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ORIGINAL ARTICLE

The role of seasonality and disturbance in bee–plant interactions in semi-arid communities of the southern Chihuahuan desert

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Abstract

1. The maintenance of interactions between plants and their floral visitors depends on factors such as resource variability, seasonality, and population dynamics. Changes in water availability along with different types and levels of anthropogenic disturbance may influence how plants and pollinators interact, especially in arid environments.
2. In a semi-arid area of the southernmost Chihuahuan Desert (Mexico), we surveyed bee–plant interactions in the dry and rainy season at sites that differed in disturbance type. We used a mutualistic network approach to analyse our data.
3. We collected 946 bee individuals belonging to 32 bee species, almost a third of the total richness previously reported for Querétaro state. We detected a strong impact of seasonality on the structure of ecological interactions, with more complex and robust interactions among bee and plant species in the rainy season.
4. We did not find statistical support for a relationship among disturbance, nestedness, or niche overlap. We did find disturbance negatively affected plant robustness to secondary extinctions.
5. Four plants: *Echinocactus platyacanthus*, *Opuntia stenopetala*, *Senna wislizeni* var. *painteri* and *Cylindropuntia imbricata* comprised the core species that were primarily responsible for the resilience of the bee communities. The following bees conformed the generalist core of species: *Diadasia rinconis*, *Lasioglossum* (*Dialictus*) sp. 1, *Apis mellifera*, and *Augochlorella pomoniella*.
6. Overall, network nestedness and robustness differed significantly between seasons but not among sites with different levels of disturbance.

KEYWORDS
ecological interactions, human activities, Mexico, network nestedness, pollinators, Querétaro, resilience

INTRODUCTION

Given changes in water availability worldwide and the impact of anthropogenic disturbance on natural ecosystems (Danneyrolles et al., 2019; Konapala et al., 2020), there is an urgent need to understand how these changes may affect ecological interactions. Mutualistic interactions may be especially prone to disruption in climate change scenarios because mutualistic species need to coordinate in

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time (Rafferty et al., 2015). A powerful tool to assess mutualistic interactions between two trophic levels is the network approach, in which species from two different trophic levels are represented as nodes and the links between the nodes symbolise their ecological interactions. Thus, mutualistic networks allow the exploration of interaction patterns at the community level. The structure of interactions in mutualistic systems is characterised by a nested pattern formed by specialist species interacting with a subset of the species that generalists interact with, making specialist-to-specialist interactions very unlikely to occur (Bascompte & Jordano, 2014). Furthermore, nestedness implies functional redundancy (i.e., there are several species interacting with the same species from the other trophic level) (Bascompte & Jordano, 2014). Therefore, functional redundancy enhances probability of species rewiring after a disturbance (i.e., species may switch interaction partners over time given changes in the pool of co-occurring species) (CaraDonna et al., 2017). Overall, the core of generalist species created by a nested pattern act as an adhesive component which keeps the entire network structure robust to random species loss (Aizen et al., 2012; Burgos et al., 2007; Dunne et al., 2002; Memmott et al., 2004). In nested networks, less-connected species are the first to go extinct when species loss is random (Bascompte & Jordano, 2014).

Mutualistic network analyses have been widely employed to study pollinator communities, especially bees and their interactions with flowers (Williams et al., 2010; Winfree et al., 2007, 2009) and have much improved our understanding on network structure. However, to appreciate the causes and consequences of network structure, it is necessary to directly address the temporal variation in which interactions arise (CaraDonna et al., 2021; Olesen et al., 2008). In highly seasonal systems (i.e., deserts), water availability may go beyond driving taxonomic turnover in bee communities but may also modify the nestedness of the network because both flowers and bees respond positively to precipitation (Pennington & Collins, 2007; Petrie et al., 2014; Snyder & Tartowski, 2006). Exploration of how seasonality is related to network patterns in highly seasonal systems may help us understand how variation in water availability results in changes in interaction patterns.

Located on both sides of the Mexico-USA border, the Chihuahuan desert is the largest warm desert of North America with marked seasonality and an extraordinary species richness of cacti (Zavala-Hurtado & Jiménez, 2020). The northwestern part of this arid region is exceptionally rich in bee species (Minckley & Ascher, 2013) with communities that exhibit great taxonomic turnover between the spring and late-summer seasons (Kazenel et al., 2020). Although some bee communities in the north and central Chihuahuan desert have been well-sampled (Droege et al., 2010; Kazenel et al., 2020; Minckley, 2008; Minckley & Radke, 2021), bees in the Queretano-Hidalguense Arid Zone (referred to hereafter as the AZQH), a subregion in southernmost Chihuahuan Desert have been poorly sampled (Ayala et al., 1993). The AZQH experiences two marked seasons in the year (i.e., dry and rainy) where average monthly rainfall varies from 5 to 103 mm, respectively. Furthermore, climate change scenarios project future precipitation events will be smaller and more numerous, along with increased duration of periods with and without rain (Petrie et al., 2014) and overall drier conditions (Rudgers et al., 2018). In addition to climate change, the AZQH faces serious conservation challenges, mostly due to human activities (Hernández-Oria et al., 2007).

Anthropogenic disturbance may result in or accelerate local species extinctions in natural systems (Ribeiro et al., 2015), but their effects on bee–plant communities seem mixed regarding species diversity and ecological interactions. On one hand, several studies report a decrease in bee interactions in areas affected by disturbance (Carman & Jenkins, 2016; Williams et al., 2010; Winfree et al., 2007, 2009). On the other hand, bee–flower interaction networks may buffer species loss if partner switching occurs and there is functional redundancy (Grass et al., 2018). Including temporal and spatial variation in network analyses may contribute to our understanding of how bee interactions respond to different disturbance levels and different seasons.

