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Hummingbird-Plant Network in a Lowland Dry Forest in Yucatan, Mexico

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Abstract

Pollination by animals contributes to the production of nearly 87.5% of the seeds and fruits in the world. Hummingbirds are one of the main groups of pollinating birds in the Americas, and they form pollination networks with the plants they visit. Few hummingbird-plant networks have been studied in tropical dry forest, which is one of the vegetation types most affected by deforestation worldwide. In this study, we describe the characteristics of the core species of a mutualistic hummingbird-plant network in a lowland dry forest located on the Yucatan Peninsula of Mexico. The study lasted a full year, from August 2017 to June 2018. Using point counts and focal observations, we identified three species of hummingbirds that visited eight plant species. The network was highly connected and had three modules—one for each hummingbird species. The core hummingbird species was *Chlorostilbon canivetii*, and the key plants were *Cordia dodecandra*, *Senna racemosa* and *Psittacanthus mayanus*. This hummingbird-plant network is apparently driven by water availability, which determines plant phenology, which in turn, determines hummingbird activity. In the context of global extinction, the conservation of core species will be critical to maintain the interactions that support all of the species in the network.

Keywords

Hummingbird-plant interaction, mutualistic network, Mexico, bird-plant network, Yucatan, core species, lowland dry forest

Introduction

Understanding and maintaining ecological interactions is now recognized to be fundamental to nature conservation (e.g. Bascompte & Jordano, 2007; Harvey et al., 2017; Rohr et al., 2014). Biodiversity is sustained not just by maintaining species and habitats, but also by keeping ecological interactions intact (Tylianakis et al., 2010). Even when all members of a community are present, if there are no significant interactions among them, their contribution to the ecosystem is virtually nonexistent; in extreme cases, if a species did not interact with others it could be considered “functionally extinct” (Valiente-Banuet & Verdu, 2013).

Interactions within a community can be mutualistic, antagonistic, commensal or neutral (Bronstein, 2015), and the nature of these interactions can be measured using network theory. Network theory uses graphs to represent the interactions among species in a community and produce patterns that can be measured, predicted, and compared (Bascompte & Jordano, 2014). The graphs also make it possible to predict what might

happen to a community if the conditions change (Dormann et al., 2017). Networks usually have core species, as well as peripheral species that depend on them (Martín González et al., 2015). The core species are the most connected with other species, and often, but not always, the most abundant ones (Chacoff et al., 2018;

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Kelly & Elle, 2020; Oleques et al., 2019). Hence, their extinction could result in the collapse of the network (Memmott et al., 2004). Identifying core species is important because doing so allows conservation measures to focus on them (Brose, 2010), and simulating extinctions of core and peripheral species within intact networks can reveal the extent of collapse (Memmott et al., 2004).

Pollination is an especially important mutualistic interaction (Ratto et al., 2018). Of all plant species, 87.5% are pollinated by animals (Ollerton et al., 2011) and several animal species depend on pollen and nectar to survive (Elle et al., 2012). An example is hummingbirds, which pollinate nearly 15% of the plant species in North and South America (Buzato et al., 2000). Due to their dependence on a specific, and often measurable, plant resource, these birds have been used as ecological indicators of disturbance (Dalsgaard et al., 2008).

There have been few studies applying network theory to hummingbird-plant systems located in lowland tropical dry forests. This ecosystem is present across North and South America and there are large portions of it in Mexico (Portillo-Quintero & Sanchez-Azofeifa, 2010). However, it has a high deforestation rate, with only 27% of its original cover remaining (Trejo & Dirzo, 2000). The Yucatan Peninsula, in southern Mexico, is covered mainly by this kind of forest (Miles et al., 2006) but it has long been impacted by human activities; and Lynch (1989) commented that in Yucatan there is no primary forest due to centuries of intense human

impact by the Maya civilization followed by environmental degradation induced by the growth of henequen cultivation at the beginning of the twentieth century.

There have been no studies of hummingbird-plant mutualistic networks in the lowland dry forest of central Yucatan, leaving even the identities of core and peripheral species unknown to date. Thus, our main objective in this study was to determine the core species and network characteristics and patterns for a hummingbird-plant network of a central Yucatan lowland dry forest. To do so, we compiled the network of hummingbirds and the plants they visit, commenting on possible hummingbird dependence on the plants and vice versa. We also discuss which species need to be considered conservation priorities in order to prevent the extinction of other species in this mutualistic network.

