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Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082918793303

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Tropical Conservation Science
Volume 11: 1–15
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Hummingbird Diversity and Assemblage Composition in a Disturbed Tropical Dry Forest of Guatemala

Michelle Bustamante-Castillo[1,2], Blanca Estela Hernández-Baños[3], and María del Coro Arizmendi[4]

Abstract

Central American dry forest has experienced high rates of deforestation and intense human-induced disturbance. As a consequence, the remaining forests exist almost entirely as small, degraded, and isolated fragments. Until now, the effect of anthropogenic disturbance on the diversity of Central American tropical dry forest is largely unexplored, making it difficult to understand the consequences for plant and animal communities and the provision of ecological services. Here, we address the impact of small-scale anthropogenic disturbance on local richness and abundance of hummingbirds in a dry forest of Guatemala. To do this, we established 15 point counts on nine transects located within patches of dry forest with different levels of human-induced disturbance. Visits to each site were done twice during the dry season and twice during the rainy season. We found differences in overall number of hummingbird registered between the dry and the wet seasons; we registered higher number of hummingbirds at the end of the wet season and beginning of the dry season, when the availability of flowers was higher. These data suggest that seasonal resource variation could be an important factor influencing the variation in the number of hummingbird present at our study area. Our results also showed resilience of hummingbirds to different levels of disturbance probably related to the generalist behavior of the dominant resident species and the availability of food resources for hummingbirds at different levels of disturbance.

Keywords

dry forest conservation, flower availability, anthropogenic disturbance, hummingbird abundance, Motagua valley, seasonality

Introduction

Anthropogenic disturbance is one of the most important threats to global bird biodiversity (Rapoport, 1993). Some studies have found that sites with less human disturbance maintain greater bird species richness and abundance (Kang, Minor, Park, & Lee, 2015; McKinney, Kick, & Fulkerson, 2010; Ntongani & Samora, 2013; Sarafadin & Oyoo-Okoth, 2016) and support more rare bird species (Fontúrbel et al., 2015; Sarafadin & Oyoo-Okoth, 2016). In disturbed landscapes, bird species richness and abundance usually decline as land use intensity increases (Elsen, Ramnarayan, Rames, & Wilcove, 2016). At more urban landscapes, anthropogenic disturbance causes lower bird densities, primarily due to simplification of vegetation structure and loss of vegetation cover (Aronson et al., 2014). Even bird flock quality (species richness, size in individuals, encounter rate, and even network characteristics) and structure have been observed to decrease as intensity of land degradation occurs a result of selective logging, agriculture, livestock grazing, our firewood collection

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Received 9 April 2018; Revised 8 July 2018; Accepted 12 July 2018

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(Goodale & Kotagama, 2005). Nonetheless, the effects of anthropogenic disturbance on bird diversity depend on several factors, including level and type of disturbance (Blair, 1996; Fontúrbel et al., 2015; Zamorano-Elgueta et al., 2014), species-specific responses (Verhulst, Báldi, & Kleijn, 2004), the characteristics of the surrounding matrix (McWethy, Hansen, & Verschuyl, 2009), among other factors. For example, long-term human disturbance may favor generalist species, capable of surviving in a wide range of environmental conditions (Chace & Walsh, 2006; Olden, Poff, Douglas, Douglas, & Fausch, 2004; Sanaphre-Villanueva et al., 2017; Sekercioglu et al., 2002). In contrast, many forest specialist species can be negatively affected by forest disturbance, and insectivorous birds can disappear from heavily transformed forests (Canaday, 1997; Chace & Walsh, 2006; Fernández-Juricic, 2004; Sekercioglu et al., 2002).

Historically, Central American dry forest has experienced high rates of deforestation (Bray, 2010), mostly due to frequent conversion to agricultural fields and pastures (Chazdon et al., 2011; Janzen, 1986; Maass, 1995; Tucker, Munroe, Nagendra, & Southworth, 2005); further disturbance has occurred due to timber and firewood extraction, selective logging, and human settlement development (Chazdon et al., 2011). As a consequence, the remaining forests exist almost entirely as small, isolated fragments (Sabogal, 1992; Sanchez-Azofeifa et al., 2005) with different degrees of human-induced disturbance. Notably, the impact of anthropogenic disturbance on the diversity of Central American tropical dry forest is largely unexplored, and research is needed to understand the consequences for plant and animal communities and the provision of ecological services (Chazdon et al., 2011). This type of studies is also needed to improve our knowledge of the overall dynamics of dry forest ecosystem to develop adequate strategies for its conservation and restoration

To assess the impact of anthropogenic disturbance on biodiversity, it is important to understand the response of organisms that provide essential ecosystem services, such as pollination (Kambach, Guerra, Beck, Hensen, & Schleuning, 2013). Pollination is especially important for ecosystem functioning, as it directly affects the survival and fitness of plant populations that form the basis of terrestrial ecosystems (Kearns, Inouye, & Waser, 1998). In consequence, the persistence, composition, and abundance of pollinators can be indicators of ecosystem health in human-altered landscapes (Abrol, 2012). In the new world tropical dry forests, hummingbirds contribute to the pollination of a variety of flowering plants (Arizmendi & Ornelas, 1990; Ortiz-Pulido, Díaz, Valle-Diáz, & Fisher, 2012), and in some areas, a high percentage of these plants are specialized for pollination by this group (Cardoso & Sazima, 2003; Machado & Lopez, 2004). Even though hummingbirds in general tend to be less affected by habitat loss and fragmentation compared with other bird guilds like insectivorous birds, there is evidence that hummingbird species richness decreases with the decreasing size of forest fragments and that the abundance of interior forest hummingbird species is lower in fragments compared with contiguous areas of forest (Borgella, Snow, & Gavin, 2001). Moreover, several studies have shown that hummingbird diversity is influenced by changes in habitat conditions and the diversity and distribution of food resources (Corcuera & Zavala-Hurtado, 2006; Cotton, 2007; Rodríguez & Rodríguez, 2015).

In this study, we describe the hummingbird assemblage composition of a disturbed tropical dry forest of Guatemala. We also analyze the influence of flower availability and seasonality on hummingbird diversity. In addition, we assessed the consequences of small-scale human-induced disturbance on richness and abundance of resident hummingbird species at the study site. We expected to find a loss in hummingbird richness and abundance with an increment of human-induced disturbance.

Methods

Study Area

The study was conducted at the Motagua valley in eastern Guatemala (Figure 1), ranging from 300 to 900 masl (Moran, 1970). Mean annual temperature at the study site is 26.9°C, with an average annual rainfall of 815 mm (Nájera, 2006). The climate is tropical subhumid, with a dry season of 5 to 7 months, usually from November to May (Nájera, 2006). The dry conditions of the valley are due to the rain shadow effect of two major mountains systems: Sierra de las Minas and Sierra Chuacus. At the landscape scale, the study area is composed of a mosaic of disturbed, dry forest patches in a matrix of anthropogenic land uses that include crops (melon, watermelon, lime, tobacco, and okra), pastures and human settlements.