Here, we explore how seasonality and chronic anthropogenic disturbance (sensu Martorell & Peters, 2005) influence mutualistic interactions among bees and flowering plants by comparing bee–plant interactions at sites that differ in disturbance type and intensity. We specifically asked: (1) How do seasonality and disturbance influence bee species composition? (2) How do seasonality and disturbance affect network nestedness, niche overlap, and robustness to species extinctions? and (3) Which are the bee and plant species that maintain the structural properties of the interactions network? We predict that the accentuated seasonality in our study area will impact the interaction patterns observed among bee and plant species, and structural change in the network properties will occur between seasons. We also predict a negative relationship between the nestedness of ecological interactions and disturbance level.

MATERIALS AND METHODS

Study site

The study was conducted in the southernmost part of the Chihuahuan desert (AZQH) in central Mexico. The geological formations in the AZQH date from the Cretaceous, mainly represented by sedimentary limestone rocks (Zamudio et al., 1992). Vegetation type is xeric scrubland, dominated by *Larrea tridentata* Sesse and Moc. ex DCC. (Zygophyllaceae) and *Fouquieria splendens* Engelman (Fouquieriaceae). The AZQH is subject to a variety of human activities that include looting of plant species, illegal wood extraction for commercial purposes, and land-use change (Hernández-Oria et al., 2007). Cattle grazing and browsing are the main human-led activities in the natural lands of the AZQH. The AZQH exhibits a high incidence of cacti species with restricted geographic distributions (Hernández & Bárcenas, 1995; Hernández & Bárcenas, 1996) and at least 17 species are listed under different protection categories in the Official Mexican Standard 0-59 (Hernández-Oria et al., 2007). We studied five localities between October 2015 and June 2016; three of these, Las Ánimas, El Banco and Higuerillas, in the municipality of Cadereyta de Montes, and the other two, Agua del Ángel and La Tinaja, in the municipality of Peñamiller (Table S1 and Figure 1). We visited the five sites four times each to document bee-flower interactions and to measure the disturbance level at each site; twice during the dry season (October 2015 and January 2016) and twice during the rainy season

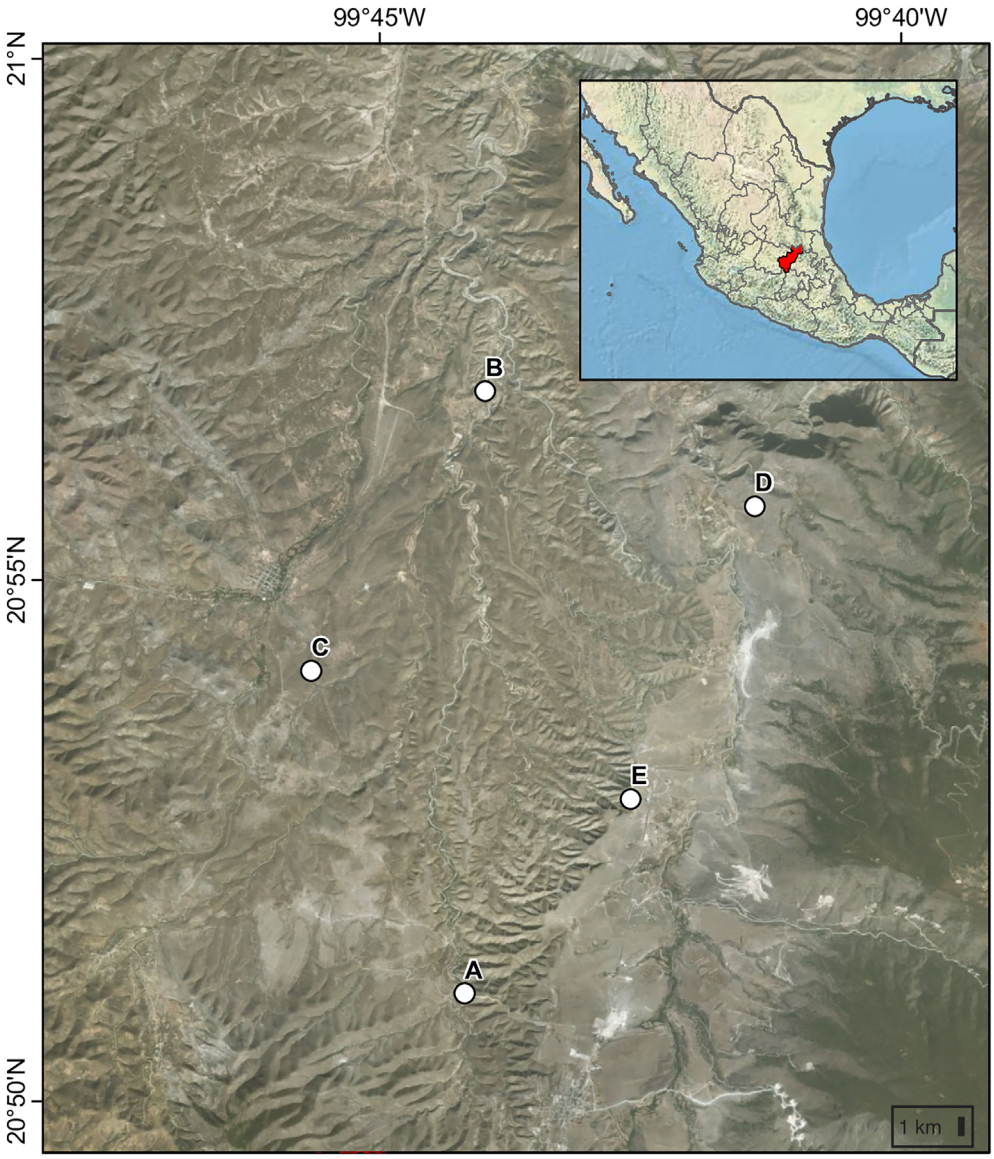


FIGURE 1 Localities of the five sites where bee–plant interactions were examined in the AZQH. Querétaro state is highlighted in red colour

(May 2016 and June 2016). Over the dry season, temperatures ranged from −1 to 26.6 °C and the greatest single rainfall event was 7.3 mm. During the rainy season, temperature ranged between 8 and 33 °C with the largest single rainfall event of 89.9 mm.

