

Changes in bee community structure (Hymenoptera, Apoidea) under three different land-use conditions

Alvaro E. Razo-León¹, Miguel Vásquez-Bolaños², Alejandro Muñoz-Urias¹,
Francisco M. Huerta-Martínez¹

1 *Departamento de Ecología, CUCBA, Universidad de Guadalajara, km 15.5 carretera Guadalajara-Nogales, Las Agujas, Zapopan, C.P. 45110, Apdo. Postal 139, Jalisco, México* **2** *Departamento de Botánica y Zoología, CUCBA, Universidad de Guadalajara, km 15.5 carretera Guadalajara-Nogales, Las Agujas, Zapopan, C.P. 45110, Apdo. Postal 139, Jalisco, México*

Corresponding author: *Alejandro Muñoz-Urias* (almurias@gmail.com)

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Abstract

Bee communities were studied with three different conditions of land-use: 1) urban area; 2) crops and livestock; and, 3) preserved vegetation. All three conditions have elements of tropical dry forest and are in the "Sierra de Quila" Flora and Fauna Protection Area and its influence zone. Sampling was carried out throughout the year (three days per month) for each land-use condition. Bee species and their abundance were registered with the intention of knowing how changes in the vegetation are related to bee community structure (richness, abundance, and α and β diversity).

A total of 14,054 individuals from 160 species were registered. A rarefaction analysis, showed that the preserved areas had significantly greater richness and diversity. Beta diversity analysis revealed a species turnover of nearly 32% among each pair of conditions. It is concluded that the changes in land-use negatively affect richness and diversity and causes major changes in species composition of the bee community. For this reason, it is recommended that the protection of the tropical dry forest, both for this study area but also in general for Mexico, is essential to guarantee the conservation of this group of insects, which are required for the reproduction of a great number wild and cultivated plant specie.

Keywords

Native bees, Mexico, tropical dry forest, bee abundance, bee diversity

Introduction

Pollinators are a key component for global biodiversity, because they assist in the sexual reproduction of many plant species and play a crucial role in maintaining terrestrial ecosystems and food security for human beings (Potts et al. 2010, van der Sluijs and Vaage 2016). Approximately 80% of angiosperms depend on biotic pollination (Klein et al. 2007, Quesada et al. 2012). Bees (Hymenoptera: Apoidea) are some of the most important pollinators (Winfree et al. 2008). It is estimated that nearly 73% of cultivated plant species and more than 75% of global vegetation are pollinated by these insects (Coro 2009), which are considered the principal pollinators in tropical regions (O'Toole and Raw 1999, Nantes-Parra 2005).

Tropical dry forest present a great bee species richness in Mexico (Ayala 1988, Ayala et al. 1996), which is explained by the high diversity of entomophilous plants (Ayala 2004), and their differentiated phenology (generally, tree species flowering in dry season while herbaceous and shrub species flowering in wet season), which provides to this group of organisms, resources for most of the year (Reyes-Novelo et al. 2009). This vegetation type covered approximately 270,000 km² in 1990 but currently there are great pressures exerted on this type of forest. For example Trejo and Dirzo (2000), reported that 50% was either fragmented or existed as relicts. Furthermore, they found changes in land use on 23% of the surface and that only 27% of this type of vegetation remained intact (Trejo and Dirzo 2000).

Land use change, such as degradation or fragmentation of tropical dry forest, could have consequences on the richness and composition of bee communities. According to previous studies, bees are susceptible to the loss of their natural habitats by the fragmentation and transformation of the landscape for agricultural, livestock and urban purposes (Martins et al. 2013, Woodcock et al. 2013, Le Féon et al. 2016, Mogren et al. 2016). For this reason, it is important to compare local bee communities from disturbed environments with one from a preserved environment in the same region, as this should provide useful information for making conservation-based decisions on bee community management (Dalmazzo 2010).

Two of the most important factors for bee communities are food availability (nectar and pollen) and nesting sites (Reyes-Novelo et al. 2009). Changes in land use are expected to affect both and consequently alter the structure of these communities. Due to this, the aims of this study were: 1) to ascertain whether landscape transformations affect bee community structure (richness, abundance, and α and β diversity) and, 2) to identify which are the bee groups most susceptible to these changes, as well as those who benefit from them.

Material and methods

Study area

The study is located at Área de protección de flora y fauna Sierra de Quila, (here and after APFFSQ) and its zone of influence, which is found in the south-central portion of Jalisco,

Mexico (Fig. 1). It is located within the Trans-Mexican Volcanic Belt physiographic region. The research was conducted in the municipalities of Tecolotlán, Tenamaxtlán, San Martín Hidalgo and Cocula. Geographically, it is found between 20°14' and 20°22'N; 103°57' and 104°07'W (DMS), with an area of 15,912 hectares (Villavicencio et al. 2012).

Data collection

Three conditions in tropical dry forest (TDF) with different land-use were selected. The first was an urbanized area (U) at Tecolotlán, a municipality with 9,189 inhabitants (IEEG 2015); the second was an agricultural area with crops and livestock (CL), which begins on the area surrounding the town, and is characterized by the presence of crops (mainly corn – *Zea mays* L.) as well as cattle ranches, which were slightly fragmented by secondary vegetation and some remaining trees of the TDF, used as living fences. The third was an area of preserved vegetation (P) of the TDF within the APFFSQ. Some of the most common trees in this area are from the following genera: *Bursera*, *Ceiba*, *Erythrina*, *Heliocarpus*, *Lysiloma*, *Stenocereus* and *Viguiera* (Fig. 1) (Guerrero-Nuño and López-Coronado 1997).