The seasonal dry forest of the study area is characterized by a tree stratum containing species such as: *Guaiacum coulteri* A. Gray, *Caesalpinia velutina* (Britton & Rose) Standl., *Cassia skinneri* Benth., *Haematoxylum brasiletto* H. Karst., *Leucaena collinsii* subsp. *zacapana* C. E. Hughes, *Bursera schlechtendalii* Engl., *Pereskia lychnidiflora* DC., and *Nopalea guatemalensis* Rose. Common shrubs include *Lippia graveolens* Kunth, *Cassia biflora* L., *Cnidoscolus urens* (L.) Arthur, *Cnidoscolus aconitifolius* (Mill.) I. M. Johnst., and *Mimosa zacapana* Standl. & Steyerm. Herbaceous plants are highly diverse; some common ones include *Cassia uniflora* Mill., *Cathestecum erectum* Vasey & Hack., *Cathestecum brevifolium* Swallen, *Heliotropium rufipilum* (Benth.) I. M. Johnst.,

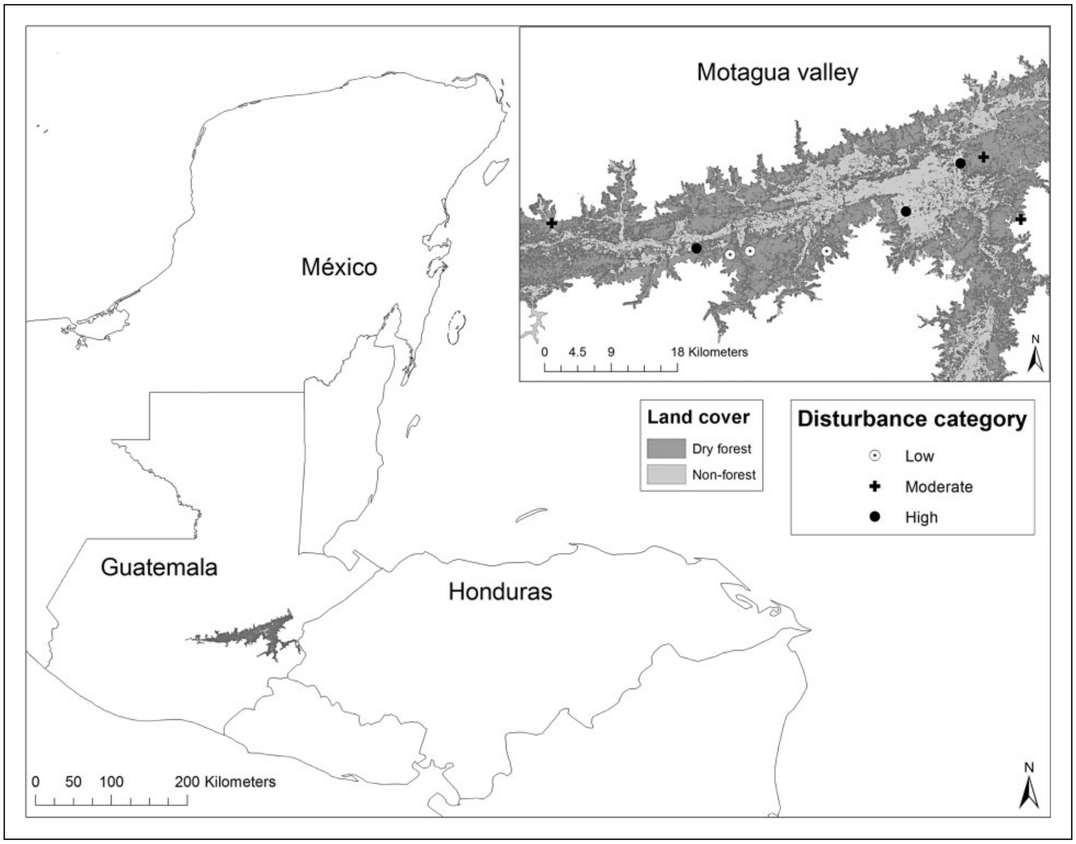

Figure 1. Map of study area, showing land cover and location of the study sites at the Motagua valley in Guatemala.

Melampodium linearilobum DC., *Melocactus curvispinus* Pfeiff., and *Hechtia guatemalensis* Mez. Epiphytes are also common and consist of several species of the genera *Tillandsia* and *Encyclia* (Veliz, García, Cóbar, & Ramírez, 2004).

Hummingbird Survey

Fieldwork was conducted from May 2013 to February 2014 at nine sites. At each site, we established a 2-km-long transect. Fifteen point counts were established along each transect. Each point count was marked and separated by at least 100 m. At each point, we recorded all hummingbirds observed for 10 min within a radius of 25 m from the central point. Visits to each site were performed from 0630 h to 1130 h. Each locality was visited twice during the dry season (May and October 2013) and twice during the rainy season (July 2013 and February 2014). In addition, we counted the number of available, open flowers within a 30-m radius from the central point. Observations were recorded for plants known or presumed to be visited by hummingbirds. Although this does not represent an absolute measure of flower availability, we believe it accurately reflects relative flower availability along the count trails. We also identified hummingbirds to species, recorded their visits to flowers, and determined the species of plants visited.

Anthropogenic Disturbance Variables

To classify the study sites according to their level of anthropogenic disturbance, we used the method proposed by Shahabuddin & Kumar (2006). We randomly selected 5 of the 15 point counts of each transect. At each point, we established a circular plot, each of 10-m radius. Consequently, we surveyed a total of 45 circular plots at the study area. Five different indicators of anthropogenic disturbance were recorded for each circular plot: proportion of trees showing signs of lopping (those with a girth at breast height >4 m), number of cut trees or bushes, number of human trails traversing the plot, signs of agriculture, and number of piles of livestock dung. Lopping on trees was categorized on a scale of 0 to 4: 0 = *no lopping on trees*, 1 = *rudimentary signs of lopping on the majority of trees* (at least 50% of them), 2 = *up to half of the main branches lopped at the majority of trees*, 3 = *more than half of main branches lopped at the majority of trees*, and 4 = *at least 50% of trees reduced to stumps*. The lopping intensity was calculated as the total lopping score divided by the total number of trees present at the five plots (taking into account the trees with a girth at breast height >4 m). In each circular plot, the total number of dung piles of livestock was recorded as an indicator of usage of the habitat by livestock. We also counted the number of separate foot-trails running through the 10-m-circular plot. Agriculture intensity at each plot was categorized on a scale of 0 to 3: 0 = *no agriculture in or near the plot* (at least 100 m away from the plot), 2 = *agriculture of any kind near the plot* (in a radius of 50 m from the plot), and 3 = *agriculture of any kind occurring inside the plot*. Each of these five variables indicating human-induced disturbance was then averaged over the five circular plots established at each site to give a single value for each study site (Table A1).

Vegetation Structure and Composition

As anthropogenic disturbance was expected to affect plant populations (Chaturvedi, Raghubanshi, Tomlinson, & Singh, 2017; Sanaphre-Villanueva et al., 2017; Zubair, Malik, Pandey, & Ballabh, 2016), at each circular plot, we recorded vegetation composition and structure of the tree layer (trees having girth at breast height >4 m; measured with a tape measure). First, tree species were identified and their relative abundances recorded in the 10-m-radius plots. In addition, we calculated the girth at breast height of each tree present in the plot. Tree density was quantified as the number of trees occurring in each plot. This information was used to calculate the number of trees per hectare and the tree basal area per m^2 (Table A1).

