UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE ECOLOGÍA

ECOLOGÍA

CONSECUENCIAS DE LA FRAGMENTACIÓN DEL PAISAJE Y LA PÉRDIDA DE HÁBITAT SOBRE LAS INTERACCIONES DE COLIBRÍES Y SUS PLANTAS ASOCIADAS EN LA REGIÓN SEMIÁRIDA DEL VALLE DEL MOTAGUA, GUATEMALA

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTORA EN CIENCIAS

PRESENTA:
MICHELLE BUSTAMANTE CASTILLO

TUTOR PRINICPAL DE TESIS: DRA. MARIA DEL CORO ARIZMENDI ARRIAGA
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CIUDAD DE MÉXICO, JUNIO, 2019.

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MÉXICO, D.F. JUNIO, 2019.

Copia del Oficio de Empaste: Es el oficio en el que se indica el jurado para el examen de grado y va dirigido a la Directora General de Administración Escolar, va después de la portadilla.

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Ciencias Biológicas

OFICIO CPCB/525/2019

Asunto: Oficio de Jurado para Examen de Grado.

M en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted, que el Subcomité de Ecología y Biología Evolutiva, en su sesión ordinaria del día 11 de marzo de 2019, aprobó, el jurado para la presentación del examen para obtener el grado de **DOCTORA EN CIENCIAS**, a la alumna **BUSTAMANTE CASTILLO MICHELLE** con número de cuenta **513451788** con la tesis titulada: **"Consecuencias de la fragmentación del paisaje y la pérdida de hábitat sobre las interacciones de colibríes y sus plantas asociadas en la Región Semiárida del valle del Motagua, Guatemala"**, bajo la dirección de la **DRA. MARÍA DEL CORO AEIZMENDI ARRIAGA:**

Presidente:	DR. ADOLFO GERARDO NAVARRO SIGÜENZA
Vocal:	DRA. KARINA BOEGE PARÉ
Secretario:	DRA. BLANCA ESTELA HERNÁNDEZ BAÑOS
Suplente:	DRA. EK DEL VAL DE GORTARI
Suplente	DRA. SILVANA MARTÉN RODRÍGUEZ

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a, 3 de mayo de 2019

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLÓGICAS
COORDINACIÓN

AGRADECIMIENTOS INSTITUCIONALES

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DEDICATORIA

A mi hermosa hermanita, *Nadeshda Bustamante*. Te extrañamos kukis.

ÍNDICE

RESUMEN

En los bosques secos del nuevo mundo, los colibríes actúan como importantes polinizadores de una amplia variedad de plantas con flor, y en algunas áreas, actúan como polinizadores efectivos y casi exclusivos de algunas especies. Actualmente, grandes extensiones de este hábitat se han convertido en tierras de cultivo y los remanentes que existen poseen distintos niveles de perturbación antrópica. Aunque los colibríes parecen ser resistentes a las perturbaciones del hábitat, poco se sabe sobre el efecto de la perturbación y la conversión de los bosques en áreas agrícolas sobre su diversidad y en las interacciones mutualistas en las que participan con sus plantas asociadas. Por ello, en este trabajo estudiamos la diversidad de colibríes en sitios con distintos niveles de perturbación antrópica en un bosque tropical seco de Guatemala. Además, realizamos un análisis de redes de interacciones planta-polinizador para discutir la influencia de la conversión de hábitat sobre la estructura y dinámica de un ensamble de colibríes-plantas en esta misma área. La recolección de datos sobre diversidad de colibríes y sus visitas a las plantas nativas del sitio de estudio se llevó a cabo en transectos ubicados en remanentes de bosque tropical seco y áreas agrícolas. Las visitas a cada sitio se realizaron dos veces durante la estación seca y dos veces durante la temporada de lluvias. Con estos datos, primero evaluamos cómo la estacionalidad y la perturbación del hábitat influyen en la diversidad de colibríes en el área de estudio. También determinamos cómo el tipo de hábitat (bosque seco tropical o agrícola) y la estacionalidad influyen sobre el número de interacciones colibrí-plantas que pueden registrarse en el sitio de estudio. Además, comparamos distintos aspectos de la red de bosque seco tropical con la red de áreas agrícolas que tienen implicaciones para la conservación de las interacciones planta-polinizador.

Encontramos que la estacionalidad influyó marcadamente sobre la riqueza y el número de colibríes que pueden registrarse en el área de estudio. Esto era de esperarse debido a los profundos cambios en la disponibilidad de alimento en estos bosques a lo largo del año. Encontramos que los colibríes son capaces de persistir en áreas con distintos tipos de perturbación antrópica; por lo que la diversidad del grupo no fue significativamente distinta en respuesta a distintos niveles de perturbación del hábitat. Esto último debido muy probablemente a la naturaleza generalista y alta movilidad de los colibríes en el área de estudio que les permite emplear recursos a través del paisaje. Por otro lado, la estacionalidad (pero no la conversión del hábitat) influyó en el número

de interacciones entre colibríes y plantas registradas. Esto probablemente está relacionado con la naturaleza generalista del conjunto de colibríes y plantas del sitio de estudio, que les permite persistir y formar nuevas interacciones en las áreas perturbadas y agrícolas. A pesar de que los colibríes muestran resiliencia a la conversión del hábitat, nuestros resultados indicaron que la conversión de hábitat a sitios agrícolas causó una reducción de la diversidad de interacciones y una red más generalista en hábitats agrícolas, lo que tiene implicaciones para la conservación de las interacciones mutualistas en hábitats transformados. Nuestros datos también señalaron la importancia de los remanentes de hábitat natural y seminatural de bosque seco tropical en el suministro de recursos esenciales para los polinizadores dentro de paisajes agrícolas.

ABSTRACT

At the new world tropical dry forests, hummingbirds act as important pollinators. Currently, large extensions of this habitat have been converted to farmlands, and the few remaining forests exist almost entirely as small, disturbed, and isolated fragments. Although hummingbirds seem to be resilient to habitat disturbance, little is known about the effect of disturbance and forest conversion to agriculture on their diversity and mutualistic interaction with native plants. Thus, in this survey, we firstly address the impact of small-scale anthropogenic disturbance on local richness and abundance of hummingbirds in a dry forest of Guatemala. We also, use ecological network analyses to discuss the influence of habitat conversion on the structure and dynamics of a plant-hummingbird assemblage at the same site. Data collection on hummingbird diversity and visits to native plants was carried out in transects located within patches of tropical dry forest and within agricultural sites. Visits to each site were done twice during the dry season and twice during the rainy season. With these data, we firstly evaluated how seasonality and human-induced disturbance influenced hummingbird diversity. Secondly, we evaluated if seasonality and habitat type (tropical dry forest and agriculture) influence the total number of hummingbird-plant interactions registered using a generalized linear model. Then, we compared distinct aspects of the tropical dry forest and agricultural networks that have implications for plant-pollinator interactions conservation. 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. Seasonality (but not habitat conversion) influence the number of hummingbird-plant interaction registered. The lack of difference in the number of mutualistic interactions in relation to habitat conversion is probably related with the generalist nature of the hummingbird-plant assemblage of the study site allows them to form new interaction in converted areas. Our results indicated that habitat conversion caused a reduction of interactions diversity and a more generalist network with implications for the conservation of mutualist interactions.

INTRODUCCIÓN

La polinización por animales es una de las interacciones bióticas más importantes para el mantenimiento de la biodiversidad global y el funcionamiento de los ecosistemas (Bascompte y Jordano, 2007; Ollerton et al., 2011) y necesaria para el bienestar de la población humana (Potts et al., 2016). En los bosques tropicales secos del nuevo mundo, los colibríes son las aves polinizadoras más especializadas, que contribuyen a la polinización de una amplia variedad de plantas con flores (Arizmendi & Ornelas, 1990; Ortiz-Pulido et al., 2012), y en algunas áreas, actúan como polinizadores efectivos y casi exclusivos de algunas especies (Machado & López, 2004). En la actualidad, los bosques secos tropicales, especialmente los de Centro América, han experimentado altas tasas de deforestación debido principalmente a su conversión en áreas agrícolas y ganaderas (Chazdon et al., 2011; Maass, 1995; Tucker et al., 2005). Bajo este extenso uso del suelo, la vegetación natural ha sido reducida a fragmentos pequeños y degradados, inmersos en una matriz agrícola, con menos del 2% en un estado más o menos intacto (Janzen, 1988). Aunque muchas especies de colibríes parecen ser resilientes a la transformación y perturbación del hábitat (Maruyama et al., 2019; Mcgregor-Fors & Schondube, 2011; Sonne et al., 2016), poco se sabe sobre el efecto de la conversión de bosques secos tropicales en áreas agricultura en la diversidad de colibríes y en sus interacciones de polinización con especies de plantas nativas. Por lo tanto, una mejor comprensión de la composición y variación de los ensambles de colibríes en ecosistemas tropicales secos transformados puede ser útil para el desarrollo de estrategias de conservación tanto de la diversidad de colibríes como de las interacciones planta-polinizador en las que participan.

Aunque el efecto de la conversión de hábitats naturales en áreas agrícolas sobre la diversidad de colibríes y sobre las interacciones mutualistas en las que participan ha sido poco explorado (pero ver Maruyama et al., 2019) algunas características distintivas del grupo pueden dar indicaciones sobre la posible respuesta de los colibríes y de las interacciones en las que participan en este tipo de ambiente perturbados. Por ejemplo, la mayoría de las especies de colibríes son muy móviles y generalistas de hábitat (Araujo & Sazima, 2003; Arizmendi & Ornelas, 1990; Feinsinger, 1976; Hadley & Betts, 2009; Ortiz-Pulido et al., 2012), lo que les permite utilizar diferentes recursos a lo largo del paisaje, dándoles la oportunidad de persistir en ambientes agrícolas e incluso formar

nuevas interacciones con plantas cultivadas. Además, dada la habitual pérdida de riqueza de especies, la homogeneización biológica y el predominio del colibríes y plantas generalistas en hábitats modificados por el hombre (Lindell et al., 2004; Maruyama et al., 2019; Mcgregor-Fors & Schondube, 2011; Mukherjee, et al. 2018), también podríamos esperar un cambio a un conjunto más generalista de interacciones colibrí-planta (Maruyama et al., 2019). También se podría esperar que dada la asociación entre la diversidad de colibríes y la disponibilidad de recursos florales (Montgomerie & Gass, 1981), los cambios en la riqueza de plantas y la abundancia de flores en hábitats transformados también podría afectar la diversidad de colibríes y el número, tipo y arreglo de la interacción colibrí-planta en estos ambientes. Es más probable que esto ocurra en hábitats altamente estacionales, como los bosques tropicales secos, donde la disponibilidad de flores está relacionada con regímenes cíclicos marcados de precipitación (Abrahamczyk & Kessler, 2015).

Además de realizar estudios básicos de diversidad, un enfoque útil para estudiar las interacciones entre los organismos y cómo cambian en relación con la conversión del hábitat es emplear el análisis de redes de interacción ecológica (Harvey et al., 2017; Kaiser-Bunbury & Blüthgen, 2015). El análisis de redes permite una mejor comprensión de la estructura y la dinámica de un conjunto de polinizadores y sus plantas asociadas que interactúan a nivel de comunidad (Harvey et al., 2017). Recientemente, se han recomendado algunas métricas de redes cuantitativas que estudian los atributos de diversidad y distribución, como la diversidad de interacciones, la diversidad de compañeros de red y el grado de especialización de la red (H'2), para describir los cambios en los patrones de redes ecológicas que tienen implicaciones para la conservación (Kaiser-Bunbury & Blüthgen, 2015). En consecuencia, en esta tesis empleamos no solo un análisis convencional de la diversidad de colibríes en respuesta a diversos niveles de perturbación de un bosque seco tropical si no también las métricas de redes como una guía para analizar la comunidad de colibríes y sus plantas asociadas en hábitats naturales y transformados en un bosque tropical seco de Guatemala.