Sampling of wild bees was conducted throughout the year, with three sampling days per month (one working day per condition, from 10:00 to 16:00 hours). Four plots, 50 × 5 m, were randomly located for each land use condition and the bees were sample walking along the transect during periods of 60 minutes per collection. Bee species presences and their abundance were recorded. Bee species that could not be determined in the field were collected using an entomological net with extension of 2.70 m on tree strata and an extension of 1.00 m for herbaceous strata. Specimens were processed according to Michener et al. (1994). Bees were then identified as precisely as possible with the help of the specialized literature, whether at a species or genus level, and then separated by morphospecies. The specimens were deposited at the Entomological Collection of Centro de Estudios en Zoología of Universidad de Guadalajara (CZUG).

Data analysis

Sampling efficiency and richness comparison

A species accumulation curve was performed to evaluate the sampling effort per site and, as well as to compare the richness among the different conditions using ESTIMATES 9.1.0. (Colwell 2016). A rarefaction curve was also prepared using the same program.

Bees abundance

Bee abundances with and without *Apis mellifera* were compared via analysis of variance (ANOVA) for the first case, and Kruskal-Wallis followed by the Nemenyi *post-hoc* test,

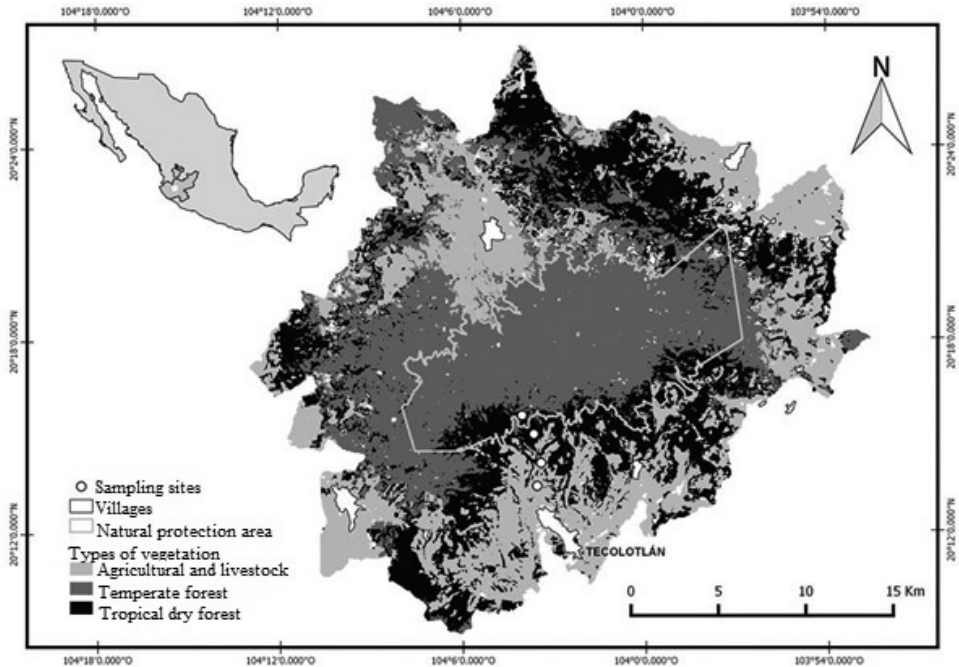


Figure 1. Location of the APFFSQ and sampling sites.

for the second case. Furthermore, Pearson's chi-squared test and residual analysis were used to compare the abundance of different bee families among the land-use conditions using the R 3.2.5 Software (R Core Team 2016).

Diversity analysis

The Shannon-Wiener index was used to compare alpha diversity of sites via a confidence interval obtained using bootstrap in PAST 3.15 software (Hammer et al. 2001). In order to contrast the composition of tribes in the study areas, beta diversity index (β_{sim}) was estimated, while non-metric multidimensional scaling (NMDS) was used with the R 3.2.5 software (R Core Team 2016) via the 'vegan' package (Oksanen et al. 2013).

Results

Sampling efficiency and comparison of specific richness

A total of 14,054 bees individuals were registered, belonging to five families, 52 genera, and 160 species (Table 1) (Appendix 1). The richest (34.9 %) and most abundant (83.3 %) family was Apidae and the poorest (7 %) and least abundant (1.2 %) fam-

Table 1. Richness and abundance of the bee families registered.

Family	Genera	Species	Abundance
Apidae	23	60	12,170
Halictidae	8	33	759
Megachilidae	13	35	739
Andrenidae	5	20	214
Colletidae	3	12	172
Total	52	160	14,054

ily was Colletidae. The bee species with the highest number of individuals were all eusocial species: *Apis mellifera*, with 7,030 individuals (49.9% of total abundance); *Partamona billineata*, with 768 individuals (5.4%); *Scaptotrigona bellwegeri* with 718 individuals (5.1%); and, *Trigona nigra* with 529 individuals (3.8 %).

The richest condition was P, with 120 species, followed by CL with 98 species and, finally U, with 81 species. The rarefaction curve among different land-use conditions indicated greater richness in P than in U and CL, although they did not present statistically significant differences (Fig. 2). Furthermore, a sampling efficiency of 88% was obtained for P (135 spp.), 77% for CL (127 spp.), and 79% for U (102 spp.) in accordance with the richness estimated by Chao 1).

Abundance of bees

The highest number of bee individuals was observed in P (5,067), followed by CL (4,786) and U (4,202). The ANOVA ($df = 2$, $F = 0.352$, $p = 0.704$) showed no significant differences between the registered abundance of bees for the different types of land-use. If only wild bees are considered (excluding *Apis mellifera*), the greatest abundance was in P (2,731), followed by U (2,418) and, finally, CL (1,876). In this case, Kruskal-Wallis test ($df = 2$, $K = 7.265$, $p = 0.026$) indicated significant differences between median abundances, while the Nemenyi *post-hoc* test demonstrated significant differences ($p = 0.023$) only in terms of the abundances of bees between P and CL.

Pearson's chi-squared test showed a dependency between land-use and bee family abundance ($df = 8$, $\chi^2 = 560.2715$, $p < 0.05$) (Table 2), while residual analysis indicated that abundance of Colletidae, Andrenidae and Megachilidae are positively related to P. The Halictidae was primarily associated with U where they were most abundant, while the Apidae registered the highest abundance in CL (Fig. 3).

