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Land-Use Change in a Mexican Dry Forest Promotes Species Turnover and Increases Nestedness in Plant-Hummingbird Networks: Are Exotic Plants Taking Over?

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Abstract

Background: Despite the increasing knowledge of plant-pollinator interaction networks, the effects of human-induced disturbances on them have barely been studied. We analyzed whether land-use changes modified the structure and topology of plant-hummingbird interaction networks or promoted the integration of exotic plant species.

Methods: Fieldwork was carried out in two vegetation areas in Mexico: a protected tropical dry forest and nearby disturbed sites. For two years we registered hummingbird-plant interactions monthly in each area. Then, we constructed interaction matrices from these data and compared their assemblage structure.

Results: The conversion of original dry forest to disturbed habitats impacted some assemblage attributes of the plant-hummingbird network. In the disturbed sites, there were more plant species, mainly exotics, and one additional hummingbird species. Most network attributes remained the same except niche width and nestedness (pattern of interactions where generalists and specialists tend to interact with generalists whereas specialist-to-specialist interactions are infrequent), which were higher in the disturbed network. The generalist core in the disturbed network contained half of the core species in the conserved network.

Implications for conservation

Exotic plants that strongly integrated into the disturbed network may exert a large influence on network dynamics in these areas. Identifying the interacting species and their role provides valuable insights for their conservation and protection. Hummingbirds attracting native plant species have a potential for practical or ornamental use, and hummingbirds presence in human-modified landscapes not only provides positive aesthetic value to people but can additionally contribute to conserving native plants and the biodiversity associated with them.

Keywords

hummingbirds, plant-hummingbird networks, spatial dynamics, plant-hummingbird interactions, bird pollination, hummingbird conservation, exotic species

Introduction

Resource availability in a habitat, whether natural or disturbed, can vary both temporally and spatially, promoting complexity in the community structure of the species that exploit the habitat's resources (Pickett & Cadenasso, 1995). Spatial heterogeneity in available resources can also determine species richness (de Souza Júnior et al., 2014) and affect the local or regional abundance of species in addition to the identity and strength

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of biotic interactions (Dupont et al., 2009). Therefore, global anthropogenic changes that affect resource availability such as habitat fragmentation, land-use changes, pollution, pesticide-use, and species invasions can affect plant-pollinator interactions (Aizen & Feinsinger, 1994; Kearns et al., 1998; Memmott et al., 2007; Mitchell et al., 2009). In tropical regions in particular, the conversion of original forests to secondary forests and/or urban, pastures, or croplands severely threatens species diversity. In this context, disturbed habitats are good models for investigating whether biotic communities are able to withstand disturbances or experience changes in their structure and composition as a result (Tylianakis et al., 2007).

With respect to plant-pollinator interactions, some studies have shown that moderate land-use changes increase pollinator richness and abundance (Tscharntke et al., 2008) by increasing habitat heterogeneity and resource availability (e.g., due to the incorporation of exotic plant species) and, in turn, niche diversity (Tews et al., 2004). In this regard, novel habitats originated due to human activities can provide new opportunities for resource exploitation and/or modify the community capacity to respond to perturbation or disturbance. For example, some pollinators that nest in natural habitats also feed in agricultural landscapes (Klein et al., 2003). Likewise, in coastal dunes the resilience of pollination networks is highest at moderate disturbance (Fantinato, 2019). However, higher pollinator diversity in modified habitats may be due to the excessive presence of common species, masking the negative effect on rare species and leading to the large-scale homogenization of species diversity (Winfree et al., 2011).

Despite the increasing knowledge on plant-pollinator interaction networks, the effects of human-induced disturbances have barely been studied (Bascompte & Jordano, 2006). Many biotic interactions are at risk of local or global extinction, yet most studies have only focused on the loss of single species rather than species interactions (Tylianakis et al., 2010). These interactions are highly relevant considering that the topology of interaction networks may affect the response of entire communities to disturbance (Thébault & Fontaine, 2010). Thus, over recent years some studies have begun to consider this aspect (e.g. Carman and Jenkins, 2016; Fantinato, 2019; Taki et al., 2007; Williams et al., 2011) focusing mainly in plant-insect pollination interactions. Some studies have shown that the introduction of exotic plant species does not have a large effect on connectance (the proportion of realized links in plant-pollinator networks), even though native plant species are affected (Aizen et al., 2008). For example, in one study, the properties of a *Heliconia*-invertebrate interaction network were maintained in human-disturbed habitats even

though the species richness, abundance, and composition and the number and quality of host plant species were affected (Benítez-Malvido et al., 2014). Other studies have found that invasive super generalist species become the central nodes (the most connected species) of interaction networks following disturbance, increasing the nestedness (the degree to which interactions of specialized species are subsets of interactions of the more generalist species in the networks) (Aizen et al., 2008; Bartomeus et al., 2008). Therefore, nestedness can be a good parameter for monitoring changes to mutualistic networks in human-modified habitats (Tylianakis et al., 2010).

Many species of hummingbirds (Trochilidae) act as habitat generalists throughout the Americas (Arizmendi & Ornelas, 1990; Feinsinger, 1976) and can be frequently found in forest edges, secondary vegetation, or open areas with abundant flower resources as well as in urban forests, parks, and gardens (Rodrigues & Araujo, 2011; Toledo & Moreira, 2008). However, few studies have examined plant-hummingbird interaction networks in human-modified habitats (Maruyama et al., 2019; Mendonça & Dos Anjos, 2003), and rarely have these studies compared these interaction networks to those of nearby conserved sites. In modified habitats, hummingbirds can use an important number of non-ornithophilous plants (i.e., mainly those pollinated by insects, bats, or other species), probably reflecting the abundance and availability of non-native resources. Such new, circumstantial interactions do not necessarily result from co-evolutionary processes (Mendonça & Dos Anjos, 2005). Given this context, it would be interesting to compare the number and identity of native and exotic plant species used by hummingbirds in order to assess their contribution to the nestedness of their interaction networks (Bascompte & Jordano, 2006, 2007).

Generally, the hummingbird species present in disturbed sites are wide-range generalists, whereas those linked with well-preserved areas are absent from human-modified sites (Mendonça & Dos Anjos, 2005). Some studies have suggested that hummingbird species that prefer non-disturbed sites usually depend and forage on specific plant species, require particular nesting sites, or are less tolerant to the environmental characteristics of modified sites (Lindell et al., 2004; Rodrigues & Rodrigues, 2015). At the same time, the absence of habitat specialists in disturbed sites would likely affect the structure of interaction networks (e.g., node changes, more generalists, etc.).