Measure and analysis of disturbance

Anthropogenic disturbances are often associated with ecosystem decline and can be compared by the disturbance index proposed by Martorell and Peters (2005). We selected and indexed seven variables to characterise chronic anthropogenic disturbance (Table S2). Based on a priori knowledge of the AZQH, we selected five sites with similar vegetation composition that encompassed different levels and types of disturbance. In each of the five sites, we established three 50 × 50 m plots. Plots at one site were no closer than 200 m apart and no farther than 500 m apart. Within each plot, we surveyed along two perpendicular 50 × 1 m transects that crossed in the middle and recorded the disturbance variables detailed in Table S2: disturbance variables can be broadly grouped into degradation due to livestock or humans and habitat deterioration. We summarised the measured variables per plot into a disturbance index (Martorell & Peters, 2005) that ranges from 0 points (little or not disturbed) to 100 points (extremely disturbed). The disturbance index for a site was scored as the mean of the transects in the three plots, considering each time we visited the sites. We characterise sites into those that were little (<20 points), moderately (>20 and <69 points), and extremely disturbed (>70 points). We calculated the disturbance index at the plot level in each site. We used principal coordinates analysis (PCA) with the disturbance data to examine the association of each variable of disturbance measured at each location surveyed.

Survey of bee–flower interactions

To quantify and describe the ecological interactions between bees and flowers, we surveyed all five study sites twice in the dry season and twice in the rainy season (Table S3). At each site, sampling was done on 1 day at temperatures when bees were active (17–25 °C), and the wind did not exceed 3 km/h. Sampling was done on the same three 50 × 50 m plots we used to quantify disturbance and mentioned above. All plots were sampled simultaneously by different collectors three times/day: 2 h in the morning, 2 h at midday, and 2 h in the afternoon. Each collector walked in a zig zag pattern through the plots and captured all bees with an aerial net at any plant in bloom, pausing the timer while the bee specimen was processed. Each bee was placed in an individual vial with ethanol and labelled with the site information, time of day, collector name, and taxonomic identity of the plant on which the bee was caught. If the plant identity was unknown, we collected a specimen for later identification. We considered a bee–plant interaction as valid when the bee physically interacted with the sexual parts of the flower (e.g., anthers or stigma). To avoid collector bias, we rotated collectors among plots every 2 h of sampling. Overall, this sampling regime resulted in 6 h of sampling/plot/day and 18 h of sampling per site per visit. Over the duration of the study, each site was visited four times and sampled for a total of 72 h. Total sampling time summed across all five sites was 360 h.

We identified the plants and bees to their lowest taxonomic level possible using taxonomic keys and expert knowledge by Dr. Ismael Hinojosa (Instituto de Biología at Universidad Nacional Autónoma de México in Mexico City) and M. Sc. Jorge Mérida (El Colegio de la Frontera Sur in San Cristóbal de las Casas, Chiapas, México).

TABLE 1 Disturbance types and level of each study site.

Site	Disturbance points	Main disturbance
A	19.72	No dominant disturbance detected
B	40.93	No dominant disturbance detected
C	79.26	Vegetation extraction, cattle grazing and goat faeces
D	83.23	Cattle faeces, human and cattle roads
E	89.13	Cattle grazing and goat faeces

Note: Disturbance level was calculated as the mean of three subplots using the Martorell and Peters (2005) index, which ranges from no (0) to high disturbance (100).

Data analysis

To assess how well our bee samples represented the known fauna in Querétaro State, we pooled together the data collected in different sites and seasons and examined the accumulative and rarefaction richness of species (Gotelli & Colwell, 2001) using the *specaccum* function in 'vegan' R package (Oksanen et al., 2020). This allowed us to represent cumulative richness as a function of the total number of plots we surveyed. To assess diversity representation in our sampling, we represented the number of individuals collected as an independent variable in a sample size-based extrapolation with 95% CI. We then standardised our sample size (Chao et al., 2014) to Hill numbers (Richness, Shannon, and Simpson Diversity Indexes), using the *ggINEXT* function in 'iNEXT' R package (Hsieh et al., 2016).