Diversity analysis

The Shannon-Wiener index (H') values presented significant differences with a $p < 0.05$, P obtained a greater level of diversity compared to the other types of land-use, followed by U and, finally CL. Evenness (J') is lower in CL, while U and P presented similar even-

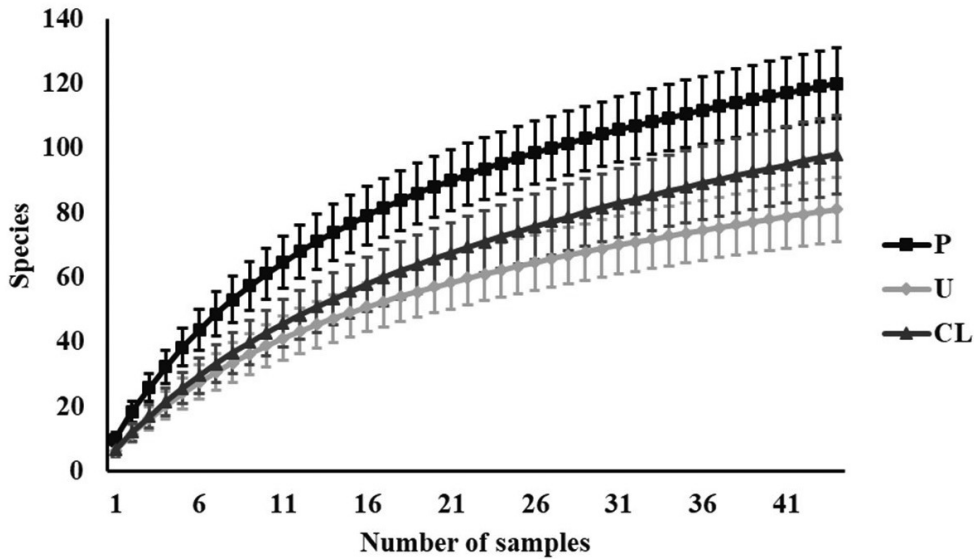


Figure 2. Rarefaction curve for bee richness among the different land-use conditions.

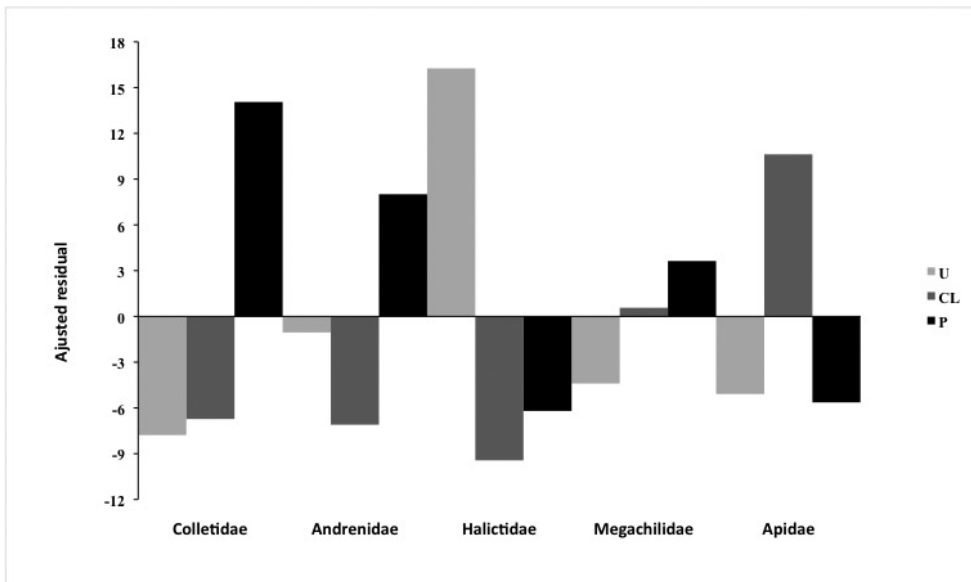


Figure 3. Residual analysis with Pearson's chi-squared test to compare independence between bee family and land use conditions.

ness. Moreover, when only wild bees were considered, diversity was higher in P. This is due to the elevated abundance of *Apis mellifera* (Table 3).

The beta diversity index (β_{sim}) showed an average species turnover rate of about 32% for each condition. In terms of bee species composition change, the highest was between U and CL (36%), followed by P and U with 30% and finally between CL and P with 27%.

Table 2. Abundance per bee family in different conditions of land-use. Abundance of Apidae without *Apis mellifera* between parentheses.

Family	U	CL	P
Apidae	3,545 (1,748)	4,345 (1,434)	4,279 (1,943)
Halictidae	427	141	192
Megachilidae	168	259	313
Andrenidae	57	24	133
Colletidae	5	17	150

Table 3. Shannon-Wiener diversity index (H') per land-use condition and their confidence intervals (IC 95%) via bootstrap, and maximum diversity (H'max), Evenness (J'), including *Apis mellifera* and excluding *A. mellifera*.

	H'	-CI 95%	+CI 95%	H'max	J'
Including <i>A. mellifera</i>					
U	2.605 ^b	2.561	2.666	4.40	0.591
CL	1.933 ^c	1.889	2.00	4.58	0.421
P	2.755 ^a	2.703	2.813	4.79	0.574
Excluding <i>A. mellifera</i>					
U	3.342 ^b	3.313	3.403	4.39	0.760
CL	3.225 ^b	3.187	3.319	4.57	0.704
P	3.830 ^a	3.790	3.878	4.78	0.800

Measurements with the same letter do not differ statistically, according to the confidence intervals.