Data Analysis

Categorization of sites. The seven measured quantitative descriptors of anthropogenic disturbances and the vegetation composition of the study sites (as a matrix of number of individuals per species of plant) were used to group them into distinct levels of human-induced disturbance using a hierarchical clustering analysis. For this, we used the function pvclust of the pvclust package in R.

Hummingbird assemblage composition. Hummingbird species were grouped into three categories according to the total hummingbird individuals observed: one to three (rare species), four to nine (occasional species), and more than nine individuals (common species). To determine whether our sampling effort was sufficient to record all hummingbird species at the study site, we generated the species accumulation curve for the study area with the function specaccum in the vegan package in R. We used the function specpool (package vegan in R) to estimate the extrapolated species richness for the collection of sample sites of the study area.

Hummingbird diversity and disturbance. Shannon–Wiener's index and Simpson's diversity index were calculated for each study site. The diversity index values were compared among disturbance categories using nonparametric Kruskal–Wallis tests for difference in means. To test whether the number of hummingbirds registered was significantly different in relation to season, month or disturbance category, we performed Kruskal–Wallis tests. When significant differences were found, we used a post hoc test using multiple comparisons based on pairwise rankings. Data from the migratory species (*Archilochus colubris*) recorded at the study site were not taken into account for the overall analysis because we wanted to describe the resident hummingbird community and because we considered that the factors affecting resident hummingbird species are probably not the same affecting latitudinal migrant species as discussed by Supp et al. (2015).

To test for a possible correlation between hummingbird individual numbers and flower richness and availability, we carried out Spearman correlation tests. In addition, we constructed a qualitative matrix of hummingbird–plant interactions for the entire Motagua valley and one for every disturbance category. Hummingbirds were placed in columns and plants in rows. In the matrix, 1 indicated that the plant was visited by the hummingbird and 0 indicated no visits. We considered an interaction to occur if the hummingbird introduced its beak into the corolla of the flower; independent of the number of flowers that the hummingbird visited in the same transect, only one visit was counted. For each disturbance category, a bipartite network was constructed and the following common network metrics were calculated: (a) links per species: mean number of links per species, (b) connectance: defined as the proportion of realized links of the total possible in each network, (c) cluster coefficient: the average cluster coefficients of its members, (d) web asymmetry: balance between numbers of plants and hummingbird in the network: positive values indicate more hummingbird species at the network, negative more plant species, (e) Nestedness: describes a topological feature where poorly linked nodes are typically linked to more general nodes, (f) Specialization asymmetry: positive values indicate a higher specialization of hummingbird in relation to plant species and negative values a higher specialization of plants species, and (g) Shannon diversity: Shannon's diversity of interactions at the network. We used R to perform all the Statistical analyses and the package Bipartite to analyze and draw the bipartite networks.

Results

Classification of Study Sites

Sites were separated into three distinct groups: one representing a low degree of anthropogenic disturbances that included two protected areas and a communal area used primarily for limited timber extraction; a second cluster representing an intermediate degree of disturbance with timber extraction, cattle grazing, and lopping; and a third one representing a high degree of use (primarily for agriculture; Figure 2).

Hummingbird Richness and Assemblage Composition

We recorded five hummingbird species for the study site: *Amazilia rutila* DeLattre (1842), *Anthracothorax prevostii* Lesson (1832), *Archilochus colubris* Linnaeus (1758), *Chlorostilbon canivetii* Lesson (1832), and *Heliomaster constantii* DeLattre (1843). Our hummingbird species accumulation curve indicates that the sampling effort was enough to detect all hummingbird species of the study site (Figure 3).

The species *Amazilia rutila* and *Chlorostilbon canivetii* were recorded at almost all sampling locations and had the largest number of records (Table A2). *Heliomaster constantii* was an uncommon species with low number of individuals when recorded. *Anthracothorax prevostii* was the rarest resident species in the area and was recorded at only three of the nine sampled sites. Finally, *Archilochus colubris* was the only latitudinal migrant species and had the fewest records (Table A2).

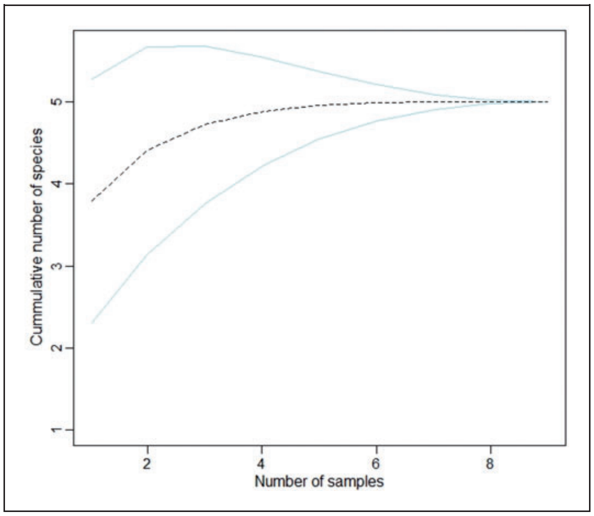

Figure 3. Hummingbird species accumulation curve for the study area at the Motagua valley in Guatemala.

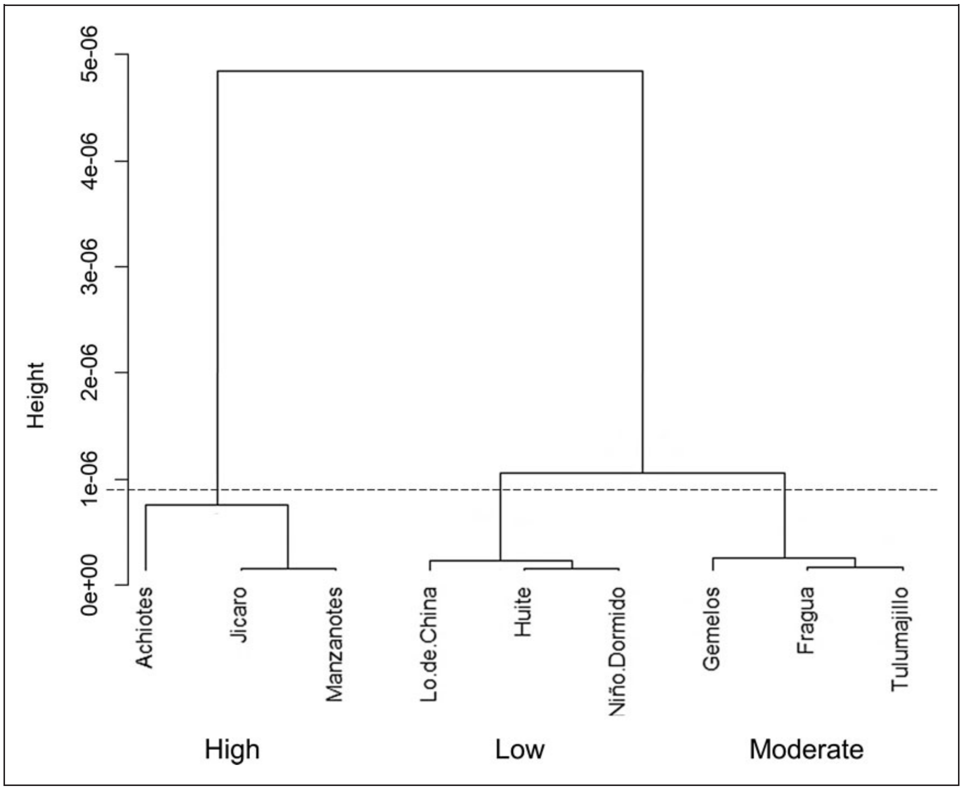

Figure 2. Cluster analyses of the sampling sites at the Motagua valley in Guatemala, obtained by war.D2 agglomerative method and correlation distance, from abundance data of plant species and values of seven measured quantitative descriptors of disturbance at each study site. Sites were separated in three groups: low (sites with low levels of anthropogenic disturbance), moderate (sites with moderate levels of anthropogenic disturbance), and high (sites with high levels of anthropogenic disturbance).

