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### Hummingbird diversity, abundance, and feeding interactions across three floral communities on Mount Totumas, Chiriquí, Panamá

Zachary Ginn  
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**Hummingbird diversity, abundance, and feeding interactions across  
three floral communities on Mount Totumas, Chiriquí, Panamá**



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**SIT Panamá: Tropical Ecology, Marine Ecosystems, and Biodiversity Conservation**

**Fall, 2022**

## Abstract

Hummingbirds (Trochilidae) are a large Neotropical bird family of nectar-feeders that have evolved as pollinators of many Neotropical plants. Interactions between hummingbirds and plants form mutualistic networks that may change in structure over environmental and anthropogenic gradients. While the unique dynamics of hummingbird diversity and floral interactions have been studied throughout the Neotropics, differing drivers between locations emphasizes the need for further local research. This deficit is especially crucial in biodiverse and understudied locations like the Western Highlands of Panamá. In this study, I investigated how hummingbird diversity, abundance, and floral interactions differed between Cloud Forest, Garden, and Oak Forest on Mount Totumas, Chiriquí Highlands, Panamá. I quantified and compared hummingbird richness, Shannon diversity, abundance, floral density, and floral visitation during three days of replicate point counts in each site. Additionally, I constructed quantitative hummingbird-plant networks, computed standard network indices, and compared hummingbird specialization at a species-level. Across study sites, I made 548 observations of 14 hummingbird species, and observed 4533 hummingbird visits to 35 plant species. Hummingbird richness was highest in the Garden, while Shannon diversity was slightly higher in the Cloud Forest. Hummingbird relative abundance, floral density, and visitation rates were significantly higher in the Garden site, and decreased in Cloud Forest and Oak Forest. Linear models suggest that floral density predicts hummingbird abundance and richness, suggesting that high floral density in the Garden likely attracts hummingbirds. While not representative of a complete elevational gradient, hummingbird diversity decreased at the higher elevation Oak Forest site. The study area hummingbird-plant network was speciose, with the Garden contributing more species and interactions than the forest sites. Across sites, nestedness (wNODF) and connectance (C) were lower than expected by null models, while network-level specialization ( $H_2'$ ) and modularity (Q) were higher. Network-level specialization was higher in the forest sites than in the Garden, possibly indicating hummingbird foraging flexibility in human-impacted landscapes. Hummingbird species specialization ( $d'$ ) varied on a species-specific level between sites, and was not significantly predicted by hummingbird body length, bill length, or bill curvature. While there are clearly structural differences in hummingbird-plant interactions between sites, further study over the entire year is essential to fully describe hummingbird dynamics at Mount Totumas.

## Acknowledgements

This project is a direct product of the encouragement and thoughtful advising of a community of friends and mentors here with SIT Panamá. I would like to thank Aly Dagang for the continual optimism, and for emphasizing joy and passion in creating an independent project. My endless gratitude to Chelina Batista Mojica, for providing sound advice, feedback, and excitement throughout the duration of this study. To Jeffrey, Alma, Mateo, Milka, and Reinaldo for making staying in the cloud forest accessible, comfortable, exciting, and delicious! This experience would not have been the same without you all, and I am truly grateful to have gotten to spend so much time at Mount Totumas. To Yuri, Yari, and Arcadio for logistical support and bus ride conversations. Finally, thank you to my loving family, Colleen Campbell, and all my friends in the USA and in Panamá for maintaining community from near and far.



Stripe-tailed Hummingbird (*Eupherusa eximia*) on *Hibiscus* spp.

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*Columnea chiricana* flower in the Oak Forest site.

## Introduction

### Panamá

Panamá is a small tropical country residing between 7° and 10° North on the isthmus between North and South America. The isthmus runs from East to West and has a central backbone of mountains that differentiate the drier, more seasonal, Pacific slope from the wet Caribbean slope (Holdridge & Bodowski, 1956). Temperatures in the lowland tropical belt exceed 24° Celsius year-round, while temperatures in the highlands can reach 0° Celsius above 3000 meters (Monro et al., 2017b). Elevations range from sea-level up to 3474 meters on the summit of Volcan Baru in Chiriquí. Given a small land area of roughly 75,000 km<sup>2</sup>, Panamá hosts a remarkably high biodiversity of over 10,000 flowering plant species (Monro et al., 2017b) and 1019 bird species (Audubon Panamá, 2022). Monro et al. (2017b) and Angehr & Dean (2010) highlight that diversity is created and maintained by varied topography over elevational gradients, giving rise to high habitat diversity. In Panamá, species richness is concentrated in zones of high endemism (Montañez & Angehr, 2007; Tokarz & Condit, 2021).

### Western Highlands and PILA

The Western Highlands, one of these endemic hotspots, consists of the eastern edge of the Talamanca Mountains. Elevations in the highlands reach over 3000 meters, and much of the land is above 2000 meters. The Western Highlands of Panamá are designated as one of the world's most biodiverse Important Bird Areas (IBAs), with over 400 species and 59 endemics (Montañez & Angehr, 2007). These montane environments compose the La Amistad International Park (PILA), which covers 401,000 ha in both Costa Rica and Panamá (Monro et al., 2017b). Precipitation on the Pacific slope ranges between 2000-2500 mm per year, while the Caribbean slope receives between 4000 and 6000 mm per year (Borge, 2004). PILA hosts at least 3046 documented vascular plant species distributed across 10 life zones, including predominant bands of cloud forest, lower-montane oak forest, upper-montane oak forest, and páramo (Monro et al., 2017b). Notably, Monro et al. (2017b) found the highest plant species richness in cloud forest between 1600 and 2100 meters, followed by lower montane oak forest between 2101 and 2600 meters. PILA also has high species richness of birds (more than 285 species), mammals (84 species), amphibians (32 species), and reptiles (25 species) (ANAM, 2004). Moreover, these estimates are likely undercounts, as research expeditions into PILA are costly and difficult given the steep topography, remoteness, and poor weather conditions (Monro et al., 2017a). While PILA retains the vast majority of its forest intact (Monro et al., 2017b), recent intensification of ranching, agriculture, road construction, and hydroelectric energy development pose threats to the wealth of biodiversity inside the park (Hofstede & Ojeda, 2013).

### Mount Totumas

Mount Totumas Cloud Forest (hereafter Mount Totumas) is a 140 hectare privately owned cloud forest reserve located at 8.9°N and 82.6°W in Chiriquí Province, Panamá. The reserve extends from 1600 to 2000 meters above sea level, directly bordering PILA. The property is predominantly primary and second growth cloud forest habitat, with around 3 hectares of coffee farm and cattle pasture on the lower slopes (Myers, 2018). Historic deforestation for pasture and select timber products constitute the land use history of the area.

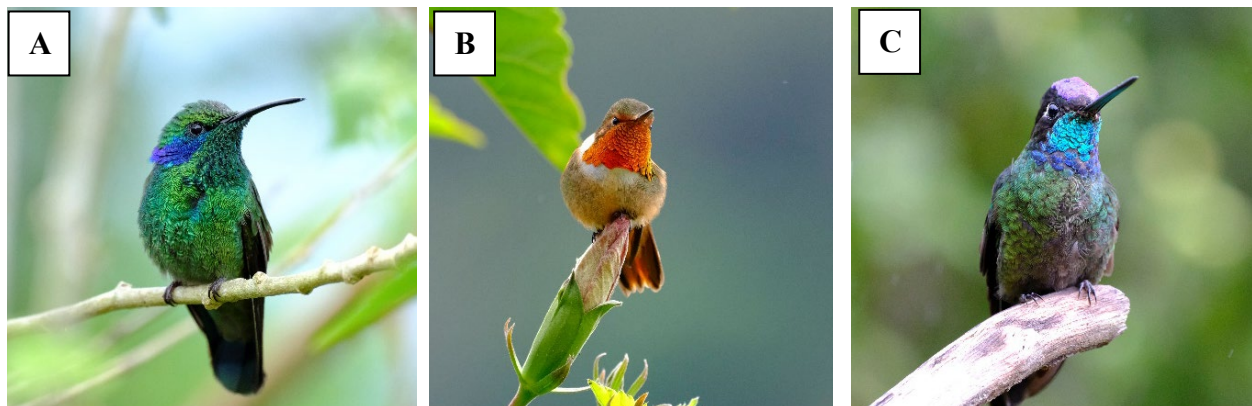
Above 2000 meters, the reserve transitions into PILA. These higher forests are less impacted by the aforementioned human impacts; however, a few small homesteads remain active in the park. The owners of Mount Totumas produce coffee and run an off-grid ecolodge, helping maintain hummingbird feeding stations and a system of around 30 km of hiking trails. Temperatures at Mount Totumas range from 10°C to 25°C, and the majority of the yearly precipitation falls during the rainy season between May and early December. During the dry season, strong winds from the Caribbean drive fine fine mist over the continental divide, facilitating the growth of epiphytic communities. Over 300 species of birds have been recorded in the surrounding area, including 19 species of hummingbird (eBird, 2022). Myers (2018) investigated avian diversity across different vegetation types on Mount Totumas, recording 43 bird species during the study period. Additionally, Mount Totumas hosts a number of other researchers interested in insect taxonomy and mammalogy. As of yet, no formal research has been conducted on hummingbirds or hummingbird-plant interactions on Mount Totumas.

## Literature Review

### Hummingbird Evolution, Physiology, and Feeding Mutualisms

Hummingbirds (Trochilidae) are a large Neotropical family of 362 species distributed across North and South America (Gill et al., 2022), with 61 species in Panamá (Audubon Panamá, 2022). Hummingbirds are most speciose in northern South America, with decreasing diversity in temperate regions (Abrahamczyk & Renner, 2015). McGuire et al. (2007) support the hypothesis that hummingbirds evolved in lowland South America, and then repeatedly colonized and speciated into highland regions. Notably, McGuire et al. (2007) also highlight that clades like the Emeralds and Bee Hummingbirds reside primarily in highland areas, while others like Hermits are predominantly lowland groups. Hummingbirds are easily recognizable by their small body sizes, bright coloration, and unique hovering flight. Hovering is metabolically taxing, especially for larger hummingbirds at high altitudes (Altshuler et al., 2004). In order to sustain this high energy expenditure, hummingbirds have evolved a primarily nectivorous foraging habit in which they consume flower nectar with long, slender bills and tongues (Tamm & Gass, 1986). Kim et al. (2011) suggest that hummingbird nectar feeding via capillary action has evolved to maximize energy intake from flower nectar with a concentration of between 35% and 45% sucrose.