Methods

Study Area

Fieldwork was done in Homun, Yucatan, Mexico (20°44'54" N, 89°17'49" W; 16 m asl), where there is a patch of relatively well-preserved lowland dry forest. The climate is hot and sub-humid. The mean annual temperature is 26°C and varies from 16°C (January) to 37°C (May; Figure 1A); mean annual precipitation is 860 mm, with 81% of the precipitation falling in the May–October rainy season (CONAGUA, 2020; INEGI, 2018) (Figure 1B). Hummingbirds whose ranges include

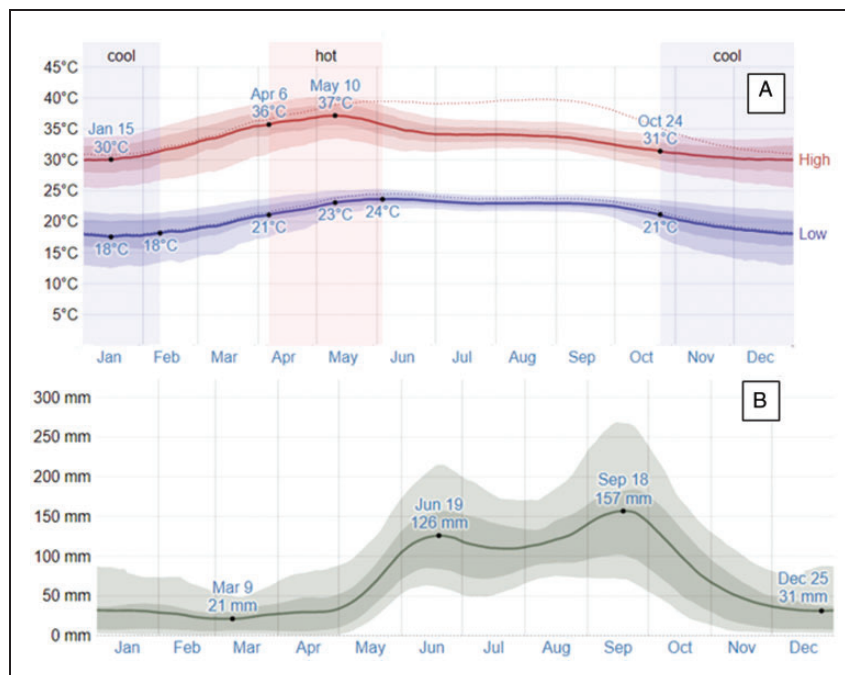


Figure 1. Climate in Homun, Yucatan, México. Variation in annual temperature (A) and rainfall (B) are shown with 25th and 75th percentile bands. Graphs are reproduced with permission from Weather-Spark (2018).

Homun are *Anthracothonax prevostii*, *Archilochus colubris* (wintering), *Chlorostilbon canivetii*, *Campylopterus curvipennis*, *Amazilia candida*, *A. yucatanensis*, and *A. rutila*, which are reported to inhabit dry forests and forest edges (Howell & Webb, 1995; Johnsgard, 1997; Williamson, 2001). There are no data about the identity of the plant species visited by hummingbirds in this landscape.

Data Collection

We established 48 equidistant point-counts in the low-land dry forest along nineteenth century Mayan paths, surveying a total area of 12 ha. The paths are no wider than 2 m and run several kilometers into the dry forest. Each point-count had a 25 m radius, was separated from other points by 50 m and was in the interior of the dry forest. Fieldwork was carried out every other month from August 2017 to June 2018. We sampled the hummingbirds and plants from each point count within two days of each other.

Hummingbirds. We surveyed all 48 point-counts for hummingbirds in one day, starting at dawn and ending around 1100 h. At each point, all the hummingbirds seen or heard for 5 minutes were recorded. Between 10 and 20% of hummingbird records were made by identifying their distinctive calls (Martínez-García et al., 2013). Both of the observers that carried out the point counts had extensive experience identifying hummingbirds using this method (RO-P > 25 years, VM-G > 15 years). For each hummingbird sighting, we recorded species, distance to the observer, and plant species with which the hummingbird interacted. To determine hummingbird species, we used specialized field guides (Arizmendi & Berlanga, 2014; Howell, 2003; Williamson, 2001) and binoculars (10 × 50 mm) and when possible, we determined sex and age.

Plants. During point counts and in transit to them, we recorded and identified the plants that were visited by hummingbirds as well as other plants that exhibited characters that are common among ornithophilous plants, such as brilliant colors (e.g. red or blue) and a tubular corolla (Johnsgard, 1997). Plant samples were collected and deposited in the Centro de Investigaciones Biológicas of the Universidad Autónoma del Estado de Hidalgo, Mexico. To determine plant identity, we collected voucher specimens, took photographs, and consulted the digital herbarium of the Centro de Investigaciones Científicas de Yucatán (Herbario CICY 2010) and Missouri Botanical Garden (<http://www.missouribotanicalgarden.org/>) and the plant plates of the SEDUMA (2018).