To calculate niche overlap, robustness to species extinctions, and weighted nestedness for our network of interactions per site and season, we used the *networklevel* function from 'bipartite' R package (Dormann et al., 2021). Niche overlap is a measure of similarity in the dietary

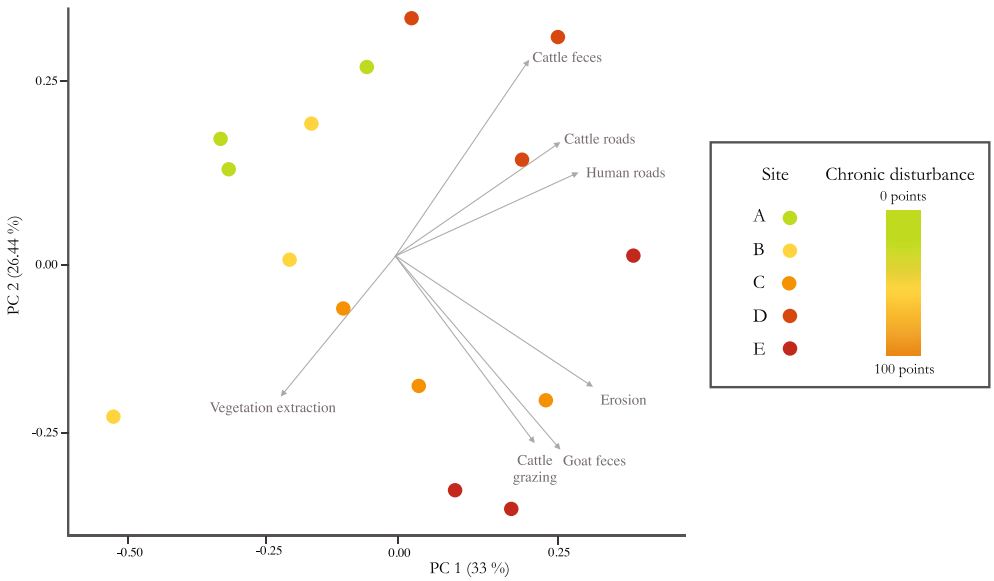


FIGURE 2 Principal coordinates analysis (PCA) of the disturbance variables measured in five sites in the AZQH. From the five sites studied, Sites A and B presented the lowest levels of disturbance and no disturbance variable. In contrast, Sites C, D, and E presented higher levels of disturbance with associations to multiple disturbance variables measured

breadth (from the bee species perspective) or of the floral visitors shared (from the plant species perspective). We obtained this metric using Horn's Index (Horn, 1966), where values of 0 indicate no niche overlap between the species of the same trophic level and 1 corresponds to full overlap. Robustness calculates the probability of species extinction in a trophic level if their interaction partners in the other trophic level go extinct (i.e., chances of secondary extinctions) (Memmott et al., 2004). To calculate robustness, we removed species according to their abundance from least to most abundant. Weighted nestedness considers interactions frequency from 1 (maximum nestedness) and 0 (minimum

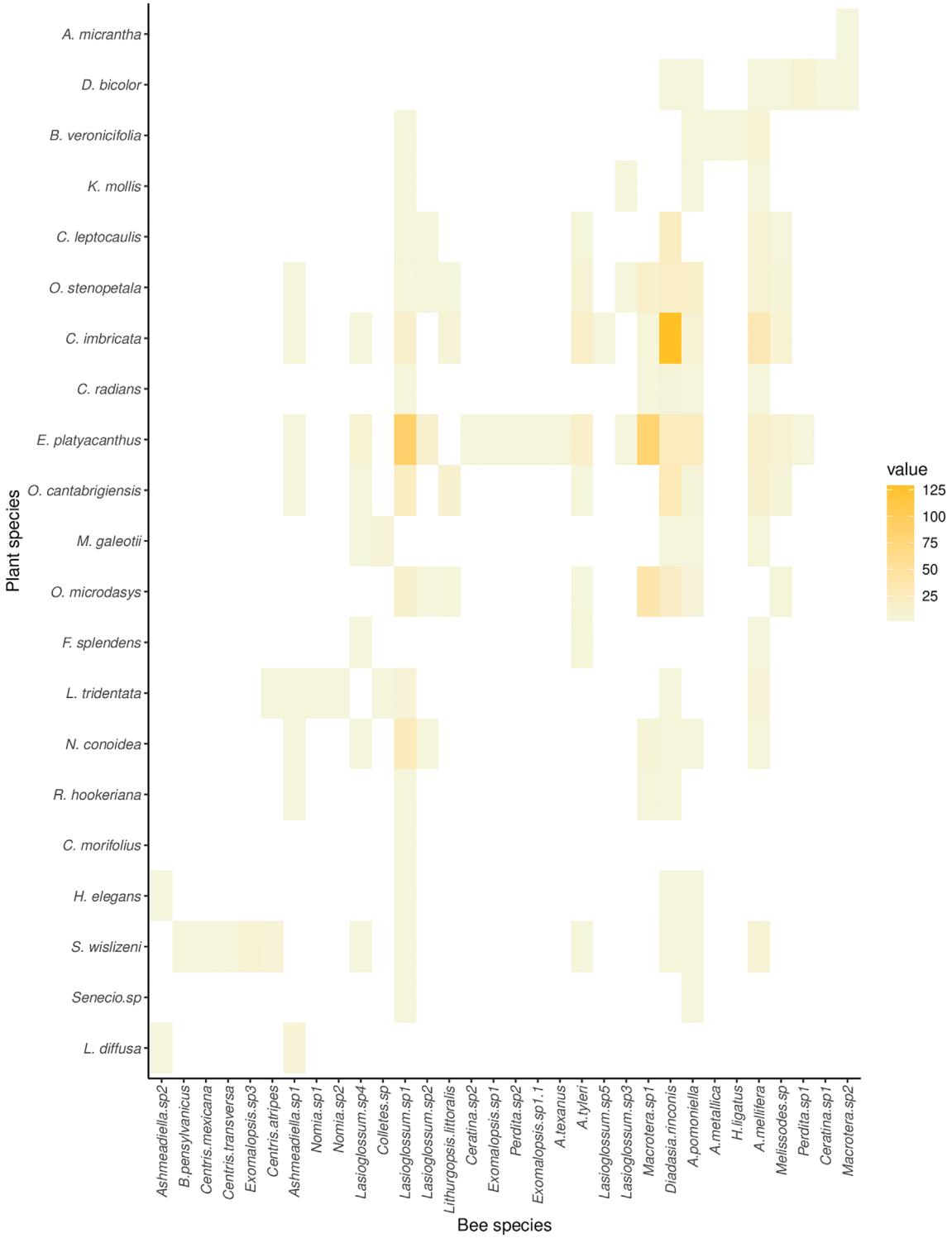


FIGURE 3 Weighted heatmap of the interactions among bees and the blooming plants present in the AZQH from October 2015 to Jun 2016. *Value* indicates number of observed interactions. Four bee species accounted for most of the visits registered: 1) *Diadasia rinconis* (Apidae), 2) *Lasioglossum* sp. 1 (*Dialictus*: Halictidae), 3) *Apis mellifera* (Apidae), and 4) *Augochlorella pomoniella* (Halictidae)