Hummingbird Diversity in Relation to Seasonality

The total number of hummingbirds recorded was higher and significantly different between the dry and rainy seasons ($\chi^2 = 5.99$, $df = 1$, $p < .05$). The largest number of individuals was recorded in February (59) and May (40), while July had the lowest number of records (12). In October, we recorded a total of 25 individuals (Figure 4).

The total number of individuals of *Amazilia rutila* and *Chlorostilbon canivetii* varied seasonally (*Amazilia rutila*: $\chi^2 = 16.5$, $df = 1$, $p < .001$; *Chlorostilbon canivetii*: $\chi^2 = 5.55$, $df = 1$, $p = .02$) and was higher during the dry season. The other resident species did not show significant seasonal variation in the number of individuals registered in relation to seasonality. The number of individuals registered per month per hummingbird species at the Motagua valley in Guatemala is shown in Figure 5.

Hummingbird Diversity and Flower Availability

We did not find a significant difference in total flower availability between seasons, but we did find significant differences between certain months ($\chi^2 = 16.6$, $df = 3$, $p = .000839$; Kruskal–Wallis post hoc: July and October $p = .00036$ and May and October $p = .0439$). The data indicated that flower abundance was greater at the end of the wet season and beginning of the dry season and lower at the end of the dry season and beginning of the wet season.

Per site, the number of plant species in bloom (total number of plants in bloom per transect) and the number of hummingbird records per transect were significantly correlated ($r = .40$, $n = 36$, $p = .0166$). Total flower availability (total number of flowers per transect) and total number of hummingbird records per transect were also significantly correlated (Spearman $r = 0.49$, $n = 36$, $p = .0026$; Figure 6). Only the relative abundance of *Amazilia rutila* was significantly correlated with flower availability ($r = .54$, $n = 36$, $p = .0007$).

In relation to disturbance, the total number of plant species in bloom (low disturbance = 64 and high disturbance = 51) and the monthly average number of plant species in bloom per site (low disturbance = 4.3 ± 2.5, high disturbance = 5.3 ± 2.7) was higher at low- and high-disturbance sites. Moderate disturbance sites showed the lowest total number of plant species in bloom (44) and the monthly average number of plant species in bloom per site (3.8 ± 0.9). However, we did not find a significant difference in the number of plant species in bloom per site ($\chi^2 = 3.05$, $df = 2$, $p = .21$) and total number of flower availability between disturbance categories ($\chi^2 = 0.054$, $df = 2$, $p = .97$).

Hummingbird Diversity in Relation to Disturbance

Bird diversity index values as measured by Shannon–Wiener's index and Simpson's diversity index were higher in low-disturbance site and moderately disturbed site in comparison to highly disturbed ones (Table A3). However, we did not find a significant difference between diversity index values among disturbance categories (Shannon diversity index: $\chi^2 = 3.2$, $df = 2$, $p = .2$ and Simpson diversity index: $\chi^2 = 3.2$, $df = 2$, $p = .201$). Meanwhile, with respect to specific sampling sites, Huite and Lo de China, two areas with low degree of disturbance, and Tulumajillo a moderate disturbed site, showed the highest diversity estimates (Table A3).

The species *Amazilia rutila*, *Chlorostilbon canivetii.*, and *Heliomaster constantii* were present in all disturbance categories (Table A2). *Anthracothorax prevostii* was detected only at moderately and highly disturbed sites (Table A2).

The total number of individuals recorded was higher at low-disturbance sites (66). Moderate- and

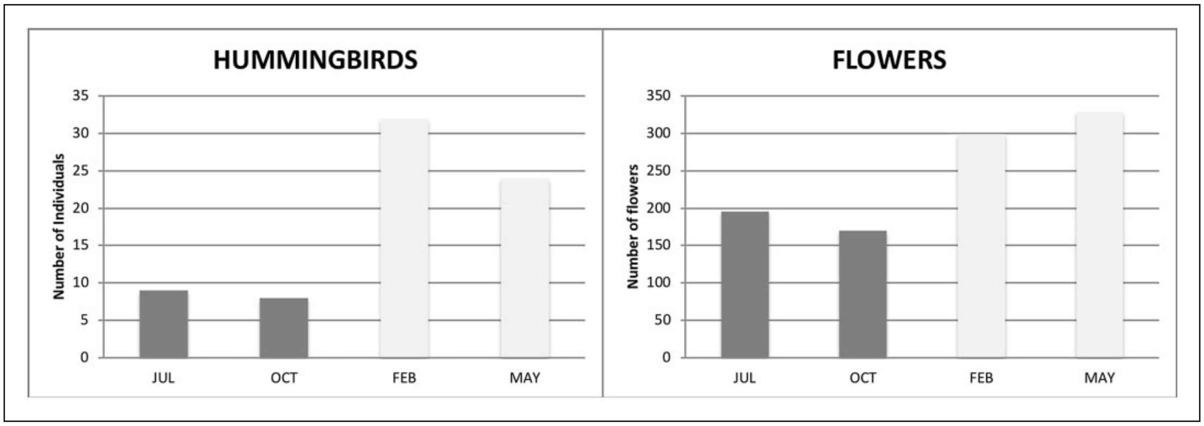

Figure 4. Hummingbird and flower seasonal availability at the Motagua Valley during wet (gray) and dry (white) seasons.