Given this context, we evaluated herein the hummingbird-plant communities inhabiting two vegetation areas along the west coast of Mexico: a protected native dry forest in the Chamela Biological Station (EBCh) as a reference for comparison, and a disturbed site (outside the protected area) influenced by human

settlements, croplands, and pastures. In both habitats, the plant-hummingbird interaction networks were generated through the inter-annual monitoring of interactions. Specifically, we aimed to assess whether land-use changes modify the structure and topology of the plant-hummingbird interaction networks or promote the integration of exotic plant species. We expected that the network in the modified habitats should experience a turnover of the interacting species: some native species will disappear whilst some new species will be introduced to the network, particularly exotic plant species and hummingbird generalists. Consequently, we expected that this turnover of interacting species would maintain most network parameters, although the incorporation of exotic plant species (specifically as core generalists interacting with the specialist hummingbird species) would increase the nestedness of the disturbed network.

Methods

Study Site

The study sites were distributed in two habitat types: 1) a protected native dry forest in the Chamela-Cuixmala Biosphere Reserve and 2) a disturbed area including secondary vegetation in different successional stages, human settlements, croplands, pastures, and paved and dirt roads.

The conserved sites were located in the conservation area of the Chamela Biological Station (EBCh; 19° 22'–19° 39'N, 104° 56'–105° 10'W; 35 to 120 m.a.s.l.) with an extension of 13,142 hectares. The average annual precipitation is 745 mm but is variable year to year (366–1320 mm) and mainly concentrated during the rainy season from June to October (Bullock, 1986). The dominant vegetation mainly consists of tropical dry forest (TDF) with trees 6 to 12 m tall on average mainly located on slopes with a dense understory. Most plants lose their leaves for 5 to 8 months during the dry season (Lott et al., 1987). Also, along creeks and valleys, tropical semi-deciduous forest (TSDF) is present, with trees taller than 20 m on average but with some individuals up to 25 or 30 m; in this vegetation cover, some trees keep their leaves all year long (Lott et al., 1987; Rzedowski, 2006). The Chamela-Cuixmala dry forest is considered one of the most diverse (\approx 1,100 plant species) in Mexico and possess a high degree of endemism (Banda et al., 2016; Lott et al., 1987).

The disturbed sites were the rural town of San Mateo, 6 km from the EBCh (19° 34'32" N–105° 05'06" W), and the ejido (a communally owned land) La Fortuna, 9 km from the EBCh (19° 59'33" N–105° 12'45" W), both in La Huerta municipality in Jalisco state. The first site has a population of 647 habitants and mainly consists of houses and businesses, with some bare plots and original

vegetation remnants. The second site mainly consists of croplands with watermelon, pepper, and sorghum; papaya, mango, and coconut orchards; and ruderal vegetation with some native trees and plants. Around houses we also observed ornamental vegetation mostly composed of exotic plants.

Plant-Hummingbird Interaction Records

In 2016 (July–December), 2017 (January–December), and 2018 (January–July), we registered the hummingbird-plant interactions in both study areas. We established 78 circular plots (39 in each area) with a 25-m radius at a distance of 200 m from each other (Hutto et al., 1986; Ralph, 1997). At monthly intervals, point counts were performed in each plot for 10 min to record the number and species of hummingbirds feeding on flowering plants. The censuses began around 7:30 a. m. and ended around 1:30 pm. Two individuals started records at different plots and walked in different directions to avoid order effects (Ralph et al., 1995). Binoculars (10 \times 40 mm) and a field guide (Arizmendi & Berlanga, 2014) were used to identify hummingbirds. Plant specimens were identified at the EBCh herbarium. The sampling completeness of the plant-hummingbird interactions recorded in both study areas was determined using the Chao2 estimator in EstimateS version 9.1 (Colwell, 2013) following Chacoff et al. (2012).

Interaction Networks

We pooled together the monthly hummingbird-plant interaction data records from each habitat (conserved and disturbed) and built two adjacency matrices, where a_{ij} = the number of interactions between an individual plant species (i) and an individual hummingbird species (j), with 0 indicating no interaction (Bascompte et al., 2003). From these matrices, we built two plant-hummingbird interaction bipartite networks using the “Bipartite” package in the R software (R Development Core Team, 2019).

To evaluate how the topological properties of the plant-hummingbird mutualistic networks changed in disturbed habitats, we calculated and compared the following metrics: connectance, network specialization, niche overlap, nestedness, and species contribution to nestedness. We chose these metrics because their results can provide an overview of community organization and be compared with previously published studies (e.g., Aizen et al., 2008; Alarcón et al., 2008; Benítez-Malvido et al., 2014; Dáttilo et al., 2013; Tylianakis et al., 2010; Villa-Galaviz et al., 2012). Also, network-level metrics such as nestedness and connectance can be related with emergent properties such as network stability (Tylianakis et al., 2010).

First, connectance was calculated as the proportion of realized links out of all possible ones (Winemiller, 1989). Then, we obtained network specialization (H_2') based on the deviation of species's realized number of interactions from their total expected number of interactions. This parameter ranges from 0 (no specialization) to 1 (perfect specialization). This index is robust to the number of interacting species and to changes in sampling intensity (Blüthgen et al., 2006). Niche overlap for plants and hummingbirds was calculated as the mean similarity in interaction pattern between species of each group according to Horn's index. Values near 0 indicate no common use of niches, 1 indicates perfect niche overlap (Horn, 1966). We assessed the significance of these network metrics comparing our results to the expectations of the r2dtable null model ($N = 1,000$), which maintains the matrix sum and row/column sums constant (Dormann et al., 2008; R Development Core Team, 2019).

To determine significant differences in the structure of the hummingbird-plant networks at both sites (i.e., connectance, specialization and niche overlap), we first obtained the difference between the observed metric in the conserved and the disturbed site. Then, we randomly generated 1,000 matrices using the Patefield algorithm (Patefield, 1981). After this, we calculated the chosen metric for each of the randomly generated matrices and obtained the difference between the 1,000 pairs of matrices. Finally, we plotted the distribution of these values to determine which proportion of these values was smaller than the real (observed) differences. If the observed differences were larger than at least 95% of the differences from the random matrices, we considered them to be significant.