**Figure 1.** Three common species: (A) Lesser Violetear (*Colibri cyanotus*), (B) Scintillant Hummingbird (*Selasphorus scintilla*), and (C) Talamanca Hummingbird (*Eugenes spectabilis*)

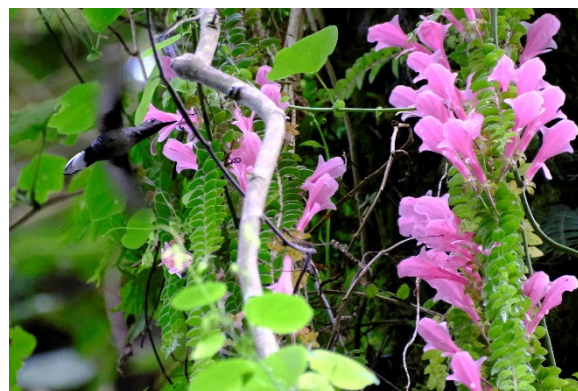


## Hummingbird Pollination and Ornithophily

Hummingbirds and flowering plants have evolved mutualistic interactions in which hummingbirds transfer pollen between flowers while feeding, aiding in pollination and sexual reproduction (Rodríguez-Flores et al., 2019). It is estimated that around 7000 plant species are hummingbird pollinated in the Americas (Abrahamczyk & Renner, 2015), representing between 10% and 15% of all flowering plant taxa on the continents (Dalsgaard et al., 2009). Within the Americas, avian pollination is most common in tropical regions, and is especially crucial for plants in cool, wet, montane environments where other pollinators like insects are less abundant (Dalsgaard et al., 2009).

Many plant species that rely on hummingbirds for pollination services have evolved a number of convergent floral traits that serve to attract hummingbirds through sensory cues. While this idea of pollination syndromes was introduced in the 1800s, Cronk & Ojeda (2008) summarize the following key features of bird pollinated, or ornithophilous, flowers. Flowers often have long, tubular, corollas with high volumes of relatively dilute nectar at the base. Red and orange coloration is most common, as these colors are highly visible for bird color-vision and do not attract bees that may rob nectar. Additionally, flowers often lack a strong scent and may be oriented in a nodding posture in order to discourage nectar robbing from other perching animals (Cronk & Ojeda, 2008). These generalized features of ornithophily have independently evolved in over 60 flowering plant families, including the Heliconiaceae, Costaceae, Musaceae, and Zingiberaceae (Cronk & Ojeda, 2008). While ornithophily in flowers clearly relates to bird pollination, recent research has also highlighted hummingbird use of non-ornithophilous flowers for food resources (Dalsgaard et al., 2009; López-Segoviano et al., 2021; Marayuma et al., 2013). Dalsgaard et al. (2009) found extensive hummingbird feeding in non-ornithophilous flowers in the Caribbean. Additionally, Maruyama et al. (2013) found that half the plant species hummingbirds regularly visit in Brazilian savanna are non-ornithophilous, underscoring the flexibility of hummingbird feeding in arid environments. López-Segoviano et al. (2021) also found that over half of hummingbird floral resources in their lowland tropical forest site in Mexico were non-ornithophilous. Further research is needed to fully understand the conditions under which hummingbirds feed from non-ornithophilous flowers at different locations.

**Figure 2.** A female Violet Sabrewing (*Campylopterus hemileucurus*) visits the conspicuously ornithophilous *Columnea chiricana* in low-elevation oak forest. This range-restricted epiphyte flowers profusely during the month of November.



## Interspecific Interactions

Interspecific interactions, such as those between plants and hummingbird pollinators, maintain ecosystem complexity and biodiversity (Bascompte, 2019). Recent intensification of global climate change and habitat loss may impact both individual species and the relationships



between them (Brambilla et al., 2020). Consequently, understanding how environmental conditions and human actions may structure these ecological interactions is of utmost importance. Tylianakis & Morris (2017) highlight three ways that interspecific interactions can shift over time and space: (1) changes in species composition, (2) differences in the frequency of interactions because of spatiotemporal overlap, and (3) alteration of coevolution. Shifts in mutualistic interactions have the potential to enhance biodiversity loss due to anthropogenic change, yet are poorly understood (Six, 2009). Field-based monitoring of ecological interactions is necessary to understand local changes in interactions over time.

### Elevational Gradients and Tropical Montane Ecology

One common environmental gradient used to study changes in interaction networks due to abiotic variables is elevation. Decreases in temperature and changes in precipitation as elevation increases help structure patterns in plant and animal biodiversity (McCain & Grytnes, 2010). Specifically, McCain & Grytnes (2010) highlight four responses of species richness as elevation increases from sea level to alpine tundra: (1) richness decreases as elevation increases, (2) low altitude richness plateaus followed by a decrease, (3) low altitude richness plateaus with a peak at moderate elevations, and (4) a bell curve pattern with a mid-elevation peak. While there are clearly richness declines at the extremes of elevation, tropical montane forests provide a more nuanced case study.

**Figure 3.** Montane cloud forest habitat in PILA.



In comparison to their lowland counterparts, tropical montane forests are generally cool and humid, supporting unique vegetative communities. In the tropical belt, Holdridge (1967) delineates the boundary of premontane forests at around 1000 meters and a transition to lower montane forest at around 2000m. He further delineates life zones by precipitation into dry, moist, wet, and rainy forests. Within these ranges, Myers (1969) further distinguishes cloud forests, which he states are physically rather than climatically defined by persistent cloud cover due to cool temperatures and low evaporation, resulting in lush epiphytic vegetation. In this way, topography and climate interact heterogeneously to create microhabitats which may deviate from strict elevational patterns of zonation (Monro et al., 2017a).

In the Neotropics, montane life zones have been shown to foster high rates of endemism, as well as unique community assemblages with high species turnover compared to lowland areas (Jankowski & Rabenold, 2007; Jankowski et al., 2009). Explanations behind this endemism include high levels of niche specialization in montane species (Jankowski et al., 2009), and narrow preferred temperature ranges (Janzen, 1967). Janzen also notes that climatic differences serve as a more intense barrier to species movement in tropical mountains because of the highly stable climate compared to temperate zones.

In La Amistad International Park, Monro et al. (2017b) found that vascular plant species richness has a mid-elevation peak between 1200m and 1600m. While Tokarz & Condit (2021)

also found a mid-elevation plateau for Panamanian tree richness, they noted the highest rates of narrow endemism in montane forests above 2000m. In Honduran cloud forest, Neate-Clegg et al. (2018) found that avian richness increased with elevation through a gradient up to 2243 meters.

### Trends in Hummingbird Diversity

Numerous studies have investigated the unique dynamics of hummingbird diversity throughout the Neotropics, including across elevational (López-Segoviano et al., 2021; Neate-Clegg et al., 2018; Rodríguez-Flores et al., 2019; Sonne et al., 2019) and land-use (Hadley et al., 2017; Morrison & Mendenhall, 2020; Tinoco et al., 2018) gradients. McGuire et al. (2007) assert that hummingbird diversity is highest in mid-elevation moist tropical forests, supporting a unimodal richness pattern (McCain & Grytnes, 2010). In Honduras, Neate-Clegg et al. (2018) found highest nectarivore (primarily hummingbird) richness at elevations above 2000m, which is a mid-elevation montane cloud forest habitat. Analyzing hummingbird visitation networks in the Ecuadorian Andes, Sonne et al. (2019) reported a decreasing hummingbird richness pattern over a 4000-meter gradient. Interestingly, Sonne et al. (2019) found a notable tradeoff between the relative richness of curve-billed specialists at below 2000m and long-straight-billed specialists above 2000m.

Investigating land-use rather than elevation, Hadley et al. (2017) found that deforestation significantly reduced hummingbird richness and abundance across a deforestation gradient in Costa Rica. Notably, deforestation especially impacting morphological specialists (Hadley et al., 2017). Finding a different result, Tinoco et al. (2018) reported highest hummingbird richness in heterogeneous mixed-use landscapes in the Andes. However, Tinoco et al. (2018) also found that functional diversity was highest in intact forest habitats. Building on the findings of Hadley et al. (2017), Morrison and Mendenhall (2020) also observed higher hummingbird richness in more forested sites across an agro-ecological gradient in Costa Rica. While species richness may generally decrease with deforestation, certain hummingbird species are highly resilient to land-use change, and may thrive in open and human-impacted environments (Morrison & Mendenhall, 2020). Morrison & Mendenhall (2020) concluded that while there was not much species turnover between open and forested landscapes, relative abundances of different species varied significantly.

### Hummingbird-plant Interaction Networks

Along with diversity, many researchers have investigated hummingbird-plant interactions and networks in the Neotropics (Bustamante-Castillo et al., 2018; Dalsgaard et al., 2009; Gonzalez & Loiselle, 2016; Hadley et al., 2017; López-Segoviano et al., 2021; Maglianesi et al., 2014; Maglianesi et al., 2015; Marayuma et al., 2013; Marayuma et al., 2019; Marín-Gómez et al., 2021; Morrison & Mendenhall, 2020; Partida-Lara et al. 2018). Prominent research themes include the impacts of hummingbird morphology, flowering phenology, floral abundance, elevation, agriculture, urbanization, and sugar-water feeders on hummingbird plant interactions. Additionally, recent advances in computational analysis of plant-pollinator networks using open-source packages like *bipartite* have enabled the computation of standardized metrics that enable comparisons of networks across space and time (Dormann et al., 2008, see methods section for metric details).

**Figure 4.** The Violet Sabrewing (*Campylopterus hemileucurus*), a large hummingbird with a long, curved bill.



Starting with morphology, Rodríguez-Flores et al. (2019) concluded in their meta-analysis that evolutionarily older clades of hummingbirds like Hermits show more specialized bill morphologies and higher floral specialization, while more recently evolved groups like the Bee Hummingbirds and Mountain Gems exhibit more standard morphologies and generalized floral choice. These conclusions corroborate local-level investigations into relationships between bill length/curvature and floral morphology conducted in the Caribbean (Dalsgaard et al., 2009), Costa Rica (Maglianesi et al., 2014; Maglianesi et al., 2015), and Mexico (López-Segoviano et al., 2021). All of these studies found evidence that hummingbirds with longer and more curved bills (high morphological specialization) were more specialized than hummingbirds with short, straight bills. Maglianesi et al., 2014 go so far as to argue that bill morphology is a primary driver that structures the patterns of hummingbird-plant interactions in the Neotropics.

Focusing on different drivers, Gonzalez & Loiselle (2016) concluded that in Andean cloud forest, the timing of flowering structured community interactions more than morphology. Gonzalez & Loiselle (2016) attributed the decreased importance of morphological trait matching at the site to the abundance of flowerpiercers (*Diglossa spp.*) that enabled hummingbirds with varying bill shapes to access most floral nectar. Bustamante-Castillo et al. (2018) found that seasonal floral abundance was the primary driver of hummingbird abundance in Guatemalan dry forest. They highlighted the role of floral abundance in attracting latitudinal hummingbird migrants. Additionally, López-Segoviano et al. (2018) reported a direct correlation between floral abundance of hummingbird-pollinated plants and the abundance of latitudinally and altitudinally migrating hummingbirds, suggesting that migration timing is connected with floral resources. In tropical cloud forests, flowering has been shown to be dispersed throughout the year, with different species flowering in different months (Sheldon & Nadkarni, 2015). However, Sheldon & Nadkarni (2015) also found a peak in ornithophilous epiphyte flowering at the end of the wet season.

Focusing on elevation, Dalsgaard et al. (2009) observed higher floral specialization in hummingbirds in the highlands of the Caribbean islands, likely due to morphological trait matching between plants and large hummingbirds with specialized bills. In a gradient of seasonal forest and cloud forest in the Sierra Madre Occidental of Mexico, Partida-Lara et al. (2018) found high hummingbird specialization at the high-altitude cloud forest site, despite predominantly generalized interactions across the study area. López-Segoviano et al. (2021) observed contrasting results in a similar area of Mexico, concluding that specialization was highest at the ecotone between low and high elevation forest. Finally, Maglianesi et al. (2015) found higher specialization across low and middle elevations in Costa Rica. They posited that

increased competition at higher elevations due to resource constraints likely increased generalization through niche-expansion (Maglianesi et al., 2015).