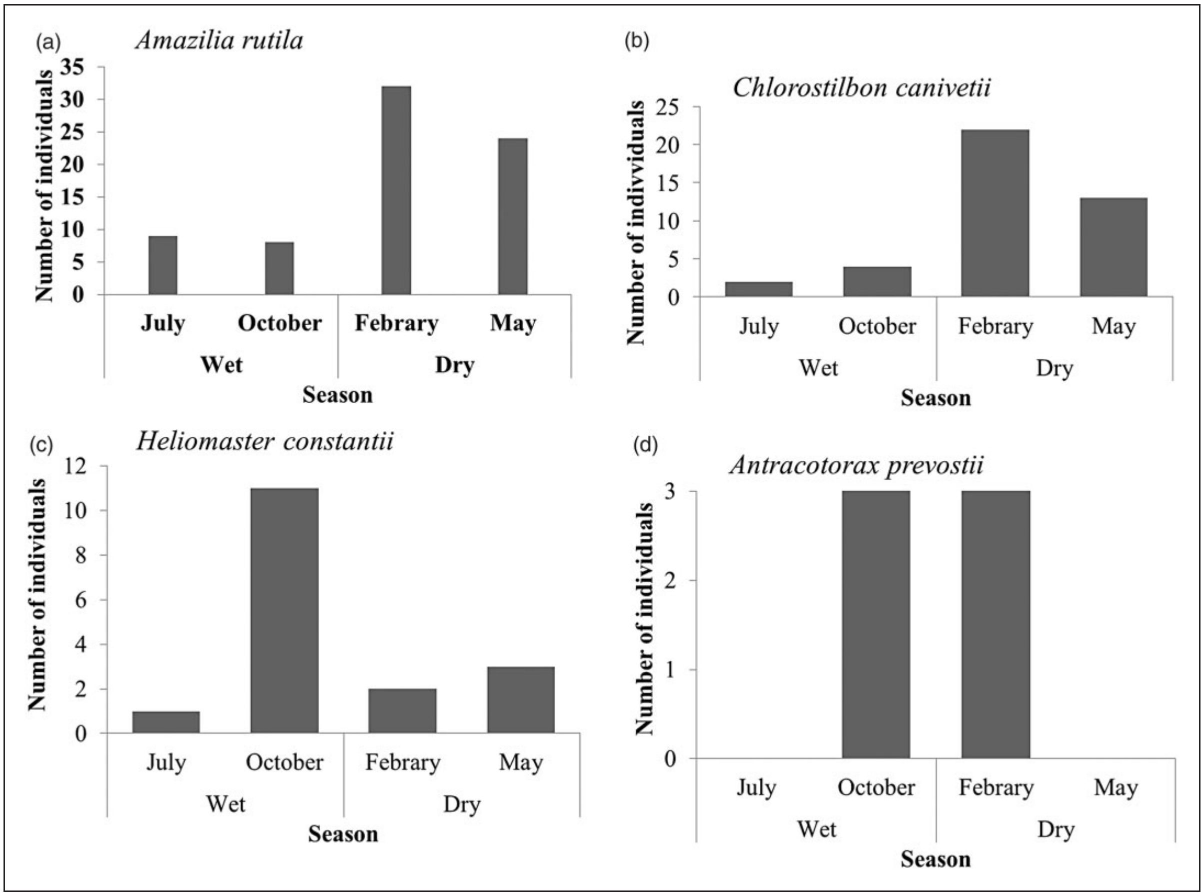

Figure 5. Number of individuals registered per month per hummingbird species at the Motagua valley in Guatemala. (a) Number of individuals registered per month for *Amazilia rutila*, (b) number of individuals registered per month for *Chlorostilbon canivetii*, (c) number of individuals registered per month for *Heliomaster constantii*, and (d) number of individuals registered per month for *Anthracothorax prevostii*.

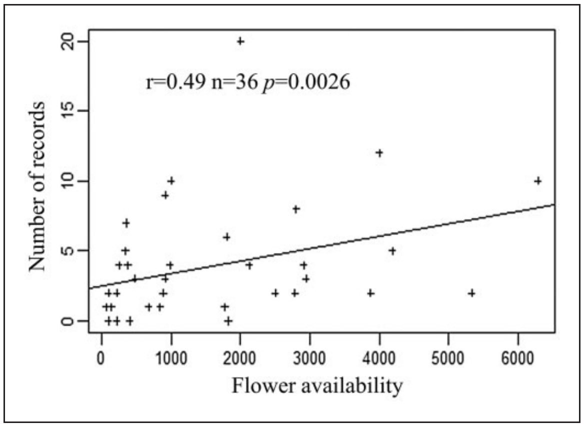

Figure 6. The correlation between the total number of hummingbird records per month and the total number of flowers (of 23 plant species) used as food resources by hummingbirds in the Motagua valley.

high-disturbance sites showed almost the same number of individuals. Nevertheless, we did not find significant differences in the number of hummingbird records among disturbance categories ($\chi^2 = 1.88$, $df = 2$, $p = .3905$).

When comparing the number of records of each hummingbird species separately in relation to disturbance, we did not find any significant difference for any of the resident hummingbird species (*Amazilia rutila* $\chi^2 = 2.67$, $df = 2$, $p = .2634$; *Anthracothorax prevostii* $\chi^2 = 2.67$, $df = 2$, $p = .1$, *Chlorostilbon canivetii* $\chi^2 = 2.68$, $df = 2$, $p = .261$, and *Heliomaster constantii* $\chi^2 = 0.620$, $df = 2$, $p = .734$).

Hummingbird–Plant Interactions in Relation to Disturbance

We recorded a total of 69 species of flowering plants along the sampled transects and 23 were used as food resources by hummingbirds (Figure 7 and Appendix A). We observed 36 interactions between them in all eight sites (Figure 7). *Amazilia rutila* was involved in 47% of the interactions, *Chlorostilbon canivetii* in 39%, *Heliomaster constantii* in 17%, and *Antracotorax prevostii* only at 3% of them. The number of plants that were visited by hummingbirds and the number of different pairwise interactions registered were almost the same between low- (16 interactions) and high-disturbance sites (17 interactions; Figure 7). The moderate disturbance sites showed the lowest number of plants visited by hummingbirds (six species) and the lowest number of different pairwise interactions (eight interactions).

Connectance was similar among the three disturbance categories, while asymmetry was higher at low- and high-disturbance sites and nestedness was higher at moderate disturbed sites (Table A4). No statistical comparisons could be made among disturbance categories due to low number of data.

Despite of disturbance, there was a trend showing more pairwise interactions as diversity of sites increase (Figure 8). However, no statistical significance could be found for Shannon–Wiener index ($y = 13.64–4.84$; $R^2 = .32$; $p = .11$) nor for Simpson index ($y = 18.95x - 2.83$; $R^2 = .16$, $p = .27$).

Discussion

Hummingbird Species Richness at the Motagua Valley

The hummingbird species richness at the Motagua valley is relatively low compared with other more humid forests