The indirect ordination performed with NMDS resulted in a stress value of 0.1326, that shows a gradual separation of the three different land-use conditions along the first axis, where on the left side are located U sites, CL sites in the center, and P sites on the right side. The tribe Anthophorini and tribes of the Halictidae were associated with the U, while tribes of the Apidae and one megachilid tribe were located principally between the U and CL areas. The Lithurgini, two tribes of the Andrenidae and two cleptoparasite tribes (Ericrocidini, Epeolini) were associated with the CL, while the Xylocopini was associated with the P and CL areas. Tribes of Colletidae, Andrenidae, and Megachilidae and two apid tribes were found in P (Fig. 4).

Discussion

The highest bee richness was registered in P while the only significant differences were recorded between U and P. The results indicate a gradient in richness related to the habitat conservation. This finding is supported by different studies which show that the destruction of the habitat, for agriculture or urbanization, is principally responsible for bee species reduction, up to the point of local extinction for some species (Frankie et al. 1997, Martins et al. 2013). Furthermore, in a meta-analysis, Winfree

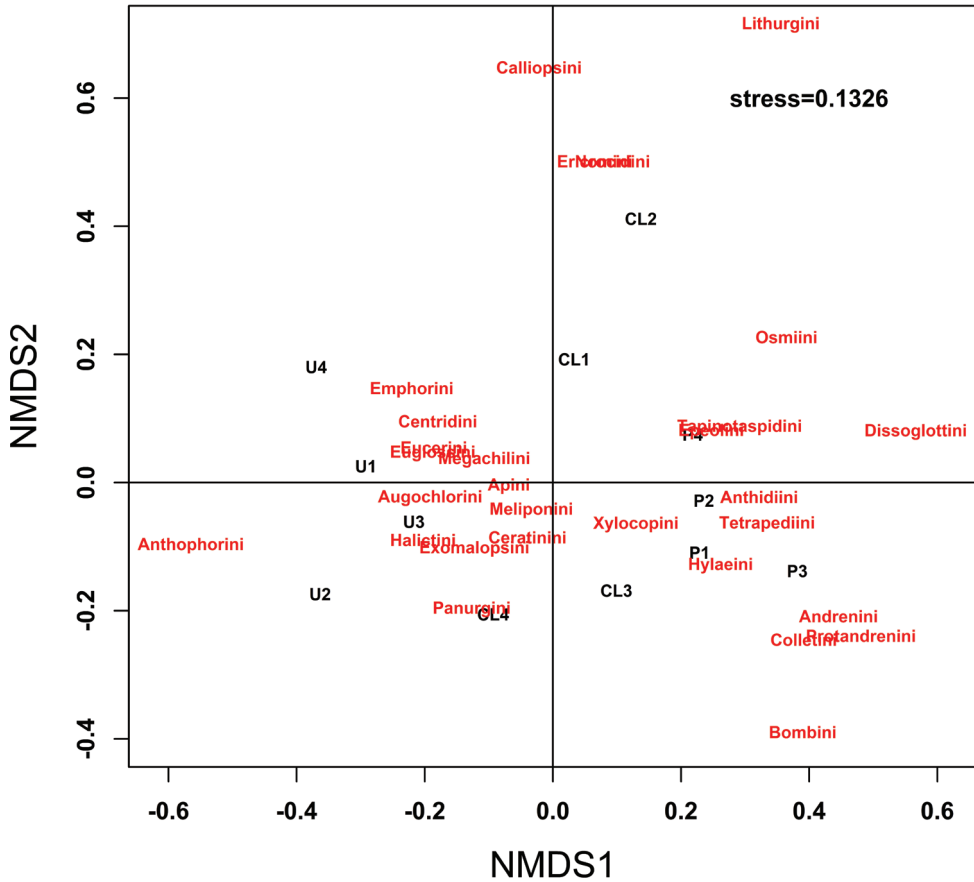


Figure 4. Ordination diagram derived from NMDS for the different land-use areas and bee tribal data.

et al. (2009), report that bee richness decreases with increasing anthropogenic disturbance, while Ricketts et al. (2008), found that on average the richness of pollinators (principally bees) in crops decreased by half as the distance from preserved habitat increased to 1500 m.

The decrease in bee richness is related to their dependence on various resources to complete their lifecycle, such as food resources (pollen and nectar) and nesting substrates (either from the soil or vegetation), and materials for constructing their nests (Winfree 2010). The reason that a greater number of bee species is registered in the preserved area is possibly due to a greater availability of plant species for food, being that bee richness has been positively related to the richness of flowers (Carper et al. 2014) and to a great floral diversity, which provide food to a great variety of specialist and generalist bee species (Martins et al. 2013).

The abundance of bees did not differ significantly between the three land-use conditions. This agrees with various studies that report a similar or greater abundance in human modified areas (Carper et al. 2014, Mallinger et al. 2016, Nantes-Parra et al. 2008, Olalde-Estrada et al. 2015, Otero and Sandino 2003, Tonhasca et al. 2002); this occurs in sites

with moderate disturbance with gaps on forest canopy, which facilitate grow of herbaceous layer (Carper et al. 2014). This also shows that urban areas could be important for bee communities, despite the modification of vegetation, because they offer ornamental and wild flowers, particularly because they are watering them in times when native vegetation is diminished, as well as nesting resources associated to human constructions (Dalmazzo 2010). The differences in abundance between the P and CL when *Apis mellifera* is excluded from analysis could be due to the same reasons that affect bee richness in addition to the use of pesticides in the crops which affect wild bees (Winfree 2010).

The number of individuals per family varied, Andrenidae, Megachilidae and Colletidae being far less abundant than the Apidae and Halictidae. Potts et al. (2003) found the Andrenidae positively associated with annual plant diversity, and Megachile with plant richness, pollen and available nectar. Vergara (2005) suggests that, in areas with agricultural activity, bee genera that nest in the soil, including andrenids and colletids, are under-represented due to plowing for agricultural activities and the presence of livestock, which affect nesting. While Halictidae presented greater abundance in the urban area, this is possibly because most of the registered bees of this family are small (<1 cm) and most of them are polilectic (Michener 2000).