While elevational trends in network structure seem to differ, hummingbird-plant communities appear to respond more predictably to land-use change and urbanization. Both Hadley et al. (2017) and Morrison & Mendenhall (2020) found that network-level specialization decreased in more disturbed agricultural landscapes.

Morrison & Mendenhall (2020) suggest that this generalization was due to (1) the loss of morphological specialists in agricultural habitats, and (2) behavioral changes favoring increased opportunistic feeding. Investigating how urbanization impacts hummingbird-plant networks, Marayuma et al. (2019) and Marín-Gómez et al. (2021) both reported decreased specialization in urban environments. The role of sugar-water feeders, which are a crucial attractant for hummingbirds in human-impacted areas, is still uncertain. Sonne et al. (2016) found that hummingbird feeders locally increased the abundance of hummingbirds within 75 meters and facilitated increased visitation to native plants surrounding the feeders. In contrast, Avalos et al. (2012) reported a clear decrease in flower feeding within 3 km of a feeding station in the highlands of Costa Rica. These data suggest that feeders may impact hummingbird-plant interactions over large spatial scales.

Clearly, trends in hummingbird plant interactions are nuanced and vary across locations. To date, limited studies on hummingbird floral interactions have been conducted in Panamá, representing a clear gap considering Panamá's speciose hummingbird assemblage and unique biogeographic history connecting North and South America. This deficit is especially noticeable in the biodiversity hotspots of the Western Highlands and PILA. Further inquiry into hummingbird diversity and floral interactions across environmental and anthropogenic gradients in Panamá may aid in unravelling the structural drivers of biodiversity in this unique country.

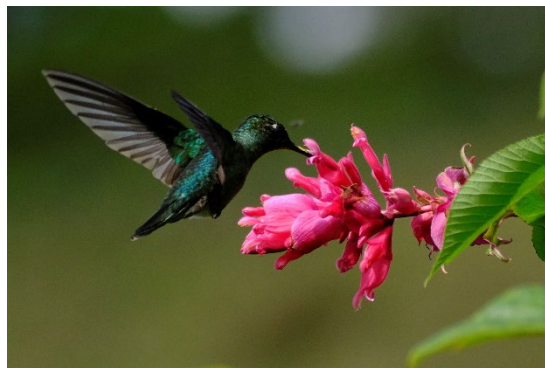
### Research Question

Do hummingbird species diversity, abundance, and nectar-feeding interactions differ between Cloud Forest, Oak Forest, and Garden sites on Mount Totumas, Chiriquí Highlands, Panamá?

### Research Objectives

1. Assess hummingbird richness, diversity, abundance, floral visitation, and floral density in each of the three sites during the duration of study in November.
2. Quantify hummingbird-plant interactions at a network level for each site for the study period and compute standardized indices to describe and compare network structure and hummingbird specialization.

**Figure 5.** *Eugenes spectabilis* pollinating the ornithophilous flower of *Salvia involucra*, a non-native garden plant close to a sugar-water feeding station. Note the yellow pollen on the hummingbird's bill.



## Methods

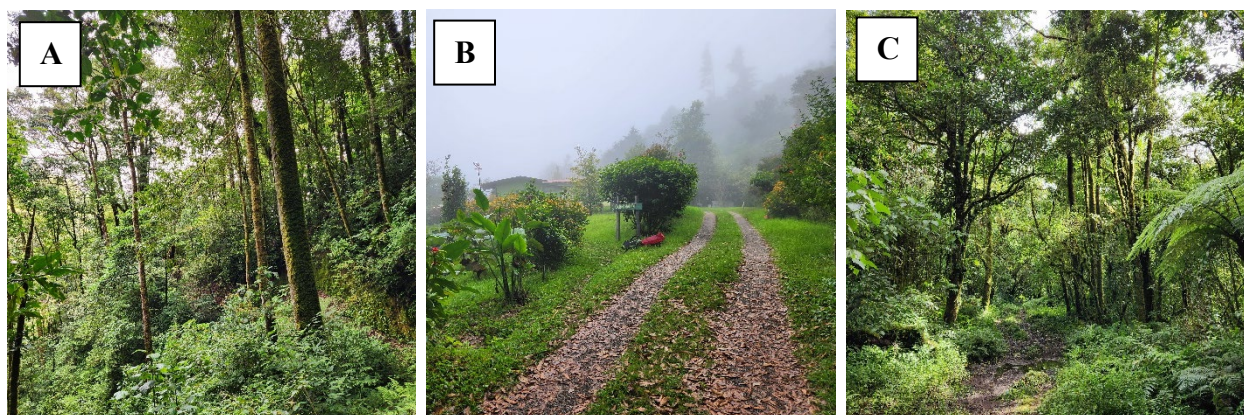
### Data Collection

I quantified (1) hummingbird diversity and abundance, (2) floral density, and (3) hummingbird floral interactions across three habitats on Mount Totumas. After three days of site exploration and the approval of the following methods by an IRB committee, I began data collection on November 16<sup>th</sup>, 2022. Three days were spent in each habitat, for a total of nine study days culminating on November 28<sup>th</sup>, 2022.

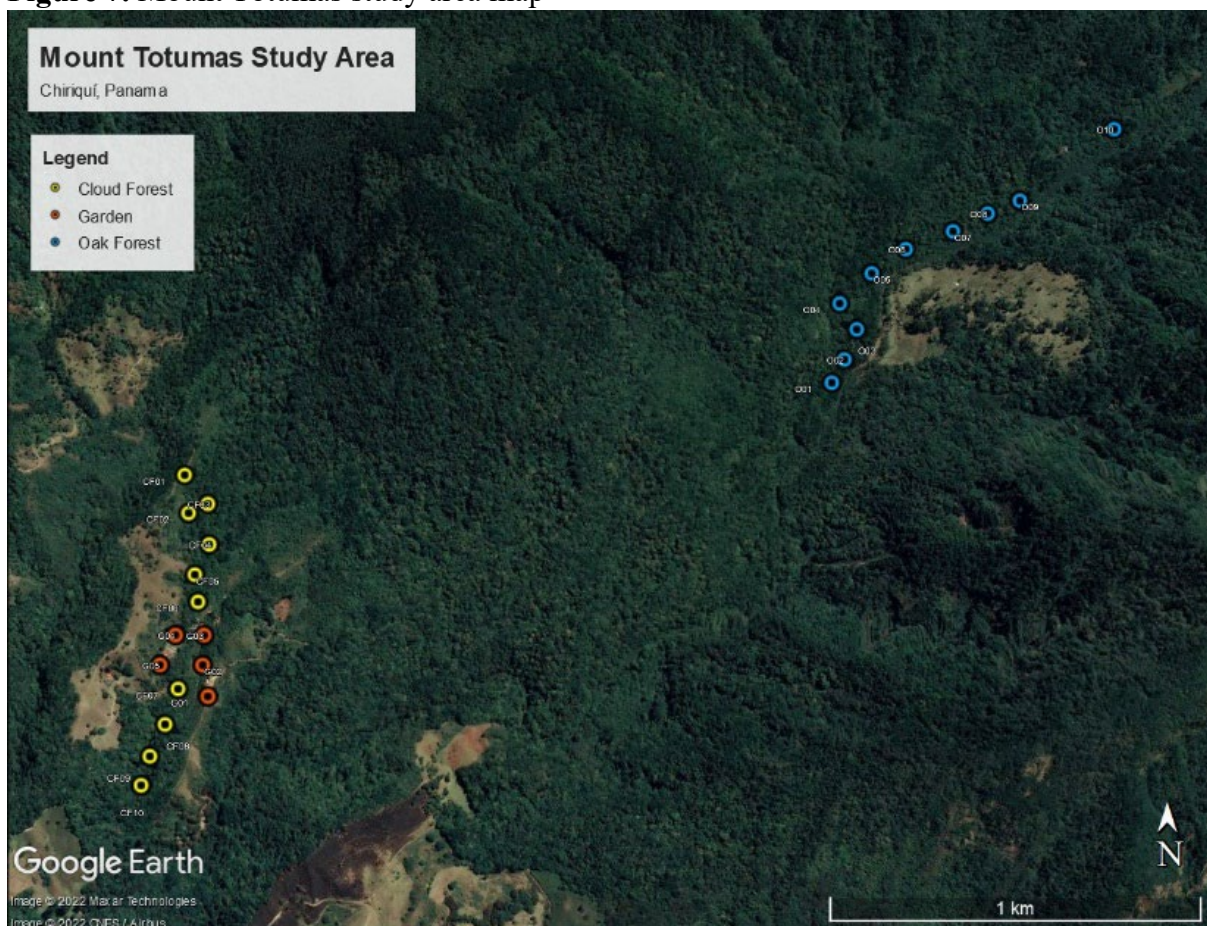
### Study Sites

To investigate hummingbird diversity and floral interactions across Mount Totumas, I established sites in three different habitats: Cloud Forest (CF), low-elevation Oak Forest (OF), and Garden (G) (Figure 6). In each site, replicate plots for observing both birds and flowers were established (Figure 7, see Table 1 in appendix for plot coordinates and vegetative characteristics). Distinguishing forest habitats was based on personal observation of tree species and general life-zone predictions detailed in Monro et al. (2017b). The Cloud Forest site extended from 1815 meters to 1975 meters on the Cascada and Bajareque trail systems. This forest consisted mainly of mixed primary/secondary growth cloud forest habitat bordering a small tributary of the Rio Colorado. Dominant tree species included *Ulmus mexicana* and *Quercus costaricensis*. The Oak Forest site covered an elevational gradient of 2050 to 2250 meters within the boundaries of PILA. I accessed this site via the 15 kilometer La Amistad trail. This forest differed in structure from the lower Cloud Forest, with a higher coverage of epiphytes and the dominance of *Quercus copeyensis* trees as detailed in Monro et al. (2017b). The Garden site provided an accessible and interesting comparison to the forest sites. The Garden covered a heterogenous patchwork of mixed native and non-native vegetation close to Mount Totumas Ecolodge. This site had limited canopy cover. However, it bordered forest edge in places, making it a heterogenous edge habitat. Many landscaped plant species were chosen specifically to attract pollinators, and consequently, floral density in the Garden was high. This site also shared close proximity with two hummingbird feeding stations (see implications in discussion).

**Figure 6.** Characteristic habitat in the (A) Cloud Forest, (B) Garden, and (C) low-elevation Oak Forest sites. Note the limited canopy cover in the Garden.



**Figure 7.** Mount Totumas study area map



### Point Counts and Visitor Watches

To observe hummingbird diversity, abundance, and floral interactions, I established replicate radial plots along trails in each site (Figure 7). Plots were separated by at least 100 meters to ensure spatial independence of plot observations (Bustamante-Castillo et al., 2018). Due to available habitat space, each forest site had ten plots, while the garden site only had five. In order to maximize the likelihood of seeing hummingbirds and their feeding interactions during the short study period, plots were non-randomly placed in areas of high floral density (Partida-Lara et al., 2018; see discussion for possible implications).