La presente tesis incluye el estudio de la diversidad de colibríes en áreas de bosque tropical seco con distinto nivel de perturbación antrópica y el análisis de la respuesta de dicha diversidad en relación a la estacionalidad. Incluye también un análisis de la influencia de la estacionalidad y el tipo de hábitat (bosque seco tropical o agrícola) sobre el número total de interacciones de colibríes-planta que se pueden registrar en el sitio del estudio. De la misma manera, se comparó la estructura

y el funcionamiento de las redes de interacciones colibríe-planta en sitios de bosque seco tropical y áreas agrícolas, con el fin de analizar el efecto de la transformación de los bosques secos tropicales en áreas agrícolas sobre distintos atributos de estas redes de interacción planta-polinizador. La información obtenida a través de esta tesis será útil para identificar la respuesta a nivel de comunidad de los colibríes de bosque seco a la perturbación antrópica y uso del suelo que puede sumarse a la información necesaria para lograr establecer planes de conservación de colibríes y de plantas nativas de bosques secos tropicales principalmente porque que se analiza la influencia de la conversión del hábitat sobre dicha diversidad y se identifica el papel tanto de las especies de colibríes como de las plantas en el mantenimiento de las interacciones mutualistas de polinización en paisajes agrícolas.

Capítulo 1. Artículo: Bustamante-Castillo, M., Hernández-Baños, B. & Arizmendi, MC. 2018. Hummingbird Diversity and Assemblage Composition in a Disturbed Tropical Dry Forest of Guatemala. Tropical Conservation Science, 11:1-15.

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.

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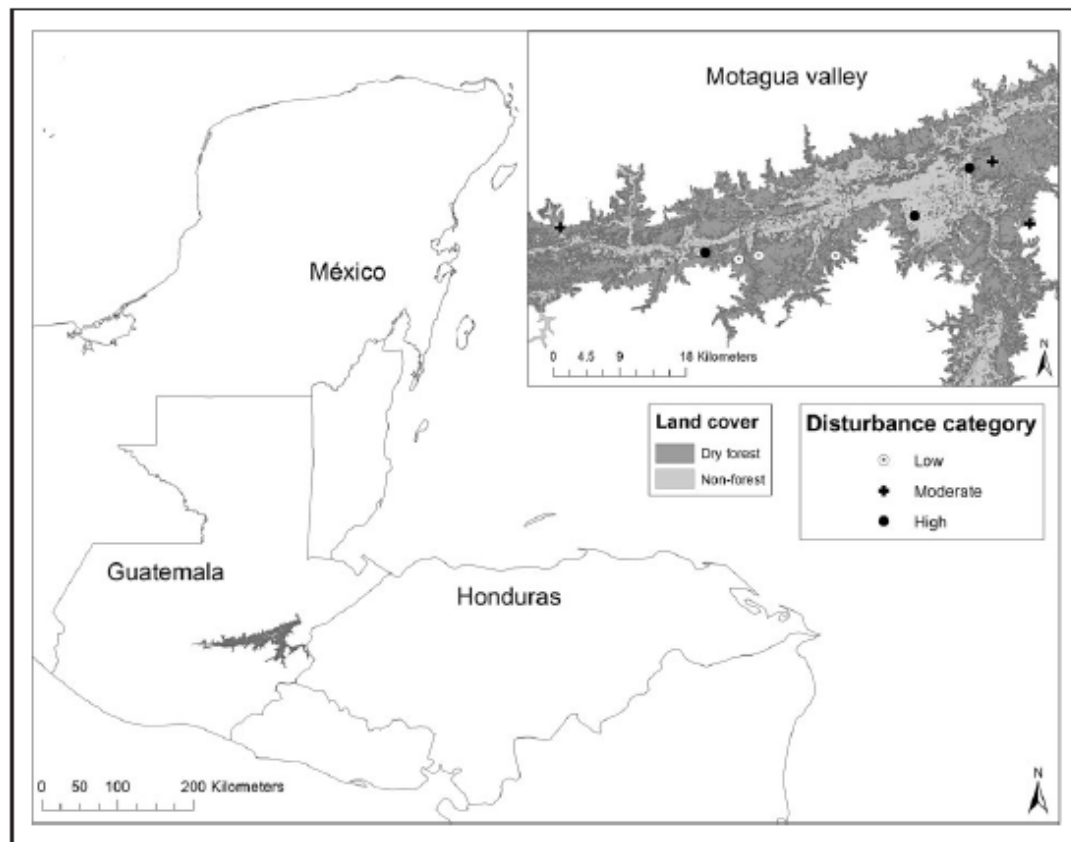
Figure 1. Map of study area, showing land cover and location of the study sites at the Motagua valley in Guatemala.

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).
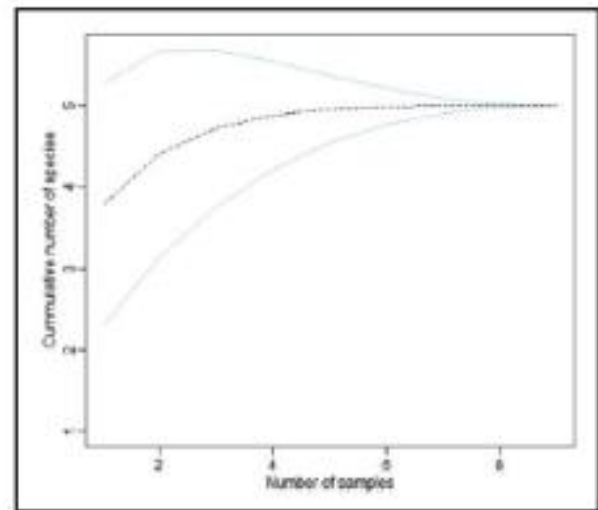
Figure 3. Hummingbird species accumulation curve for the study area at the Motagua valley in Guatemala.
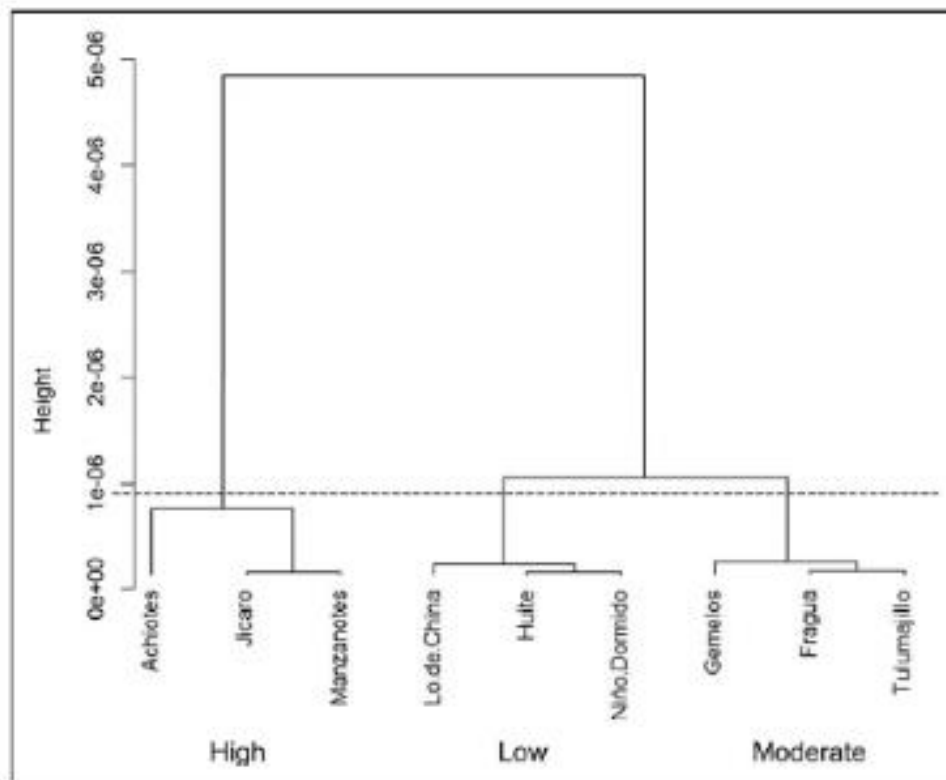
Figure 2. Cluster analyses of the sampling sites at the Motagua valley in Guatemala, obtained by warD2 agglomerative method and correlation distance, from abundance data of plant species and values of seven measured quantitative descriptors of disturbance at each study site. Sites were separated in three 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
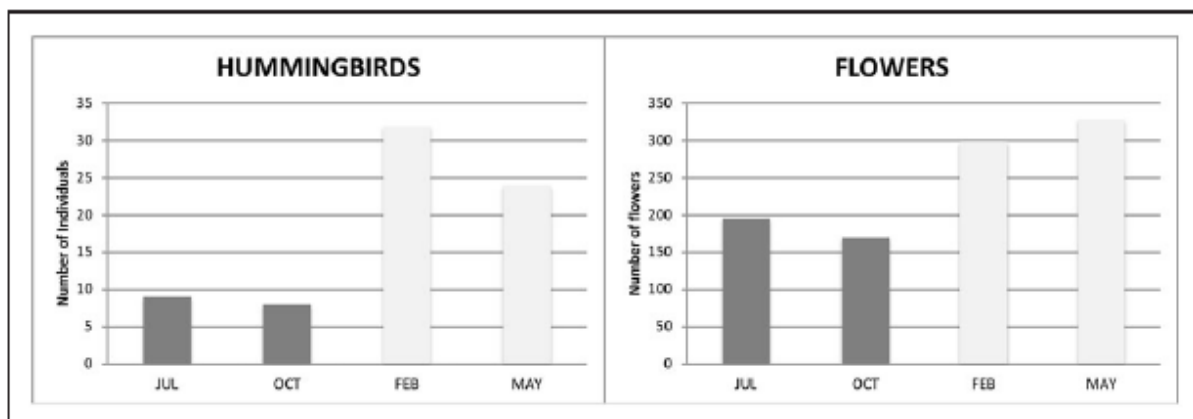