Banaszak-Cibicka and Zmihorski (2012), reported that urban areas contain small green isolated island (parks and gardens), that promote the abundances of small bees, which require only a small amount of food. Winfree et al. (2009), indicate that they do not have problems in finding nesting sites in disturbed areas.

Total bee abundance tends to decline at disturbed sites, while individual species present different responses, some of them show drastic reduction in their populations, while others remain stable or even increase with land-use change (Winfree et al. 2008). For this reason, the use of the habitat according to bee species plays an important role. Bees that require specific conditions for their development, become the most vulnerable to the disappearance of their habitat. On the other hand, if the resources generated by the modification of the habitat is exploited by the bees, they could survive in disturbed areas (Winfree 2010). That is the reason why bees that can use a wide variety of resources are often able to compensate when circumstances change, although some species disappear due to land use changes. The higher richness and evenness patterns in preserved areas is supported by Reyes-Novelo et al. (2009), who explain that in disturbed areas some species disappear locally and the abundance of others decreases, which modifies dominance.

Finally, β diversity showed a medium level of species turnover rate among conditions, despite the maximum distance between sampling sites was 6 km. The structure of bee community contrasts with P and U, in which tribes such as Halictini and Anthophorini (due to the high abundance of *Anthophora squammulosa*) are associated with the urban area. The tribes of the Andrenidae, Colletidae, Megachilidae and Apidae, such as bumblebees (Bombini), are strongly associated with P, while the CL area is found at the mid-point of the gradient. This suggests that disturbance, with its variations in micro-environments and food and nesting resource has a significant effect on bee community species composition.

The bee fauna of the TDF in Mexico is one of the richest and most diverse in the country (Ayala 2004), so, the protection of this type of vegetation is crucial for the conservation of this group of insects, given that the reduction of these native pollinators could have a negative economic impact on crops (Maass et al. 2005). As the expansion of human settlement and the population growth or production activities have led to the process of deforestation, fragmentation and degradation of this forest (Maass et al. 2010), Trejo and Dirzo (2000) report that approximately 3.7% of the TDF of the total area of Mexico (72,850 km²) remains relatively intact and with a high annual deforestation rate of 2.02% of the total coverage.

Conclusions

The APFFSQ is an important site for maintaining wild bee diversity, given that 200 species of bees were registered in the area, of which 160 are present in the TDF (Razo-León 2015). According to Ortega, (2007), the TDF covered 19.84% of APFFSQ (2,797 ha) in 1993, by the year 2000, it only covered 15.25% (2,149 ha), this means that the TDF lost 23.2% of its area in seven years, because it is rounded by agricultural or livestock production areas which make it more vulnerable to transformation. This leads to the conclusion that change in land-use negatively affects the richness, abundance, and diversity of species of bee community, for this reason it is recommended that the TDF in Mexico should be protected in order to guarantee the conservation of this group of insects.

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References

- Ayala R (1988) Abejas silvestres (Hymenoptera: Apoidea) de Chamela, Jalisco, México. *Folia Entomologica Mexicana* 73: 395–493.
- Ayala R, Griswold TL, Yanega D (1996) Apoidea (Hymenoptera). In: Llorente J, García A, González E (Eds) *Biodiversidad, taxonomía, y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento*. UNAM-CONABIO, Ciudad de México, 423–464.
- Ayala R (2004) Fauna de abejas silvestres (Hymenoptera: Apoidea). In: García AN, Ayala R (Eds) *Artrópodos de Chamela*. UNAM, Ciudad de México, 193–219.

- Banaszack-Cibicka W, Zmihorski M (2012) Wild bees along an urban gradient: winners and loser. *Journal of Insect Conservation* 16(3): 331–343. <https://doi.org/10.1007/s10841-011-9419-2>
- Campos-Navarrete MJ, Parra-Tabla V, Ramos-Zapata J, Díaz-Castelazo C, Reyes-Novelo E (2013) Structure of plant–Hymenoptera networks in two coastal shrub sites in Mexico. *Arthropod Plant Interaction* 7(6): 607–617. <https://doi.org/10.1007/s11829-013-9280-1>
- Carper AL, Adler LS, Warren PS, Irwin RE (2014) Effects of suburbanization on forest bee communities. *Environmental Entomology* 43(2): 253–262. <https://doi.org/10.1603/EN13078>
- Colwell RK (2016) EstimateS 9.1.0. University of Connecticut, Storrs, USA. <http://purl.oclc.org/estimates>
- Coro AM (2009) La crisis de los polinizadores. *Biodiversitas* 85: 1–5.
- Dalmazzo M (2010) Diversidad y aspectos biológicos de abejas silvestres de un ambiente urbano y otro natural de la región central de Santa Fe, Argentina. *Revista de la Sociedad Entomológica Argentina* 69(1–2): 33–44.
- Frankie GW, Vinson SB, Rizzardi MA, Griswold TL, O’Keefe S, Snelling RR (1997) Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. *Journal of the Kansas Entomological Society* 70(4): 281–296.
- Guerrero-Nuño JJ, López-Coronado GA (1997) La vegetación y la flora de la Sierra de Quila. Universidad de Guadalajara, Guadalajara, 134 pp.
- Hammer Ř, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis *Palaeontologia Electronica*. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- IIEG (2015) Instituto de Información Estadística y Geográfica del Estado de Jalisco con base en INEGI, censos y conteos nacionales. <http://www.iieg.gob.mx/contenido/Municipios/Tecolotlan.pdf>
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of Royal Society B* 274(1608): 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Le Féon V, Poggio SL, Torretta JP, Bertrand C, Molina GA, Burel F, Ghersa CM (2016) Diversity and life-history traits of wild bees (Insecta: Hymenoptera) in intensive agricultural landscapes in the Rolling Pampa, Argentina. *Journal of Natural History* 50(19–20): 1175–1196. <https://doi.org/10.1080/00222933.2015.1113315>
- Maass M, Balvanera P, Castillo A, Daily GC, Mooney HA, Ehrlich P, Quesada M, Miranda A, Jaramillo VJ, Garcia-Oliva F, Martinez-Yrizar A, Cotler H, Lopez-Blanco J, Perez-Jimenez A, Burquez A, Tinoco C, Ceballos G, Barraza L, Ayala R, Sar J (2005) Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the Pacific Coast of Mexico. *Ecology and Society* 10(1): 17–39. <https://doi.org/10.5751/ES-01219-100117>
- Maass M, Búrquez A, Trejo I, Valenzuela D, González MA, Rodríguez M, Arias H (2010) Amenazas. In: Ceballos G, Martínez L, García A, Espinoza E, Creel JB, Dirzo R (Eds) *Diversidad, amenazas y áreas prioritarias para la conservación de las Selvas Secas del Pacífico de México*. FCE-CONABIO-TELMEX-CONANP-WWF México-EcoCiencia SC, Ciudad de México, 321–346.