TABLE 2 Total bee species collected at flowering plants in the rainy and dry season.

Family	Species	Rainy	Dry	Total
Apidae	***Apis mellifera*** Linnaeus	90	12	101
Halictidae	*Agapostemon texanus* Cresson	2	0	2
Halictidae	*Agapostemon tyleri*	42	3	45
Megachilidae	*Ashmeadiella* sp. 1	16	0	16
Megachilidae	*Ashmeadiella* sp. 2	2	0	2
Halictidae	***Augochlorella pomoniella*** Cockerell	62	6	68
Halictidae	*Augochloropsis metallica* Fabricius	0	2	2
Apidae	*Bombus pensylvanicus* Degeer	1	0	1
Apidae	*Centris atripes* Mocsáry	7	0	7
Apidae	*Centris mexicana* Smith	1	0	1
Apidae	*Centris transversa* Pérez	1	0	1
Apidae	*Ceratina* sp. 1	0	1	1
Apidae	*Ceratina* sp. 2	1	0	1
Colletidae	*Colletes* sp. 1	6	0	6
Apidae	***Diadasia rinconis*** Cockerell	253	1	254
Halictidae	*Halictus ligatus* Say	0	1	1
Apidae	*Exomalopsis* sp. 1	2	0	2
Apidae	*Exomalopsis* sp. 2	1	0	1
Apidae	*Exomalopsis* sp. 3	9	0	9
Halictidae	***Lasioglossum* sp. 1**	178	3	181
Halictidae	*Lasioglossum* sp. 2	15	0	15
Halictidae	*Lasioglossum* sp. 3	4	0	4
Halictidae	*Lasioglossum* sp. 4	15	1	16
Halictidae	*Lasioglossum* sp. 5	2	0	2
Megachilidae	*Lithurgopsis littoralis* Cockerell	19	0	19
Andrenidae	*Macrotera* sp. 1	142	1	142
Andrenidae	*Macrotera* sp. 2	0	3	2
Apidae	*Melissodes* sp. 1	31	2	32
Halictidae	*Nomia* sp. 1	1	0	1
Halictidae	*Nomia* sp. 2	0	1	1
Andrenidae	*Perdita* sp. 1	1	8	9
Andrenidae	*Perdita* sp. 2	1	0	1

Note: Rainy, dry, and total columns indicate the number of individuals collected respectively. Bee species in bold were identified as core species for the bee–flower interactions network.

nestedness). To determine the bee and plant species that belong to the generalist core (*Gc*) of interacting species, we employed the z-score formula to describe the number of interactions of a given species relative to the mean number of interactions of all species in that trophic level. Species with Z scores greater than 1 had larger number of interactions and were considered core species in the trophic level (Dáttilo et al., 2013).

We used generalised linear mixed models (GLMMs) to analyse how seasonality, disturbance, and site influences the following response variables: (a) bee species abundance, (b) network nestedness, (c) network niche overlap for both trophic levels, and (d) robustness to secondary extinctions for both trophic levels. For the species abundance model, we used a negative binomial GLMM distribution to account for overdispersion of the residuals in our dataset. To prevent pseudoreplication, we acknowledge as random effects the nested structure of our field design (e.g., plots within sites), sampling season, and variation in counts between species. For all the network indexes models, we used Gaussian distribution and accounted as random effects our plots nested into sites and sampling season. In all models, we considered as fixed effects site, season, and disturbance. To inspect for over or underdispersion in our models' residuals, we used the function *simulateResiduals* from the DHARMa R package (Hartig, 2021). We conducted all GLMMs with the *glmmTMB* function from the identically named R package (Brooks et al., 2017).

To compare niche overlap for both trophic levels among sites, we conducted pairwise comparisons using the *pairs* function from the emmeans R package (Lenth et al., 2022).

TABLE 3 Number of flowering plant species associated that bee visited in the rainy and dry season.

Family	Species	Number of bee species associated	Season
Cactaceae	***Echinocactus platyacanthus*** Link and Otto	17	Rainy
Cactaceae	***Cylindropuntia imbricata*** Haworth	11	Rainy
Cactaceae	***Opuntia stenopetala*** Engelm	11	Rainy
Fabaceae	***Senna wislizeni* var. *painter*** Britton and Rose	11	Rainy
Cactaceae	*Opuntia cantabrigiensis* Lynch	9	Rainy
Cactaceae	*Opuntia microdasys* Lehmann	8	Rainy
Cactaceae	*Neolloydia conoidea* De Candolle	8	Rainy
Zygophyllaceae	*Larrea tridentata* Moç. and Seseé ex DC.	8	Both
Fabaceae	*Dalea bicolor* Humb. and Bonpl. ex Willd	7	Dry
Cactaceae	*Cylindropuntia leptocaulis* De Candolle	6	Rainy
Asteraceae	*Brickellia veronicifolia* Kunth	5	Dry
Cactaceae	*Coryphantha radians* De Candolle	5	Rainy
Cactaceae	*Mimosa galeotii* Bentham	5	Rainy
Acanthaceae	*Ruellia hookeriana* Nees	5	Rainy
Rhamnaceae	*Karwinskia mollis* Schlechtendal	4	Rainy
Malvaceae	*Hibiscus elegans* Standley	4	Rainy
Fouquieriaceae	*Fouquieria splendens* Engelmann	3	Dry
Cactaceae	*Lophophora diffusa* Croizat	2	Rainy
Asteraceae	*Senecio* sp. 1	2	Dry
Malvaceae	*Ayenia micrantha* Standley	1	Dry
Euphorbiaceae	*Croton morifolius* Willdenow	1	Rainy