Figure 4. Hummingbird and flower seasonal availability at the Motagua Valley during wet (gray) and dry (white) seasons.
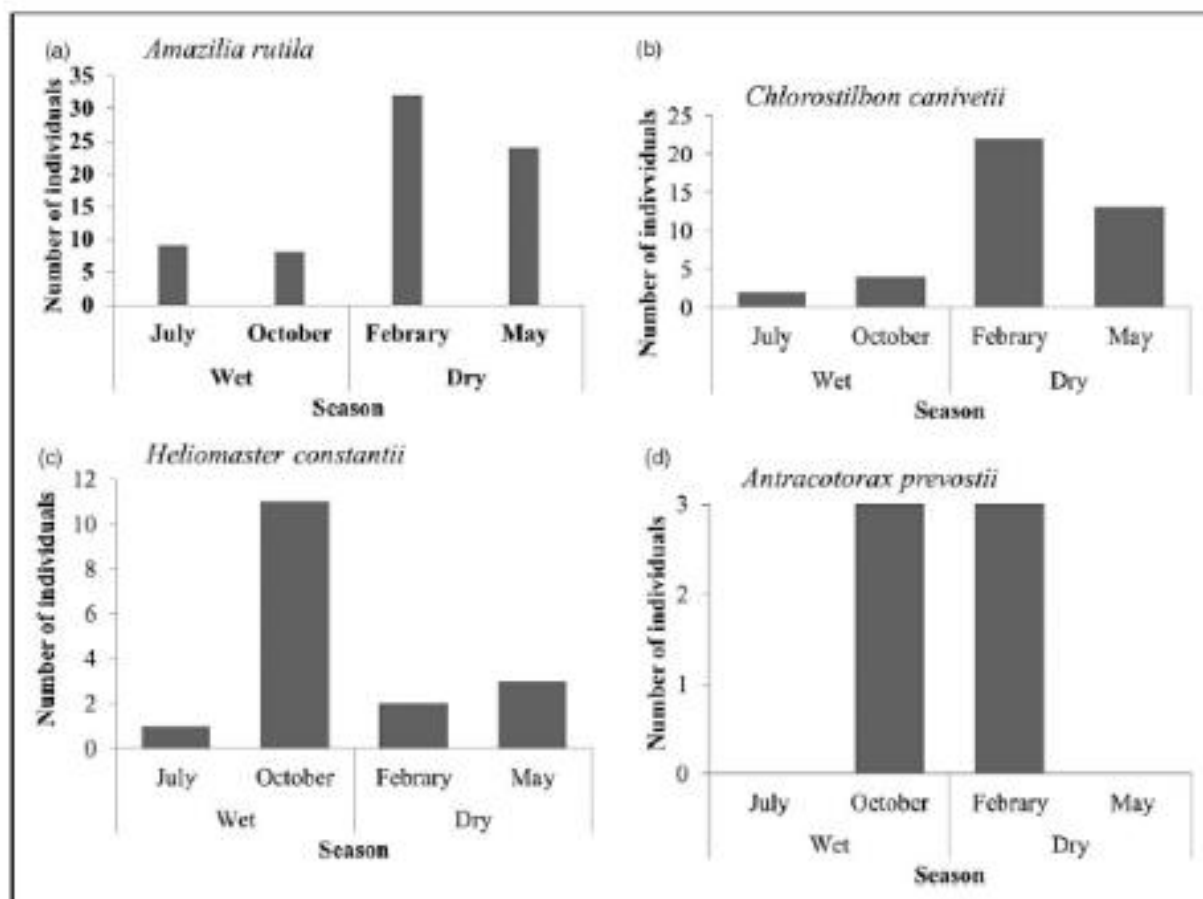
Figure 5. Number of individuals registered per month per hummingbird species at the Motagua valley in Guatemala. (a) Number of individuals registered per month for *Amazilia rutila*, (b) number of individuals registered per month for *Chlorostilbon canivetii*, (c) number of individuals registered per month for *Heliomaster constantii*, and (d) number of individuals registered per month for *Anthracothorax prevostii*.
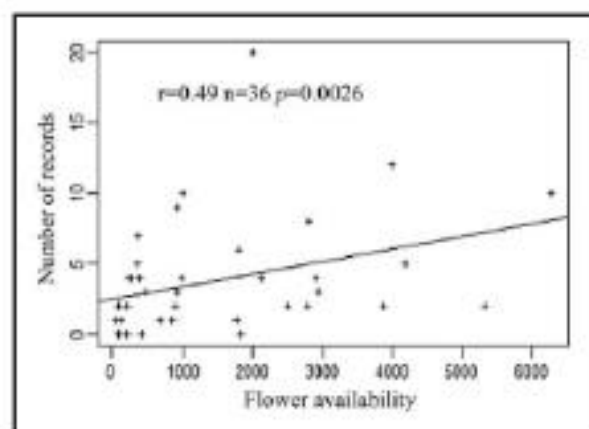
Figure 6. The correlation between the total number of hummingbird records per month and the total number of flowers (of 23 plant species) used as food resources by hummingbirds in the Motagua valley.

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
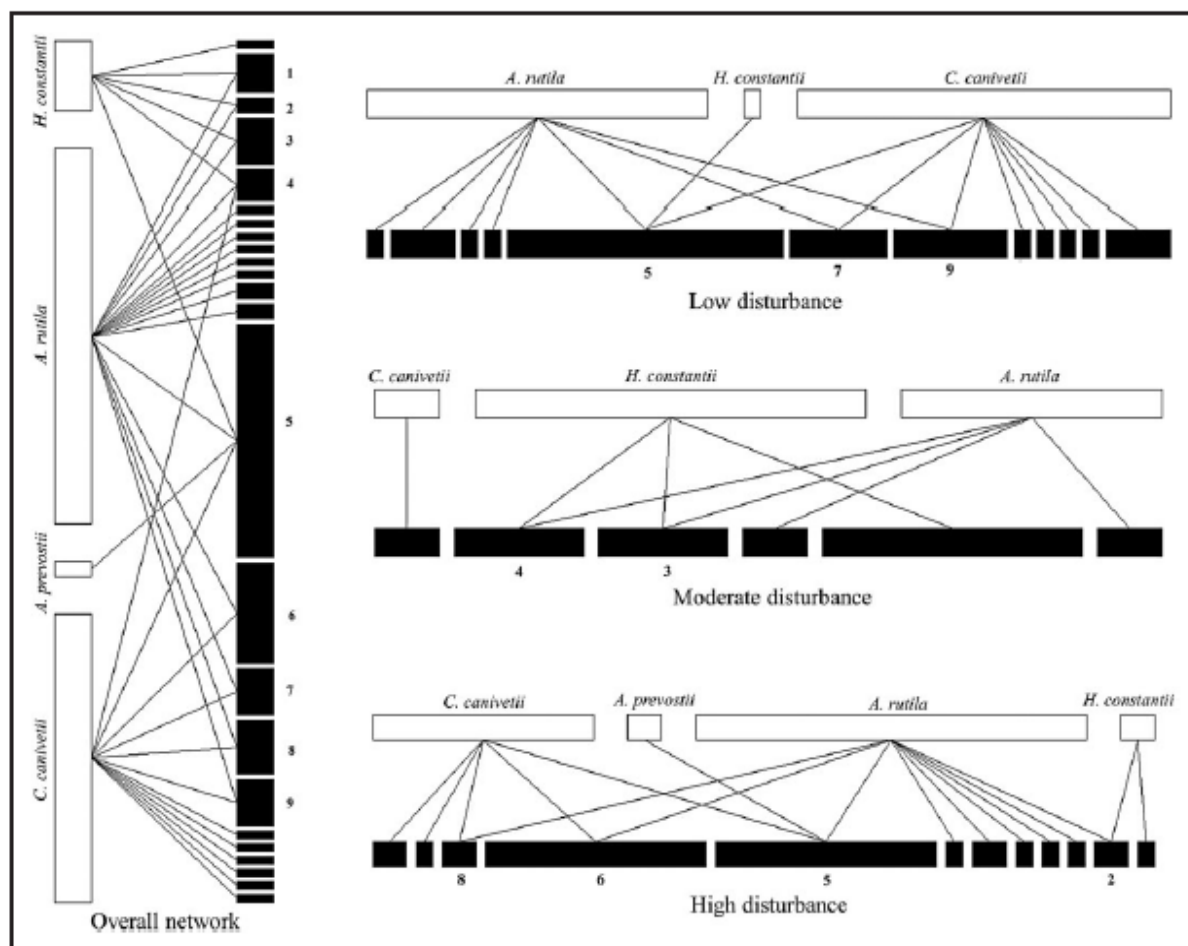
Figure 7. Hummingbird–plant visitation networks of the Motagua valley in Guatemala. The white boxes represent hummingbird species and the black boxes represent the plant species visit by them. The lines linking the boxes represent pairwise interactions. The overall network was obtained by pooling all 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*.
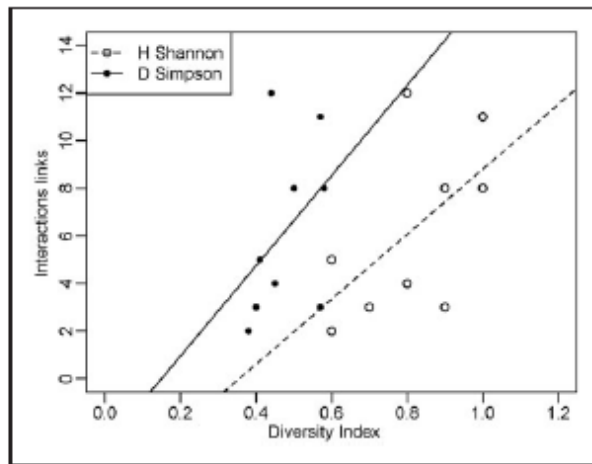
Figure 8. Correlations between diversity indexes, Shannon–Wiener (open circles; $y = 13.64 - 4.84$; $R^2 = .32$, $p = .11$) and Simpson (dark circles; $y = 18.95x - 2.83$; $R^2 = .16$, $p = .27$).

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 m²
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

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.

Disturbance category	Site	Species richness	Species richness estimation		H′	D′	Effective number of species
			Jack1 (±SE)	ACE (±SE)			
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.

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Capítulo 2. Artículo: Hummingbird-plant visitation networks in agriculture and forested areas in a tropical dry forest of Guatemala.

Hummingbird-plant visitation networks in agricultural and forested areas in a tropical dry forest region of Guatemala

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ABSTRACT

In the present study, we evaluated how seasonality and habitat conversion affect the total number of recorded hummingbird-plant interactions in a tropical dry forest of Central America. We used network analysis to assess the effects of habitat conversion on the structure and dynamics of the plant-hummingbird assemblages at our study sites. Data on hummingbird visitation to native flowering plants were collected along four transects located in patches of tropical dry forest and four transects in agricultural areas. Each transect was visited twice during the dry season and twice during the rainy season. Our data suggest that, at a local scale, seasonality is a stronger predictor than habitat type of the recorded number of hummingbird-plant interactions at our study sites. The lack of differences in the number of interactions with respect to habitat type is probably related to the generalist nature of our studied hummingbird-plant assemblages, allowing plants and hummingbirds to persist and form new interactions in the transformed environment. Our data also suggest that, although hummingbird-plant assemblages can persist in agricultural environments, habitat conversion to agriculture can cause changes in network patterns such as lower interaction diversity, lower partner diversity, and a higher level of generalization, which have negative

implications for the conservation of mutualist pollination interactions. Therefore, our data highlight the importance of natural and semi-natural tropical dry forest remnants within agricultural landscapes for the conservation of pollinators and pollination services necessary for the reproduction of native plants.

INTRODUCTION

Pollination by animals is one of the most important biotic interactions because it is essential for the maintenance of global biodiversity and ecosystem functioning (Bascompte and Jordano 2007; Ollerton et al. 2011) and the welfare of the human population (Potts et al. 2016). In New World tropical dry forests, hummingbirds are the most specialized bird pollinators, contributing to the pollination of a wide variety of flowering plants (Arizmendi and Ornelas 1990; Ortiz-Pulido et al. 2012). In some areas, hummingbirds act as effective and nearly exclusive pollinators of some plant species (Machado and Lopez 2004). Presently, tropical dry forest, especially in Central America, has experienced high rates of deforestation primarily due to conversion to agriculture (Maass 1995; Tucker et al. 2005; Chazdon et al. 2011). Natural dry forest has been reduced to small or degraded fragments immersed in an agricultural matrix, and less than 2% of the original forest remains in a more or less intact state (Janzen 1988). Many hummingbird species seem to be resilient to habitat transformation (Mcgregor-Fors and Schondube 2011; Sonne et al. 2016; Bustamante-Castillo et al. 2018; Maruyama et al. 2019), yet little is known about the effects of the conversion of tropical dry forest to agriculture on the pollination interactions between hummingbirds and native plants. A better understanding of hummingbird-plant communities in transformed tropical dry forest ecosystems can be useful for the development of conservation strategies to maintain hummingbird diversity and plant-pollinator interactions.

As mentioned, the effects of the conversion of natural habitats to agriculture on hummingbirds and their mutualistic interactions has been little explored (see Bustamante-Castillo et al. 2018 and Maruyama et al. 2019), but some distinctive characteristics of hummingbirds may indicate the possible outcomes of land use change for hummingbird populations. For instance, most

hummingbird species are highly mobile habitat generalists (Feinsinger 1976; Arizmendi and Ornelas 1990; Araujo and Sazima 2003; Hadley and Betts 2009; Ortiz-Pulido et al. 2012), so many hummingbirds are able to use different resources throughout the landscape and form new interactions in agricultural areas. Following the usual loss of species richness and the biological homogenization and dominance of generalist hummingbird and plant species in human-modified habitats (Lindell et al. 2004; Mcgregor-Fors and Schondube 2011; Mukherjee et al. 2018; Maruyama et al. 2019), we could also expect a shift toward a more generalist set of hummingbird-plant interactions (Maruyama et al. 2019). Furthermore, given the association between hummingbird diversity and flower resource availability (Montgomerie and Gass 1981), changes in plant richness and flower abundance in transformed habitats could affect the number, type, and arrangement of hummingbird-plant interactions. These changes are more likely to occur in highly-seasonal habitats, such as tropical dry forests, where flower availability is related with the marked cyclical rainfall regime (Abrahamczyk and Kessler 2015). Accordingly, seasonality and habitat conversion as well as their interaction may have consequences for hummingbird mutualisms in transformed tropical dry forest areas.