To determine changes in the use of available resources, we calculated the hummingbirds' niche width in both networks according to Shannon's niche breadth index, which measures the diversity of resources used, in the R software using the *spaa* package. Then, we calculated the percentage variance between these two values by subtracting the benchmark number (the niche width value at the conserved site) and dividing the result by the benchmark number. Additionally, to evaluate changes in species roles in network structure at both sites, we classified plant and hummingbird species as either core or periphery using the following formula: $Gc = (k_i - k_{mean}) / \sigma_k$, where k_i = mean number of links for a given plant/hummingbird species, k_{mean} = mean number of links for all plant/hummingbird species in the network, and σ_k = standard deviation from the number of links for a given plant/hummingbird species. $Gc > 1$ are species with a larger number of interactions in relation to other species of the same trophic level and are therefore considered to be part of the generalist core. $Gc < 1$ are species with a lower number of interactions in relation to other

species of the same trophic level and are therefore considered to be periphery species (Dáttilo et al., 2013).

We also calculated the degree of nestedness of each network according to the NODF parameter (Almeida-Neto et al., 2008) in Aninhado 3.0 (Guimarães & Guimarães, 2006). Nestedness describes a pattern in which a core of generalist species interacts with each other, and with extreme specialist species interacting only with generalists. NODF values close to 1 indicate a high degree of nestedness (Bascompte et al., 2003; Guimarães et al., 2007). NODF's significance was estimated using null model 2 (Bascompte et al., 2003), which generates random matrices from the original one. The probability of interaction between any pair of species is calculated proportionally to the total number of interactions (i.e., their degree of interactions). The P value was obtained for the random matrices that had a NODF value equal to or larger than the original matrix.

Finally, we calculated species contribution to nestedness with the *nestedcontribution* function in the Bipartite package. A value larger than 0 indicates a positive contribution to nestedness and a lower value indicates a negative contribution. With this parameter, we identified the proportion of idiosyncratic species (i.e., species with negative values, thus with interaction patterns tending away from a perfectly nested pattern) (Atmar & Patterson, 1993) in addition to the contribution of exotic plant species to network nestedness.

Results

The interaction network of the conserved area consisted of 44 plant species and 6 hummingbird species, with a total of 375 hummingbird visits to plants and 78 unique interactions. The network of the disturbed area consisted of 57 plant species and 7 hummingbird species, with a total of 602 hummingbird visits to plants and 113 unique interactions (Figure 1). Of the 87 plant species visited by hummingbirds (Appendix), only 14 (16%) were shared between the two study areas. In the disturbed area, 30 plant species recorded in the conserved network were absent, yet 43 unique ones were present (mostly exotic species), indicating high species turnover (Figure 2). In the case of hummingbirds (Figure 1), the 7 species recorded throughout the study were present in the disturbed network, but only 6 of these were present in the conserved network. It should also be noted that due to the difficulty of correctly distinguishing females and juveniles of *Archilochus alexandri* and *A. colubris*, we simply treated them as *Archilochus* sp.

We detected only 64.25% of the interactions estimated for the conserved network and 69.42% of those estimated for the disturbed network according to the Chao2 estimator (Figure 3). However, the observed number of