To estimate flower density of each plant species, at each point count, we set up two 6 m² quadrats separated by 20 m and counted the flowers of each species. We report these values as flowers/m² bimonthly (i.e., the mean number of flowers recorded in the 96 quadrats sampled every two months). We also measured flower characteristics (corolla length and width and nectar volume and concentration) of up to 10 flowers on 10 individuals of each plant species. The volume of nectar contained in flowers of each plant species was obtained by inserting a 75-microliter Lauka microcapillary tube into the flower and measuring the height of the nectar in the tube using a caliper. The amount of energy contained in the nectar obtained was measured using a portable refractometer (Vee Gee from 0 to 32 Brix), and transforming the °Brix to calories using a conversion table (VINOLAB, 2018).

Interactions. To characterize hummingbird-plant interactions, we recorded all interactions that occurred during the point count surveys (sampling effort = 10 hours every two months) and in the 6 m² quadrats (sampling effort = 6 hours every two months). In addition, we performed focal plant observations (sampling effort = 16 hours every two months), which consisted of revisiting the sites where we had recorded plant species being visited by hummingbirds from dawn to 1100 h and from 1600 h to sunset and observing each plant species for one hour, recording the hummingbird visitor species and the number of flowers visited by each hummingbird species. We conducted these additional observations after completing the point count surveys (on the same day and the following day) during each sampling month.

The relative abundance of each hummingbird species and density of flowers of each plant species each month was obtained from the data collected during the 48 hummingbird point counts and the 96 quadrats, respectively.

Data Analysis

We built an interaction matrix of plants and hummingbirds (Jordano, 1987) and calculated macro- and micro-scale relevant metrics for the network or for each participating species (Simmons et al., 2019). For the macro scale (network level), we calculated connectance and modularity. Connectance is the proportion of all of the possible interactions in the network that were actually observed. Modularity is a structural characteristic of the network that represents to what extent the overall network is divided into sub-groups; modularity values are high when small groups of species interact with each other more intensely than with the rest of the species, forming modules that can be considered independent within the community of species that comprise the

full network (Martínez-Falcón et al., 2019; Olesen et al., 2007).

For the micro scale (species level) analysis, we calculated the strength, specialization, normalized degrees, closeness centrality, and betweenness centrality (Bascompte et al., 2006; Bascompte & Jordano, 2014; Blüthgen et al., 2006; Burgos et al., 2007; Dormann et al., 2008; Dunne et al., 2002; Emer et al., 2016; González et al., 2010; Memmott et al., 2004; Newman & Girvan, 2004). Strength is the importance of each species in the network depending on a quantification of how much other species rely on it for food or pollination. Specialization is the probability that one species is dependent on few resources. Normalized degree is calculated by dividing the number of species the focal species interacts with by the total possible interactions in the network; high normalized degree value is a potential indicator of core species. Closeness centrality (CC) and betweenness centrality (BC) are measures of centrality of each species. CC is calculated for each species by summing the shortest distances between that species and the rest of the species in the network, then dividing that total distance by the number of species in the network minus 1. BC is calculated by doubling the sum of the fractions of the shortest paths that pass through the focal species in the network, divided by the number of all shortest paths that link any two species, which is then divided by the product of the number of species minus one and the number of species minus 2.

We also calculated robustness to extinction, which is the area under the curve of simulated extinctions (see Figure 4A) and represents the number of species that remain in the network after the simulated extinction of one or more species. To do this, we simulated sequential hierarchical extinctions by deleting species one by one in order of connectedness, beginning with the most connected species in both groups (i.e. hummingbirds and plants). For example, in our simulated extinction we eliminated one pollinator, which causes the extinction of the plant species that were pollinated only by such pollinator; then we eliminated a second pollinator, which causes the extinction of its exclusive pollinated plants; etc. We simulated this pattern of extinction because although it is the worst-case scenario (Memmott et al., 2004), it unfortunately appears to be happening in several places around the world (Potts et al., 2010). The extinction model of Memmott et al. (2004) applied to mutualistic networks has some limitations; for example, it assumes that species go extinct if and only if all of the species with which it interacts have gone extinct. This is an unrealistic assumption with problematic implications, because extinction cascades cannot be captured in the model; for example, the extinction of a pollinator which leads to extinction of a plant cannot lead to any further extinctions, because the plant

will no longer be interacting with any other species. However, even with these limitations, the model is useful in that it provides some sense of the robustness of the network in a simplified scenario.

All of the calculations were carried out using the bipartite package in R following previous protocols (Bascompte et al., 2006; Bascompte & Jordano, 2014; Blüthgen et al., 2006; Burgos et al., 2007; Dormann et al., 2008; Dunne et al., 2002; Emer et al., 2016; González et al., 2010; Memmott et al., 2004; Newman & Girvan, 2004). We did not relate the relative abundance of hummingbirds to flower density (Ortiz-Pulido & Lara, 2012), because that was not the objective of this study.

Finally, we also evaluated if precipitation was related to hummingbird-plant interactions in Homun using Pearson correlation tests between monthly precipitation and number of paired interactions recorded by month (i.e. unique paired interactions between two species in the mutualistic network). To do it we obtained Homun precipitation values to the study year from Weather-Spark (2018) and we used the Program PAST (Hammer et al., 2001) to perform the test.