One useful approach for studying ecological interactions between organisms and how they change following habitat conversion is network analysis (Kaiser-Bunbury and Blüthgen 2015; Harvey et al. 2017). Network analysis enables a better understanding of the structure and dynamics of an assemblage of pollinators and plants interacting at the community level and therefore enables identification of more appropriate conservation targets for maintaining ecosystem integrity (Harvey et al. 2017). Recently, some quantitative metrics that are descriptive of the diversity and distribution attributes of an ecological interaction network were recommended for describing changes in network patterns: partner diversity, interaction diversity, and network complementary specialization. These attributes have important implications for conservation (Kaiser-Bunbury and Blüthgen 2015). We used these metrics to guide our analysis of a hummingbird-plant community in a tropical dry forest of Guatemala.

First, we assessed the influence of seasonality and habitat type (tropical dry forest and agriculture) on the total number of hummingbird-plant interactions that could be recorded in our study area. Second, we compared the structure and functioning of the hummingbird-plant network between

tropical dry forest and agricultural areas. Additionally, we established which hummingbirds and flowering plants are most important in the maintenance of the hummingbird-plant community in our study area. Finally, we discuss the implications of the conversion of native habitats, particularly dry forest, to agriculture and the role of specific plants/pollinators as organizers of the identified plant-pollinator assemblage. Our findings are useful for the long-term conservation of hummingbirds and native plants and can be subsequently used in conservation efforts in agriculture landscapes.

METHODS

Data on hummingbird visitation to flowers were collected in 8 sites in the Motagua Valley of eastern Guatemala ranging from 300 to 900 masl (Moran 1971) (Fig. 1). The mean annual temperature of this area is 26.9 °C, and the average annual rainfall is 815 mm (Najera 2006). The climate is tropical sub-humid, with a dry season lasting 5–7 months, usually from November to May (Najera 2006). The study area is composed of a mosaic of disturbed tropical dry forest patches in a matrix of anthropogenic land uses including crops (melon, watermelon, lemon, tobacco, and okra), pastures, and human settlements. We selected 4 sites in tropical dry forest and 4 sites in agricultural areas. To record hummingbird-plant interactions, a transect of approximately 2 km was established in each site. Fifteen observation points were marked along each transect and spaced 150 m from each other. Visits to each site were performed from 06:30 to 11:30. Each transect was visited twice during the dry season (May and October 2013) and twice during the rainy season (July 2013 and February 2014).

Each point was observed by two observers for a 10-min period during which all hummingbird visits to flowers were recorded. A visit was recorded when a hummingbird probed a flower from the corolla opening, touching the reproductive structures of the flower. We also recorded the number of flowers visited by each observed hummingbird and the time spent at each flower. In addition, we counted the number of available, open flowers within a 30-m radius from the central point. Observations were focused on plants know or presumed to be visited by hummingbirds. Because the number of flowers varies among individuals and species, we considered a visit every time a hummingbird approached an individual plant and fed on at least one flower of that plant species.
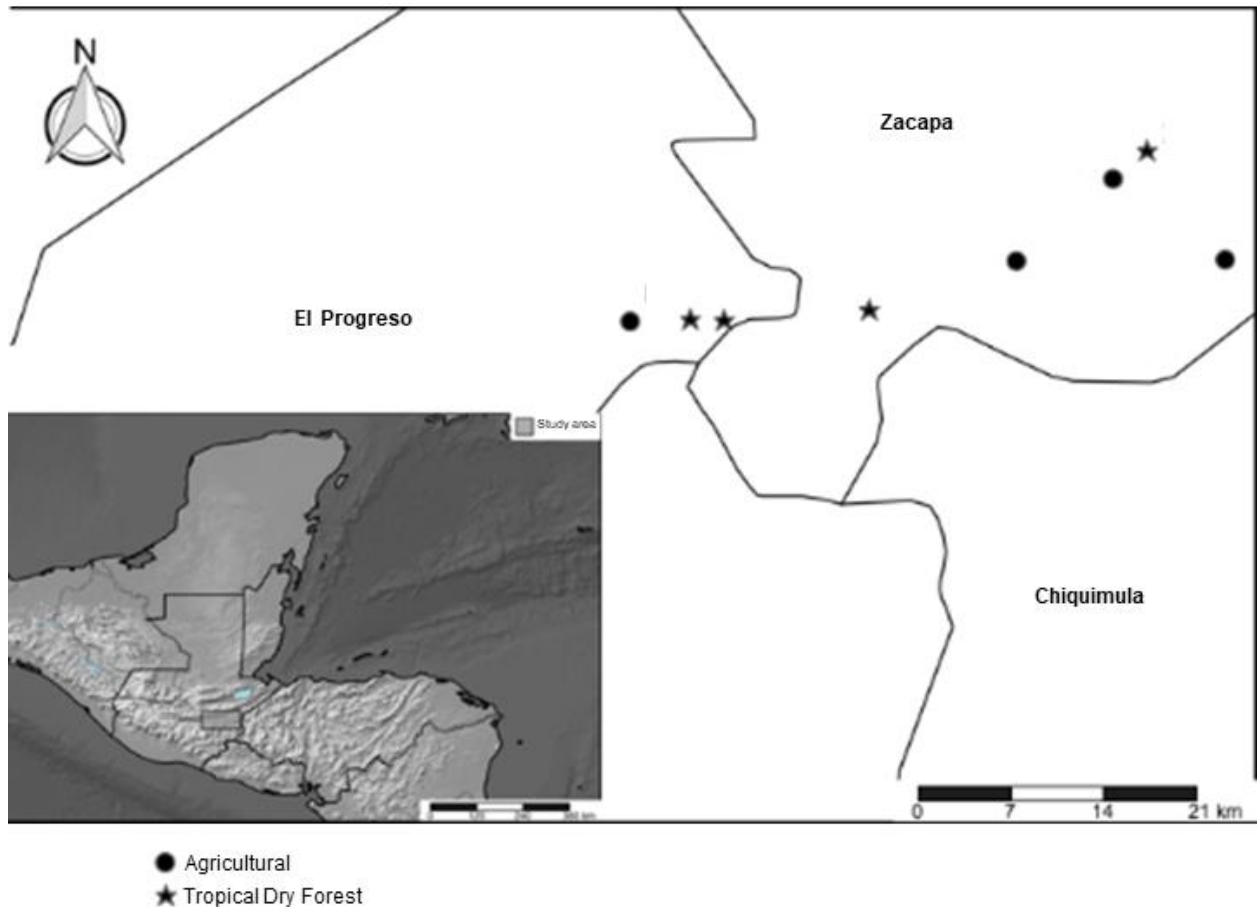
Fig. 1 Map of the study sites in Motagua Valley, eastern Guatemala.

A cumulative curve of interactions was plotted to determine whether our sampling effort was sufficient for recording all hummingbird-plant interactions in the study area. The expected number of unobserved hummingbird-plant interactions was estimated using the Bootstrap estimator, which is recommended when the community includes many rare species (in this case, rare interactions) (Poulin et al. 1993). A matrix with the observed hummingbird-plant interactions in the columns and the four sampling months in the rows was constructed. Then, a direct estimation of the unobserved pairwise interactions was performed using the specpool function in the Vegan package in R.

To test for possible correlations between the number of recorded hummingbirds and flower richness and availability, we used Kendall's correlation, which is a rank-based measure of association for data that do not necessarily have a bivariate normal distribution. We tested whether

the monthly total number of recorded hummingbirds at each study site was correlated with the total number of flowering plant species and available flowers.

We also evaluated how seasonality and habitat type (and the possible interaction between these two factors) affected the total number of recorded hummingbird-plant interactions by fitting a generalized linear-mixed model (GLMM, package lme4 in R) with a Poisson error distribution and a log-link function to the experimental data. Sites were included as a random factor considering that counts were performed four times at each study site. After analyzing which factors influenced the number of hummingbird-plant interactions recorded, we removed from the final model those factors (or the interaction between them) that did not show a significant effect ($p>0.05$).

Network analysis

divWe built quantitative interaction networks per site (combining data from both seasons) and per habitat type (combining data of all habitat type replicates), considering the number of visits as a measure of the strength of the interactions. We then calculated five network metrics for each of these networks that characterize distinct aspects of the networks structure: 1) Connectance (C) describes the realized proportion of possible links in a network (Dunne et al. 2002). 2) Nestedness (NODF) quantifies the degree to which interactions between specialized species are subsets of the interactions between more generalist species in the network. Nestedness describes the topological feature of poorly-linked nodes typically being linked to more generalist nodes. This structure tends to buffer poorly-linked species from becoming extinct (Bascompte et al. 2003). To calculate nestedness and its level of significance in the tropical dry forest and agricultural networks, we used the Ce null model in ANINHADO (Guimarães and Guimarães 2006). This latter model assumes that the probability of occurrence of an interaction is proportional to the level of generalization of both interacting species. 3) Shannon diversity (S) represents the diversity of interactions in the entire network. 4) Complementary specialization (H'2) is an index designed to measure network-wide specialization for quantitative interaction matrices. It describes how species restrict their interactions with respect to those randomly expected based on partner availability (Blüthgen et al. 2006). 5) Robustness (R) is a metric that measures the tolerance of a system to species loss. It is calculated using the area below the extinction curve (Memmott et al. 2004) based on the likelihood that the elimination of a given fraction of species in one guild will lead to the extinction of a

number of species in another guild dependent upon their interactions. The curve provides a graphic description of the tolerance of a system to the extinction of component species. A value of 1 corresponds with a curve that decreases very mildly until a point at which almost all animal species are eliminated, which is consistent with a very robust system. Conversely, a value of 0 corresponds with a curve that decreases abruptly as soon as any single species is lost, which is consistent with a fragile system. Additionally, and only for the habitat type networks we calculate species strength (Es) and Partner diversity metrics (PD). The first one assesses the role of species within networks and its variance between habitats. Corresponds to the sum of the proportion of interactions of a given species with all interaction partners. Higher values indicate that more plants depend on a specific hummingbird species or vice versa (Bascompte et al. 2006). partner diversity is the (weighted) mean Shannon diversity of the number of interactions for the species of that level. All metrics except for nestedness were calculated using the bipartite package (Dormann et al. 2008) in R. Finally, to test for differences between network parameters between habitat types we performed a t-test analysis.

