile) sp 1		 			 					-	So	С
Meg	Megachile (Austromegachile) sp 2	-				 						So	С
Meg	Megachile (Chelostomoides) texensis Mitchell, 1956			-		 						So	С
Meg	Megachile (Leptorachis) sp 1	-	 									So	С
Meg	Megachile (Melanosarus) nigripennis Spinola, 1841		 				-					So	С
Meg	Megachile (Neochelynia) chichimeca Cresson, 1878		 			 		-				So	С
Meg	Megachile (Pseudocentron) azteca Cresson, 1878			-			-			-		So	С
Meg	Megachile (Pseudocentron) inscita Mitchell, 1930		 -			 	•					So	С
Meg	Megachile (Pseudocentron) sp 4		 -				•					So	С
Meg	Megachile (Sayapis) zaptlana Cresson, 1878		 	-		 						So	С
Meg	Megachile (Sayapis) frugalis Cresson, 1872		 -			 	-					So	С
Meg	Megachile (Sayapis) sp1		 	-		 						So	С
Meg	Megachile sp 1		 	•		 						So	С
Meg	Megachile sp 2		 			 						So	С
Meg	Megachile sp 3		 			 						So	С

Api Melipona yucatanica Camargo, Moure and Roubik, 1988 <	A	pi <i>Melipona beecheii</i> Bennett, 1831								•					Eu	С
Api Melitama marginella (Cresson, 1872) -	A	pi Melipona yucatanica Camargo, Moure and Roubik, 1988		-				-				-			Eu	С
Api Nannotrigona perilampoides (Cresson, 1878) -	Α	pi Melissodes tepaneca Cresson, 1878	-			•		-							So	G
Api Osiris semiatratus Shanks, 1987 <td>Α</td> <td>pi Melitoma marginella (Cresson, 1872)</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td>-</td> <td></td> <td>So</td> <td>G</td>	Α	pi Melitoma marginella (Cresson, 1872)									-		-		So	G
Api Paratetrapedia (Lophopedia) apicalis (Cresson, 1878)	Α	pi Nannotrigona perilampoides (Cresson, 1878)	-		-			-	-		-	-	-	-	Eu	С
Api Paratetrapedia (Paratetrapedia) calcarata (Cresson, 1878) -<	Α	pi Osiris semiatratus Shanks, 1987				-						-			Cl	
Api Paratetrapedia (Paratetrapedia) moesta (Cresson, 1878)	A	pi Paratetrapedia (Lophopedia) apicalis (Cresson, 1878)		-											So	G
Api Paratetrapedia (Xanthopedia) swainsonae (Cockerell, 1909) <	Α	pi Paratetrapedia (Paratetrapedia) calcarata (Cresson, 1878)	-	-		-	-	-			-	-	-	-	So	G
Api Peponapis limitaris (Cockerell, 1906) <td< td=""><td>Α</td><td>pi Paratetrapedia (Paratetrapedia) moesta (Cresson, 1878)</td><td></td><td></td><td>-</td><td>•</td><td></td><td>-</td><td>-</td><td>•</td><td></td><td>-</td><td></td><td></td><td>So</td><td>G</td></td<>	Α	pi Paratetrapedia (Paratetrapedia) moesta (Cresson, 1878)			-	•		-	-	•		-			So	G
Api Peponapis sp 1 </td <td>A</td> <td>pi Paratetrapedia (Xanthopedia) swainsonae (Cockerell, 1909)</td> <td></td> <td></td> <td></td> <td>-</td> <td>-</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>So</td> <td>G</td>	A	pi Paratetrapedia (Xanthopedia) swainsonae (Cockerell, 1909)				-	-								So	G
Api Peponapis utahensis (Cockerell, 1905) So G Api Plebeia frontalis (Friese, 1911) Eu C Api Plebeia pulchra Ayala, 1999 Eu C Hal Pseudaugochloropsis graminea (Fabricius, 1804) Eu C Col Ptiloglossa mexicana (Cresson, 1878) So G Col Ptiloglossa eximia (Smith, 1861) So G Api Scaptotrigona pectoralis (Dalla Torre, 1896) So G Api Triepeolus cameroni (Meade-Waldo, 1913)	A	pi Peponapis limitaris (Cockerell, 1906)												-	So	G
Api Plebeia frontalis (Friese, 1911) Eu C Api Plebeia pulchra Ayala, 1999 Eu C Hal Pseudaugochloropsis graminea (Fabricius, 1804) Eu C Col Ptiloglossa mexicana (Cresson, 1878) So G Api Scaptotrigona pectoralis (Dalla Torre, 1896) So G Api Tetrapedia (Tetrapedia) maura Cresson, 1878 So C Api Triepeolus cameroni (Meade-Waldo, 1913) So C Api Trigona fulviventris Guérin-Méneville, 1845 Eu C	A	pi Peponapis sp 1												-	So	G
Api Plebeia pulchra Ayala, 1999 Eu C Hal Pseudaugochloropsis graminea (Fabricius, 1804) Ps G Col Ptiloglossa mexicana (Cresson, 1878) Ps G Api Scaptotrigona pectoralis (Dalla Torre, 1896) <	A	pi Peponapis utahensis (Cockerell, 1905)											-		So	G