Note: With bee species by season surveyed. Plant species in bold were identified as core species that maintain the bee–flower interaction network.

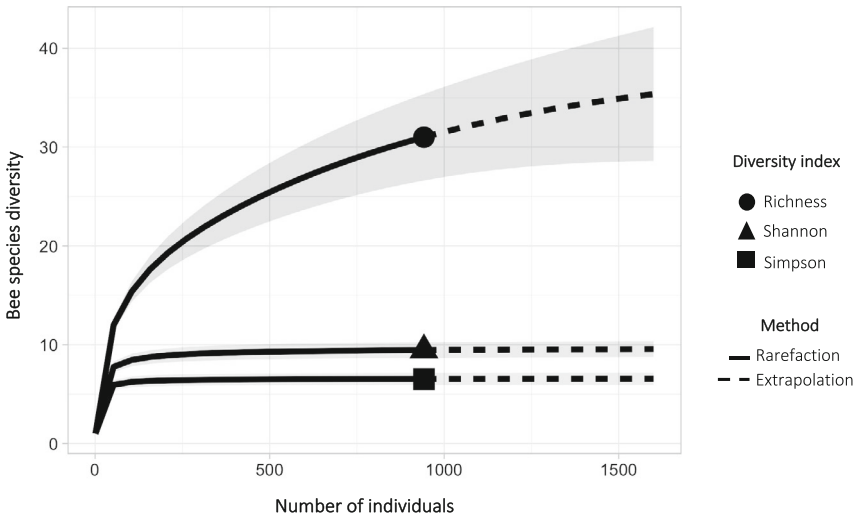


FIGURE 4 Sample-size-based rarefaction (solid line segment) sampling curves with 95% confidence intervals (shaded areas) for the bee species richness and diversity collected in the AZQH. As shown here, the curves approached an asymptote as sampling effort increased, indicating our sampling provided a robust estimate of species richness

RESULTS

Disturbance in the studied sites

The five sites we studied ranged from little-disturbed (Site A) to moderately disturbed (Site B) to highly disturbed due to multiple different stressors (Sites C, D, and E) (Table 1). The first two dimensions of the PCA (Figure 2) explained 59.44% of the total variation and further suggest how different disturbance factors are at play across our sites and the AZQH in general.

Bee and plant species

Thirty-two bee species were represented among the 946 individuals we collected at 20 flowering plant species (Figure 3, Table 2). Based

on *z* scores, the following bees comprised the generalist core set of species (*Gc* > 1): (1) *Diadasia rinconis* (Apidae), (2) *Lasioglossum* (*Dialictus*) sp. 1 (Halictidae), (3) *Apis mellifera* (Apidae), and (4) *Augochlorella pomoniella* (Halictidae) (Table 2). These four species constituted 71% of all individuals we sampled and were present at all the study sites interacting with the same host. Rare species represented by one individual amounted to 3% of the species pooled across samples at all sites. Rare bee species were observed across all sites, regardless of disturbance level or type. Among plants, the generalist core species (*Gc* > 1) were *Echinocactus platyacanthus*, *Opuntia stenopetala*, *Senna wislizeni* var. *painteri* and *Cylindropuntia imbricata* (Table 3). All these species but *S. wislizeni var. painteri* were present at all five sites. *S. wislizeni var. painteri* was only found in Site D, where it was visited not only by generalist bee species but by bee species observed only at this site (*Centris mexicana*, *Centris atripes*, *Centris transversa* and *Nomia* sp1).

Sampling thoroughness assessment

Species accumulation and sample-size-based extrapolation curves for the AZQH showed that the sampling effort was adequate to capture the maximum species diversity in terms of Shannon's entropy index and the inverse of Simpson's dominance index (Figure 4). The 32 species in our pooled samples were below the estimated 36 species predicted when extrapolating with 95% CI (Chao et al., 2014). Furthermore, species accumulation curves based on individuals (Figure 4) and plots Figure (S3) both approached an asymptote as sampling increased, indicating our sampling provided a robust estimate of species richness.

Role of seasonality on bee abundance and interactions

Consistent with our predictions, seasonality was an important factor in this desert area. Species abundance and nestedness were both higher during the rainy season (fixed effect: 0.48, df = 319, $p = 0.05$, GLMM; Figures S1, S2; Tables S4 and S5), as was the nested structure of the interactions and robustness to secondary extinctions (fixed effect: 0.52, df = 21, $p < 0.01$ 0.04, GLMM; Figures, S1, S2 and Tables S5–S7). During the dry season, *Dalea bicolor* was the only plant species regularly visited by bees (Figure S1), whereas in the rainy season, four plant species were most visited (*O. stenopetala*, *E. platyacanthus*, *C. imbricata* and *S. wislizeni* var. *painteri*) (Figure S2). During the dry season, 12 bee species interacted with six plant species, establishing 19 bee–plant interactions. During the rainy season, 28 bee species interacted with 16 plant species and formed 114 interactions. There was little overlap of bees and flowering plants in the dry and rainy season. Only 25% ($N = 9$) of the bee species were sampled in both seasons, and one plant (*Larrea tridentata*) bloomed in both the dry and rainy seasons (Table 3). Despite very different bee faunas and flora, niche overlap of bee species did not differ between seasons (fixed effect: 0.098, df = 21, $p > 0.05$, GLM; Table S7). For flowering plants, niche overlap (i.e., similarity in bee species visitors) in the rainy season was significantly greater (fixed effect: 0.10, df = 21, $p < 0.001$, GLM; Table S6).