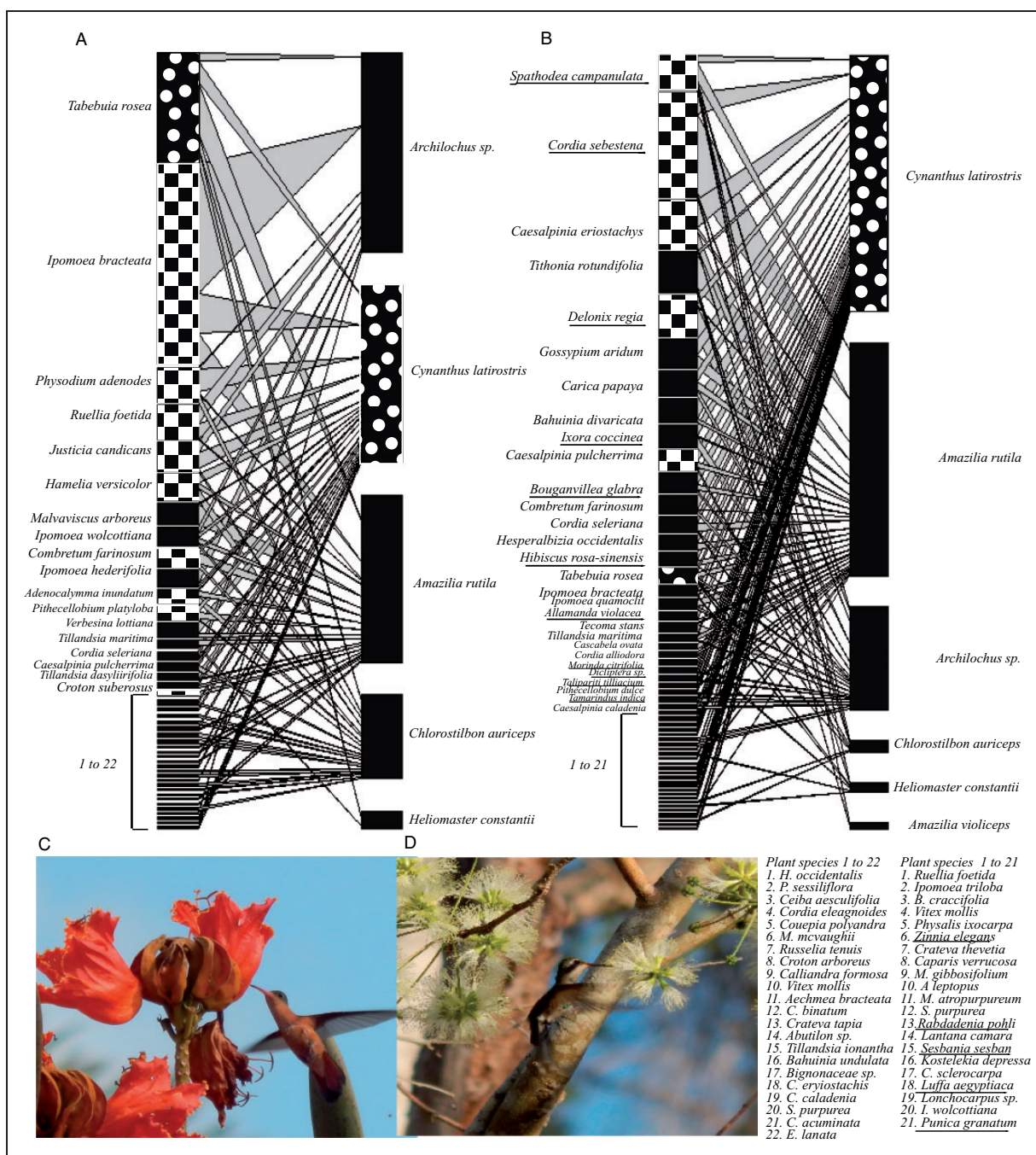


Figure 1. Bipartite Plant-Hummingbird Interaction Networks in the Chamela Region, Mexico. Nodes on the left of each network represent different plant species, and on the right hummingbird species. Chequered nodes represent core species in one habitat; dotted nodes represent core species in both habitats. The thickness of each link (gray lines) indicates the frequency of each pairwise interaction (hummingbird-flower visits). (A) Network from the conserved forest. (B) Network from the disturbed habitats (fields, pastures and rural zones nearby the Chamela preserve; underlined plant species are exotics). (C) *Amazilia rutila* visiting a *Spathodea campanulata* flower, an exotic tree native to Africa. (D) *Chlorostilbon auriceps* (a hummingbird rarely seen in disturbed areas) visiting a native tree. Photographs by Sergio Díaz Infante.

unique interactions appeared to reach an asymptote with respect to our sampling effort.

The identity of the core and periphery species in both networks differed (Figure 1). Only one hummingbird was a core species in both areas: *Cynanthus latirostris*

($G_c = 1.05$ in conserved area and 1.58 in disturbed area). In the conserved network, 10 out of 45 plant species (22.7%) were core species, and in the disturbed network, only 6 out of 57 (10.5%). Only one plant was a core species in both sites: *Tabebuia rosea*.

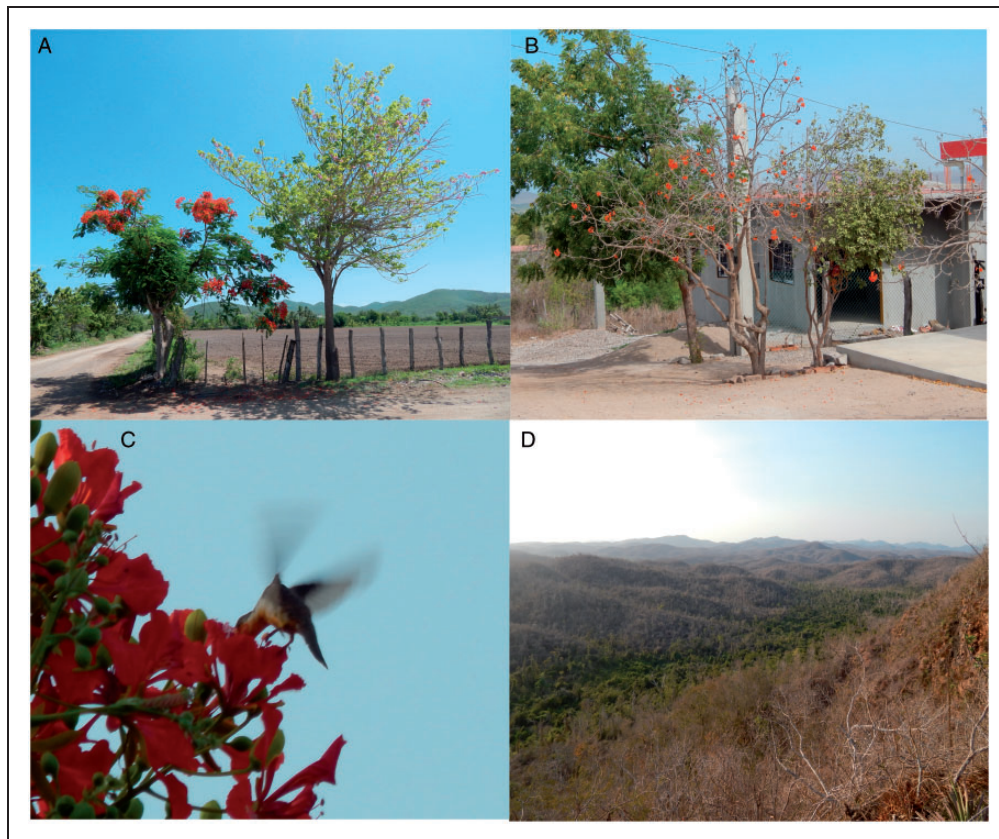


Figure 2. Hummingbird Habitats in the Chamela Region. (A) Two of the tree species whose flowers are visited by hummingbirds in agricultural fields near the Chamela's protected dry forest: *Delonix regia* (left), an exotic tree from Africa, and *Tabebuia rosea* (right) a native tree, and the only core plant species in both habitats (conserved and disturbed). (B) A *Cordia sebestena* tree, another exotic from southern Mexico whose flowers are highly appreciated by hummingbirds around rural towns (C) *Amazilia violiceps*, a very rare and vagrant hummingbird (with a considerable amount of pollen on its belly) visiting *D. regia* flowers. (D) Chamela's Tropical Dry Forest (with greener Tropical Semi-deciduous Forest in valley bottoms).

The interaction network was significantly nested in the disturbed network (58.49, $P < 0.05$). Contrarily, nestedness was not significant in the conserved network (44.6, $P = 0.27$) (Table 1). The disturbed network also had a smaller percentage of idiosyncratic species (14%) compared to the conserved network (42.5%). Of the 43 species that positively contributed to nestedness in the disturbed network, 34.9% were exotic plant species, which comprised 83% of the total number of exotic species.

Table 2 shows the hummingbirds' niche width values. All values were larger in the disturbed network, except for *Chlorostilbon auriceps*, with the largest differences being found for *Helimaster constantii* and *Archilochus* sp. (59.6% and 46.5%, respectively).

Discussion

Local and landscape environmental conditions, as well as plants' spatial aggregation and animal mobility, are important factors that structure plant-animal

interactions (Dáttilo et al., 2013). We found that the conversion of original dry forest to other land uses (croplands, pastures and human settlements) impacted some structural parameters of the plant-hummingbird network. Most differences are associated with the higher number of plant species, mainly exotic species, in the disturbed sites. Also there, one additional hummingbird species (*A. violiceps*) was registered. Most network attributes remained the same, although niche width increased in the disturbed network along with nestedness, which was only significant at the disturbed site. Finally, it is notable that the generalist species core in the conserved network contained twice as many species as the disturbed network.