RESULTS

We recorded five hummingbird species in the Motagua Valley: Canivet's Emerald (*Chlorostilbon canivetii* [Lesson, R, 1832]), the Cinnamon Hummingbird (*Amazilia rutila* [Delattre, 1843]), the Green-breasted Mango (*Anthracothorax prevostii* [Lesson, R, 1832]), the Ruby-throated Hummingbird (*Archilochus colubris* [Linnaeus, 1758]), and the Plain-capped Starthroat (*Heliomaster constantii* [Delattre, 1843]). These hummingbirds visited a total of 19 plant species. We observed 80 interactions between hummingbirds and plants in the 8 study sites (Fig. 2). The Cinnamon Hummingbird was involved in 45% of interactions, Canivet's Emerald in 39%, the Plain-capped Starthroat in 9%, the Ruby-throated Hummingbird in 4%, and the Green-breasted Mango in only 3%.
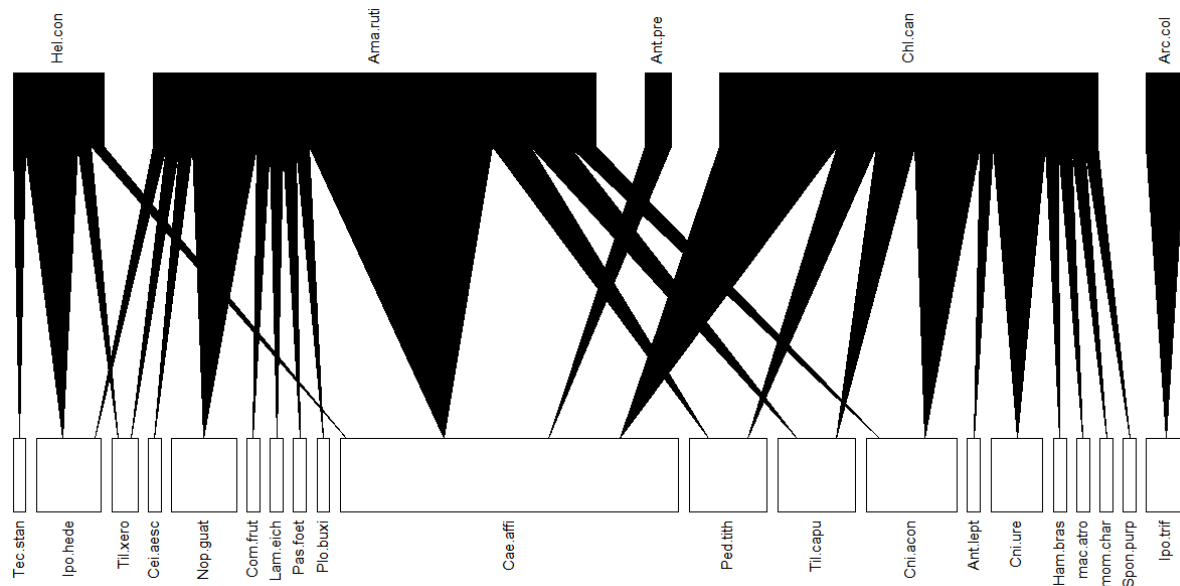
Fig. 2 Graphical representation of the overall hummingbird-plant visitation network of the study area. The lines represent the 80 recorded interactions, and the size of the boxes is proportional to the number of species with which each species is interacting. The width of the links is proportional to the number of hummingbird visits observed for a particular plant species. Hummingbird species abbreviations: Ama.rut (*Amazilia rutila* [Delattre, 1843]), Ant.pre (*Anthracothorax prevostii* [Lesson, R, 1832]), Arc.col (*Archilochus colubris* [Linnaeus, 1758]), (*Chlorostilbon canivetii* [Lesson, R, 1832]), and Hel.con (*Heliomaster constantii* [Delattre, 1843]). Plant species abbreviations: Art.lep (*Antigonon leptopus* Hook and Arn.), Cae.aff (*Caesalpinia affinis* Hemsl.), Cei.aes (*Ceiba aesculifolia* [Kunth] Britten and Baker f.), Cni.aco (*Cnidoscolus aconitifolius* [Mill.] I.M. Johnst.), Cni.ure (*Cnidoscolus urens* [L.] Arthur), Com.fru (*Combretum fruticosum* L.), Ipo.hed (*Ipomoea hederifolia* L.), Ipo.tri (*Ipomoea trifida* [Kunth] G. Don), Lam.eich (*Lemaireocereus eichlamii* Britton and Rose), Mac.atr (*Macroptilium atropurpureum* [Moc. and Sessé ex DC.] Urb.), Mom.cha (*Momordica charantia* L.), Nop.gua (*Nopalea guatemalensis* Rose), Pass.foe (*Passiflora foetida* var. *gossypifolia* L.), Ped.tit (*Pedilanthus tithymaloides* [L.] Poit.), Plo.bux (*Plocosperma buxifolia* Benth.), Spo.pur (*Spondias purpurea* L.), Tec.sta (*Tecoma stans* [L.] Juss. Ex Kunth), Till.cap (*Tillandsia caput-medusae* C.J. Morren), and Till.xer (*Tillandsia xerographica* Rohweder).

We registered approximately 79% of the estimated interactions for the study area (Bootstrapp= 46.87, stdv=7.2, n=4). The accumulation curve (Fig. 3) indicates that if we had sampled more days or more study sites, we would have detected more links in our network.
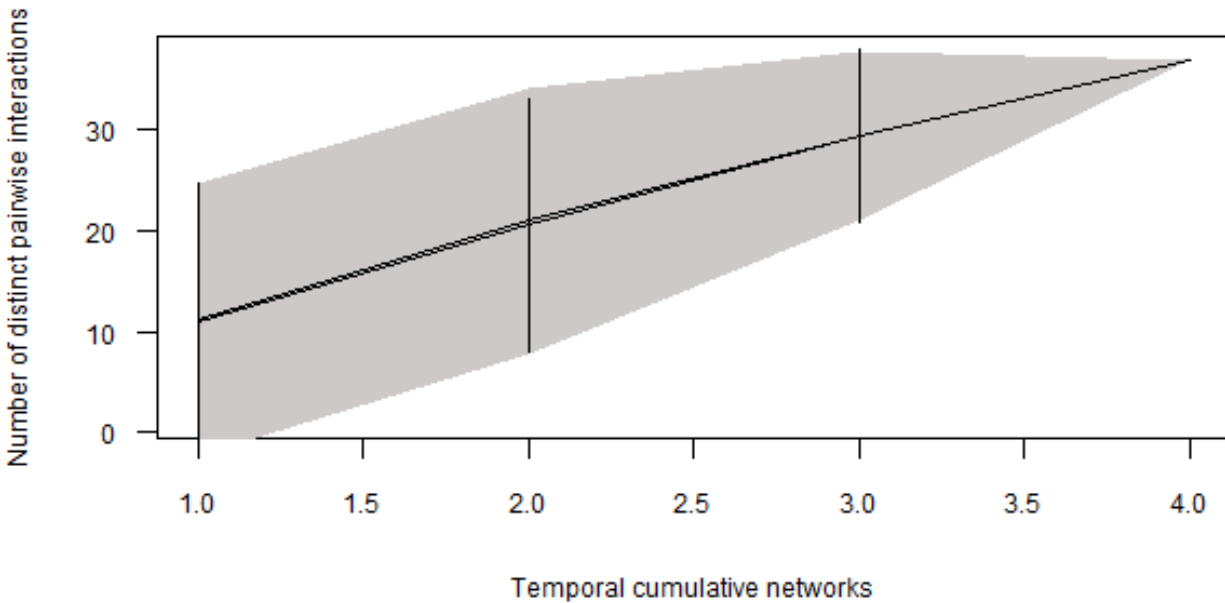

Fig. 3. Cumulative plant-hummingbird interactions in a) tropical dry forest and b) agricultural habitats in the Motagua Valley of Guatemala. The lines represent the recorded interactions, and the size of the boxes is proportional to the number of species with which each species is interacting. The width of the links is proportional to the number of hummingbird visits observed for a particular plant species. The species abbreviations are detailed in Fig. 2.

The number of hummingbird species (X^2=8.1476, df=1, P=0.0043), the number of hummingbird individuals (X^2=7.7686, df=1, P=0.0053), and the number of plant species used by hummingbirds (X^2=8.3738, df =1, P=0.0038) were significantly higher during the dry season. Only the total number of available flowers did not significantly differ between seasons (X^2=0.41051, df=1, P=0.5217).

The variables mentioned above did not significantly vary in relation to habitat type (number of hummingbird species X^2=0.42789, df=1, P=0.513; number of hummingbird individuals X^2=1.3676, df=1, P=0.2422, number of plant species used by hummingbirds X^2=1.9249, df=1, P=0.1653; and number of flowers available X^2=0.24006, df=1, P=0.6242). However, we did find an additional significant and positive association between the monthly number of hummingbird

species and individuals in each study site with the number of blooming plant species (z=2.0626, P=0.039, r=0.31; z=2.1352, P=0.033, *r*=0.30) and the total number of available flowers (z=2.0103, P=0.04, r=0.28; z=1.9958, P=0.04, *r*=0.30).

With respect to the hummingbird-plant interactions, we recorded a total of 67 interactions during the dry season and 13 during the rainy season. A higher number of interactions was observed in the tropical dry forest sites (N=52) than in the agricultural sites (N=23). On average, we recorded a higher number of hummingbird-plant interactions during the dry season and in the tropical dry forest (Fig. 4).
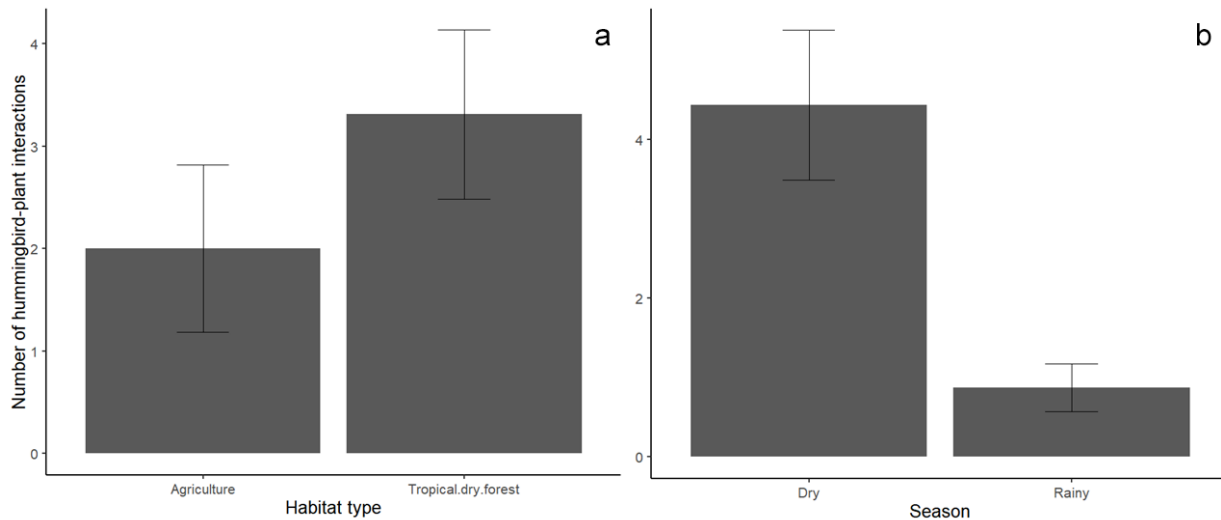
Fig. 4 Average number of hummingbird-plant interactions and standard deviation recorded in the Motagua Valley of Guatemala. a) Average number of hummingbird-plant interactions per season and b) average number of hummingbird-plant interactions in agricultural and tropical dry forest (forest) habitats.

Once again, seasonality, but not habitat type, significantly contributed to predicting the number of hummingbird-plant interactions in the Motagua Valley (Table 1). The GLMM indicated that, during the dry season, it is possible to record almost twice the number of hummingbird-plant interactions in the study area (Table 1).

Table 1 Results from the generalized linear mixed-effects model showing the relationship between seasonality and the number of hummingbird-plant interactions recorded in the study area. Habitat type and the interaction between habitat type and Seasonality did not show a significant effect ($p<0.05$) so they were excluded from the model.

	Coefficient B	Standard error	z	p
Intercept	1.3205	0.2523	5.234	$1.66e^{-07}$
Rainy season	−1.6236	0.2885	−5.628	$1.83e^{-08}$

Network analysis

All individual networks were relatively small, and had a high connectance value (Table 2). All of them showed low nestedness value and were not significantly nested, meaning that the partners of the most specialized species were not a subset of those interacting with the most generalist species. All of the networks showed a high robustness to the random extinction of species. In addition, we did not find significant differences in any of the network parameters between habitat types (Table 2). Nonetheless, the mean values of the Shannon diversity index, Robustness and Network specialization were slightly higher at tropical dry forest (Table 2). Only the mean connectance value was marginally higher at agricultural sites.

Table 2 Values of the hummingbird-plant visitation networks parameters per site at the Motagua Valley of Guatemala.