To evaluate hummingbird diversity and abundance at each plot, replicate observations were conducted. During these 20-minute point counts, I noted the species and number of any hummingbirds observed within a 25-meter radius from plot center (Bustamante-Castillo et al., 2018; López-Segoviano et al., 2021). Hummingbirds were visually identified using 10x42 binoculars and *The Birds of Panamá: A field guide* for reference (Angehr & Dean, 2010). I also identified hummingbirds by distinctive songs. To avoid double-counting these fast-moving and active birds, I counted the maximum number of individuals of each species visible at the same time during the point count. I also made additions to abundance totals when I could distinguish clear morphological differences between individuals due to sex or age.

During these point counts, I also recorded hummingbird visits to flowers in the first 10 meters of canopy, including the number of visits and the plant species (Bustamente-Castillo et al., 2018; López-Segoviano et al., 2021). Only feeding events where hummingbirds made clear contact with floral reproductive structures while drinking nectar were counted as a visit, but nectar robbing behavior was also noted (Dalsgaard et al., 2009). As I was not able to identify plant species in the field, I assigned morphospecies names/codes to all flowers and took photos of key morphological features to aid in species identification later (Partida-Lara et al., 2018). Plant species were identified to maximum possible taxonomic resolution using Monro et al. (2017b) and Gargiullo et al. (2008), as well as help from Mount Totumas staff and guides knowledgeable with the area. In order to bolster the chances of viewing uncommon interactions, I also observed hummingbird-flower interactions while walking between plots using an informal belt transect along the trail (Ortiz-Pullido et al., 2012). These data were used when considering site richness and floral interactions, but were not incorporated into assessments of hummingbird relative abundance.

At each forest site, I sampled every radial plot on three mornings and one afternoon to account for potential differences in temporal feeding patterns between species (Dalsgaard et al., 2009). Morning watches occurred between 06h30 and 12h00, while afternoon watches were between 13h00 and 16h00. I carried out observations in sun, clouds, and light rain, however not during intense rain, high wind, or when visibility was significantly reduced. In order to randomize the sampling order on each day, I assigned a number to each plot based on locations on the trail (see Figure 7). In forest plots, I created four possible sampling orders: one (1,2,3,4,5,6,7,8,9,10), two (10,9,8,7,6,5,4,3,2,1), three (6,7,8,9,10,5,4,3,2,1), and four (5,4,3,2,1,6,7,8,9,10). Each morning, I used a random number generator to select a number between one and four, corresponding to each of these treatments. As there was less available time to sample in the afternoons, I observed half the plots (1,2,3,4,5) on one afternoon, and the other half (6,7,8,9,10) on another afternoon in the forest sites.

Since there were half the number of Garden plots, I sampled each plot twice each morning for three days to yield an equivalent sampling effort to the forest sites. I randomized garden plot sampling order using the same process, with plot orders as follows: one (1,2,3,4,5,5,4,3,2,1), two (5,4,3,2,1,1,2,3,4,5), three (1,2,3,4,5,1,2,3,4,5), and four (5,4,3,2,1,5,4,3,2,1). In the garden, I observed all plots on two separate afternoons, switching the sampling order. As Sonne et al. (2016) found that hummingbird feeders locally inflate hummingbird abundance within 75 meters, I removed all sugar-water feeders for each day during the Garden sampling period. I address the potential biases of this decision further in the discussion.

### Floral Density and Diversity

To understand floral resource density for hummingbirds at each site, I counted and identified all conspicuous flowers in replicate rectangular plots adapted from López-Segoviano et al. (2021). Specifically, I quantified floral density within 5 meters of the trail on both sides for 20 meters, resulting in an effective sampling area of 20 meters by 10 meters (200m<sup>2</sup>). This method accounted for varying trail/road widths. At each site, plots were established at regular intervals of 50 meters, resulting in half the plots also landing on radial plots, while the other half

landed in between these plots. I established 18 plots in each forest site, and 9 plots in the Garden. As the goal of this methodology was to quantify relative floral availability for hummingbirds, inconspicuous flowers such as *Piper spp.* were not counted or included in analysis. Species were identified using the process detailed above.

### Vegetation Assessment

To provide a description of habitat space in each site, I conducted a rapid vegetation assessment adapted from Van Bael et al. (2013). At each radial plot, I recorded canopy height with a digital rangefinder five times at five-meter intervals. I also recorded canopy density in each cardinal direction from plot center using a spherical densitometer. Next, I classified understory vegetation growth on a scale of zero to four, with higher numbers corresponding to more dense underbrush (Myers, 2018). Finally, I assessed epiphyte percent coverage at each plot on a scale of zero to four, with higher values indicating higher epiphyte coverage.

### **Statistical Analysis**

#### Community Ecology Metrics

Statistical analyses were conducted in R (version 4.2.2) and R-studio (R Core Team, 2022). Diversity and community ecology indices were calculated using the *vegan* package (Oksanen et al., 2022). Sampling completeness was assessed by plotting species accumulation curves for hummingbird species at each site and for the entire study area. I estimated hummingbird species richness values based on sampling effort using a bias-corrected Chao estimator (Chao, 1987; Oksanen et al., 2022). Unlike López-Segoviano et al. (2021), I did not attempt to assess sampling completeness for plant species or interactions, as I surveyed a small spatial area over a short time frame. To assess hummingbird diversity, I calculated Shannon-Weiner diversity ( $H'$ ) and Pielou's Evenness ( $J'$ ) at each site due to their popularity within community ecology (Oksanen et al., 2022). To compare hummingbird community composition between sites, I calculated pairwise Bray-Curtis Dissimilarity values (Morrison & Mendenhall, 2020). This index is advantageous over binary indexes like Sorenson's similarity because it takes into account the abundance of each species, instead of simply species presence or absence (Schroeder & Jenkins, 2018).

#### Statistical Tests for Significance

Due to (1) high variance between sites, (2) generally small sample sizes, and (3) right-skewed data due to a high proportion of zeros, I used non-parametric statistical tests to examine differences between sites in vegetative characteristics (undergrowth, epiphyte coverage, canopy height, and canopy density), per-watch hummingbird abundance, hummingbird visitation rates, and floral density. After testing for normality to ensure that I could not use parametric tests, I ran Kruskal-Wallis tests on all three sites, then followed up with pairwise Wilcoxon rank sum tests to underscore which sites differed (Bustamante-Castillo et al., 2018). For the same reasons of using non-parametric tests, I also report medians rather than means for these metrics. Due to the non-random placement of plots in areas of high floral density, as well as the possibility of double-counting territorial individuals in each plot on different sampling days, I did not calculate hummingbird density values or attempt to extrapolate hummingbird abundance to larger areas. Moreover, as the goal of collecting floral density data was to understand available floral



resources for hummingbirds, rather than total floral density, floral density analyses were conducted on a subset of flowering plant species deemed of particular importance to hummingbirds (Bustamante-Castillo et al., 2018). Hereafter referred to as hummingbird flowers, this subset included (1) all plant species visited by hummingbirds in the site, and (2) plant species with a clear ornithophilous floral syndrome (see introduction and Cronk & Ojeda, 2008 for definition of ornithophilous syndrome). Finally, in order to examine compositional differences between floral communities in each site, I calculated pairwise Bray-Curtis Dissimilarity values.

### Linear Models

To examine the potential factors driving differences in hummingbird abundance and richness between plots, I constructed linear models with elevation, floral density, and site as explanatory variables and per-watch hummingbird abundance and richness as response variables:

1. Hummingbird Abundance or Richness ~ Elevation + Site + Floral Density
2. Hummingbird Abundance or Richness ~ Elevation + Floral Density
3. Hummingbird Abundance or Richness ~ Elevation + Site
4. Hummingbird Abundance or Richness ~ Site + Floral Density
5. Hummingbird Abundance or Richness ~ Elevation
6. Hummingbird Abundance or Richness ~ Floral Density
7. Hummingbird Abundance or Richness ~ Site

After testing for collinearity and checking the assumptions of linear models (normality, homoskedasticity, homogeneity of variance), I computed Akaike Information Criterion (AIC) values to select the models that explained the highest amount of variability for hummingbird abundance and richness respectively. I then summarized the findings of the best-fit models.

### Hummingbird-Plant Network Analysis

All hummingbird-plant interaction data were compiled and analyzed using the *bipartite* package in R (Dormann et al., 2008). For these analyses, I created data-matrixes representing hummingbird species on one axis, plant species on the other, and the total number of visits observed between them as the interaction strength (López-Segoviano et al., 2021). I visualized these quantitative networks for each site separately, as well as the entire study area, using the function *plotweb*.

For each of the four networks, I computed commonly reported network-level indices using the function *networklevel*, including nestedness (wNODF), connectance (C), network-level specialization ( $H2'$ ), and network modularity (Q). Nestedness is a property of species networks in which specialized species interact with generalists, and vice-versa (Bascompte et al., 2003; Dormann et al., 2009). The metric weighted nestedness overlap and decreasing fill (wNODF) ranges from 0 to 100, with higher values indicating increased nestedness (Dormann et al., 2008). More nested networks have high redundancy, and thus, are resilient to disturbance (Bascompte et al., 2003). Connectance represents a ratio between the observed interactions within a system and the total number of possible interactions based on the network size, with higher values indicating higher network stability (Dormann et al., 2009). As connectance relates to network size, larger networks usually have lower connectance (Olesen & Jordano, 2002). Network-level

specialization is a metric ranging from 0 to 1, which examines the observed specialization between all members in the network in relation to the possible minimum and maximum specialization (Blüthgen et al., 2006). Modularity, calculated using the Beckett formula, ranges from 0 to 1, with higher values occurring when isolated sub-communities within the network interact primarily with each other (Dormann & Strauss, 2014). I visualized network modularity using the commands *computemodules* and *plotmoduleweb*. All of these indices shed light on the structure of hummingbird plant communities, and also enable comparisons with similar studies. In order to test if the computed metrics differed significantly from randomly generated networks, I compared each index to null models with 1000 replicates using the command *nullmodel*, method *r2d*, and Z-tests as detailed in Dormann et al. (2008).

Additionally, I analyzed hummingbird specialization at a species level using the function *specieslevel* and the metrics degree (p) and specialization (d') (Blüthgen et al., 2006). The species degree is the number of plant species each hummingbird visited, while d' is a standardized specialization index ranging from 0 to 1 that accounts for sampling effort and plant specialization as well (Blüthgen et al., 2006). I compared these indices between sites for each hummingbird species.

In order to investigate if hummingbird morphology influences specialization, I performed a linear regression and Spearman rank correlation with body length as the explanatory variable and both degree and d' as the dependent variable. As I did not mist-net or handle hummingbird species, I used the body length values in Angehr & Dean (2010) for reference. To investigate bill morphology more specifically, I observationally grouped hummingbird species by bill length (short and long) and curvature (straight and curved). After checking for parametric assumptions of normality and equal variances, I ran two-factor ANOVAs with bill length and curvature as explanatory variables and degree and specialization as dependent variables. For these analyses, I only included hummingbird species with at least five feeding observations, as rare species may have had inflated specialization values. This resulted in excluding the Brown Violetear (*Colibri delphinae*), White-tailed emerald (*Elvira chionura*), Long-billed Starthroat (*Heliomaster longirostris*), Fiery-throated Hummingbird (*Panterpe insignis*), and Magenta-throated Woodstar (*Philodice bryantae*) from the analysis.