Species Turnover and Network Parameters

Mutualistic networks are typically characterized by fewer observed than possible interactions (e.g., Chacoff et al., 2012; Gonzalez & Loiselle, 2016), as observed herein. In the present study, most native plant species

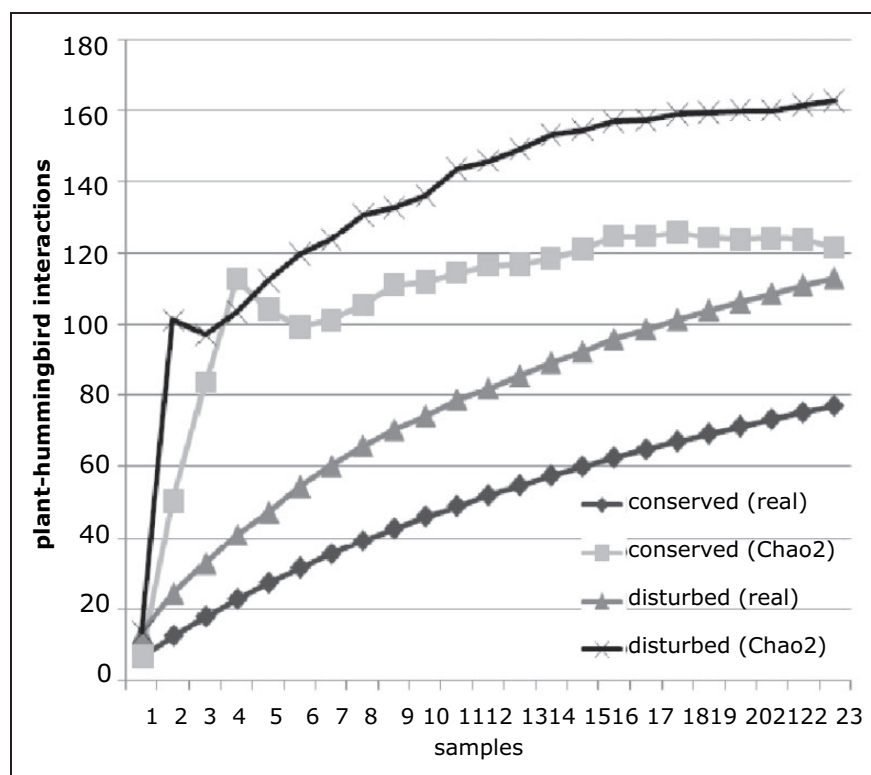


Figure 3. Sampling Completeness of the Plant-Hummingbird Interactions Recorded in Both Habitat Types (Conserved and Disturbed). Graphic shows the real plant-hummingbird interactions accumulated along the study and those estimated with Chao2.

Table 1. Parameters Describing the Plant-Hummingbird Interaction Networks in the Conserved and Disturbed Areas.

Habitat	Conserved	Disturbed
Plant species	44	57
Hummingbird species	5	6
Links	78	113
Connectance	0.35	0.32
Specialization H_2'	0.34	0.35
Hummingbirds' niche overlap	0.40	0.24
Plants' niche overlap	0.35	0.50
Nestedness (NODF)	46.7*	56.6*
Idiosyncratic plants proportion	34.1	15.8
Exotics' contribution to NODF	0.0	43.8

Note. Asterisks (*) indicate significant differences among networks in a specific attribute.

were lost in the disturbed network (68%), and the conserved and disturbed sites only shared a few plant species (16%). Most native plant species remaining in the disturbed network were trees, which besides being present in the conserved area also grow outside the Chamela reserve along roads, in spare lots, or around town. Such countryside habitats may preserve elements necessary for the conservation of some species or, at best,

sustain a moderate fraction of the native biota (Daily et al., 2001) (e.g., *Tabebuia rosea*, *Caesalpinia eryos-tachys*, and *Hesperalbizia occidentalis*).

Hummingbird richness was higher in the disturbed area outside the Chamela reserve, possibly as a result of several factors, including the greater density of floral resources compared to forested areas, and hummingbirds' capacity to explore new available resources provided mainly by the exotic species (Mendonça & Dos Anjos, 2005). Some ornamental plant species, for instance, can bloom all year long (e.g., *Bougainvillea glabra* and *Hibiscus rosa-sinensis*), providing constant, readily available resources that can be used, especially when resources inside the reserve become scarce. Even though standard measures such as species richness and abundance were higher in the disturbed area, these metrics tend to mask important compositional shifts associated with agricultural intensification, as forest-dependent species are often replaced by generalists or disturbance-adapted species (DeClerck et al., 2010).

Overall, the hummingbird community of the Chamela region mostly included generalist species with a wide distribution throughout Mexico. Most of these species are found in dry forests but also in open areas, edges (Arizmendi & Berlanga, 2014), and other human-

Table 2. Niche Width and Its Variation per Hummingbird Species in the Conserved and Disturbed Areas.

Species	Habitat	<i>A. rutila</i>	<i>C. latirostris</i>	<i>C. auriceps</i>	<i>H. constantii</i>	<i>Archilochus</i> sp.	<i>A. violiceps</i>
Conserved		2.34	2.66	2.73	0.50	1.30	NA
Disturbed		2.52	3.35	2.01	1.83	2.45	0.63
Variation		7.1%	20.6%	26.4%*	72.7%	46.9%	NA

Note. Variation values in bold indicate a larger than 5% increase; asterisks (*) a larger than 5% decrease

modified landscapes, such as gardens and urban tree-scapes. Typically, moderate urban development increases ornamental vegetation, water sources, primary productivity, and the amount of edge between habitats (Mooney & Gulmon, 1983; Whitney & Adams, 1980). Because bird abundance and distribution are associated with resource availability, changes in resources influence the presence of individual hummingbird species and the hummingbird community as a whole. Resident hummingbird species such as *Cynanthus latirostris* and *Amazilia rutila* are perfectly adapted to and very common in human settlements (del Olmo, 2007; Des Granges, 1979). These species might be considered “urban exploiters” or species adept at exploiting urban habitats and, consequently, may reach their highest densities in these sites (Blair, 1996).

Other hummingbird species such as *Archilochus* spp. can use a wide variety of habitats along their migratory routes and are commonly linked with disturbed areas (Arizmendi & Berlanga, 2014; Finch, 1991; Udvardy & Farrand, 1994). These “suburban adaptable” species can exploit resources characteristic of moderate levels of urban development, such as ornamental vegetation (Blair, 1996).