Habitat type	Site ((number of hummingbird species/ number of plant species)	Size	link per specie	C	NODF Er (p)	S	R	H'2
Agriculture	Achiotes	3 x 4	0.75	0.4	21.78 (0.76)	1.74	0.64	0.5
	Jicaro	2 x 2	0.75	0.75	28 (0.8)	1.03	0.75	0
	Manzanotes	3 x 4	1.1	0.52	-----	2.13	0.74	0.1
	Fragua	1 x 1	0.5	1	----	1.03	-----	0
	mean (SD)		0.77(0.24)	0.67(0.26)		1.48(0.54)	0.71(0.06)	0.15(0.23)
Tropical dry forest	Gemelos	1 x 1	0.8	0.66	----	1.15	-----	0
	Huite	6 x 3	0.88	0.44	21.38 (0.42)	1.97	0.73	0.3
	Lo de China	4 x 8	0.92	0.34	13.33 (0.64)	2.21	0.7	0.5

Niño Dormido	2 x 7	0.88	0.57	21.28 (0.94)	2.03	0.77	0.6
mean (SD)		0.87(0.05)	0.5(0.14)		1.84(0.47)	0.73(0.03)	0.35(0.27)
t		0.75478	1.0993		-0.99119	-0.5754	-1.1239,
(*p* value)		(0.47)	(0.31)		(0.35)	(0.59)	(0.30

Upon comparing the overall networks of both habitats (networks built with the data collected in the four replicates of each habitat type) both showed a connectance value around 36% (Table 3). In addition, both networks showed a low nestedness. The tropical dry forest network had a slightly higher diversity value than the agricultural network (Table 3). In relation to the diversity of interaction partners for individual species in the networks, hummingbirds interact with a more diverse set of flowering plant resources in the tropical dry forest network than in the agricultural network. On the other hand, plants have a higher diversity of interaction partners in the agricultural network.

Table 3 Values of the hummingbird-plant visitation networks parameters per habitat type at the Motagua Valley of Guatemala.

	Habitat	
Network parameter	**Tropical dry forest**	**Agriculture**
Size (number of hummingbird species/ number of plant species)	4×13	4×9
C	0.35	0.36
NODF*	27.05	20.63
S	2.61	2.38
Partner diversity (hummingbird/plants)	1.50/0.49	1.28/0.63
H'2	0.47	0.24

*No significantly nested (P>0.05).

Overall, with respect to the resistance of the networks to different extinction scenarios, both networks were almost equally sensitive to the random and simultaneous extinction of plant and hummingbird species (Table 4). The tropical dry forest network was more robust to the loss of plant species than to the loss of hummingbird species. The agriculture network better resisted the loss of hummingbirds when the most connected species went extinct first and was more robust to the loss of plants when the least abundant went extinct first.

Table 4 Robustness of the hummingbird-plant visitation networks in the Motagua Valley of Guatemala to different extinction scenarios per habitat type: (1) random deletion of species; (2) extinction of the least to most abundant species; and (3) extinction of the best to least connected species.

	Extinction scenario	Tropical dry forest	Agriculture
Both	Random	0.31	0.33
Hummingbird species	Random	0.61	0.72
	Degree	0.40	0.65
	Abundance	0.72	0.83
Plant species	Random	0.72	0.72
	Degree	0.65	0.57
	Abundance	0.83	0.90

Canivet's Emerald (*Chlorostilbon canivetii*) and the Cinnamon Hummingbird (*Amazilia rutila*), which were shared between habitats, were the most relevant species in the networks (Table 4). *Ipomea trifida* and *Caesalpinia affinis* were the most relevant plant species along with additional herbs and shrubs in each network (Table 5).

Table 5 Species strength values for plant and hummingbird species in tropical dry forest and agricultural habitats in the Motagua Valley of Guatemala.

		Species strength	
Group	Species	Tropical dry forest	Agriculture
Hummingbirds	*Amazilia rutila*	4.51	5.55
	Archilochus colubris	1	-
	Chlorostilbon canivetii	6.62	1.72
	Heliomaster constantii	0.86	1.50
	Anthracothorax prevostii	-	0.22
Plants	*Antigonon leptopus*	0.043	
	Caesalpinia affinis	0.93	1.71
	Cnidoscolus aconitifolius	0.31	
	Cnidoscolus urens	0.18	
	Ipomoea hederifolia	0.84	
	Ipomoea trifida	1	
	Momordica charantia	0.045	
	Nopalea guatemalensis	0.19	
	Plocosperma buxifolia	0.05	
	Spondias purpurea	0.047	

Tillandsia caput-medusae	0.27	
Pedilanthus tithymaloides	0.04	0.73
Ceiba aesculifolia	0.04	0.076
Combretum fruticosum		0.077
Lemaireocereus eichlamii		0.076
Macroptilium atropurpureum		0.17
Passiflora foetida var gossypifolia		0.077
Tecoma stans		0.50
Tillandsia xerographica		0.57

DISCUSSION

Effects of seasonality and habitat type on the number of hummingbird-plant interactions

As expected, seasonality notably and significantly impacted the number of hummingbird-plant interactions recorded in the Motagua Valley of Guatemala. We found that the recorded total numbers of hummingbirds and flowering plants used by hummingbirds were higher during the dry season, consequently resulting in a higher number of species interactions during this season. Similar results were found in other tropical dry forests in Mexico where hummingbird species were more abundant during the dry season, which is presumably related with the greater abundance of food resources (Arizmendi and Ornelas 1990). Additionally, the effect of seasonality on the number of hummingbird-plant interactions in tropical dry forest is partially related to the cyclical rainfall regime and the marked dry season, which lead to flowering patterns that can, in turn, affect the richness and abundance of hummingbirds (Abrahamczyk and Kessler 2015). The positive correlation found in the present study between the recorded number of hummingbirds per season and flower availability supports these latter findings. In tropical dry forests, flowering commonly occurs during the dry season (Frankie et al. 1974; Borchert 1996; Bennett et al. 2014), and many deciduous plants produce large numbers of flowers during this time of the year when rainfall is at a minimum (Holbrook et al. 1995). The explanation for this flowering pattern has been related with biotic factors such as the lack of interference of the flowering process with the vegetative process, increased flower visibility, and reduced competition for pollinators during this season (Gentry 1974; Janzen 1982; Augspurger 1980). As observed in other tropical dry forests (Stiles and Wolf 1970; Arizmendi and Ornelas 1990), the hummingbirds of the Motagua Valley

apparently move to surrounding areas in response to seasonal changes in resource abundance, consequently affecting the number of interactions formed over time.

Meanwhile, habitat type was not an important determining factor of the number of hummingbird-plant interactions in the study area. Our data suggest that, at a local scale, the number of interactions between hummingbirds and plants does not change significantly between tropical dry forest and agricultural habitats. This finding is probably partially related to the generalist habits of the most abundant hummingbird species in the study area (Cinnnamon Hummingbird, Cavinet's Emerald, and Plain-capped Starthroat) that are involved in the majority of the recorded interactions (93%). These species are often present in human-disturbed and transformed habitats as well as in more preserved natural vegetation (del Hoyo et al. 2018; Stiles et al. 2018; Weller et al. 2018). In addition, the majority of plant species with which hummingbirds interact are herbs or shrubs growing at the edge of tropical dry forests, in open areas, or in patches left undisturbed by farmers following the clearing of vegetation for agricultural activities, including *Caesalpinia affinis* Hemsl., *Pedilanthus tithymaloides* (L.) Poit., *Nopalea guatemalensis* Rose, and herbs of the genus *Ipomea*. In addition, the majority of the agricultural sites have remnants of tropical dry forest with distinct regeneration statuses, so floral resources were available across sites despite differing levels of disturbance, as evidenced by the non-significant differences in flower abundance between habitats.

The generalist hummingbird-plant assemblages in the study area appear to be reflective of the high level of anthropogenic disturbance that characterizes many tropical dry forest areas of Central America. Many of these areas have been seriously degraded for hundreds of years as a result of conversion to agriculture or extensive cattle ranching (Martinez 1985; Janzen 1988). Given such extensive land-use changes, the natural vegetation has been reduced to small and degraded fragments, and less than 2% of the original vegetation remains in a more or less intact state (Janzen 1988). As a consequence, species that are more sensitive to habitat loss, degradation, and fragmentation may have already been lost, whereas bird and plant species assemblages more tolerant of a wider range of conditions may have persisted (Owens and Bennett 2000). In relation to this, Sanaphre-Villanueva et al. (2017) found that the patterns of plant functional variation at the landscape scale in a tropical dry forest of Mexico were mostly driven by dominant generalist

species (in terms of number and relative abundance) across successional stages, possibly reflecting the long history of disturbance in the tropical dry forests of the region (Rico-Gray and García-Franco 1992, Mizrahi et al. 1997).

Network analysis in relation to habitat type

No differences in the connectance values were found in the hummingbird-plant interaction networks of the forested and agricultural sites. This result suggests that, in the Motagua Valley, the number of links between hummingbird and plant species is mostly retained after natural habitats are transformed to crops, which has also been reported in other studies examining the response of pollination networks to disturbances (Aizen et al. 2008; Heleno et al 2012). In the context of our study sites, this also suggests the existence of a landscape effect: hummingbird and plant assemblages do not change drastically because most of the Motagua Valley's hummingbird species are generalist and highly mobile and because agricultural sites harbor a subset of generalist plants from tropical dry forest and other flowering resources. The level of connectance of our networks was relatively low and similar to the ones reported for other hummingbird-plant visitation networks in tropical dry forests in Mexico (mean ± SE=0.38 ± 0.09, Lara-Rodriguez et al., 2012; C=0.21, recalculated for the entire network in Ortiz-Pulido et al. 2012) and a dry ecosystem in Brazil (C=0.33, Maruyama et al. 2019). The similarities in the connectance values of different tropical dry forest networks could be related to the small size of these networks, as small networks are usually highly connected. Several studies have found a relation (to a certain extent) between species richness and connectance values (Jordano 1987; Sugihara et al. 1989; Olsen and Jordano 2002).

With respect to nestedness, some studies have found higher nestedness in the hummingbird-plant networks of transformed or disturbed sites compared to more natural locations (Lara-Rodríguez et al. 2012; Maruyama et al. 2019). However, in the Motagua Valley, both the tropical dry forest and agricultural networks had similar nestedness values and were not significantly nested compared to null models. This result is probably related to the small size of our networks. As various authors have pointed out, small networks tend not to be significantly nested (Bascompte et al. 2003). Guimarães et al. (2006) reported a logarithmic relationship between network size and nestedness and suggested that species-rich systems are likely more highly nested. The explanations for this

pattern may be that nestedness is undetectable below a certain threshold of species richness and that species-poor assemblages do not have enough species for specialized interactions to evolve between specialized and generalist species. Some additional studies have raised the possibility that greater disturbance increases the nestedness of hummingbird-plant networks (Maruyama et al. 2019), yet more studies are needed to determine the effect of conservation on nestedness values in hummingbird mutualistic networks.

As previously observed for other hummingbird-plant visitation networks (Aizen et al. 2012; Maruyama et al. 2019), natural habitat transformation to agriculture in the Motagua Valley has led to slightly more generalized hummingbird-plant interaction network. Higher generalization indicates the lower dependency of species on one or several exclusive partners. The increase in generalization at agricultural sites is likely due to the lower plant species richness and the lower selectiveness of hummingbirds in these sites, thereby decreasing the complementarity specialization of the network. In this context, anthropic habitats are characterized by species that are less selective in their ecological links, resulting in greater connectivity within the networks (Santo de Araujo 2018). Therefore, these data suggest that tropical dry forest transformation has led to a less functionally diverse community and, consequently, to a more generalized interaction network. The generalization of the agricultural network may have contrasting effects in relation to the conservation and robustness of plant-pollinator interactions. In terms of conservation value, networks with more specialized interactions are important for conservation. In terms of community robustness to disturbance and anthropogenic perturbations, high specialization may reduce competition between hummingbirds, increasing the probability of pollen transfer among conspecific plants and thus benefiting both hummingbirds and plants. On the other hand, in networks with high resource specialization, hummingbirds and plant may also be more vulnerable to the extinction of their mutualistic partners (Dalsgaard et al. 2018).