## Ethics

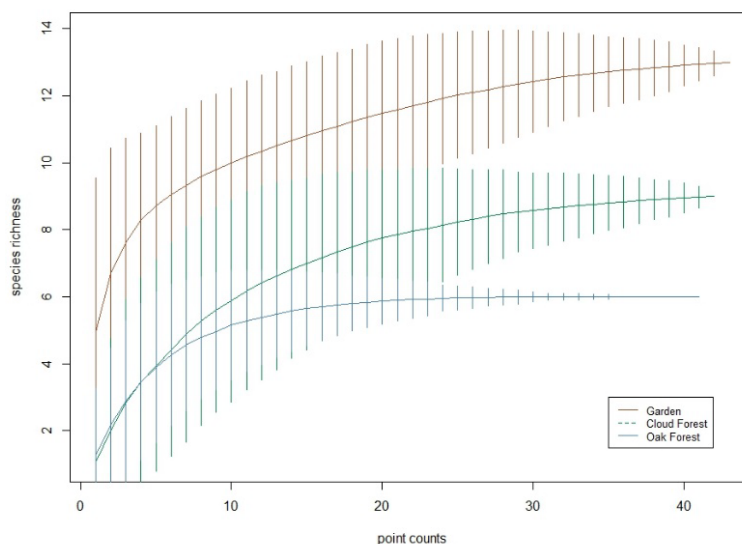
Before initiating data collection, I submitted necessary IRB forms to ensure approval of my methods. Because I did not conduct interviews with humans, this project did not require a full IRB review. Moreover, I utilized non-invasive observational sampling techniques, and thus, posed little negative environmental impact. Hummingbirds were not captured, touched, or handled, and I did not collect plants for identification. As for any field study, the potential for habitat degradation by trampling vegetation in the study plots was possible, especially while searching for flowers. I minimized trampling by using existing trails to get to study sites. Additionally, movement between ecosystems brought the risk of introducing invasive plants or pathogens. To avoid transferring seeds between sites, I conducted regular boot and pant checks to remove any burrs each day.

## Results

### Sampling Effort

Over nine field days, I observed hummingbirds and their floral interactions for a total of 2400 minutes (40 hours). All forest plots received 80 minutes of observation each, while garden plots received 160 minutes to account for the halved number of plots. Consequently, I observed each site an equivalent 800 minutes (13.33 hours). In total, I recorded 548 hummingbirds from 14 species (Table 2), as well as 67 flowering plant species belonging to 33 families (Table 3, Appendix). All three sites (Figure 8), and the study area as a whole (Figure 9, Appendix), reached or began to reach an asymptotic hummingbird species accumulation curve. This indicates an adequate sampling effort for estimating total species richness of hummingbirds during the study period.

**Figure 8.** Hummingbird Species Accumulation Curves (SAC) for each site.



### Hummingbird Richness and Diversity

Hummingbird richness and diversity values are summarized in Table 4. Across all three sites, I observed a total of 14 hummingbird species, with 13 in the Garden, 9 in the Cloud Forest, and 6 in the Oak Forest. Six species were Western Highland endemics (Angehr & Dean, 2010). Observed richness values exceeded 88% of the estimated Chao richness, indicating high sampling completeness. Shannon diversity values were higher in the general study area ( $H' = 2.02$ ) than the individual sites. Cloud Forest ( $H' = 1.95$ ) had the highest Shannon diversity, followed by Garden ( $H' = 1.92$ ), and finally Oak Forest ( $H' = 1.64$ ). Conversely, Oak Forest ( $J' = 0.92$ ) had the highest evenness, followed by Cloud Forest ( $J' = 0.89$ ), and Garden ( $J' = 0.75$ ). Pairwise Bray-Curtis dissimilarity values reveal that the two forest sites have more similar hummingbird species compositions than each with the garden site (Table 5).

**Table 4.** Hummingbird species diversity and richness by study site.

	Cloud Forest	Garden	Oak Forest	General
Hummingbird observed richness ( $S_{obs}$ )	9	13	6	14
Hummingbird estimated richness (Chao; $S_{est}$ )	9.5	13.2	6.0	16.0
Hummingbird sampling completeness ( $S_{obs}/S_{est}$ )	0.95	0.98	1.00	0.88
Hummingbird records ( $A$ )	60	427	61	548
Shannon Diversity ( $H'$ )	1.95	1.92	1.64	2.02
Pielou's Evenness ( $J'$ )	0.89	0.75	0.92	0.77

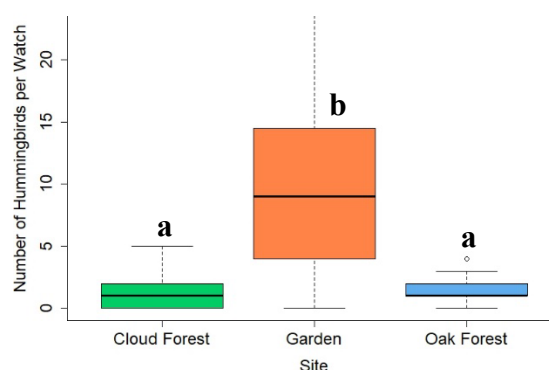
**Table 5.** Pairwise Bray-Curtis Dissimilarity values for hummingbird and floral composition between study sites.

	Cloud Forest- Garden	Cloud Forest- Oak Forest	Garden- Oak Forest
Hummingbird Composition	0.78	0.39	0.79
Flower Composition	0.87	0.83	0.77

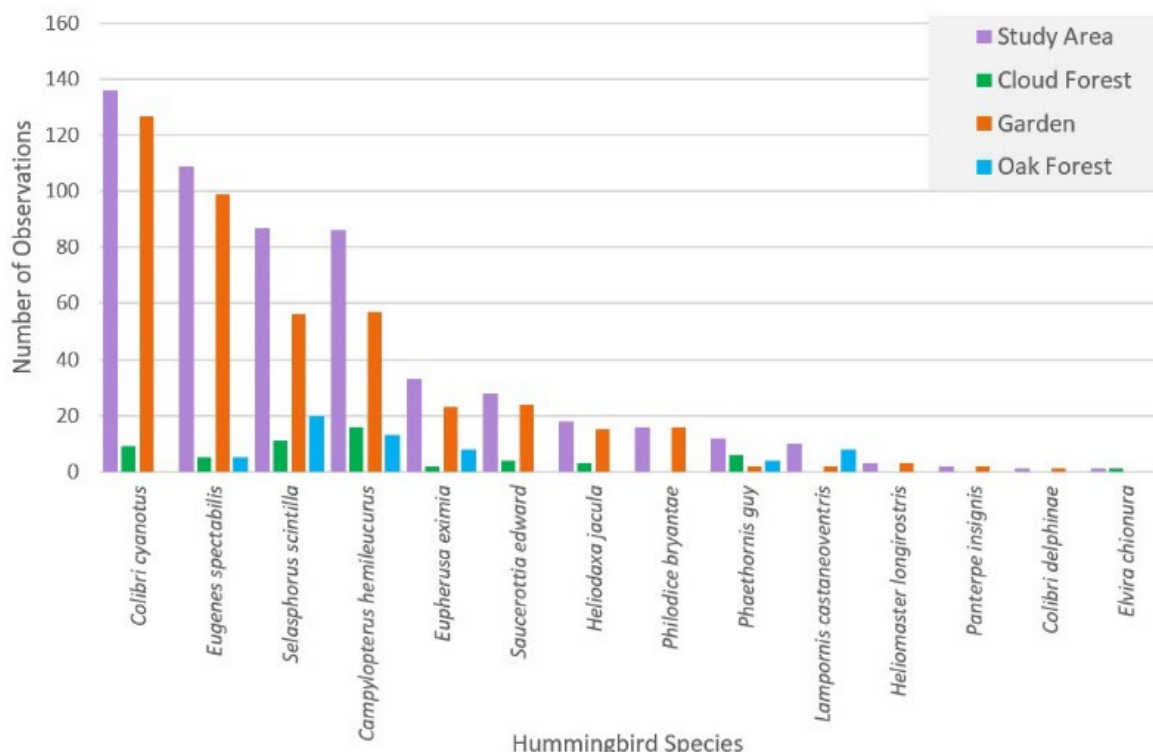
### Hummingbird Abundance

Over 120 separate 20-minute watches, I recorded 548 hummingbirds, with 60 in Cloud Forest, 427 in the Garden, and 61 in Oak Forest (Table 4). A Kruskal-Wallis test revealed significant differences between sites in the number of hummingbirds observed per watch ( $\chi^2(2) = 60.38, p < 0.001$ ). Follow up pairwise Wilcoxon rank sum tests found significantly more hummingbirds per watch in Garden plots (median=9) than in Cloud Forest (median=1,  $p < 0.001$ ) and Oak Forest (median=1,  $p < 0.001$ ), however the two forest sites did not significantly differ ( $p = 0.67$ ) (Figure 9).

**Figure 9.** Hummingbird abundance per watch by study site. Letters indicate significant difference ( $p < 0.001$ ).



**Figure 10.** Hummingbird species observations by species for the entire study area and each



Hummingbird records per site are visualized in Figure 10. For the entire study area, the Lesser Violetear (*Colibri cyanotus*), Talamanca Hummingbird (*Eugenes spectabilis*), and Scintillant Hummingbird (*Selasphorus scintilla*) were the most commonly observed (see photos in Figure 1). While this trend held true for the Garden, the forest sites differed. In Cloud Forest, the Violet Sabrewing (*Campylopterus hemileucurus*) was most abundant (Figure 2 & 4), followed by the Scintillant and Lesser Violetear. Finally, the Scintillant was the most commonly observed in the Oak Forest, followed by the Violet Sabrewing and White-throated Mountain Gem (*Lampornis castaneiventris*).

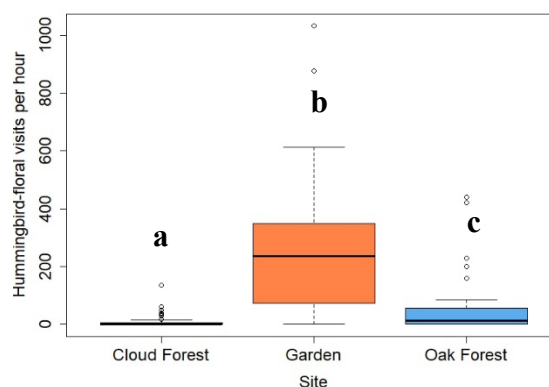
### Floral Visitation

A Kruskal-Wallis test found that floral visitation rates on a per-watch basis differed significantly between study sites ( $\chi^2(2) = 61.43$ ,  $p < 0.001$ ). Follow-up pairwise Wilcoxon rank sum tests showed that all three sites differed significantly from each other (Cloud Forest-Garden:  $p < 0.001$ , Cloud Forest-Oak Forest:  $p = 0.001$ , Garden-Oak Forest:  $p < 0.001$ ; Figure 11). Floral visitation was highest in the Garden (median=237 visits/hour), followed by the Oak Forest (median= 12 visits/hour), and finally Cloud Forest (median= 0 visits/hour). Notably, floral visitation was significantly positively correlated with hummingbird abundance (Spearman rank correlation:  $R = 0.80$ ,  $p < 0.001$ ).