On the other hand, *H. constantii* had a low abundance in both study sites. This species is highly insectivorous, and its presence is usually linked with abundant plant resources (Arizmendi & Ornelas, 1990; Des Granges, 1979), such as *Tabebuia rosea*. Meanwhile, *A. violiceps* is a wanderer and altitudinal migrant (Des Granges, 1979; Lopez-Segoviano, 2018) that is very rare in the area (Arizmendi & Ornelas, 1990); however, it may be present in disturbed areas when exotic tree species with broad floral displays such as *Spathodea campanulata* or *Delonix regia* are in bloom. Overall, all hummingbird species responded positively to the higher number of plant species in the disturbed sites, widening their niche. The only exception was *Chlorostilbon auriceps*, which did not seem to benefit from the extra resources in the disturbed sites, as evidenced by its reduced niche width and more common occurrence inside the conserved forest. This “urban avoider” species can be particularly sensitive to human-induced changes in the landscape and, consequently, reaches its highest densities in the most natural sites (Blair, 1996). In Brazil, hummingbird communities in natural areas were categorized

according to their varying preferences for open savannah, forest habitats (Maruyama et al., 2014), and even urban areas (Maruyama et al., 2019). Something similar occurs with *C. auriceps*: This species seems to prefer forest habitats and is less commonly found in open, human-modified landscapes. Accordingly, it is likely more vulnerable to habitat loss, which can highlight the importance of maintaining natural areas such as the Chamela-Cuixmala Biosphere Reserve and other conserved dry forests.

Spatial differences in the number and identity of species forming interaction networks have been previously reported. For example, according to Hagen and Kraemer (2010), the species richness and abundance of plant and bee communities and their mutualistic flower-visitor networks strongly differed between structurally diverse farmland habitats and the neighboring forest understory in Western Kenya. Specifically, the largest networks, diversity, and abundance of bees and plants were found at the forest edge and in farmlands (i.e., disturbed sites). According to Villa-Galaviz et al. (2012), the plant-herbivore network in the Chamela area in Mexico showed high resilience: Differences were only found in recently abandoned fields, as most network descriptors of secondary and mature forest did not differ. Also, no significant nestedness or modularity in the network structure was found. Plant-herbivore network properties appear to quickly reestablish after disturbance despite changes to species richness and composition. Dáttilo et al. (2013) showed that, although the ant and plant composition of networks changed spatially following disturbance, the central core of generalist species and network structure remained unaltered over a geographic distance up to 5,099 m in the southern Brazilian Amazonia. Meanwhile, Benítez-Malvido et al. (2014) assessed the topological structure of individual *Heliconia*–invertebrate networks in Chiapas, Mexico, and found that *H. collinsiana* richness was greater in riparian vegetation and that no differences existed in the diversity of the invertebrates associated with particular *Heliconia* species and habitats. Invertebrate abundance was, however, greater on *H. latispatha* in gaps and on *H. collinsiana* in riparian vegetation, indicating species turnover in human-disturbed habitats. Therefore, *Heliconia*–invertebrate network properties appear to be maintained in human-disturbed habitats despite

differences in species richness, abundance, and composition and host number and quality. Finally, Tinoco et al. (2017) analyzed the similarity of hummingbird species in three Andean valleys in Ecuador and found, on average, a hummingbird species turnover of 33% between networks.

Integration of Exotic Plant Species Into the Network

In the disturbed network, around 40% of plant species were exotic (22 spp.), a smaller percentage in comparison to other hummingbird studies in human-modified landscapes. For example, Mendonça and Dos Anjos (2005) reported that 60% of species were exotic (22 spp.) in the University of Parana, Brazil, including some species in common with the present study such as *Hibiscus rosa-sinensis* and *Spathodea campanulata*. Marcon (2016) also reported 61% of plant species as exotic in another disturbed habitat in the south of Brazil. However, most studies on hummingbird-plant interactions in disturbed landscapes do not specify whether the plant species visited by hummingbirds are natives or exotics. In one review, Maruyama et al. (2016) found that only around 8% of plants in hummingbird networks were exotic, but this review mostly included studies in conserved areas where exotic plants are not common. This highlights the need to continue to study hummingbird-plant networks in disturbed areas and to explicitly identify whether plants are native or exotic. A global data set study that explored the integration of exotic plants into plant-insect pollination networks showed that these networks are characterized by greater total, plant and pollinator richness, as well as higher values of relative nestedness (Stouffer et al., 2014).

Some important changes in the core plant species were also noted. The number of core plant species in the disturbed site was half of the conserved network even though there were more species at the disturbed site. The plant species lost from the generalist core seemed to be forest-dependent, and they were core generalist because of their varied interactions with hummingbirds but not necessarily because of their ability to grow everywhere. Also, when some exotic species become increasingly abundant and/or increase their interaction strength, they increase their chance of interacting with a large number of partners sequestering interaction frequency and links from the original network (Aizen et al., 2008). Thus, this augmented strength of invasive plants may result not only from its high density, but also from the tendency of these species to produce exuberant flower displays and offer superabundant flower resources (Chittka & Schürkens, 2001). Therefore, these exotic plants become network hubs (super generalist species) occupying a central role in the community (Bartomeus et al., 2008), and making it

more difficult for other plant species to become core species.

Also, whereas inside the forest only two of the core species were trees (20%), in the disturbed area, five out of six core species (83%) were trees. This agrees with prior hummingbird studies in natural areas where pollinators are rarely associated with trees and more commonly associated with herbs and shrubs (Arizmendi & Ornelas, 1990; Buzato et al., 2000; Stiles, 1978). Even though trees were less important in the conserved forest, the only core plant shared between the sites was the tree *Tabebuia rosea*. Therefore, this tree species contributes toward conserving pollinators in both locations and should be considered in reforestation programs, as part of live fences/corridors in agricultural areas, or as an ornamental/shade tree in rural or urban zones.