However, the tropical dry forest network did show a higher diversity of partners and interactions, which reflects a richer community and a more even distribution of links in the network (Kaiser-Bunbury and Bluthgen 2015). The latter condition is associated with higher functional robustness at a community level given that the risk of losing a link or an entire species is spread more evenly across the network (Kaiser-Bunbury and Bluthgen 2015). Higher partner diversity can also

contribute to the persistence and functioning of an ecosystem because the diversity of both plants and pollinators can, for instance, contribute to the reproductive success and persistence of plant communities (Fontaine et al. 2005). Higher partner diversity in tropical dry forest reduces the reliance of hummingbirds on few plant species, thus increasing the robustness of hummingbirds to different types of stochastic and anthropogenic disturbances in more natural habitats (Kaiser-Bunbury and Bluthgen 2015). Hummingbirds' higher number of partner species in tropical dry forest also explains the higher resistance of this network to the loss of plant species than to the loss of hummingbird species.

Key hummingbird and plant species for conservation purposes

To conserve and even restore (Menz et al. 2011) pollination interactions in human-modified landscapes, two important steps are 1) to establish which pollinator species are the most important in the maintenance of the plant-pollinator community and 2) to establish which plant species are preferred by pollinators at a given location in order to improve resource availability (Mukherjee et al. 2018). In the present survey, Canivet's Emerald (*Chlorostilbon canivetii*) and the Cinnamon Hummingbird (*Amazilia rutila*) were the most abundant resident hummingbird species in the Motagua Valley (Bustamante-Castillo et al. 2018) and also the most relevant hummingbird pollinator species in the study area. These generalist species were involved in the majority of recorded interactions and functioned as important network connectors. In both networks, they had connections with half or more than half of the recorded plant species (Martínez-Gonzáles et al. 2010). Because of their generalist behavior, resident status, and high abundance (Bustamante-Castillo et al. 2018), these two hummingbirds are good targets for plant-hummingbird conservation efforts. Highly connected species like these are essential for network cohesion because their elimination may trigger a cascade of secondary extinctions, strongly impacting the plant community and the integrity of the entire network (Memmott et al. 2004; Kaiser-Bunbury et al. 2010). These generalist species are also considered to play a key role in the evolution and persistence of pollination communities (Bascompte et al. 2003; Memmott et al. 2004). In the present study, the most relevant pollinators in the hummingbird-plant networks were mainly chosen by selecting the species with the highest proportions of interactions considering all interaction partners. This indicates that more plant species depend on these particular species for pollination (Bascompte et al. 2006). Nevertheless, it is important to take into consideration that

the effectiveness of a pollinator at setting seeds can be influenced by many other factors such as visit duration to flowers (Ivey et al. 2003; Boyd 2004), body size (Garibaldi et al. 2015), and even foraging behavior (Bosch and Blas 1994).

Notably, as pointed out by Mukherjee et al. (2018), the selection of plant species for the conservation of pollinator populations is considered to be more significant than the selection of pollinators for the conservation of plants. In the absence of certain pollinators, pollination may still be performed by other pollinator species, but the availability of flowering plants is essential for the survival of many pollinators. In the case of the Motagua Valley, as observed in other tropical forests (Stiles 1985; Arizmendi and Ornelas 1990; Cardoso-Araujo and Sazima 2003), the majority of plants species visited by hummingbirds were herbs, shrubs, and epiphytes. In particular, herbs such as *Ipomea trifida* and *Ipomoea hederifolia* and shrubs such as *Caesalpinia affinis*, *Cnidoscolus urens*, and *Pedilanthus tithymaloides* were identified as relevant resources for the hummingbird assemblage of the study area. Most of the flowering plants used by hummingbirds presented a high abundance of flowers per individual and were frequently located at the edges of tropical dry forest or in secondary growth vegetation and open areas. Consequently, generalist hummingbirds that often use this set of flowers (Stouffer and Bierregaard 1995) were highly attracted to them. Notably, none of the plants visited by hummingbirds were cultivated; rather, in the agricultural areas, the hummingbirds visited flowers growing on the edges of crops or in nearby remnants of tropical dry forest. This observation highlights the importance of natural and semi-natural habitat remnants for providing essential resources for pollinators in agricultural landscapes, which may help to maintain pollination services in agroecosystems (Jauker et al. 2009).

Finally, we believe that to achieve the conservation of pollinators and native plants in the Motagua Valley, it is necessary to legally protect a greater number of natural and semi-natural areas. However, since only a small amount of these lands are likely to be protected legally, we recommend converting agricultural lands into more biodiversity-friendly areas that combine agricultural production with biodiversity protection (Kearns et al. 1998). Agricultural lands can be managed to support pollinator populations by providing a seasonal succession of suitable forage plants, including, for example, the plants identified as good flower resources for hummingbirds in the present survey. Also, the enrichment of floral resources for hummingbirds and other pollinators

could be carried out in agricultural environments through the establishment of living fences or even gardens for pollinators.

In summary, our data suggest that seasonality is a stronger predictor than habitat type of the number of hummingbird-plant interactions recorded at a local scale in the Motagua Valley of Guatemala. The apparent lack of response of the number of interactions to habitat type is probably a consequence of the generalist nature of the hummingbird-plant assemblages of the study area, enabling plants and hummingbirds to persist and form new interactions in disturbed and transformed environments. Our data also suggest that although hummingbird-plant assemblages can persist in agricultural environments, the conversion of natural habitats to agriculture can cause changes in interaction patterns, such as a higher level of generalization, which has implications for the conservation of mutualist pollination interactions. Therefore, our data highlight the importance of conserving remnants of dry forest around farmlands to guarantee the persistence of hummingbirds and the pollination services they provide to native plants. We also recommend the implementation of strategies that contribute to the conservation of hummingbirds in degraded and transformed tropical dry forest areas, including the enrichment of sites with attractive plants for hummingbirds.

Declaration of Conflicting Interests
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DISCUSIÓN GENERAL

Diversidad de colibríes en distintos niveles de perturbación antrópica

La riqueza de especies de colibríes y el número de registros que obtuvimos en el área de estudio no cambió en relación al nivel de perturbación antrópica. La alta resiliencia de colibríes ante distintos niveles de perturbación antrópica se ha observado en otros ensambles de colibríes en ambientes alterados (Snow & Snow, 1972; Stouffer & Bierregaard, 1995) y posiblemente se relacione con el comportamiento generalista de las especies de colibríes dominantes del área de estudio (Snow & Snow, 1972) y la plasticidad de varias de estas para emplear ecotonos y áreas de borde como sitios de forrajeo (Banks-Leite, *et al.*, 2010). Características como la alta capacidad de vuelo de los colibríes, que les permite cruzar áreas abiertas y perturbadas (Hadley & Betts, 2009), y una dieta generalista, les permite ser más resistentes a la perturbación en comparación con otros gremios de aves como los insectívoros (Stouffer y Bierregaard, 1995; Thiollay, 1997). El ensamble de colibríes del Valle de Motagua probablemente perciba el paisaje de esta área como moderadamente modificado, en comparación con especies con capacidades de dispersión más pobres (Mcintyre & Hobbs, 1999). Sin embargo, la persistencia de los colibríes en hábitats alterados no implica necesariamente que la perturbación no tenga un impacto sobre ellos. Por ejemplo, dos estudios diferentes realizados en paisajes agrícolas, encontraron que incluso los colibríes altamente móviles evitan cruzar áreas muy abiertas en su camino hacia parches de bosque (Hadley & Betts, 2009; Volpe *et al*., 2016). Un impedimento en la movilidad de los colibríes en este tipo de hábitats podría tener un impacto en su efectividad para transferir el polen entre las plantas de una misma especie (Hadley & Betts, 2009), afectando así la reproducción de las plantas.

La baja riqueza relativa y la naturaleza generalista del conjunto de colibríes en el valle de Motagua podrían ser el resultado de la pérdida de especies sensibles a la perturbación en respuesta a la intensa transformación del hábitat y altos niveles de perturbación inducidos por el hombre (Ewers & Didham, 2006) que han estado presentes en el área por más de 100 años (Bray, 2010; Chazdon et al., 2011; Janzen, 1986; Maass, 1995). En su estudio, MacGregor-Fors y Schondube (2011) encontraron que las áreas de bosque seco tropical transformados en campos de cultivo y pastizales tenían comunidades de aves con menor riqueza de especies que los encontrados en bosques primarios. Especies endémica y especies de aves quasi-endémicas, que tienden a ser más sensibles.

a la perturbación (Julliard, Jiguet, & Couvert, 2003), estuvieron mal representados en estos hábitats estructuralmente simplificados. Además, Gillespie (2000) encontró que las especies de aves que requieren de los bosques secos sólidos no estaban presentes en áreas grandes pero perturbadas, lo que sugiere que la perturbación puede tener un papel importante para determinar la presencia de especies de aves sensibles en este tipo de hábitat. No obstante, debido a que los bosques secos tropicales de Mesoamérica han tenido una historia muy similar de perturbación y debido a que los registros colibríes antes de la intensa degradación de estos bosques son escasos, no es posible llegar a conclusiones precisas sobre el papel de la degradación del hábitat en la posibilidad de pérdida de especies de colibríes en el valle de Motagua. Adicionalmente, sería necesario determinar si los colibríes se están reproduciendo en hábitats alterados del sitio de estudio o si requieren áreas sin perturbaciones para reproducirse. En este respecto, se necesitan más estudios para documentar sus requisitos específicos de reproducción, ya que estos pueden limitar su distribución y abundancia.

Efecto de la estacionalidad sobre el número de interacciones colibrí-planta registradas en el área de estudio

La estacionalidad mostró un impacto notable en el número de interacciones colibrí-planta registradas en el valle de Motagua. Encontramos que el número de colibríes registrados y el número total de plantas con flores utilizadas por los colibríes fue mayor durante la estación seca. Esto dio lugar a un mayor número de especies que pudieron interactuar, lo que condujo a un aumento de las interacciones en esta temporada. Aparentemente, el efecto de la estacionalidad en el número de interacciones colibrí-planta en el bosque seco tropical está en parte relacionado con los regímenes cíclicos de precipitación y una estación seca marcada que crean patrones de floración que a su vez pueden afectar la riqueza y abundancia de colibríes (Abrahamczyk & Kessler, 2015). La correlación positiva encontrada en este estudio entre el número de colibríes registrados y la disponibilidad de flores apoya esta idea. En los bosques secos tropicales, la floración ocurre comúnmente durante la estación seca (Bennett *et al*., 2014: Borchert, 1996; Frankie *et al*., 1974); y muchas plantas de hoja caduca producen grandes cantidades de flores durante la época del año cuando la precipitación es mínima (Holbrook *et al*., 1995). Seguramente, y como ha sido señalado por otros estudios, durante los periodos de baja disponibilidad de recursos las especies de colibríes del valle del Motagua expanden su área de forrajeo o se movilizan latitudinalmente en busca de recursos alimenticios (Arizmendi & Ornelas, 1990).

Efecto de del tipo de hábitat (bosque tropical seco o área agrícola) sobre el número de interacciones colibrí-planta registradas en el área de estudio

El tipo de hábitat no influyó en el número de interacciones colibrí-planta registradas en el sitio de estudio. Este dato sugiere que, a escala local, el número de interacciones resultantes entre los colibríes y sus plantas asociadas no cambia significativamente si el hábitat es un bosque seco tropical o es área agrícola. Esto probablemente se relaciona en parte con el hecho de que las especies de colibríes más abundantes en el área de estudio (*Amazilia rutila* y *Chlorostilbon canivetii*), que estuvieron involucradas en la mayoría de las interacciones registradas, son especies generalistas que están presentes en hábitats transformados y perturbados por el hombre, así como en una vegetación natural más preservada (del Hoyo *et al.*, 2018; Stiles *et al.*, 2018; Weller *et al.*, 2018). Además, la mayoría de las especies de plantas que interactúan con estos colibríes son hierbas y arbustos que crecen en los bordes de bosques secos tropicales, áreas abiertas o áreas verdes que los agricultores dejan cuando realizan la limpieza para actividades agrícolas. Entre algunas de ellas estan *Caesalpinia affinis* Hemsl., *Pedilanthus tithymaloides* (L .) Poit., *Nopalea guatemalensis* Rosa y hierbas del género *Ipomea*. Asimismo, la mayoría de los sitios agrícolas tienen remanentes de bosque seco tropical en distintos estados de regeneración cercanos, por lo que los recursos florales estaban disponibles a través de los niveles de perturbación, como lo demuestra la diferencia no significativa en la abundancia de flores entre hábitats. Además, como se mencionó anteriormente, estos resultados también podrían estar reflejando la pérdida de especies de colibríes y plantas más sensible a la perturbación debido a la degradación histórica de los bosques secos de la región, y por ende la posible pérdida de interacciones colibrí-plantas en el sitio de estudio.