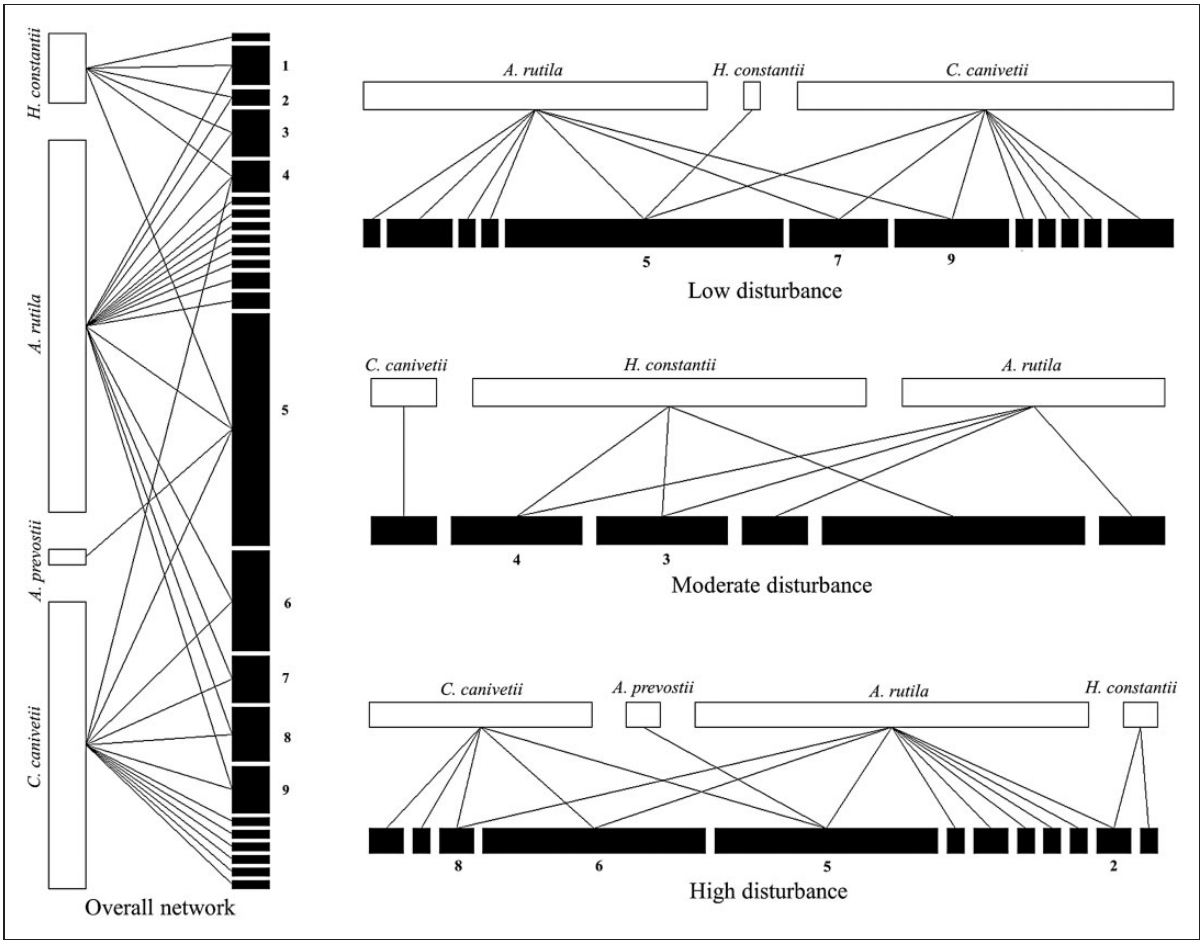

Figure 7. Hummingbird–plant visitation networks of the Motagua valley in Guatemala. The white boxes represent hummingbird species and the black boxes represent the plant species visit by them. The lines linking the boxes represent pairwise interactions. The overall network was obtained by pooling all interactions across all the sampling sites. The other networks show the visitation interactions registered at each level of human-induced disturbance. Hummingbird species: *H. constantii* (*Heliomaster constantii*), *A. rutila* (*Amazilia rutila*), *A. prevostii* (*Antracotorax prevostii*) and *C. canivetii* (*Chlorostilbon canivetii*). Main plant species: 1. *Ipomoea hederifolia*, 2. *Tillandsia xerographica*, 3. *Nopalea guatemalensis*, 4. *Tabebuia donnell-smithii*, 5. *Caesalpinia affinis*, 6. *Pedilanthus tithymaloides*, 7. *Tillandsia caput-medusae*, 8. *Cnidoscolus urens*, and 9. *Cnidoscolus aconitifolius*.

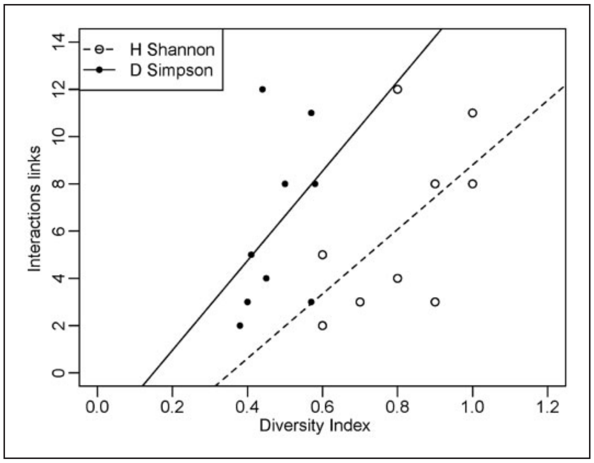

Figure 8. Correlations between diversity indexes, Shannon–Wiener (open circles; $y = 13.64 - 4.84$; $R^2 = .32$, $p = .11$) and Simpson (dark circles; $y = 18.95x - 2.83$; $R^2 = .16$, $p = .27$).

of Guatemala, where up to 22 species may be present (Howell & Webb, 1995). These data are in concordance with several studies that report higher hummingbird diversity in humid rain forests in comparison to drier deciduous forests (Kessler & Kromer, 2000; Rahbek & Graves, 2000). This pattern is presumably related to the marked seasonal and phenological patterns in dry forests that are driven by cyclical regimes of precipitation. Seasonality affects hummingbird diversity, as hummingbirds require a continuous supply of food due to their high metabolic rates (Abrahamczyk, Kluge, Gareca, Reichle, & Kessler, 2011).

The hummingbird species richness at the Motagua valley is similar to other tropical dry forests of Mesoamerica where hummingbird richness ranges from five to nine species (Arizmendi & Espinoza de los Monteros, 1996; Arizmendi & Ornelas, 1990; Gillespie & Hartmut, 2004; Ortiz-Pulido et al., 2012; Wolf, 1970). The Motagua valley also shares many species with other tropical dry forests of the region. For example, it shares 67% of its species with the Chamela Biosphere Reserve in Jalisco, Mexico (Arizmendi & Ornelas, 1990), 57% with Cerro Colorado in Veracruz, Mexico (Hernández, 2009), 67% with La Flor Reserve in Nicaragua (Gillespie & Hartmut, 2004), and 56% with The Granja Experimental Jiménez, at Guanacaste in Costa Rica (Wolf, 1970). This similarity in hummingbird communities reflects the history of lowlands ranging from 0 to 900 m asl, as these previously formed a continuous strip from the Pacific Coast of Mexico to Costa Rica (Janzen, 1986). Chazdon et al. (2011) indicate that the Mexican Pacific, Central American Pacific and interior valleys, and the Caribbean constitute a major tropical dry forest region as a whole, based on their floristic similarities. These similarities in plant composition could also explain similarities in the hummingbird assemblages of these areas. Unfortunately, dry tropical forests throughout this region have also been subjected to high levels of alteration, fragmentation, and deforestation as a result of human activities, which has resulted in a loss of continuity among these areas (Chazdon et al., 2011).

Hummingbird Assemblage Composition at the Motagua Valley

Generally, hummingbird communities are mainly composed of medium-sized species (Stiles, 1981) of which resident species tend to be the most abundant (Arizmendi & Ornelas, 1990). At our study site, three of five hummingbird species may be considered medium to large sized (Arizmendi & Berlanga, 2014; Téllez, Meneses, & Torres, 2017), including *Amazilia rutila*, which was the most abundant species in our study area. As the dominant species, *Amazilia rutila* actively defends clumped flowers and its feeding territory, from *Chlorostilbon canivetii*, with which it shares various food resources, including *Cesalpinia affinis*, *Pedilanthus tithymaloides*, and *Tillandsia caput-medusae*. *Heliomaster constantii* was uncommon and observed mostly at forest edges. *Anthracothorax prevostii* was the rarest species in the area. This species is an uncommon to very common hummingbird in different parts of its range and in many areas, usually expands its range with deforestation (Stiles, Boesman, & Kirwan, 2018). At the Motagua valley, it is apparently an altitudinal migrant that also uses other habitat types to search for resources that are unavailable during part of the year. *Archilochus colubris* was the only latitudinal migrant species recorded.