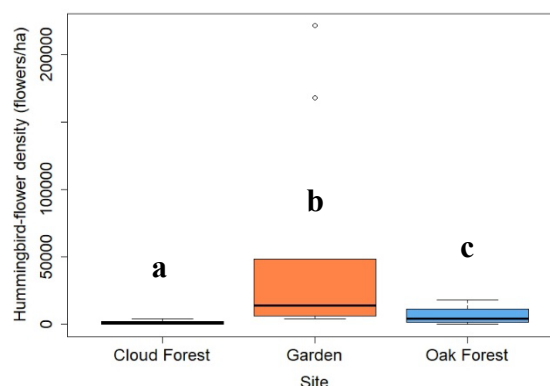
### Floral Density and Composition

A Kruskal-Wallis test determined that floral density of hummingbird flowers differed significantly between each of the three sites ( $\chi^2(2) = 20.67$ ,  $p < 0.001$ ). Follow-up pairwise Wilcoxon rank sum tests revealed that the floral density in Cloud Forest and Garden ( $p < 0.001$ ), Cloud Forest and Oak Forest ( $p = 0.0065$ ), and Oak Forest and Garden ( $p = 0.025$ ) all differed significantly (Figure 12). The Garden had the highest median floral density (14200 flowers/ha), followed by Oak Forest (4400 flowers/ha), and finally Cloud Forest (1425 flowers/ha). High Bray-Curtis dissimilarity values reveal clear compositional differences between sites (Table 5). The plant species with the highest floral densities for each site are summarized in Table 6 (Appendix).

**Figure 11.** Hummingbird visitation per watch by study site. Letters indicate significant difference ( $p < 0.01$ ).



**Figure 12.** Hummingbird-flower density per hectare by study site. Letters indicate significant difference ( $p < 0.01$ ).



## Vegetation

Kruskal-Wallis tests revealed significant differences between sites in undergrowth ( $\chi^2(2) = 6.37, p=0.04$ ), epiphyte coverage ( $\chi^2(2) = 17.91, p<0.001$ ), and canopy density ( $\chi^2(2) = 16.36, p<0.001$ ). Undergrowth and epiphyte coverage were both highest in the Oak Forest, followed by Cloud Forest and finally Garden. Canopy height was marginally higher in Oak Forest, and canopy density was significantly higher in Oak Forest ( $p=0.008$ ).

## Linear Models

Akaike Information Criterion (AIC) values were lowest for model four, which incorporated site and floral density as explanatory variables (Table 7, Appendix). Model four explained the highest amount of variance in the response variables ( $R^2=0.85$  and  $R^2=0.77$  for abundance and richness respectively). Holding site constant, floral density significantly predicted both hummingbird abundance per watch ( $p<0.001$ ) and floral richness ( $p<0.001$ ). Holding floral density constant, Garden plots had a mean abundance ( $p<0.001$ ), and mean richness ( $p<0.001$ ) exceeding forest plots. The model using only elevation as an explanatory variable predicted the least variation in the response variables, however was still significant ( $p<0.001$ ).

## Hummingbird-plant Network

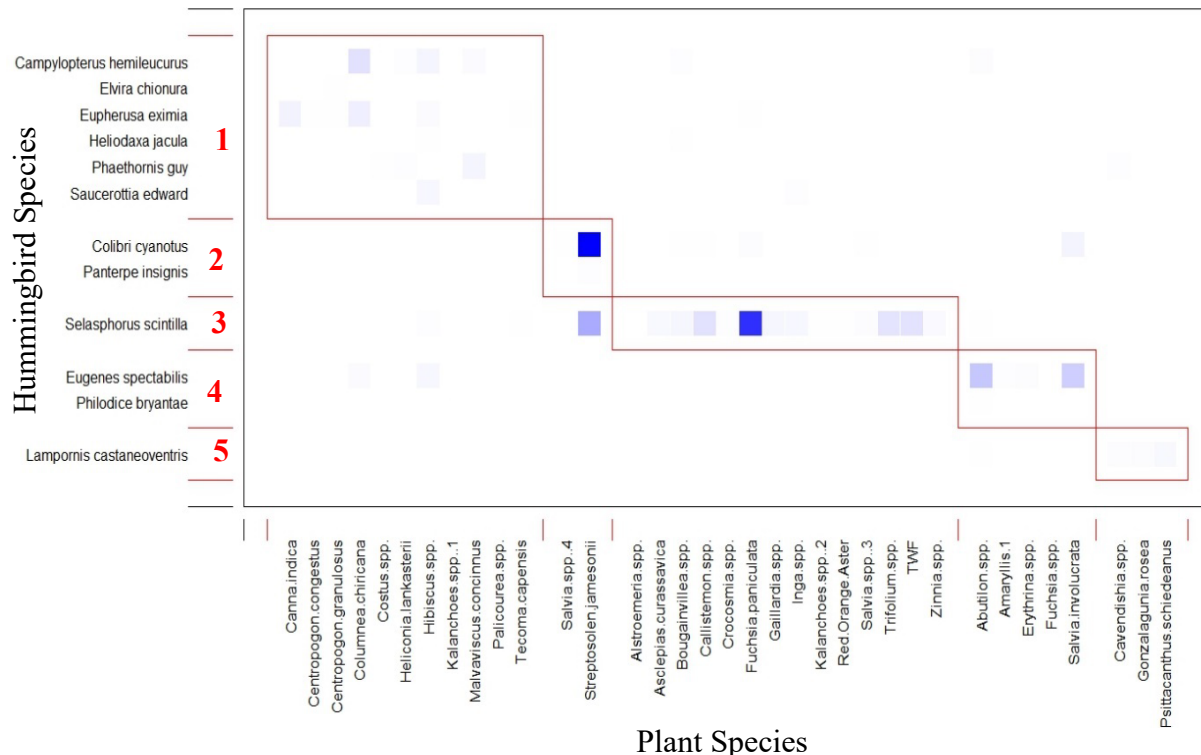
Across all three study sites, I recorded 4533 visits made by 12 hummingbird species to 35 plant species, composing a total of 72 unique interactions (Table 8, Figure 14). The individual sites represented smaller subsets of the general network, with the cloud forest having 9 interactions between 6 hummingbird species and 8 plant species, the Garden site having 53 interactions between 11 hummingbird species and 26 plant species, and the Oak Forest having 13 interactions between 6 hummingbird species and 8 plant species (Table 8, Figure 14). All computed indices for each network differed significantly from computed null models (Z test,  $p<0.001$ ). Nestedness (wNODF) was highest in the Garden and lowest in the Cloud Forest. Connectance (C) was highest in the Oak Forest site and lowest in the General network. Network-level specialization ( $H_2'$ ) was also highest in the Oak Forest and lowest in the Garden. Finally, modularity (Q) was similar between sites. The modularity output for the general network computed five modules that differed significantly from null models (Z test,  $p<0.001$ ; Figure 13).

**Table 8:** Hummingbird-plant network indices for the entire area and each study site.

	General	Cloud Forest	Garden	Oak Forest
Hummingbird richness	12	6	11	6
Plant Richness	35	8	26	8
Interactions	72	9	53	13
Nestedness (wNODF)	18.51*	8.33*	22.87*	17.44*
Connectance (C)	0.17*	0.21*	0.18*	0.27*
Network-level Specialization ( $H_2'$ )	0.69*	0.75*	0.67*	0.91*
Modularity (Q)	0.56*	0.53*	0.51*	0.55*

\* Indicates significant deviation from null models (Z test,  $p<0.001$ ).

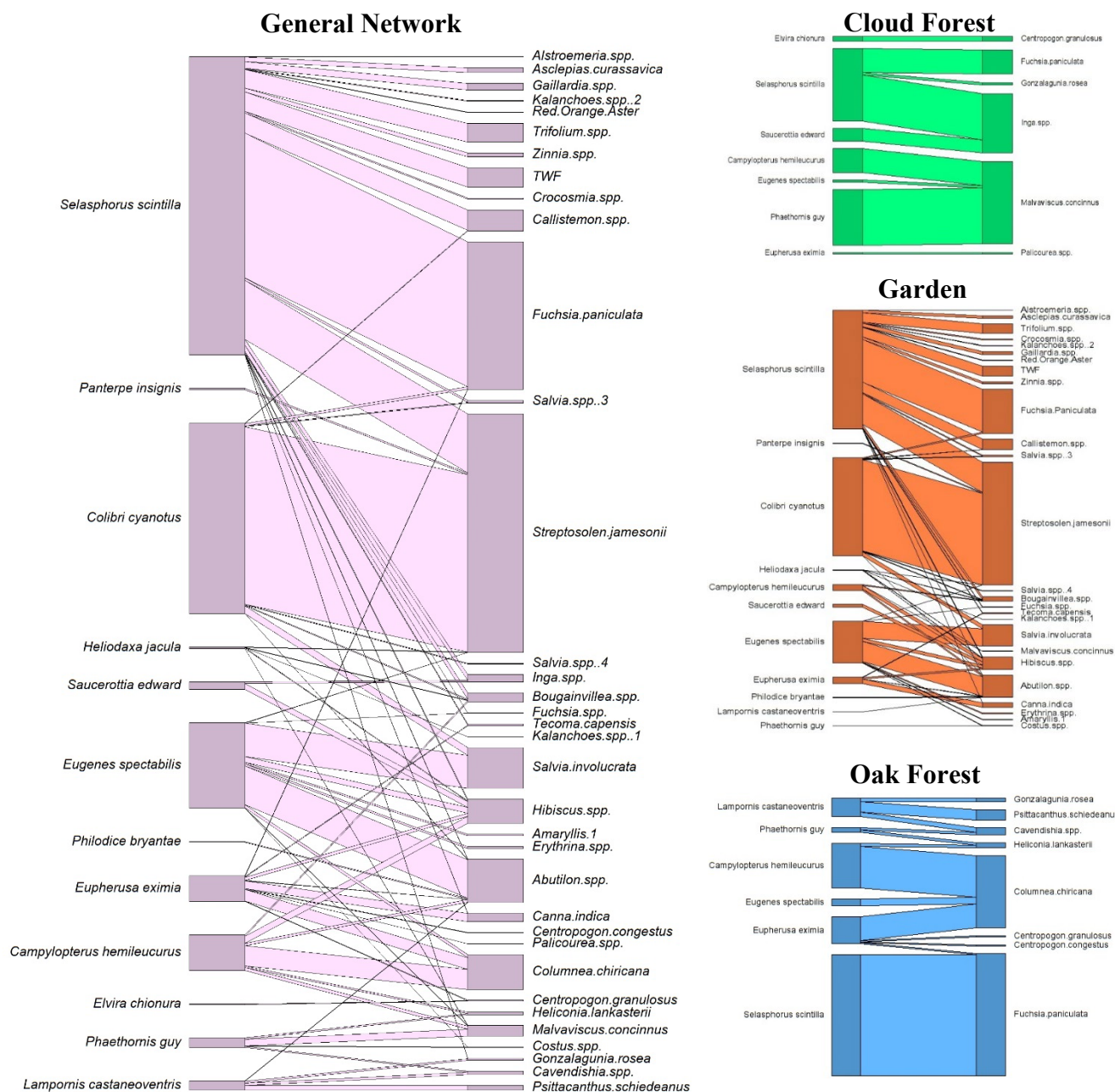
**Figure 13.** Hummingbird-plant network modularity. Hummingbird species are represented on the y-axis and plant species on the x-axis. Shading intensity corresponds to the interaction strength measured by cumulative visits. Red boxes indicate computed modules where species within each module are statistically more likely to interact with other species within the module than species outside.