- Mallinger RE, Gibbs J, Gratton C (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology* 31(7): 1523–1535. <https://doi.org/10.1007/s10980-015-0332-z>
- Martins AC, Gonçalves RB, Melo GA (2013) Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years. *Zoologia (Curitiba)* 30(2): 157–176. <https://doi.org/10.1590/S1984-46702013000200006>
- Michener CD, McGinley RJ, Fanforth BN (1994) *The Bee Genera of North and Central America (Hymenoptera: Apoidea)*. Smithsonian Institution Press, Washington, 208 pp.
- Mogren CL, Rand TA, Fausti SW, Lundgren JG (2016) The effects of crop intensification on the diversity of native pollinator communities. *Environmental Entomology* 45(4): 865–872. <https://doi.org/10.1093/ee/nvw066>
- Nantes-Parra G (2005) Abejas silvestres y polinización. *Manejo Integrado de Plagas y Agroecología* 75: 7–20.
- Nantes-Parra G, Palacios E, Parra A (2008) Efecto del cambio del paisaje en la estructura de la comunidad de abejas sin aguijón (Hymenoptera: Apidae) en Meta, Colombia. *Revista de Biología Tropical* 56(3): 1295–1308.
- O'Toole C, Raw A (1999) *Bees of the world. Facts on file*, New York, 192 pp.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Henry M, Stevens H, Szoecs E, Wagner H (2013) Package 'vegan' version 2.0–10. En *Community ecology package*. <http://www.r-project.org>.
- Olalde-Estrada I, Cano-Santana Z, Castellanos-Vargas II, Balboa-Aguilar CC (2015) Variación Espacio-Temporal en la Densidad y Diversidad de Abejas en sitios de Bosque Tropical Caducifolio Sujetos a Disturbio en el Ejido San José Tilapa, Puebla. *Entomología Mexicana* 2: 533–539.
- Ortega CCA (2007) Estudio Temporal de la Fragmentación Forestal del Área de Protección de Flora y Fauna "Sierra de Quila" en el Estado de Jalisco, Mediante Sistemas de Información Geográfica (SIG). Thesis. Universidad de Guadalajara, Guadalajara.
- Otero JT, Sandino JC (2003) Capture Rates of Male Euglossine Bees across a Human Intervention Gradient, Chocó Region, Colombia. *Biotropica* 35(4): 520–529.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impact and drivers. *Trends in Ecology and Evolution* 25(6): 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P (2003) Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84(10): 2628–2642. <https://doi.org/10.1890/02-0136>
- Quesada M, Rosas F, Lópezaraiza M, Aguilar R, Ashworth L, Rosas GV, Sánchez MG, Martín RS (2012) Ecología y Conservación Biológica de Sistemas de Polinización de Plantas Tropicales. In: del Val E, Bouge K (Eds) *Ecología y Evolución de las Interacciones bióticas*. Fondo de Cultura Económica, CIECO y UNAM. Ciudad de México, 75–100.
- R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Reyes-Novelo E, Meléndez VR, Ayala R, Delfín HG (2009) Abejas Silvetres (Hymenoptera: Apoidea) como Bioindicadores en el Neotrópico. *Tropical and Subtropical Agroecosystems* 10(1): 1–13.

- Ricketts TH, Regetz, J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Morandin LA (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology letters* 11(5): 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Tonhasca Jr A, Blackmer JL, Albuquerque GS (2002) Abundance and Diversity of Euglossine Bees in the Fragmented Landscape of the Brazilian Atlantic Forest. *Biotropica* 34(3): 416–422. <https://doi.org/10.1111/j.1744-7429.2002.tb00555.x>
- Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* 94(2): 133–142. [https://doi.org/10.1016/S0006-3207\(99\)00188-3](https://doi.org/10.1016/S0006-3207(99)00188-3)
- van der Sluijs JP, Vaage NS (2016) Pollinators and Global Food Security: The Need for Holistic Global Stewardship. *Food Ethics* 1(1): 75–91. <https://doi.org/10.1007/s41055-016-0003-z>
- Vergara CH (2005) Effects of Agriculture on Bee Community (Hymenoptera: Apoidea). *Journal of Agronomy* 4(4): 277–280. <https://doi.org/10.3923/ja.2005.277.280>
- Villavicencio R, Santiago AL, Godínez JJ, Chávez JM, Toledo SL (2012) Efecto de la fragmentación sobre la regeneración natural en la Sierra de Quila, Jalisco. *Revista Mexicana de Ciencias Forestales* 3(11): 9–23.
- Winfree R, Williams NM, Gaines H, Ascher JS, Kremen C (2008) Wild Bee Pollinators Provide the Majority of Crop Visitation across Land-Use Gradients in New Jersey and Pennsylvania, USA. *Journal Applied Ecology* 45(3): 793–802. <https://doi.org/10.1111/j.1365-2664.2007.01418.x>
- Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90(8): 2068–2076. <https://doi.org/10.1890/08-1245.1>
- Winfree R (2010) The conservation and restoration of wild bees. *Annals of the New York Academic of Sciences* 1195: 169–197. <https://doi.org/10.1111/j.1749-6632.2010.05449.x>
- Woodcock BA, Edwards M, Redhead J, Meek WR, Nuttall P, Falk S, Pywell RF (2013) Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems and Environment* 171: 1–8. <https://doi.org/10.1016/j.agee.2013.03.005>

Appendix I

Table AI. Number of individuals per bee species registered in different land use conditions.