In the conserved sites, most exotic plant species were trees (11 spp.). Of these, *Spathodea campanulata*, *Delonix regia*, and *Cordia sebestena* were also among the five most visited plant species in the disturbed sites, garnering almost 30% of hummingbird visits and the last one being the most visited of all plants. In Brazil, trees were found to be more important than other growth forms for the maintenance of hummingbirds in urban settings because they can provide high amounts of nectar (Maruyama et al., 2019). However, besides attracting hummingbirds (de Andrade et al., 2007; Martínez, 2008; Mendonça & Dos Anjos, 2005; Percival, 1974; Rangaiah et al., 2004) it has been reported in other countries that these tree species attract several other flower visitors such as non hovering birds (Banks, 1997; Dalsgaard et al., 2016; Du Puy et al., 1995; Faegri & Van Der Pijl, 2013; Gentry, 1974; Maruyama et al., 2019), bees (Fohouo et al., 2011), butterflies (Cruden & Jensen, 1979; Percival, 1974), and even mammals such as bats (Ayensu, 1974) and lemurs (Sussman & Raven, 1978) in the case of *S. campanulata*. Thus, Old World plants with adaptations to bird pollination, such as *S. campanulata* and *D. regia*, can more easily integrate into plant-hummingbird interaction networks in the Americas, or at least more so than alien plant species without bird pollination (Maruyama et al., 2016). Thus, some shared traits associated with hummingbird pollination such as odorless flowers with bright colors, copious and diluted amounts of nectar, and exerted anthers, are favored (Banks, 1997; Gentry, 1974) (e.g. Caribbean native tree *C. sebestena* (Askins et al., 1987; Johnston, 1949).

In addition to the exotic species *Spathodea campanulata*, *Delonix regia*, and *Cordia sebestena* representing one-half of the core species in the disturbed network, overall, exotic plant species in this network received about one-third of all hummingbird visits, making them important resources. Maruyama (2016) stated than an average alien plant is more important for

hummingbirds than an average native plant in terms of relative interaction frequency. There is also a tendency for alien plants to have more partners and for some hummingbird species to interact more exclusively with these plants than natives. In the present study, exotic plants played a key role in the disturbed area and strongly integrated into the plant-hummingbird network. Nestedness was only significant outside the reserve, where the exotic plants' contribution to nestedness was more than double. According to Maruyama et al. (2016), exotic plants have more partners, and hummingbirds show greater dependency on them than on average native plant species (e.g., *A. rutila* with *C. sebestena* and *D. regia*). Thus, exotic plants are important and act as core generalists in disturbed networks (Aizen et al., 2008; Bartomeus et al., 2008; Stouffer et al., 2014; Vila et al., 2009).

Maruyama et al. (2016) also suggest that other plant traits, such as a different flowering phenology with respect to native plants or higher nectar secretion rates, could be important factors that explain the integration of exotic species in these networks (see Chittka & Schürkens, 2001; Godoy et al., 2009). By acting as core generalist species in these networks, exotic plants may impact the entire plant-pollinator network (Traveset et al., 2013) and even modify its eco-evolutionary dynamics (Guimarães et al., 2011). Although exotic plants represent important food resources for hummingbirds in disturbed areas, they could also have negative effects. They may usurp pollinators and reduce visitation to nearby native plants (Bartomeus et al., 2008; Cunningham-Minnick et al., 2020). Thus, a different experimental approach will be helpful to elucidate if hummingbirds (or other pollinators) do prefer exotics over native plant species. Likewise, disturbed habitats may act as ecological traps for hummingbirds if, for example, they prefer to nest at sites where egg and/or nestling survivorship shrinks due to higher exposure to predators (Battin, 2004). Alternatively, floral displays of exotic plants may facilitate or increase the pollination success in adjacent plants by attracting more pollinators to the area (Bartomeus et al., 2008; Cunningham-Minnick et al., 2020). Given this, patches of disturbed habitat may enhance landscape heterogeneity, providing complementary resources to the native remnants (Fonturbel et al., 2017) or provide complementary resources when they are scarce at the conserved areas (Bartomeus et al., 2008).

As a consequence of land-use changes, an increasing number of native species are being "forced" to inhabit human-modified landscapes composed of a mosaic of natural and anthropic land covers (Galán-Acedo et al., 2019). Unfortunately, for many of these species, studies have mostly focused on their ecology within their

primary habitat, especially in protected areas, thus limiting our understanding of their use of and tolerance to human-modified landscapes (Galán-Acedo et al., 2019). Therefore, the continued study of these species and their interactions in both natural and modified landscapes is important.

Implications for Conservation

The number and identity of interacting species in the hummingbird-plant network of a dry forest in Chamela, Mexico, changed in nearby human-modified landscapes. Change was primarily observed in the plant community where many native species were lost in the disturbed site and many exotics were introduced. In the case of hummingbirds, an additional species (*Amazilia violiceps*) was recorded. Overall, most network structure parameters remained unchanged, with the exception of nestedness and niche width, which increased. Exotic plants were strongly integrated in the plant-hummingbird networks in the disturbed area and, thus, may have a significant influence on network dynamics in these adjacent rural towns and agricultural areas. Finally, *Tabebuia rosea* was identified as an important plant species for conserving the plant-hummingbird interaction network in the Chamela region. The spatial perspective of this study provides unique insights into the effects of some land use changes in plant-hummingbird networks in areas close to the conserved dry forest.

Aside the scientific value of understanding species interactions in natural and human-modified landscapes, identifying the interacting species and their role in the interaction networks can provide valuable insights for their conservation and protection. For example, besides its ecological value in maintaining interaction networks, native plants can also have an ornamental use in private or public gardens. Native plants are easier to maintain, generally require less water than exotic and cultivated plant species, and often possess beautiful flowers and foliage (Kruckeberg, 2001). Moreover, native plants can sustain a greater abundance and diversity including birds and butterflies in managed landscapes (Burghardt et al., 2009). Having a hummingbird garden can be a way to conserve both birds and native plants in human modified habitats. Managing the landscape to be more hospitable to pollinators in general has the potential to mitigate the negative impact of habitat loss and fragmentation (Dicks et al., 2016). Some examples of hummingbird-attracting native plant species from the Chamela area with this potential are: *Ipomoea bracteata*, *Physodium adenodes*, *Ruellia foetida*, *Justicia candicans* and *Hamelia versicolor*. Trees are also integral to the environmental quality of cities and towns around the world (Bolund & Hunhammar, 1999). They are

important components of the modified landscapes of the Chamela area providing shade to humans and cattle, helping to maintain higher moisture levels and lower temperatures (Livesley et al., 2016), and providing floral resources to bees, hummingbirds and other pollinators. In agricultural areas, trees such as *Caesalpinia eryostachys*, *Tabebuia rosea*, *Gossypium aridum* and *Hesperalbizia occidentalis* can also be used as live fences while, during blooming season, they also provide beautiful sights. Green corridors could also be maintained in these areas including small trees such as *Bahinia unguolata* and *Cordia sekeriana* or herbs such as *Tithonia rotundifolia* with its ornamental and ecological value. Since hummingbirds also contribute to pollination, attracting them to these areas can be of benefit to domesticated crops such as papaya (*Carica papaya*), tamarind (*Tamarindus indicus*) and green tomatoes (*Physalis ixocarpa*). Finally, the presence of hummingbirds in human-modified, landscapes not only provides positive aesthetic value to people, but can additionally contribute to conserving native plants and the biodiversity associated with them.