### Hummingbird Species Specialization

On a species level, hummingbird degree ( $p$ ) and specialization ( $d'$ ) for each site are visualized in Table 9. In general, hummingbird species had fewer partners in forest environments than in the Garden site. Hummingbird specialization varied at a species-specific level between sites. Across the entire network and including only species with adequate sampling effort, the White-throated Mountain Gem (*Lampornis castaneiventris*) had the highest specialization ( $d'=0.91$ ), while the Green-crowned Brilliant (*Heliodaxa jacula*) had the lowest ( $d'=0.40$ ). Trends in hummingbird degree did not always match trends in specialization, as  $d'$  takes into account the specialization of the plants as well as the hummingbirds. A Spearman rank correlation found that body length did not significantly predict the number of partners ( $R=-0.32$ ,  $p=0.39$ ) or specialization ( $R=0.32$ ,  $p=0.40$ ). As expected, these metrics showed opposite trends, as the number of partners non-significantly decreased with body length (Figure 15a), but specialization non-significantly increased (Figure 15b). A two factor ANOVA with bill length and curvature as explanatory variables found no significant effects of either variable on degree (length:  $p=0.45$ , curve:  $p=0.81$ ) or specialization (length:  $p=0.67$ , curve:  $p=0.72$ ).

**Figure 14.** Visualized hummingbird-plant visitation networks for the entire study site, Cloud Forest, Garden, and Oak Forest sites. Hummingbird species are arranged on the left axis and plant species are arranged on the right. The thickness of connection between hummingbirds and plants represents the interaction strength measured through cumulative hummingbird visits.





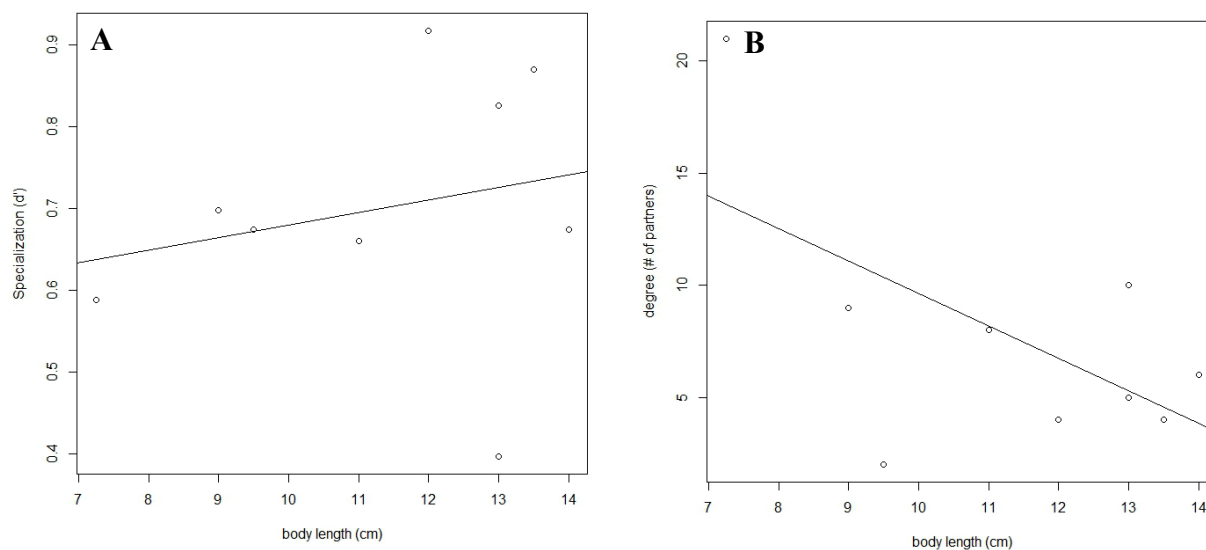
**Table 9.** Hummingbird species degree and specialization in general and for each study site.

S= entire Study Area, CF= Cloud Forest, G=Garden, OF=Oak Forest.

Hummingbird species	Degree (# Partners)				Specialization (d')			
	S	CF	G	OF	S	CF	G	OF
<i>Campylopterus hemileucurus</i> *	6	1	4	2	0.67	0.37	0.58	0.66
<i>Colibri cyanotus</i> *	8	0	8	-	0.66	0	0.6	-
<i>Colibri delphinae</i>	0	-	0	-	0	-	0	-
<i>Elvira chionura</i>	1	1	-	-	0.89	1	-	-
<i>Eugenes spectabilis</i> *	10	1	8	1	0.83	0.13	0.86	0.31
<i>Eupherusa eximia</i> *	9	1	4	4	0.7	1	0.81	0.44
<i>Heliodaxa jacula</i> *	5	0	5	-	0.4	0	0.43	-
<i>Heliomaster longirostris</i>	0	-	0	-	0	-	0	-
<i>Lampornis castaneiventris</i> *	4	-	1	3	0.92	-	0.3	0.96
<i>Panterpe insignis</i>	1	-	1	-	0.13	-	0.1	-
<i>Phaethornis guy</i> *	4	1	1	2	0.87	0.66	0.96	0.76
<i>Philodice bryantae</i>	1	-	1	-	0.37	-	0.36	-
<i>Saucerottia edwardii</i> *	2	1	1	-	0.67	0.4	0.68	-
<i>Selasphorus scintilla</i> *	21	3	19	1	0.59	0.81	0.51	0.98

- indicates the species was not present at the site.

\* indicates adequate sampling effort (&gt;5 observed feeding bouts)

**Figure 10.** Linear regressions between (A) body length and specialization, and (B) body length and degree (# partners).

## Discussion

### Hummingbird community

Throughout the study period, I observed clear differences in hummingbird richness and diversity between Cloud Forest, Garden, and Oak Forest on Mount Totumas (Table 4). Additionally, I observed significant differences in hummingbird abundance (Figure 9), vegetation characteristics, floral density (Figure 12), and floral visitation (Figure 11) between sites ( $p < 0.05$ ). High sampling completeness, assessed through hummingbird species accumulation curves and Chao richness estimations, suggests that these data provide a thorough representation of hummingbird richness for the period of study (Table 4). However, all reported results are inherently limited to the study period in November, at the end of the wet season. Further study is required to understand hummingbird diversity dynamics over the entire year.

Hummingbird richness was highest in the Garden (Table 4). Additionally, relative abundance (Figure 9), and visitation rates (Figure 11) were both significantly higher in the Garden than in the forest sites ( $p < 0.05$ ). Shannon diversity peaked in the Cloud Forest ( $H' = 1.95$ ); however, the Garden was very similar ( $H' = 1.92$ ). Pielou's evenness peaked in the Oak Forest ( $J' = 0.92$ ) and the Garden was noticeably lower ( $J' = 0.75$ ). These data suggest that the Garden supports a more speciose assemblage of hummingbirds than the forest. However, forest sites may have higher Shannon diversity and evenness because hummingbird species are more evenly abundant in the forest sites.

Depending on a focus of strictly species richness or Shannon diversity, these results may corroborate either Tinoco et al. (2018) or Hadley et al. (2017) and Morrison & Mendenhall (2020). The Garden, which is a heterogenous/human-influenced habitat, had higher species richness. This echoes the conclusions of Tinoco et al. (2018) that heterogenous environments support the greatest hummingbird richness in the Andes. However, focusing on Shannon diversity, the Cloud Forest had a slightly more diverse hummingbird community. This underscores the findings of Hadley et al. (2017) and Morrison & Mendenhall (2020) that forest communities support more diverse hummingbird assemblages than human-impacted landscapes. Tempering these comparisons, however, is the fact that Tinoco et al. (2018), Hadley et al. (2017), and Morrison & Mendenhall (2020) focused on broader areas of human-impacted habitat that likely had lower floral abundance than the Garden. Therefore, direct comparisons between the Mount Totumas Garden and other human-impacted/ agricultural landscapes in the Neotropics may produce skewed conclusions.

The most commonly observed species across the study area, the Lesser Violetear (*Colibri cyanotus*), showed a clear habitat preference for the Garden site. Other common species like the Talamanca Hummingbird (*Eugenes spectabilis*), the Scintillant Hummingbird (*Selasphorus scintilla*), and the Violet Sabrewing (*Campylopterus hemileucurus*) were found across all three sites; however, abundance was highest in the Garden. Four species: the Brown Violetear (*Colibri delphinae*), Long-billed Starthroat (*Heliomaster longirostris*), Fiery-throated Hummingbird (*Panterpe insignis*), and Magenta-throated Woodstar (*Philodice bryantae*), were seen exclusively in the Garden. Notably, three of these species are altitudinal migrants who travel to Mount Totumas during certain times of year. Only one species, the White-tailed Emerald (*Elvira chionura*) was exclusive to the Cloud Forest. No species were exclusive to the Oak Forest. While

species turnover was low between sites, abundance-based Bray-Curtis dissimilarity values suggest that the forest sites had clear compositional differences from the Garden (Table 5). While seen occasionally in the Garden, the Green Hermit (*Phaethornis guy*) and the White-throated Mountain Gem (*Lampornis castraneovenstris*) were both much more abundant in Cloud Forest and Oak Forest, respectively. These results echo those of Morrison & Mendenhall (2020), who asserted that human-impacted landscapes foster unique hummingbird communities compared to forest habitats. Notably, forest specialists may be more vulnerable to habitat destruction than human-tolerant species (Morrison & Mendenhall, 2020).

Floral density differed significantly between sites ( $p < 0.001$ ), with the Garden having nearly three times more floral resources than the forest sites per hectare (Figure 12). Bray-Curtis dissimilarity values also suggest clearly different floral communities in each site (Table 5). Linear models and AIC suggest that observed differences in hummingbird richness and abundance on a watch-level were best explained by site and floral density (Table 7, Appendix). This result suggests that (1) hummingbirds may be attracted to the Garden area because of the bounty of nectar resources, and (2) the plentiful resources in the garden may support a higher population density. This finding is interesting, as many of the flowers in the Garden are non-native. Three of the four most visited flower species across the area: *Streptosolen jamesonii*, *Abutilon spp.*, and *Salvia involucrata*, were all non-native garden plants (Table 3, Appendix). The most visited native plant, *Fuchsia paniculata*, was found in all sites, had very high floral densities, and was visited primarily by *Selasphorus scintilla*. I also observed hummingbird visitation to both ornithophilous and non-ornithophilous flowers in all sites (Table 3, Appendix). This finding supports the importance of non-ornithophilous flowers for hummingbirds discussed in Dalsgaard et al. (2009), Marayuma et al. (2013), and López-Segoviano et al. (2021). High rates of floral visitation to non-native and non-ornithophilous flowers suggests that hummingbirds at this site are highly adaptable to changing floral resources. This underscores the observations of Marayuma et al. (2019), Morrison & Mendenhall (2020), and Marín-Gómez et al. (2021) that hummingbirds may increase opportunistic feeding in human-impacted landscapes.