Hummingbird Diversity in Relation to Seasonality and Flower Availability

Previous studies of the annual dynamics of hummingbirds in lowlands report that seasonality is one of the main factors that affect the abundance of individuals, mainly due to the availability of food resources (Arizmendi & Ornelas, 1990; Gutiérrez, Rojas-Nossa, & Stiles, 2004; Poulin, Lefebvre, & Mcniel, 1993). At our study site, we found differences in overall number of hummingbirds registered between the dry and the wet seasons; we registered a higher number of hummingbirds during February at middle of the dry season coinciding with the period when the availability of flowers was also high. These data suggest that seasonal resource variation could be an important factor influencing the variation in the number of hummingbird present at our study area. Nevertheless, a more complete assessment of the distribution across space and time of the plants used for food by hummingbirds would be necessary to reach conclusions about the role of food availability in hummingbird diversity at our study site.

Differences in the number of hummingbirds registered between seasons were primarily due to changes in the number of records of the most abundant resident species such as *Amazilia rutila* and *Chlorostilbon canivetii*. Variation in number of records of these species is probably reflecting changes in density, as they must expand their territory when food resources are scarce (Arizmendi & Berlanga, 2014). This assumption is supported by the significant relationship found between the number of records of *Amazilia rutila* and flower availability at the study site. On the other hand, we did not found differences in the number of records for the other two resident species, even though reports indicate that both of them expand their range or perform altitudinal migrations in respond to seasonal changes in food availability (Stiles, Boesman, et al., 2018; Stiles, Kirwan, & Boesman, 2018). It is possible that the sampling effort of our study was not enough to detect trends in relation to seasonality for these species, taking into account that both are usually rare and uncommon species (Stiles, Boesman, et al., 2018; Stiles, Kirwan, et al., 2018). In this context, some authors have indicated that the study of rare and low-density bird species (that usually have low detection probabilities) requires more sampling effort in point counts surveys, particularly in those studies relating bird presence or abundance with habitat use (Buskirk & McDonald, 1995).

Hummingbird Diversity in Relation to Disturbance

Contrary to what we expected, hummingbird species richness and number of records did not change in relation to disturbance. This lack of response of hummingbirds to disturbance has been observed for other hummingbird assemblages in altered environments (Snow & Snow, 1972; Stouffer & Bierregaard, 1995) and has presumably been related with the plastic habitat preference of dominant species (Snow & Snow, 1972) and the preferences of several species to forest ecotones (Banks-Leite, Ewers, & Metzger, 2010). This could be the case for hummingbirds at the Motagua valley as all species present can be found in different habitat types with different degrees of human-induced disturbance. Features like high mobility allow hummingbirds to cross open and disturbed areas (Hadley & Betts, 2009), and a generalist diet increases their resilience to disturbance in comparison to other bird guilds, such as insectivores (Stouffer & Bierregaard, 1995; Thiollay, 1997). The hummingbird assemblage at the Motagua valley likely perceives the landscape as moderately modified, compared to species with poor dispersal capabilities (Mcintyre & Hobbs, 1999). Nevertheless, the persistence of hummingbirds in altered habitats does not necessarily imply that disturbance does not have an impact on them. For example, two different studies conducted in agricultural landscapes found that highly mobile hummingbirds avoid crossing open matrix in favor of longer forested detours (Hadley & Betts, 2009; Volpe, Robinson, Frey, Hadley, & Betts, 2016). Disruption of hummingbird's movement as a function of landscape disturbance could have an important impact on hummingbird's effectiveness to transfer pollen among plants (Hadley & Betts, 2009), thus affecting plant reproduction and fitness. In addition, it would be necessary to determine whether hummingbirds are breeding in altered habitats at the study site or whether they require undisturbed areas to breed. In this respect, more studies are needed to document their specific breeding requirements, as these may ultimately limit their distribution and abundance.

Compared with other better-preserved tropical dry forests of Mesoamerica such as those in Santa Rosa and Palo Verde in Costa Rica (Gillespie & Hartmut, 2004) and Tehuacán-Cuicatlán in México (Lara-Rodríguez et al., 2012), the Motagua valley has a less diverse hummingbird community composition. The relative low richness and the generalist nature of the hummingbird assemblage at the Motagua valley could be the result of the loss of disturbance-sensitive species in response to the intense forest transformation and high levels of human-induced disturbance (Ewers & Didham, 2006) that have been present at the area for more than 100 years (Bray, 2010; Chazdon et al., 2011; Janzen, 1986; Maass, 1995). In their study, MacGregor-Fors and Schondube (2011) found that tropical dry forest areas transformed into crop fields and pastures had bird communities with lower species richness and lower evenness values than those found in primary forests. Endemic and quasi-endemic bird species, which tend to be more sensitive to disturbance (Julliard, Jiguet, & Couvert, 2003), were poorly represented in these structurally simplified habitats. In addition, Gillespie (2000) found that bird species that require solid dry forest were not present at large but disturbed reserves, suggesting that disturbance may play an important role in the presence of sensitive bird species at this type of habitat. Nonetheless, because tropical dry forests of Mesoamerica have had a very similar history of disturbance and because records of hummingbird species prior to the intense degradation of these forests are scarce, it is not possible to reach accurate conclusions about the role of habitat degradation on the possibility of hummingbird species loss at the Motagua valley.

Hummingbird–Plant Interactions in Relation to Disturbance

The number of hummingbird–plant interactions was lower at moderately disturbance sites. Low- and high-disturbance sites were similar regarding interaction structure (Nestedness and asymmetry). The reason behind this result is probably related to the fact that high- and low-disturbance sites present a higher number of plant species that are more attractive to hummingbirds to visit. Our highly disturbed sites, mainly agricultural, are dominated by scattered trees and several pioneer species such as *Cnidoscolus aconitifolius* (Mill.) I. M. Johnst, *Cnidoscolus urens* (L.) Arthur, *Macroptilium atropurpureum (*DC.) Urb. and *Pedilanthus tithymaloides* (L.) Poit, which were visited by various hummingbird species. Less disturbed sites were dominated by trees and shrubs typical of more mature forest that were visited by hummingbirds but they also presented several herbs and pioneer species. At moderately disturbed sites, the average number of plant species for hummingbirds was lower and pioneer species were scarcer. The lower number of plant species available as food resources for hummingbirds at moderately disturbed sites could be a consequence of heavy grazing and selective logging that occurs at these areas. In a dry tropical forest of Costa Rica, Stern, Quezada, and Stoner (2002) found significantly fewer plant species and a less diverse floristic composition at an area with intermittent cattle grazing compared with an area with no grazing. Their results indicate that cattle grazing has an impact on the dry forest by reducing the relative abundance and density of larger tree species and by changing the species composition and structure of the plant community that can have effects on the abundance of pollinators due to lower availability of flowers.

Implication for Conservation

In general, our study results showed resilience of hummingbirds to different levels of disturbance probably related with the generalist behavior of dominant resident species and the availability of food resources for hummingbirds at different levels of disturbance. However, these data should be taken with caution as our study was conducted on a small-scale and a large-scale spatial analysis could provide a better understanding of the effect of human-induced disturbance on hummingbird richness and abundance at the study site. It should also be taken into account that our sampling sites are immersed in a mosaic of dry forest patches, pastures, and areas with other land uses that surely provide nesting and breeding sites for hummingbirds. Therefore, in future studies, we recommend studying reproductive aspects of hummingbird populations at the study site and the role of forested areas in the breeding and survival of hummingbird populations.