Comparación de atributos de redes de bosque seco tropical y áreas agrícolas del Valle del Motagua

Como se ha observado anteriormente en otras redes polinizador-planta (Aizen et al., 2012; Maruyama *et al.*, 2019), en el Valle de Motagua, la transformación del hábitat natural condujo a una red más generalista. Una mayor generalización indica una menor dependencia de cada especie en unos pocos socios exclusivos. El aumento de la generalización en los sitios agrícolas se debe

probablemente a la menor riqueza de especies de plantas y la menor selectividad en las visitas de colibríes a estas especies de plantas, lo que disminuyó la especialización de la complementariedad de la red. En este contexto, los hábitats antrópicos se caracterizan por tener especies que son menos selectivas en sus vínculos ecológicos, lo que resulta en una gran conectividad dentro de estas redes (Santo de Araujo, 2018). Este dato sugiere que la transformación del bosque seco tropical conduce a una comunidad menos funcionalmente diversa y, en consecuencia, a una red de interacción más generalizada. La generalización de la red agrícola puede tener efectos contrastantes en relación con la conservación y la solidez de las interacciones planta-polinizador. En términos de valor para la conservación, es importante preservar redes con interacciones especializadas. En términos de solidez de la comunidad ante las perturbaciones antropogénicas, una alta especialización puede reducir la competencia entre colibríes, lo que aumenta la probabilidad de transferencia de polen entre plantas conspecíficas, lo que beneficia tanto a los colibríes como a las plantas. Por otro lado, la alta especialización de recursos también puede hacerlos más vulnerables a las extinciones de sus socios mutualistas (Dalsgaard, *et al*., 2018).

En nuestro sitio de estudio, la red de bosque seco tropical mostró una mayor diversidad de socios mutualistas y una mayor diversidad de interacciones, lo que refleja una comunidad más rica y una distribución más uniforme de enlaces en esta red en comparación con la red de áreas agrícolas (Kaiser-Bunbury & Bluthgen, 2015). Esta última condición está asociada con una mayor robustez funcional a nivel de comunidad, dado que los riesgos de perder un enlace o una especie completa se distribuyen de manera más uniforme en toda la red (Kaiser-Bunbury & Bluthgen, 2015). Una mayor diversidad de socios también puede contribuir a la persistencia y el funcionamiento de un ecosistema, ya que la diversidad funcional de las plantas y los polinizadores pueden, por ejemplo, contribuir al éxito reproductivo y la persistencia de las comunidades de plantas (Fontaine *et al*., 2005). Nuestros resultados también mostraron que en el bosque seco tropical los colibríes tienen un conjunto más diverso de especies de plantas con flores que interactuar. Un mayor número de diversidad de socios en el bosque seco tropical reduce la dependencia de los colibríes en unas pocas especies de plantas, aumentando así la robustez de los colibríes a diferentes tipos de alteraciones estocásticas y antropogénicas en hábitats más naturales (Kaiser-Bunbury & Bluthgen, 2015). El mayor número de especies asociadas a los colibríes en el bosque tropical seco también explica la mayor resistencia de esta red a la pérdida de plantas.

Especies de Colibríes y plantas clave con fines de conservación

Para conservar, e incluso restaurar (LaBarColin *et al*., 2014), las interacciones de polinización dentro de paisajes modificados por el hombre, un paso importante es obtener información sobre las especies polinizadoras más importantes para el mantenimiento de una comunidad planta-polinizador y establecer qué plantas son preferidas por los polinizadores en un lugar determinado para mejorar la disponibilidad de recursos (Mukherje *et al*., 2018). En este estudio, se identificó a *Amazilia rutila* y *Chlorostilbon canivetii*, las dos especies de colibríes residentes más abundantes en el Valle de Motagua, como los polinizadores más relevantes en el sitio de estudio. Estas especies generalistas realizaron la mayoría de interacciones registradas y funcionaron como importantes conectores de red, ya que en ambas redes (de bosque seco tropical y agrícola) contribuyeron a conectar la mitad o más de la mitad de las especies de plantas (Martínez-Gonzáles *et al*., 2010). Debido a su comportamiento generalista, condición residente y a su gran abundancia, estas dos especies de colibríes son una buena opción como objetos de conservación para la preservación de la comunidad de plantas-colibríes en el área de estudio.

Especies altamente conectadas como estas son esenciales para la cohesión de la red, porque su eliminación puede conducir a cascadas de extinciones secundarias, con un fuerte impacto en la comunidad de plantas y en la integridad de las redes de interacciones (Kaiser-Bunbury *et al*., 2010; Memmott *et al*., 2004). También se considera que estas especies generalistas tienen un papel clave en la evolución y persistencia de las comunidades de polinización (Bascompte *et al*., 2003; Memmott *et al*., 2004). En este estudio, los polinizadores más relevantes para las redes de colibríes se seleccionaron principalmente en base a que presentaron las mayores proporciones de interacciones entre todos sus compañeros de interacción. Esto indica que más especies de plantas dependen de estas especies específicas para la polinización (Bascompte *et al*., 2006). Sin embargo, es importante tener en cuenta que la efectividad de un polinizador (para contribuir a la producción de semillas de las plantas visitadas) puede verse influida por muchos otros factores, como la duración de la visita a las flores (Boyd, 2004; Ivey *et al*., 2003), el tamaño corporal del polinizador (Garibaldi *et al*., 2015), e incluso el comportamiento de forrajeo del polinizador (Bosch & Blas, 1994). Adicionalmente, nuestros datos también señalan la importancia de conservar a las especies de colibríes menos abundantes del área ya que para estas especies se registraron interacciones

únicas en el área, como en el caso de *Archilocus colubris* e *Ipomea trífida* y *Heliomaster constantii* y *Tecoma stans*.

En relación a las especies de plantas importantes como recurso para los colibríes y la estructura de las redes de polinización, como se observa en otros bosques tropicales (Arizmendi & Ornelas, 1990; Cardoso-Araujo & Sazima, 2003; Stiles, 1985), la mayoría de las especies de plantas visitadas por colibríes fueron hierbas, arbustos y epífitas. Hierbas como *Ipomea trifida* e *Ipomoea hederifolia*, y arbustos como *Caesalpinia affinis*, *Cnidoscolus urens* y *Pedilanthus tithymaloides* se identificaron como recursos relevantes para el ensamble de colibríes en el sitio de estudio. La mayoría de las plantas con flores utilizadas por los colibríes presentaron una gran abundancia de flores por individuo y se ubicaron con frecuencia en los bordes del bosque seco tropical, vegetación de crecimiento secundario y áreas abiertas. De hecho, ninguna de las plantas visitadas por colibríes fue cultivada, en cambio, en áreas agrícolas visitaron flores que crecen en los bordes de los cultivos o en los bordes de los remanentes del bosque seco tropical cercano. Esto último señala la importancia de los remanentes de hábitat naturales y seminaturales para proporcionar recursos esenciales para los polinizadores dentro de los paisajes agrícolas que pueden ayudar a mantener los servicios de polinización en los ecosistemas (Jauker *et al*., 2009). En este sentido, también es posible emplear las especies de plantas nativas identificadas en este estudio como importantes recursos alimenticios para colibríes en actividades de restauración de los bosques secos del área con iniciativas como corredores verdes y cercos vivos. Además, en áreas semiurbanas y urbanas se pueden implementar jardines para colibríes empleando las plantas registradas en este estudio como recursos atractivos para las especies más generalistas.

CONCLUSIONES GENERALES

Los resultados del estudio mostraron la persistencia de los colibríes en áreas con distintos niveles de perturbación antrópica, probablemente relacionado con el comportamiento generalista de las especies residentes dominantes del lugar y debido a la disponibilidad de recursos alimenticios para colibríes en diferentes niveles de perturbación. Sin embargo, estos datos deben tomarse con precaución pues el estudio se realizó a una escala local y los resultados a una escala mayor podrían

ser distintos. El análisis espacial podría proporcionar una mejor comprensión del efecto de la perturbación inducida por el hombre en la riqueza y abundancia de colibríes en el sitio de estudio.

Nuestros datos sugieren que, a escala local, la estacionalidad es un predictor más fuerte, que el tipo de hábitat, del número de interacciones de colibrí-planta que se pueden registrar en el Valle de Motagua. La aparente falta de respuesta del número de interacciones en relación con el tipo de hábitat probablemente esté relacionada con la naturaleza generalista del ensamblaje de colibríes y plantas del sitio de estudio que permite que las plantas y los colibríes persistan y formen nuevas interacciones en similar número en ambientes perturbados y transformados.

Nuestros datos también sugieren que, aunque los conjuntos de colibríes-plantas pueden persistir en ambientes agrícolas, la conversión de los hábitats naturales puede causar cambios en los patrones de las interacciones mutualistas. En el estudio observamos que la red de bosque seco tropical mostró una mayor diversidad de socios mutualistas y una mayor diversidad de interacciones, lo que refleja una comunidad más rica y una distribución más uniforme de enlaces. Esta condición está asociada con una mayor robustez funcional a nivel de comunidad, dado que los riesgos de perder un enlace o una especie completa se distribuyen de manera más uniforme en toda la red. Una mayor diversidad de socios también puede contribuir a la persistencia y el funcionamiento de un ecosistema, ya que la diversidad funcional de las plantas y los polinizadores pueden, por ejemplo, contribuir al éxito reproductivo y la persistencia de las comunidades de plantas. Nuestros resultados también mostraron que en el bosque seco tropical los colibríes tienen un conjunto más diverso de especies de plantas con flores con las que interactuar, lo que aumenta la robustez de los colibríes a diferentes tipos de alteraciones antropogénicas en hábitats más naturales.

Nuestros datos también indican la importancia de conservar los restos de bosque seco alrededor de las tierras de cultivo para la persistencia de los colibríes y el servicio que brindan a las plantas nativas. También recomendamos la implementación de estrategias que contribuyan a la conservación de colibríes en áreas de bosques tropicales secos degradados y que se transformen, como el enriquecimiento de sitios con plantas atractivas para colibríes como las registradas en este

estudio incluyendo a *Ipomea trífida*, *Ipomoea hederifolia*, *Caesalpinia affinis*, *Cnidoscolus urens* y *Pedilanthus tithymaloides*.

RECOMENDACIONES GENERALES

Proponemos que para lograr la conservación de los polinizadores y plantas nativas del bosque seco tropical del Valle de Motagua en Guatemala, es necesario incorporar un mayor número de áreas naturales y seminaturales al Sistema Nacional de Áreas Protegidas del país. Sin embargo, dado que es una pequeña cantidad de tierra que aún tiene potencial para esta actividad, se recomienda convertir las tierras agrícolas de esta región en áreas más amigables con la biodiversidad, combinando la producción con la protección de la biodiversidad (Kearns *et al*., 1998). Las tierras agrícolas podrían gestionarse para alentar a las poblaciones de polinizadores proporcionando una sucesión estacional de plantas forrajeras adecuadas, incluidas las registradas en este estudio como un buen recurso floral para los colibríes. El enriquecimiento de los recursos florales para colibríes y otros polinizadores se podría realizar tanto en entornos agrícolas mediante el establecimiento de cercas vivas e incluso jardines para polinizadores.

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