Results

Hummingbirds

We recorded three species of hummingbirds in Homun: *C. canivetii*, *A. yucatanensis* and *A. rutila* (Table 1). Hummingbird abundance peaked in December and dropped from February to June, with no hummingbirds recorded between August and October (Table 1).

Plants

Eight flowering plant species (Table 2) were visited by hummingbirds. There were no flowers detected in August and October. In Homun, the density of flowers utilized by hummingbirds barely surpasses 0.015 flowers/m²/month (Table 2). The flowers that were visited by hummingbirds had variable traits (Table 3).

Interactions

We observed 10 interactions between hummingbirds and plants in Homun (Figure 2). The strongest hummingbird species was *C. canivetii* and the strongest plant species were *Cordia dodecandra* and *Psittacanthus mayanus* (Figure 2, Table 4). The total connectance of the network was 0.416. There were three modules in the network, each of which contained a single hummingbird species (Figure 3). *Chlorostilbon canivetii* was the most connected species, considering the number of visits (Figure 2), and had the largest normalized degree, closeness and betweenness (Table 4). *Amazilia rutila* was the most specialized (*d'*, Table 4). Among the plants,

Table 1. Records of Hummingbird Species in Homun, Yucatan, Mexico (August 2017–June 2018).

Species	August	October	December	February	April	June	Total
<i>Chlorostilbon canivetii</i>			7	3	5	2	17
<i>Amazilia yucatanensis</i>			1	1		1	3
<i>Amazilia rutila</i>			4		4		8
Unknown			4			1	5
Total			16	4	9	4	33

Note. Each number is the sum of the hummingbird records per species in 48 monthly point counts and at least 16 h of focal plant observations.

Table 2. Bimonthly flower density (individuals/m²) of plant species visited by hummingbirds in Homun, Yucatan, Mexico (August 2017–June 2018).

Family	Species	August	October	December	February	April	June	Total
Boraginaceae	<i>Bouyeria pulchra</i>				0.0035			0.0035
Fabaceae	<i>Clitoria</i> sp.			0.0017				0.0017
Euphorbiaceae	<i>Cnidoscolus</i> sp.				0.0017			0.0017
Boraginaceae	<i>Cordia dodecandra</i>					0.0069		0.0069
Acanthaceae	<i>Dicliptera sexangularis</i>				0.0069			0.0069
Rubiaceae	<i>Morinda royoc</i>					0.0087		0.0087
Loranthaceae	<i>Psittacanthus mayanus</i>			0.0017			0.0035	0.0052
Fabaceae	<i>Senna racemosa</i>			0.0035				0.0035

Note. To express densities as individuals per square meter, the sum of flowers was recorded and divided by 96 × 6 m² plots per month.

Table 3. Flower traits of six plant species visited by hummingbirds in Homun, Yucatan, Mexico.

Species	N	Corolla length (mm)	Corolla width (mm)	Nectar volume (mL)	Sucrose cc (g/L)
<i>Bouyeria pulchra</i>	2	9.105 ± 0.94	5.17 ± 0.382	0.01 ± 0	0 ± 0
<i>Cnidoscolus</i> sp.	1	5.48 ^a	1.43 ^a	0 ^a	–
<i>Cordia dodecandra</i>	7	34.88 ± 2.266	4.441 ± 0.448	1.098 ± 0.673	184.2 ± 82
<i>Dicliptera sexangularis</i>	5	15.94 ± 1.424	1.662 ± 0.448	0.002 ^a	216.6 ^a
<i>Morinda royoc</i>	10	5.781 ± 0.772	1.433 ± 0.221	0.007 ± 0.004	31.48 ± 102
<i>Senna racemosa</i>	5	11.94 ± 1.879	1.384 ± 0.193	1.09 ± 2.431	145.7 ± 206

Note. Values given are the mean ± 1 standard error.

^aStandard error not shown because measurements were taken from a single flower. – data not obtained.

C. dodecandra was the most specialized (*d'*, Table 4), forming a notable module with *A. rutila* (Figure 3). *Senna racemosa* and *P. mayanus* tied for the largest values of normalized degrees, closeness and betweenness (Table 4).

In our extinction simulation, we found that if the most connected hummingbirds are removed sequentially from the network, the system would collapse more quickly (*R* = 0.566, Figure 4A) than if the most connected plants were removed (*R* = 0.754, Figure 4B).

Finally, we recorded that monthly precipitation was negatively related to monthly number of paired interactions (*r* = −0.84, *n* = 4, *P* = 0.04).

Discussion

Our results suggest that the Homun network is small and highly connected. We also found that the structure of

this network shows seasonal differences probably driven by water availability (see below).