Role of disturbance on bee abundance and interactions

Contrary to our predictions, disturbance was not correlated with bee species abundance (fixed effect: 0.007, df = 319, $p > 0.05$, GLMM; Table S5) nestedness, or niche overlap index ($p < 0.05$ for all network GLMMs; df = 21; see fixed effects in Tables S6–S8). However, we did find that plant species robustness to the loss of bee species and secondary extinctions decreases in sites with greater disturbance (fixed effect: −0.003, df = 21, $p = 0.05$ GLMM; Table S9). In comparison, bee species robustness to the loss of plant species and secondary extinctions did not differ among sites with different disturbance levels (fixed effect: 0.001, df = 21, $p > 0.05$, GLMM; Table S10). Some bee species were dominant at specific sites. For instance, *D. rinconis* was most abundant in a highly disturbed site (Site C) where vegetation extraction and cattle grazing were the dominant disturbance pressures (Table 1). In this site, *D. rinconis* was strongly associated with *C. imbricata*, a common plant at all sites. Although niche overlap for bees and plants is apparently higher in the sites with higher disturbance level (Table S9), our pairwise comparisons did not detect any statistical difference among sites in niche overlap for bees or plants ($p > 0.05$, df = 21, see coefficients in Tables S11–S12).

DISCUSSION

In spite of the biological diversity hotspot that the AZQH represents for cacti and succulent plants, an assessment of the pollinator's community structure was lacking before this study. Bee richness (32 species) represented approximately 26% of the 128 bee species found for the state of Querétaro (Ayala et al., 1993) However, our assessment of sampling thoroughness revealed that the AZQH harbours a greater species richness than we found (Figure 4). This emphasises the importance of the AZQH as a biodiversity reservoir even at the small scales studied here. Cactaceae were the plants that received the highest number of bee species ($n = 20$), mainly *E. platyacanthus*, *C. imbricata*, *O. stenopetala*, *O. cantabrigiensis*, and *O. microdasys*. *Opuntia* is the most species-rich genus of the Cactaceae and is most diverse in Mexico (Mandujano et al., 2013). The identification of three *Opuntia* species as core species (*Gc* > 1) in our network analyses highlights the ecological importance that *Opuntia* flowers constitute to the pollinator community in semi-arid systems. Bees may prefer *Opuntia* flowers because they constituted the most abundant floral resource available during our sampling season.

Relationship between seasonality and frequency of bee interactions

Arid environments are strongly water limited and precipitation is an important cue for bee emergence and plant bloom (Danforth, 1999). Increased floral resources in the rainy season lead to a greater abundance and richness of bee species (Olesen et al., 2008; Potts et al., 2003; Vergara & Ayala, 2002). We found higher bee species

richness in the rainy season (Table 2). Furthermore, the network of interactions became much more robust in the rainy season, due to the emergence of a nested pattern related to higher bee species and flowering plant richness than in the dry season (Table S6). High seasonal turnover in interactions may indicate that a single pollinator species can play different roles at different time frames, such as among blooming periods (CaraDonna et al., 2017) and within the same blooming season (Bramon Mora et al., 2020). Thus, network characteristics vary in temporally predictable ways. Interannual sampling seasons of the bee–flower interactions in the AZQH may reveal higher species turnover and enable the identification of more nested modules of species (Rudgers et al., 2018; Schwarz et al., 2020). We recommend that bee–flower interactions in the AZQH be sampled across different blooming seasons to evaluate how nestedness and modularity relate to network stability in this highly seasonal environment.

Our results suggest that the drier scenarios for the Chihuahuan Desert predicted by climate change projections (Rudgers et al., 2018) will lead to decreased complexity and greater vulnerability of bee-plant interactions in the AZQH. Although niche overlap did not differ among seasons for bees (Table S8), niche overlap differed among seasons for plants meaning that bee species share more flower resources in the rainy season than they do in the dry season. Thus, functional redundancy of bee species and nestedness is enhanced in the rainy season. The lack of evidence for niche overlap among seasons for bees may indicate bees have greater partner flexibility and interaction rewiring (Biella et al., 2019; Vizentin-Bugoni et al., 2020) than plants and may provide some buffer for secondary extinctions among floral hosts.