Species	U	CL	P
<i>Agapostemon leunculus</i> Vachal, 1903	20	6	21
<i>Agapostemon nasutus</i> Smith, 1853	9	0	1
<i>Ancyloscelis apiformis</i> (Fabricius, 1793)	35	2	8
<i>Andrena</i> sp. 1	0	0	25
<i>Andrena</i> sp. 2	0	0	12
<i>Andrena</i> sp. 3	0	0	1
<i>Andrena</i> sp. 4	0	1	0
<i>Anthidiellum apicale</i> (Cresson, 1878)	1	13	42
<i>Anthidiellum azteca</i> (Urban, 2001)	0	0	2
<i>Anthidium parkeri</i> González & Griswold, 2013	0	0	8
<i>Anthodioctes gualanensis</i> (Cockerell, 1912)	0	0	1
<i>Anthodioctes</i> sp. 1	0	4	7
<i>Anthophora capistrata</i> Cresson, 1878	0	0	1
<i>Anthophora squamulosa</i> Dours, 1864	160	39	0
<i>Anthophorula serrata</i> (Friese, 1899)	0	31	26
<i>Apis mellifera</i> Linnaeus, 1758	178	2910	2336
<i>Ashmeadiella buconis</i> (Cresson, 1878)	0	29	0
<i>Ashmeadiella opuntiae</i> (Cockerell, 1879)	0	0	1
<i>Augochlora aurifera</i> Cockerell, 1897	42	0	0
<i>Augochlora quiriguensis</i> Cockerell, 1913	6	17	28
<i>Augochlora sidaefolia</i> Cockerell, 1913	9	6	4
<i>Augochlora smaragdina</i> Friese, 1917	13	11	12
<i>Augochlora</i> sp. 1	29	2	34
<i>Augochlora</i> sp. 2	37	0	0
<i>Augochlora</i> sp. 3	0	0	2
<i>Augochlorella neglectula</i> (Cockerell, 1897)	25	28	3
<i>Augochloropsis ignita</i> (Smith, 1861)	4	1	0
<i>Augochloropsis metallica</i> (Fabricius, 1793)	30	11	39
<i>Aztecantidium xochipillium</i> Michener & Ordway, 1964	0	0	2
<i>Bombus diligens</i> Smith, 1861	0	1	3
<i>Bombus steindachneri</i> Handlirsch, 1888	0	1	9
<i>Calliopsis hondurasica</i> Cockerell, 1897	0	2	0
<i>Calliopsis</i> sp. 1	1	0	0
<i>Calliopsis</i> sp. 2	0	0	1
<i>Centris agilis</i> Smith, 1874	0	0	3
<i>Centris aterrima</i> Smith, 1854	0	6	0
<i>Centris atripes</i> Mocsáry, 1899	0	1	4
<i>Centris flavofasciata</i> Friese, 1899	0	4	0
<i>Centris nitida</i> Smith, 1874	37	30	68
<i>Centris trigonoides</i> Lepeletier, 1841	125	14	3
<i>Centris varia</i> (Erichson, 1848)	18	0	0
<i>Ceratina arizonensis</i> Cockerell, 1898	1	3	5
<i>Ceratina capitosa</i> Smith, 1879	1	1	6
<i>Ceratina excimia</i> Smith, 1862	3	0	7
<i>Ceratina</i> sp. 1	1	47	42
<i>Ceratina</i> sp. 2	20	9	12
<i>Ceratina</i> sp. 3	20	5	10
<i>Ceratina</i> sp. 4	7	0	0
<i>Coelioxys aztecus</i> Cresson, 1878	1	1	1
<i>Coelioxys</i> sp. 1	0	1	0
<i>Coelioxys</i> sp. 2	0	1	0