The lowland dry forest in Homun, Yucatan, has few species of hummingbirds and plants; in hummingbirds we detected three of the eight species that are reported to occur in Yucatan (sensu Howell & Webb, 1995; Johnsgard, 1997; Williamson, 2001). Hummingbirds are often rare in this area; for example Santamaría-Rivero et al. (2013) excluded them from their study in this region because they had very few records. Though there are records of hummingbirds in other localities in Yucatan (CONANP, 2007; MacKinnon, 2005), they are from more humid vegetation types in northern and southern Yucatan (e.g. Medina-van Berkum et al., 2016; Ortega-Pimienta, 2014; Ortiz-Pulido et al., 2002; Puch-Chavez, 2012; Santamaría-Rivero et al., 2013). With respect to plant species, the Homun dry forest has fewer species than more humid sites

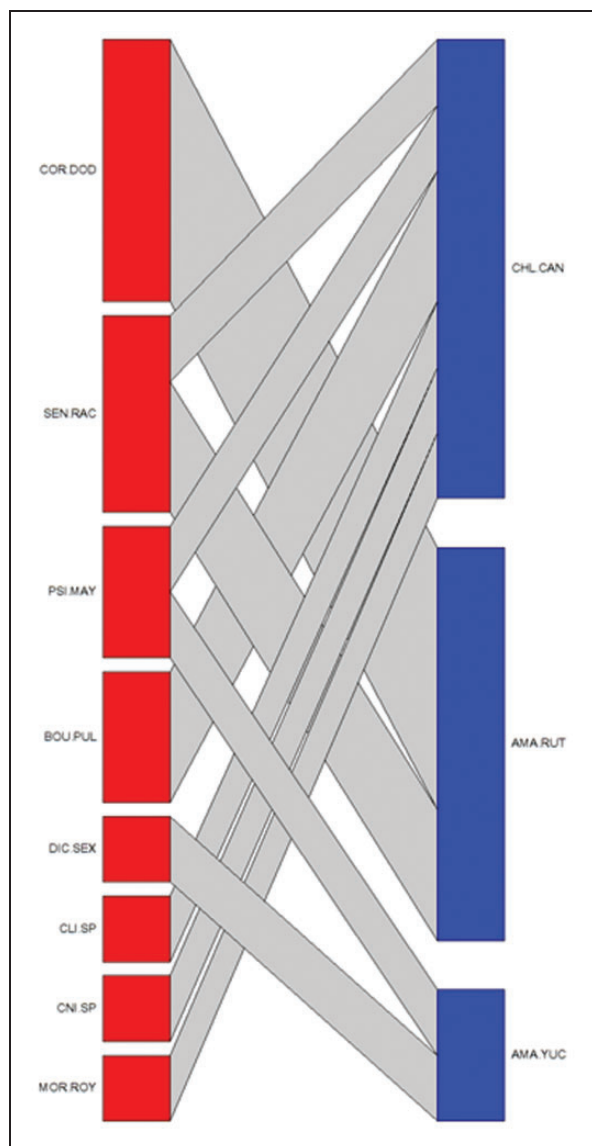


Figure 2. Hummingbird-Plant Interaction Network in Homun, Yucatan, Mexico, Recorded From August 2017 to June 2018. Plants are in red and hummingbirds are in blue.

(Lara-Rodríguez et al., 2012). Unfortunately, there is no way to compare the hummingbird and plant richness with other contiguous Yucatan sites, since this kind of information is lacking in other lowland dry forest sites in the region.

We detected one core hummingbird species in the hummingbird-plant network of the dry forest of Homun, *C. canivetii*. This is the first time to our knowledge that *C. canivetii* has been reported as a core species in a hummingbird-plant network. However, that could be due to a lack of studies using a network focus, because this is the most common hummingbird on the central Veracruz coast of Mexico, where it occupies a wide array of natural and disturbed habitats and is

common year-round at a range of elevations (Ortiz-Pulido & Díaz, 2001). In other tropical dry forests, *C. canivetii* is known to visit flowers of at least seven or eight species of plants (none of them in Homun) (Arizmendi & Ornelas, 1990; Wolf, 1970).

Contrary to what has been reported elsewhere (Martín González et al., 2015), the hummingbird core species was not the competitively dominant species. It is possible that in small and strongly seasonal systems the core species may be the non-territorial and less aggressive species. This may happen in systems with low resource competition, for example, when there are few species and they have low abundances; besides, it helps if the potential core species can visit several plant species, which depends on its behavior and spatial flower availability. In the Homun network, the core species, *C. canivetii*, is not aggressive (Feinsinger et al., 1979), and it is usually a subordinate in other ecosystems (Arizmendi & Ornelas, 1990; Feinsinger, 1976), where it is excluded from clumped flowers by other hummingbirds (Feinsinger & Chaplin, 1975). Johnsgard (1997) considered *C. canivetii* a “wanderer” while Feinsinger and Chaplin (1975) classified the species as a trap-liner; both foraging behaviors were consistent with our observations of the species in Yucatan’s tropical dry forest, despite the occurrence of defendable flower clumps. The fact that there are few hummingbird species in the study site and that they have low abundance probably allows *C. canivetii* to forage without being driven off by other hummingbirds, which in addition to its lack of aggression and traplining behavior, could facilitate its core role.