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Appendix. Plants Visited by Hummingbirds in Conserved and Disturbed Areas

Family	Plant species	Conserved	Disturbed	Growth form
Acanthaceae	<i>Dicliptera</i> sp.		x	Shrub
	<i>Justicia candicans</i>	x		Shrub
	<i>Mexacanthus mcvaughii</i>	x		Vine
	<i>Ruellia foetida</i>	x	x	Shrub
	<i>Thunbergia grandiflora</i>		x	Vine
Anacardiaceae	<i>Mangifera indica</i>		x	Tree
	<i>Spondias purpurea</i>	x	x	Tree
Apocynaceae	<i>Allamanda violacea</i>		x	Shrub
	<i>Cascabela ovata</i>	x	x	Tree
	<i>Crateva thevetia</i>		x	Tree
	<i>Mandevilla sanderi</i>		x	Vine
	<i>Rhabdadenia pohlii</i>		x	Vine
Arecaceae	<i>Dypsis lutescens</i>		x	Tree
Asteraceae	<i>Tithonia rotundifolia</i>		x	Herb
	<i>Verbesina lottiana</i>	x		Herb
	<i>Zinnia elegans</i>		x	Herb
Bignoniaceae	<i>Adenocalymma inundatum</i>	x		Vine
	<i>Bignoniaceae</i>	x		Vine
	<i>Clytostoma binatum</i>	x		Vine
	<i>Spathodea campanulata</i>		x	Tree
	<i>Tabebuia rosea</i>	x	x	Tree
Boraginaceae	<i>Tecoma stans</i>		x	Tree
	<i>Cordia alliodora</i>		x	Tree
	<i>Cordia eleagnoides</i>	x		Tree
	<i>Cordia sebestena</i>		x	Tree
	<i>Cordia seleriana</i>	x	x	Tree
Bromeliaceae	<i>Aechmea bracteata</i>	x		Epiphyte
	<i>Tillandsia bartrami</i>	x		Epiphyte
	<i>Tillandsia dasyliirifolia</i>	x		Epiphyte
	<i>Tillandsia ionantha</i>	x		Epiphyte
	<i>Tillandsia maritima</i>	x	x	Epiphyte
	<i>Tillandsia paucifolia</i>	x		Epiphyte
Cactaceae	<i>Nopalea karwinskiana</i>		x	Shrub
Capparaceae	<i>Capparis verrucosa</i>		x	Tree
	<i>Capparis indica</i>	x		Tree
	<i>Crateva tapia</i>	x		Tree
Caricaceae	<i>Carica papaya</i>		x	Tree
Chrysobalanaceae	<i>Couepia polyandra</i>	x		Tree
Combretaceae	<i>Combretum farinosum</i>	x	x	Vine
Convolvulaceae	<i>Ipomoea bracteata</i>	x	x	Vine
	<i>Ipomoea hederifolia</i>	x		Vine
	<i>Ipomoea quamoclit</i>		x	Vine
	<i>Ipomoea triloba</i>		x	Vine
	<i>Ipomoea wolcottiana</i>	x	x	Tree
Cucurbitacea	<i>Luffa aegyptiaca</i>		x	Vine
Euphorbiaceae	<i>Croton arboreus</i>	x		Tree
	<i>Croton suberosus</i>	x		Shrub
	<i>Jatropha multifida</i>		x	Shrub
Fabaceae	<i>Pithecellobium platyloba</i>	x		Vine
	<i>Bauhinia divaricata</i>		x	Tree
	<i>Bauhinia unguolata</i>	x		Tree
	<i>Caesalpinia caladenia</i>	x	x	Tree
	<i>Caesalpinia eriostachys</i>	x	x	Tree

(continued)

Continued.

Family	Plant species	Conserved	Disturbed	Growth form
	<i>Caesalpinia pulcherrima</i>	x	x	Tree
	<i>Caesalpinia sclerocarpa</i>		x	Tree
	<i>Canavalia acuminata</i>	x		Vine
	<u><i>Delonix regia</i></u>		x	Tree
	<i>Erythrina lanata</i>	x		Tree
	<i>Macroptilium gibbosifolium</i>		x	Vine
	<i>Hesperalbizia occidentalis</i>	x	x	Tree
	<i>Lonchocarpus</i> sp.		x	Tree
	<i>Macroptilium atropurpureum</i>		x	Vine
	<i>Calliandra formosa</i>	x		Shrub
	<i>Pithecellobium dulce</i>		x	Tree
	<u><i>Sesbania sesban</i></u>		x	Tree
	<u><i>Tamarindus indica</i></u>		x	Tree
Lythraceae	<u><i>Punica granatum</i></u>		x	Tree
Malpigiaceae	<i>Birsonima crassifolia</i>		x	Tree
Malvaceae	<i>Abutilon mcvaughii</i>	x		Shrub
	<i>Ceiba aesculifolia</i>	x		Tree
	<i>Gossypium aridum</i>		x	Tree
	<u><i>Hibiscus rosa-sinensis</i></u>		x	Shrub
	<i>Kosteletzkia depresa</i>		x	Shrub
	<i>Malvaviscus arboreus</i>	x		Shrub
	<u><i>Talipariti tiliaceum</i></u>		x	Tree
Moringaceae	<i>Moringa oleifera</i>		x	Tree
Nyctaginaceae	<u><i>Bougainvillea glabra</i></u>		x	Shrub
Polygonaceae	<i>Antigonon leptopus</i>		x	Vine
Rubiaceae	<i>Hamelia versicolor</i>	x		Shrub
	<u><i>Ixora coccinea</i></u>		x	Shrub
	<u><i>Morinda citrifolia</i></u>		x	Tree
Sapindaceae	<i>Paullinia sessiliflora</i>	x		Vine
Scrophulariaceae	<i>Russelia tenuis</i>	x		Herb
Solanaceae	<i>Physalis ixocarpa</i>		x	Herb
Sterculiaceae	<i>Physodium adenodes</i>	x		Shrub
Verbenaceae	<i>Lantana camara</i>		x	Shrub
	<i>Vitex mollis</i>	x	x	Tree

Note. Species in bold were registered inside and outside the reserve. Exotic plant species are underlined.