HalPseudaugochloropsis graminea (Fabricius, 1804)PsGColPtiloglossa mexicana (Cresson, 1878)SoGColPtiloglossa eximia (Smith, 1861)SoGApiScaptotrigona pectoralis (Dalla Torre, 1896)II<	A	pi Plebeia frontalis (Friese, 1911)	-	-	-			-	-			-			Eu	С
Col Ptiloglossa mexicana (Cresson, 1878) <td< td=""><td>A</td><td>pi Plebeia pulchra Ayala, 1999</td><td></td><td>-</td><td>-</td><td></td><td>-</td><td>-</td><td>-</td><td>-</td><td></td><td></td><td></td><td></td><td>Eu</td><td>С</td></td<>	A	pi Plebeia pulchra Ayala, 1999		-	-		-	-	-	-					Eu	С
ColPtiloglossa eximia (Smith, 1861)SoGApiScaptotrigona pectoralis (Dalla Torre, 1896)EuCApiTetrapedia (Tetrapedia) maura Cresson, 1878SoCApiTriepeolus cameroni (Meade-Waldo, 1913)ClApiTrigona fulviventris Guérin-Méneville, 1845ClApiTrigona fuscipennis Friese, 1900EuCApiTrigonisca pipioli Ayala, 1999EuCApiXylocopa (Neoxylocopa) mexicanorum Cockerell, 1912PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879PsW	H	al Pseudaugochloropsis graminea (Fabricius, 1804)				•			-	•		-			Ps	G
ApiScaptotrigona pectoralis(Dalla Torre, 1896)Image: Construction of the second of th	C	ol Ptiloglossa mexicana (Cresson, 1878)													So	G
ApiTetrapedia (Tetrapedia) maura Cresson, 1878SoCApiTriepeolus cameroni (Meade-Waldo, 1913)ClApiTrigona fulviventris Guérin-Méneville, 1845ClApiTrigona fuscipennis Friese, 1900EuCApiTrigonisca pipioli Ayala, 1999EuCApiXylocopa (Neoxylocopa) mexicanorum Cockerell, 1912PsWApiXylocopa (Neoxylocopa) nautlana Cockerell, 1904PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879	C	ol Ptiloglossa eximia (Smith, 1861)			-			-	-						So	G
ApiTriepeolus cameroni (Meade-Waldo, 1913)ClApiTrigona fulviventris Guérin-Méneville, 1845ClApiTrigona fulviventris Guérin-Méneville, 1845EuCApiTrigona fuscipennis Friese, 1900EuCApiTrigonisca pipioli Ayala, 1999EuCApiXylocopa (Neoxylocopa) mexicanorum Cockerell, 1912PsWApiXylocopa (Neoxylocopa) nautlana Cockerell, 1904PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879PsW	A	pi Scaptotrigona pectoralis (Dalla Torre, 1896)	-									-		-	Eu	С
ApiTrigona fulviventrisGuérin-Méneville, 1845Image: Subscription of the state o	A	pi Tetrapedia (Tetrapedia) maura Cresson, 1878				-	-								So	С
ApiTrigona fuscipennis Friese, 1900EuCApiTrigonisca pipioli Ayala, 1999EuCApiXylocopa (Neoxylocopa) mexicanorum Cockerell, 1912PsWApiXylocopa (Neoxylocopa) nautlana Cockerell, 1904PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879PsW	A	pi Triepeolus cameroni (Meade-Waldo, 1913)				-	-								Cl	
ApiTrigonisca pipioli Ayala, 1999Image: Second conditional description of the second des	A	pi Trigona fulviventris Guérin-Méneville, 1845	-	-	-	-	-	-	-	-	-	-	-	-	Eu	С
ApiXylocopa (Neoxylocopa) mexicanorum Cockerell, 1912PsWApiXylocopa (Neoxylocopa) nautlana Cockerell, 1904PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879PsW	A	pi Trigona fuscipennis Friese, 1900			-										Eu	С
ApiXylocopa (Neoxylocopa) nautlana Cockerell, 1904PsWApiXylocopa (Schoenherria) subvirescens Cresson, 1879PsW	A	pi Trigonisca pipioli Ayala, 1999	-	-	-			-				-			Eu	С
Api Xylocopa (Schoenherria) subvirescens Cresson, 1879 Ps W	A	pi Xylocopa (Neoxylocopa) mexicanorum Cockerell, 1912						-							Ps	W
	A	pi Xylocopa (Neoxylocopa) nautlana Cockerell, 1904													Ps	W
Api Xylocopa (Schoenherria) muscaria Fabricius, 1775 E E E Ps W	A	pi Xylocopa (Schoenherria) subvirescens Cresson, 1879						-		-					Ps	W
	A	pi Xylocopa (Schoenherria) muscaria Fabricius, 1775				•		•		•					Ps	W

F= Family, Api= Apidae, Coll= Colletidae, Hal= Halictidae and Meg= Megachilidae. Months: Ja= January, Fe= February, Ma= March, Ap= April, My= May, Ju= June, Jl= July, Ag=August, Se= September, Oc= October, No=November and Dc= December. LS=Lifestyle: So=Solitary, Ps=Parasocial, Eu= Eusocial and Cl= Cleptoparasitic. Nb=Nesting behavior: C= Preexisting cavity, G=Ground and W=Wood. Specie: = present, -- = absent