The other hummingbird species recorded in Homun—*A. rutila* and *A. yucatanensis*—are known for their aggressive behavior (Johnsgard, 1997). However, they visited fewer flowers than *C. canivetii* (Figure 2). Lynch (1992) reported that *A. rutila* in Yucatan preferred coastal scrub to old field habitats, dry forest or pastures, and it is mostly distributed on the coast (Johnsgard, 1997), which could account for the low number of records of this species in our dry forest study site. In a dry forest of Costa Rica, it is highly aggressive towards both conspecifics and other hummingbird species (Wolf, 1970), but in the non-breeding season, territorial behavior is not evident (Stiles & Wolf, 1970). On the other hand, Lynch (1989) mentions that the other species, *A. yucatanensis*, is very frequent among pastures and secondary forest vegetation, which is evident in Veracruz (Ortiz-Pulido & Díaz, 2001). We suggest that the dry forest of Homun could be a marginal habitat for this species, which could explain the low number of records there.

There are three core plant species in our network: *C. dodecandra*, *S. racemosa* and *P. mayanus* (Table 4). *Cordia dodecandra* was visited by *A. rutila* and had the

Table 4. Strength and specialization measurements for species participating in the hummingbird-plant network recorded in Homun, Yucatan, Mexico.

Species	Strength	Specialization d'	Normalized degrees	Closeness	Betweenness
Hummingbirds					
<i>Chlorostilbon canivetii</i>	4.83	0.53	0.75	0.4	1
<i>Amazilia yucatanensis</i>	1.5	0.72	0.25	0.3	0
<i>Amazilia rutila</i>	1.66	0.79	0.25	0.3	0
Plants					
<i>Bourreria pulchra</i>	0.286	0.329	0.333	0.134	0
<i>Clitoria</i> sp.	0.143	0	0.333	0.134	0
<i>Cnidoscolus</i> sp.	0.143	0	0.333	0.134	0
<i>Cordia dodecandra</i>	0.666	0.675	0.333	0.086	0
<i>Dicliptera sexangularis</i>	0.5	0.643	0.333	0.086	0
<i>Morinda royoc</i>	0.143	0	0.333	0.134	0
<i>Psittacanthus mayanus</i>	0.642	0.0645	0.666	0.145	0.5
<i>Senna racemosa</i>	0.476	0.065	0.666	0.145	0.5

highest measure of species strength, but did not have high values in other indexes, such as normalized degrees, closeness, betweenness or specialization, which means that *C. dodecandra* had few paired interactions relative to other plants (Figure 2). Those other metrics were similarly high between *S. racemosa* and *P. mayanus*; even so, *C. dodecandra* is likely the most important core plant species in our network because it had the highest nectar volume (Table 3), and *C. dodecandra* has been reported to be visited by *C. canivetii* in other Yucatan sites (Santamaria in Canché-Collí & Canto, 2014). On the other hand, although *S. racemosa* is adapted to buzz pollination by bees (Marazzi et al., 2007; Marazzi & Endress, 2008), we did observe hummingbirds visiting it in our study site, and it had nearly the same nectar volume as *C. dodecandra* (Table 3). The mistletoe *P. mayanus* flowered more frequently than the other plants (Table 2) and it belongs to a family where all plants are dependent on animal pollinators (Vidal-Russell & Nickrent, 2008), but we did not find literature reports of this species' pollinators.

Other plant species in Homun require more studies in the future. For example, *Dicliptera sexangularis* was dismissed by Austin (1975) as a plant pollinated by the hummingbird *Archilochus colubris*, stating that it could be pollinated by other organisms. However, the species was used by *A. yucatanensis* and had the highest sucrose concentration at our study site (Table 3), thus it could be important for hummingbirds. Given our low sample size for nectar metrics (note in Table 3) we recommend further research on the nectar properties and pollination of *D. sexangularis*. The other plants in the network, *B. pulchra* and *M. royoc*, could not be core species in the Homun network because *B. pulchra* is a cultivated plant that reproduces vegetatively (Campos-Ríos, 2005) and *M. royoc* is ant-pollinated (Percival, 1974). Even though we recorded hummingbirds interacting with

these two species, it is possible that these plants are only an occasional resource for them.