Relationship between disturbance and bee interactions

The disturbance pressures that impacted our study sites were very different (Figure 2) and reflect the spatially heterogeneous patterns of disturbance in the AZQH reported by others (Hernández-Oria et al., 2007). Thus, chronic disturbance pressures may be widespread across the AZQH which raises the need to evaluate how these conditions influence biological communities other than bees and plants. Other studies that have examined the effect of anthropogenic disturbance on natural bee communities have reported a decrease in bee abundance and diversity that is more pronounced where there was high levels of disturbance (Carman & Jenkins, 2016; Winfree et al., 2007, 2009). However, we did not find a relationship between disturbance and bee species abundance, network nestedness, nor niche overlap which may be explained by the following six non-exclusive factors: (1) the main factor that shapes bee–plant interactions in arid environments is water availability because it is the main driver that cues plant reproduction and bee activity; (2) some bees preferentially nest where soils are disturbed and more easily excavated (Poveda-Coronel et al., 2018; Williams et al., 2010; Winfree et al., 2007); (3) the natural areas surrounding our study sites may function as a natural reservoir for bees that disperse to and forage in more disturbed sites (Chiawo et al., 2017); (4) although disturbance was high in most of the studied localities, the core plant species (*E. platyacanthus*, *O. stenopetala*, *S. wislizeni* var. *painteri* and *C. imbricata*) were shared among the studied sites regardless of the disturbance level or type. These remnants have allowed the network of bee–plant interactions to remain nested despite the high level of human disturbance these sites have and continue to experience (Vázquez & Simberloff, 2003; Yoshihara et al., 2008); (5) some blooming plants that are attractive to bees are common in disturbed areas. For instance, different Asteraceae thrive in the roads along agricultural landscapes attracting then more bee species than the crops (Montagnana & Campos, 2020); and (6) given that we only sampled a small portion of the AZQH over 10 months and in 1 year, it is possible that more intensive surveys may reveal disturbance effects that we did not find.

Our findings do not entirely exclude the possibility of a rapid collapse of the entire mutualistic network. If species loss is not random and targeted to the species in the generalist core then rapid network collapse could occur (Tylianakis et al., 2010). For example, a realistic scenario in the AZQH is that anthropogenic disturbances such as vegetation extraction and cattle grazing might target the plant species that comprise the generalist core of the network. Early extinction of the core species due to these uncontrolled and prolonged anthropogenic disturbance pressures should increase the potential of rapid network collapse.

The AZQH harbours a diverse plant community (Hernández-Magaña et al., 2012; Sánchez Martínez et al., 2008) with many species under significant risk. The giant barrel cactus *E. platyacanthus* is an endemic species with a wide distribution in the AZQH. However, the giant barrel cactus populations face high pressure from human activities as it is commonly used to feed livestock (Hernández-Oria et al., 2007). The current status of the giant barrel cactus in the Official Mexican Standard 0-59 is 'In Danger of Extinction' (Semarnat, 2010). Populations of other cacti species are directly targeted by illegal collecting for the commercial cactus market (Bárcenas Luna, 2003). Given that our analyses identified *E. platyacanthus* as a core species, its loss may lead to secondary extinctions that can trigger parallel declines of other species present in the system (Biesmeijer et al., 2006). Furthermore, *S. wislizenn*i var. *painteri*, another native plant identified as a core species, is not protected in the current Mexican legislation. As our model on robustness against species extinctions showed, plant species in the AZQH are more vulnerable to bee species extinction than vice versa (Table S9) under disturbance scenarios. We strongly suggest considering the ecological role that the identified core plants have in the maintenance of the bee community as an argument to keep the protection category of 'In Danger of Extinction' for *E. platyacanthus* and to evaluate the population demography of *S. wislizenni* var. *painteri* in the AZQH to determine whether it requires protection or not. However, network collapse in this system may be buffered if extinctions are random and if interaction rewiring occurs after the loss of a species in the network (Vizentin-Bugoni et al., 2020). Species loss followed by rewiring has been shown to complicate the ability to predict secondary network extinctions in subalpine meadows (Brosi & Briggs, 2013).

Another caveat of our analysis of network maintenance is the honeybee, *Apis mellifera*, as a core species ($Gc > 1$). This introduced species from the eastern hemisphere is widespread in Mexico and an

ineffective pollinator of many wildflowers that may negatively impact populations of native bee species (Geldmann & González-Varo, 2018; Magrach et al., 2017). Given that the generalist core metric (*Gc*) is based on observed floral visits, the metric does not guarantee that pollination is indeed occurring from those visits. Thus, we suggest a cautious interpretation of the generalist core metric (*Gc*) and recommend further work on the pollination effectiveness of core bee species.

CONCLUDING REMARKS

We found a positive relationship between network nestedness and seasonality, and a negative relationship between disturbance and plant robustness to secondary extinctions. Specifically, network nestedness significantly increased in the rainy season, but we did not detect any relationship between disturbance and network nestedness. Thus, our results suggest that water availability may be the main determinant factor for nestedness of the ecological interactions among bees and plants in the southernmost Chihuahuan Desert. In addition, our findings emphasise the importance of the shared plant species among sites with different levels and types of disturbance. Among the plants present in the area, *E. platyacanthus*, *O. stenopetala*, *C. imbricata*, and *S. wislizeni* var. *painteri* were identified as part of the generalist core of plant species responsible for the maintenance of the network of interactions among bees and flowers. Given the negative relationship found between disturbance and plant robustness against secondary extinctions. We suggest the incorporation of the ecological role of these species as a criterion for the assignment and maintenance of protection categories in Mexican legislature. Since our study sites were visited only four times in a year, we did not account for potential variation of species interactions within seasons and among years. We encourage other researchers to study the AZQH to help close the gap in sampling thoroughness compared to the central and northernmost portions of the Chihuahuan desert.

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CONFLICT OF INTEREST

All authors declare they have no potential conflict of interest involved with the development of this study.

AUTHORS CONTRIBUTION

M. Argueta-Guzmán, J. Golubov, Z. Cano-Santana, and R. Ayala participated in the conceptualization of this study. M. Argueta-Guzmán and J. Golubov collected field data. M. Argueta-Guzmán analysed the data. M. Argueta-Guzmán and J. Golubov wrote the first draft of the manuscript and all authors contributed with comments.

DATA AVAILABILITY STATEMENT

Data available in article supplementary material

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Supporting information

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