<i>Colletes macconnelli</i> Metz, 1910	0	0	16
<i>Colletes</i> sp. 1	0	0	42
<i>Colletes</i> sp. 2	1	1	5
<i>Colletes</i> sp. 3	0	0	1
<i>Colletes</i> sp. 4	0	0	1
<i>Colletes</i> sp. 5	0	0	8
<i>Diadasia australis</i> (Cresson, 1878)	56	159	5
<i>Diadasia</i> sp. 1	0	1	0
<i>Dianthidium macrurum</i> (Cockerell, 1913)	0	70	20
<i>Dianthidium</i> sp. 1	0	1	10
<i>Dieunomia micheneri</i> (Cross, 1958)	0	1	0
<i>Epicharis elegans</i> Smith, 1861	6	0	0
<i>Eufriesea micheneri</i> Ayala and Engel, 2008	0	0	3
<i>Euglossa viridissima</i> Friese, 1899	76	8	66
<i>Eulaema polychroma</i> (Mocsáry, 1899)	6	0	11
<i>Exomalopsis similis arida</i> Cockerell, 1929	0	1	0
<i>Exomalopsis similis moesta</i> Timberlake, 1890	51	25	2
<i>Exomalopsis</i> sp. 1	0	21	33
<i>Exomalopsis</i> sp. 2	26	2	3
<i>Exomalopsis</i> sp. 4	8	0	7
<i>Exomalopsis</i> sp. 5	0	0	4
<i>Frieseomelitta nigra</i> Cresson, 1878	122	320	87
<i>Halictus ligatus</i> Say, 1837	113	0	3
<i>Heriades bruneri</i> Titus, 1904	0	0	1
<i>Heriades variolosa</i> Cockerell, 1929	0	6	20
<i>Hylaeus</i> sp. 1	2	5	26
<i>Hylaeus</i> sp. 2	1	4	0
<i>Hylaeus</i> sp. 3	0	0	4
<i>Hylaeus</i> sp. 4	1	0	0
<i>Hylaeus</i> sp. 5	0	0	4
<i>Hypanthidium mexicanum</i> (Cresson, 1878)	0	0	1
<i>Lasioglossum acarophyllum</i> McGinley, 1986	1	0	11
<i>Lasioglossum desertum</i> Smith, 1879	1	0	0
<i>Lasioglossum</i> sp. 1	0	3	0
<i>Lasioglossum</i> sp. 2	0	3	0
<i>Lasioglossum</i> sp. 3	2	0	2
<i>Lasioglossum</i> sp. 4	0	18	2
<i>Lasioglossum</i> sp. 5	0	4	0
<i>Lasioglossum</i> sp. 6	0	0	5
<i>Lasioglossum</i> sp. 7	1	3	0
<i>Lasioglossum</i> sp. 8	0	2	4
<i>Lasioglossum</i> sp. 9	0	0	5
<i>Lasioglossum</i> sp. 10	1	0	6
<i>Lasioglossum</i> sp. 11	3	16	3
<i>Lasioglossum</i> sp. 12	0	0	3
<i>Lasioglossum</i> sp. 13	9	0	0
<i>Lasioglossum</i> sp. 14	2	1	1
<i>Lasioglossum</i> sp. 15	4	1	0
<i>Lasioglossum</i> sp. 16	0	0	1
<i>Lithurgopsis apicalis</i> Cresson, 1875	0	52	5
<i>Megachile albitarsis</i> Cresson, 1872	13	0	8
<i>Megachile concinna</i> Smith, 1879	2	5	2
<i>Megachile exilis</i> Cresson, 1878	38	0	11
<i>Megachile flavihirsuta</i> Mitchell, 1939	2	1	14
<i>Megachile frugalis</i> Cresson, 1872	0	17	10
<i>Megachile gentilis</i> Cresson, 1872	23	13	62

<i>Megachile otomita</i> Cresson, 1878	69	0	0
<i>Megachile parallela</i> Smith, 1853	2	1	2
<i>Megachile petulans</i> Cresson, 1878	5	4	9
<i>Megachile reflexa</i> (Snell, 1990)	8	36	4
<i>Megachile</i> sp. 1	0	0	1
<i>Megachile</i> sp. 2	1	0	0
<i>Megachile zapoteca</i> Cresson, 1872	0	1	16
<i>Melissodes morrilli</i> Cockerell, 1918	46	18	8
<i>Melissodes</i> sp. 1	0	1	0
<i>Melissodes</i> sp. 2	3	6	7
<i>Melissodes</i> sp. 3	20	12	12
<i>Melissodes</i> sp. 4	0	2	0
<i>Melissodes tepaneca</i> Cresson, 1878	1	28	7
<i>Melitoma marginella</i> (Cresson, 1872)	70	1	49
<i>Mesochora bicolor</i> (Fabricius, 1804)	0	5	0
<i>Mexalictus</i> sp. 1	0	0	3
<i>Mydosoma serratum</i> (Friese, 1899)	0	7	43
<i>Panathidium jugatorium</i> (Say, 1824)	0	2	14
<i>Panathidium vespoidea</i> (Friese, 1921)	3	0	54
<i>Paratetrapedia moesta</i> (Cresson, 1878)	0	4	9
<i>Partamona bilineata</i> (Say, 1837)	439	84	245
<i>Peponapis azteca</i> (Hurd and Linsley, 1966)	125	49	1
<i>Peponapis utahensis</i> (Cockerell, 1905)	1	0	0
<i>Perdita</i> sp. 1	0	2	20
<i>Plebeia cora</i> Ayala, 1999	0	0	145
<i>Protandrena</i> sp. 1	12	1	41
<i>Protandrena</i> sp. 2	37	0	16
<i>Protandrena</i> sp. 3	0	11	0
<i>Protandrena</i> sp. 4	3	3	0
<i>Protandrena</i> sp. 5	0	0	2
<i>Protandrena</i> sp. 6	1	0	0
<i>Pseudaugochlora graminea</i> (Fabricius, 1804)	66	6	2
<i>Pseudopanurgus</i> sp. 1	1	1	14
<i>Pseudopanurgus</i> sp. 2	0	2	0
<i>Pseudopanurgus</i> sp. 3	1	0	0
<i>Pseudopanurgus</i> sp. 4	0	0	1
<i>Pseudopanurgus</i> sp. 5	1	1	0
<i>Scaptotrigona bellwegeri</i> (Friese, 1900)	134	388	196
<i>Stelis costaricensis</i> Friese, 1921	0	0	1
<i>Tetraloniella balluca</i> LaBerge, 2001	0	2	1
<i>Tetraloniella donata</i> (Cresson, 1878)	0	6	19
<i>Tetraloniella pomonae</i> (Cockerell, 1915)	5	14	22
<i>Tetraloniella salviae</i> LaBerge, 1989	0	2	32
<i>Tetrapedia maura</i> Cresson, 1878	0	23	8
<i>Trachusa pectinata</i> Brooks and Griswold, 1988	0	1	38
<i>Triepeolus</i> sp. 1	2	0	25
<i>Trigona fulviventris</i> Guérin, 1835	0	14	172
<i>Xenoglossa gabbii</i> (Cresson, 1878)	1	0	0
<i>Xylocopa guatemalensis</i> Cockerell, 1912	0	1	214
<i>Xylocopa mexicanorum</i> Cockerell, 1912	134	43	124
<i>Xylocopa muscaria</i> (Fabricius, 1775)	1	1	53
<i>Xylocopa tabaniformis tabaniformis</i> (Smith, 1854)	0	0	108
Total	4202	4786	5067