In a conservation context, our analysis suggests that attention should be focused more on hummingbirds than on plants. Our extinction simulation suggests that hummingbird extinctions will have more severe consequences for the network than plant extinctions (Figure 4). This may be because hummingbirds have higher strength and closeness (Table 4) and more paired interactions than plants (Figure 2), because each hummingbird species interacts with more plant species (2.9 on average) than plant species with hummingbird species (1.2; Figure 2), as can be seen in Figure 2. In addition, we detected three modules (Figure 3) that reflect how one hummingbird species interacts with multiple plant species but not vice versa. Thus, on the whole, our results suggest that, if the hummingbirds were the only pollinators, the extinction of a hummingbird species could result in the loss of pollination for multiple plants, but if a plant species were to go extinct, hummingbirds could still consume nectar from other species.

Impact of Seasonality on the Hummingbird-Plant Network

Our results suggest that the Homun hummingbird-plant network is a small network that is influenced by seasonality, functioning from early December to late June, because hummingbirds are forced to forage opportunistically by the lack of flowers in the humid season and the reduced bloom in the dry season. Seasonality is a strong predictor of other pollination networks' structure (Petanidou et al., 2018; Robinson et al., 2018; Takemoto et al., 2014). For example, in a dry forest on Mexico's Pacific coast, 96% of ornithophilous plant species bloomed during the rainy season (Arizmendi & Ornelas, 1990), and a similar pattern was found in

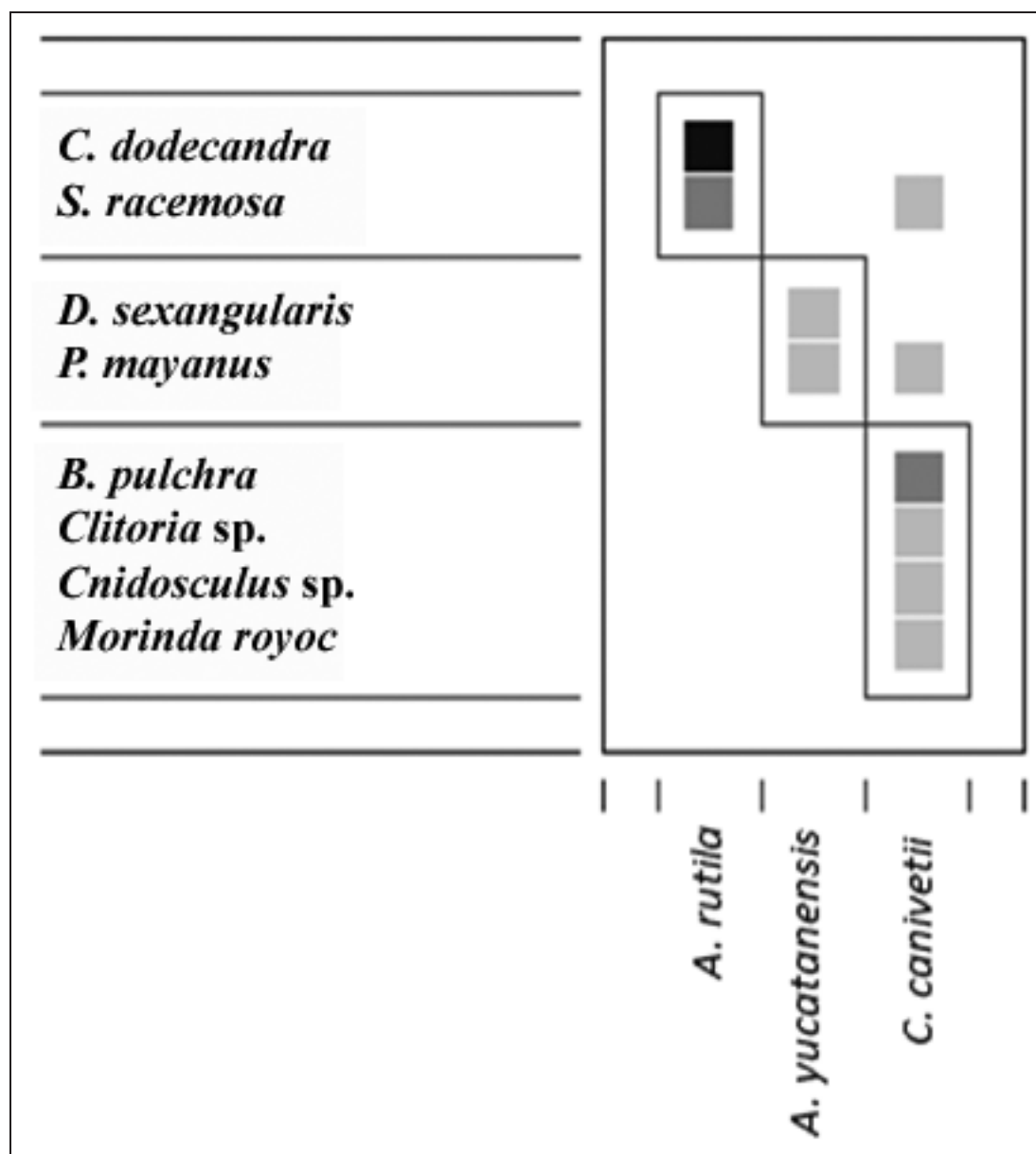


Figure 3. Modules of Plants and Hummingbirds in Homun, Yucatán, Mexico, Recorded From August 2017 to June 2018. Square color represents the intensity of the interaction between each species pair, with darker color indicating more recorded interactions.