As part of our results, we identified some important food resources for hummingbird in the Motagua valley. *Caesalpinia affinis* Hemsl. and *Tabebuia donnell-smithii* Rose, two common tree species present at forested areas, were particularly important to hummingbirds. When in bloom, both species produce large numbers of flowers that are intensely visited by all the hummingbird species at the study site. These species are particularly important for the overall hummingbird community and could be preferentially used in reforestation programs to promote the conservation of hummingbird communities at the study site. Other potentially useful plant species that could be used at dry forest restoration programs are *Nopalea guatemalensis* Rose, *Tillandsia caput-medusae* E. Morren, and *Tillandsia xerographica* Rohweder. Even though these plant species were visited only by some of the hummingbird species at the study site, they are native Neotropical dry forests species that could contribute to the recovery of the structure and complexity of the vegetation at disturbed areas. *T. xerographica* is an endangered plant species in Guatemala and its conservation could be further boosted because of its role as a hummingbird floral resource.

Appendices

Appendix A

Interaction matrix of hummingbirds and their nectar resources at the Motagua valley, Guatemala. The interactions represented data registered during direct observations. 1 = presence of interaction and 0 = lack of interaction.

Table A1. Mean Values and Standard Error of Selected Disturbance Indicators and Number of Trees and Basal Area (Per Hectare) in the Nine Study Sites at the Motagua Valley in Guatemala.

Site	Lopping	Average no. of dung clusters	Average no. of trails	Average scale of agriculture	Average no. of trees cut	No. of trees per hectare	Basal area per m^2
Lo de China (14°54′23N 89°50′23W)	0.04 ± 0.04	0.2 ± 0.44	1 ± 0	0.6 ± 0.89	1.2 ± 1.64	191.0	4.7
Huite (14°′54′46N 89°36′59W)	0.296 ± 0.02	1.2 ± 1.09	1.2 ± 0.84	0	4 ± 4.24	133.7	3.5
Niño Dormido (14°54′20N 74°0′21W)	0.54 ± 0.05	2 ± 0	1.2 ± 0.44	0	0.6 ± 0.89	140.1	3.8

(continued)

Table A1. Continued

Site	Lopping	Average no. of dung clusters	Average no. of trails	Average scale of agriculture	Average no. of trees cut	No. of trees per hectare	Basal area per m^2
Fragua (14°′56′46N 89°36′59W)	0.08 ± 0.43	1.7 ± 0.5	2.6 ± 0.54	3 ± 0	1.6 ± 3.6	89.1	2.9
Tulumajillo (14°′55′52N 89°43′2W)	0.05 ± 0.03	0.4 ± 0.89	2.8 ± 0.44	0.8 ± 0.44	4.2 ± 3.7	140.1	5.1
Gemelos (15°1′18N 89°33′1W)	0.34 ± 0.043	2.6 ± 3.28	1.5 ± 0.89	0.6 ± 1.34	3.2 ± 2.95	178.3	5.5
Jicaro (14°′54′17N 89°28′25W)	0.09 ± 0.12	1.6 ± 1.51	2.6 ± 0.55	3 ± 0.44	3.6 ± 6.5	101.9	9.5
Achiotes (14°′56′49N 89°31′37W)	0.13 ± 0.09	0	2.8 ± 0.44	0	2 ± 2.82	89.1	4.3
Manzanotes (15°0′8N 89°50′23W)	0.05 ± 0.08	3.2 ± 1.09	2 ± 0	2.6 ± 0.54	0.8 ± 1.78	114.6	9.7

Table A2. Number of Individuals Per Hummingbird Species at Each Study Site at the Motagua Valley in Guatemala.

Disturbance category	Sites	*Amazilia rutila*	*Anthracothorax prevostii*	*Archilochus colubris*	*Chlorostilbon canivetii*	*Heliomaster constantii*	Total
Low	Lo de China	21	0	3	14	1	39
	Huite	9	0	1	5	1	16
	Niño Dormido	10	0	0	3	2	15
Moderate	Fragua	9	0	0	3	0	12
	Tulumajillo	1	3	0	5	0	9
	Gemelos	2	0	0	2	10	14
High	Achiotes	0	0	0	5	2	7
	Jicaro	9	2	0	0	1	12
	Manzanotes	12	1	0	4	0	17
	Total	73	6	4	41	17	141

Table A3. Total Resident Species Richness Observed, Estimated Species Richness, and Diversity Index Values of Hummingbirds for the Nine Study Sites at the Motagua Valley in Guatemala.

			Species richness estimation				
Disturbance category	Site	Species richness	Jack1 (±SE)	ACE (±SE)	H′	D′	Effective number of species
Low	Lo de China	4	5.5 ± 1.06	5.1 ± 0.93	1	0.57	2.7
	Huite	4	5.5 ± 1.06	6.3 ± 1.27	1	0.58	2.8
	Niño Dormido	3	3.8 ± 0.75	3 ± 0	0.9	0.50	2.4
Moderate	Fragua	2	2.8 ± 0.75	3 ± 2.57	0.6	0.38	1.8
	Tulumajillo	3	4.5 ± 0.75	3.6 ± 0.70	0.9	0.57	2.6
	Gemelos	3	3.8 ± 0.75	3 ± 1.49	0.8	0.45	2.2
High	Jicaro	3	4.5 ± 1.06	4.2 ± 1.01	0.7	0.40	2.1
	Achiotes	2	2 ± 0	2 ± 0	0.6	0.41	1.8
	Manzanotes	3	3.8 ± 0.75	4.1 ± 0.86	0.8	0.44	2.1

Note. Species richness estimation according to jackknife of first order (Jack 1) and ACE. Diversity index values according to Shannon–Wiener's index (H′), Simpson's diversity index (D′), and effective numbers of species. ACE = abundance-based coverage estimator.

Table A4. Species Interaction Matrix Metrics.

	Low	Moderate	High
Links per species	1.066667	0.8888889	1.0625
Connectance	0.4444444	0.4444444	0.3541667
Cluster coefficient	0.3333333	0.3333333	0.25
Web asymmetry	0.6	0.3333333	0.5
Nestedness	25.81525	30.55266	25.04765
Specialisation asymmetry	1	0.09400543	0.01958073

Note. No statistical comparison could be done due to low data numbers.

Acknowledgments

The authors want to thank the Biological Science Postgraduate Department of the National Autonomous University of Mexico (Posgrado en Ciencias Biológicas: Universidad Nacional Autónoma de México) for facilities given to M. Bustamante during her PhD studies and for offering financial support for travel (PAEP-CEP-UNAM). The authors also want to thank Biologist Victor Vargas from CONABIO (Comisión nacional para el conocimiento y uso de la biodiversidad, México) for making the map of the surveyed area and two anonymous reviewers whose comments improved the quality of the manuscript.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was financially supported by National Council of Science and Technology (Consejo Nacional de Ciencia y Tecnología) and the Government of Guatemala through the National Fund for Science and Technology (Fondo Nacional de Ciencia y Tecnología [FODECYT 45-2013]).

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