Guatemala (Bustamante-Castillo et al., 2020). However, in our study in Homun, we found the opposite. Flowers were absent during the wettest months of the year, August–October. This could depend on plant water storage. In a semi desert located in central Mexico, a similar pattern of flowering during the dry season was reported by Ortiz-Pulido et al. (2012), in which several cactus species were found to store water during the rainy season and use it during the dry season to produce flowers. Something similar could be happening in Homun, as all the plant species visited by hummingbirds bloom during the dry season (Table 2). Future research could help to test this idea. In any case, phenology, in

particular the timing of plant flowering, is a strong driver of the structure of this network, as has been found in other hummingbird-plant networks (Vizentin-Bugoni et al., 2014; Gonzalez & Loiselle, 2016). In other dry forests, hummingbirds are highly affected by the seasonality of dry and wet seasons (Arizmendi & Ornelas, 1990; Wolf, 1970). The strong seasonality in Homun (in this case, flowering during the dry season) may force hummingbirds to visit whatever plants offer floral resources at the time, which could explain the high overall connectance of the network (0.416) compared to other networks (Lara-Rodríguez et al., 2012), and why subnetworks involving four to five species are more

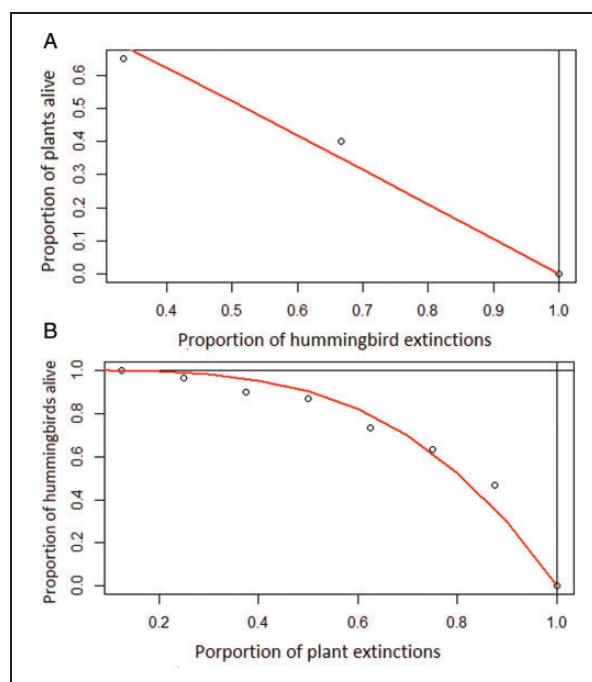


Figure 4. Extinction Curve of (A) Plants in the Case of Hummingbird Extinctions ($R = 0.566$) and (B) Hummingbirds in the Case of Plant Extinctions ($R = 0.754$) in Homun, Yucatan, México. In both cases, the extinctions were simulated in order from most connected to least connected species.

common than those with three species or fewer (Figure 2).

Implications for Conservation

Given the apparent importance of phenology, and in particular, the seasonality of precipitation, this pollination system may be vulnerable to climate change, particularly to changes in rainfall patterns (Nagaishi & Takemoto, 2018). Reduction in water availability due to decreased precipitation and increased evapotranspiration can affect flower production phenology in tropical dry forests, which is known to vary with soil water availability during the dry season (Borchert et al., 2004). This is a plausible future scenario in the Homun area; according to the mean estimation of several climate change models (CNRMCM5, MPI_ESM_LR, GFDL_CM3 and HADGEM2_ES) (Intergovernmental Panel on Climate Change, 2019), Homun could receive between 4% (RCP 4.5) and 5.7% (RCP 8.5) less precipitation in the next 80 years (CONABIO, 2020), and temperature in the Homun region is expected to increase by 1.1 °C–4.2 °C (CONABIO, 2020), resulting in increased evapotranspiration, which in turn is going to affect negatively water availability in the site.

In order to maintain the functionality of this pollination network, we recommend focusing future

conservation actions on the core species, *C. canivetti*, for hummingbirds, and *C. dodecandra*, *S. racemosa* and *P. mayanus*, for plants. We suggest studying the effects of reduced flower production on these mutualist interactions, especially in the context of decreasing water availability in the future. In tropical dry forest, the flowering season has been shown to be determined largely by the timing of the first rains (Borchert et al., 2004). Experimental manipulation in the field in Homun, for example by using irrigation to simulate earlier or later rains could be informative in determining how the flower production of each species relates to the timing of rains, and how this in turn affects relationships with hummingbirds.

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