Between the forest sites, hummingbird visitation (Figure 11) and floral density (Figure 12) were significantly higher in the Oak Forest ( $p < 0.001$ ), while hummingbird abundance was statistically similar between the two sites (Figure 9,  $p = 0.67$ ). This difference is likely due to high floral density and visitation of hummingbirds to *Columnea chiricana* in the Oak Forest (Figure 2). The importance of floral density in impacted hummingbird communities supports the findings of Gonzalez & Loiselle (2016) in Andean cloud forest and Bustamante-Castillo et al. (2018) in Guatemalan dry forest. Moreover, while this study had a short temporal duration, differences in floral density over time and space relate closely with altitudinal and latitudinal migration of hummingbirds (López-Segoviano et al., 2018). The number of altitudinal migrants found exclusively in the Garden could indicate that these species prioritize floral density when moving between locations. Further study over the course of the year could elucidate the nuances of the relationship between floral density and hummingbird altitudinal migration in Panamá.

While it explained less of the variance in hummingbird abundance and richness than floral density and site together, elevation by itself significantly predicted hummingbird richness and abundance ( $p < 0.01$ ). The lower elevation Cloud Forest site had both a higher richness and Shannon diversity than the Oak Forest site. Additionally, a single day of informal observation on

the summit of Mount Totumas (2625 meters) yielded only a single hummingbird species: the Fiery-throated Hummingbird (*Panterpe insignis*). These data support a general decreasing richness pattern with elevation (McCain & Grytnes, 2010, Sonne et al., 2019). However, the complete trend is unclear due to a lack of sampling at lower elevations in this study.

Elevation also explained some of the compositional differences in hummingbird species seen between sites. The higher incidence of the White-throated Mountain Gem (*Lampornis castaneiventris*) at the Oak Forest site makes sense as this species is generally reported from higher elevations during the wet season, descending lower during the dry season. Additionally, the single report of the White-tailed Emerald was from my lowest radial plot at 1817 meters. This species is known to be more abundant in foothill elevations (Angehr & Dean, 2010); as such, Mount Totumas may represent the upper boundary of its elevational range. Numerous other species found within the study area were higher in elevation than their projected ranges from Angehr & Dean (2010). The Green Hermit (*Phaethornis guy*) is generally observed between 600 and 1650 meters, yet I saw it regularly in both the Cloud Forest (1800-2000 meters) and Oak Forest (2050-2250 meters). Similarly, the Violet Sabrewing (*Camplyopterus hemileucurus*) is expected between 900 and 1650 meters, and was common across all sites. The Brown Violetear (*Colibri delphinae*, 900 to 1350 meters), Long-billed Starthroat (*Helio-master longirostris*, to 1500 meters), and Magenta-throated Woodstar (*Philodice bryantae*, 900 to 1750 meters) were all observed at around 1900 meters at the Garden site. These deviations from elevational expectations could indicate attractive effects of high floral density/sugar water feeders (Avalos et al., 2012, potential hummingbird upsloping due to climate change (Yoon, 2019), or simply historic misreporting of hummingbird ranges in the Western Highlands, where they may deviate from patterns across the rest of Panamá.

#### Hummingbird-Plant Network

Considering the short observational period of this study, the high number of observed feeding hummingbird species (12), hummingbird-visited plant species (35) and interactions (72) indicates that this network is speciose (Table 8). Network parameters for both hummingbird and plant species from 9 days of observation exceeded the size of published networks from the Caribbean (Dalsgaard et al., 2009), Guatemalan dry forest (Bustamante-Castillo et al., 2018), Brazilian Cerrado (Marayuma et al., 2013), and Mexican highlands (Ortiz-Pulido et al., 2012). As expected, network size more closely resembled studies from Costa Rica (Maglianesi et al., 2014; Maglianesi et al., 2015; & Morrison & Mendenhall, 2020), and the Andes (Gonzalez & Loiselle, 2016; Sonne et al., 2019). Further study through the rest of the year would undoubtedly increase the network size further, especially in the forest sites with the inclusion of plant species that flower other times of year due to dispersed flowering (Sheldon & Nardkani, 2015).

Between sites, the Garden network had more hummingbird species, plant species, and interactions than the two forest sites. The forest sites had the same number of hummingbirds and plants, but the Oak Forest site had more interactions. Across all sites and the general network, all of the computed indices deviated significantly from null-model expectations (Table 8). This result is similar to other sampled hummingbird-plant networks (Gonzalez & Loiselle, 2016; López-Segoviano et al., 2021). Deviations from null models indicate that the Mount Totumas hummingbird-plant networks have distinctive structure and organization. For the entire study site, nestedness (wNODF= 18.51) was significantly lower than expected by chance. Nestedness

was very low in the Cloud Forest site ( $wNODF=8.33$ ), and marginally higher in the Garden ( $wNODF=22.87$ ) and Oak Forest ( $wNODF=17.44$ ). Networks with low nestedness are known to be more susceptible to disturbance because of higher specialization and less redundancy in interactions (Bascompte et al., 2003). This could indicate that hummingbird-plant interactions in the forest sites are more vulnerable to change. However, low nestedness could also be a result of poor sampling effort from the short study duration (Bascompte et al., 2003). Connectance for the entire area ( $C=0.17$ ) was also lower than expected by chance ( $p<0.001$ ), and was similar to observed values from Gonzalez & Loiselle (2016) and López-Segoviano et al., (2021). Differing from nestedness, connectance values were higher in the forest sites (Cloud Forest:  $C=0.21$ , Oak Forest:  $C=0.27$ ) than in the Garden ( $C=0.18$ ). This deficit is likely due to the fact that network connectance is usually lower in more speciose networks (Olesen & Jordano, 2002).

Network modularity values were fairly similar between sites and the entire study area ( $Q=0.56$ ), all of which were significantly more modular than random networks (Table 8, Figure 13). All modularity values exceeded those published in López-Segoviano et al., (2021). Hummingbirds were generally not grouped into modules by site, as many of the same species were present across the study area. Additionally, modules did not show any clear grouping by bill morphology, as both the long-billed Talamanca Hummingbird (*Eugenes spectabilis*) and short-billed Magenta-throated Woodstar (*Philodice bryantae*) occupied the same module (module 4). The Scintillant Hummingbird (*Selasphorus scintilla*), and the White-throated Mountain Gem (*Lampornis castaneiventris*) both occupied single-species modules, indicating unique foraging preferences. In contrast, plant species showed more grouping by site, with modules 2, 3, and 4 being comprised nearly exclusively of Garden plants, and module 5 being exclusively flowers found in the Oak Forest. Module 1 consisted of a mix of species from all three sites, with high representation from the forest habitats. These findings corroborate those of López-Segoviano et al. (2021) that plant species were grouped by site in their module analysis.

Specialization

Network-level specialization was significantly higher than expected by chance in all sites (Table 8,  $p<0.001$ ), and was also higher than published values from Maglianesi et al. (2014), Gonzalez & Loiselle (2016), Partida-Lara et al. (2018), and López-Segoviano et al., (2021). The Oak Forest, especially, had a very high specialization index of ( $H_2'=0.91$ ). In contrast, the Garden had the lowest network level specialization ( $H_2'=0.67$ ). The high observed specialization across these networks asserts that hummingbird-plant interactions during the study period were highly specialized. However, network-level specialization would likely decrease with a longer study duration as hummingbirds visited more plant species. Understanding that comparisons with year-round networks may yield different results, these findings may still provide insight into the effects of elevation and human-influence on hummingbird-plant interactions. These data are similar to the findings of Dalsgaard et al. (2009) and Partida Lara et al. (2018) that hummingbird specialization was highest at their high-elevation sites. Additionally, the decrease in specialization in the human-impacted garden site echoes Hadley et al. (2017), Marayuma et al. (2019), Morrison & Mendenhall (2020), and Marín-Gómez et al.'s (2021) findings that specialization decreases in non-forest environments. While specialization may be advantageous for individuals within the network, it also leaves species vulnerable to potential changes in their relationships with specialized partners (Blüthgen et al., 2006). For example, if a forest plant

species is only visited by a single hummingbird, and that hummingbird stops foraging in the forest because there are more nectar rewards in the Garden, then the forest plant will not be pollinated and will not be able to reproduce. Similarly, if the forest plant shifts in range due to climate change, the specialized hummingbird may not have a food resource.

On a species level, the most specialized hummingbirds across the entire study area with adequate sampling effort were the White-throated Mountain Gem (*Lampornis castaneiventris*,  $d'=0.92$ ), Green Hermit (*Phaethornis guy*,  $d'=0.87$ ), and Talamanca Hummingbird (*Eugenes spectabilis*,  $d'=0.83$ ) (Table 9). Notably, *Phaethornis guy* is part of the hermit clade, which have long decurved bills and are known to be highly specialized (Rodríguez-Flores et al., 2019). The hummingbird with the greatest number of partners by far was the Scintillant Hummingbird (*Selasphorus scintilla*), visiting 21 plant species. The short and straight bill of *Selasphorus scintilla* enabled it to visit many small flowers that did not attract other hummingbirds. One of these species, *Fuchsia paniculata*, had abundant small flowers in all three study sites and attracted over 1000 observed visits from *Selasphorus scintilla*. Also fitting with larger generalizations at the clade level, *Selasphorus scintilla* is a member of the Bee-hummingbird clade, which are known to be quite generalized (Rodríguez-Flores et al., 2019).

Hummingbird species differed in both their number of floral partners and their specialization between sites. The species present in all sites (Violet Sabrewing/ *Campylopterus hemileucurus*, Talamanca Hummingbird/*Eugenes spectabilis*, Stripe-tailed Hummingbird/ *Eupherusa eximia*, Green Hermit/*Phaethornis guy*, and Scintillant Hummingbird/*Selasphorus scintilla*), differed in their patterns of specialization (Table 9). *Campylopterus hemileucurus* and *Selasphorus scintilla* were most specialized in the Oak Forest. *Eugenes spectabilis* had the highest specialization in the Cloud Forest, while both *Eupherusa eximia* and *Phaethornis guy* were most specialized in the Garden. Notably, trends in the number of partners for each species did not always match trends in specialization. This discrepancy had to do with the reciprocal specialization of certain plant species. For example, even though *Panterpe insignis* only interacted with a single plant species (*Streptosolen jamesii*), it had a low specialization index ( $d'=0.13$ ) because many other hummingbirds visited *Streptosolen jamesii*. In contrast, *Selasphorus scintilla* visited 19 flowering plant species in the garden, yet still had a moderate specialization index ( $d'=0.51$ ) because it was the sole visitor of many of those plants. These data highlight clear species-specific differences between specialization in different habitats that warrant further inquiry.

I detected no significant relationships between body length, bill length, or bill curvature and species degree or specialization. Species degree and specialization responded in opposite manners to increasing body length, with degree decreasing and specialization increasing (Figure 15a, 15b). Generally, this finding makes sense as having more partners is likely to decrease generalization, and vice versa. While non-significant, these trends in body length partially support Dalsgaard et al.'s (2009) claim that larger hummingbirds are more specialized. However, these results are insufficient to draw broader conclusions regarding the role of hummingbird morphology in structuring species-specialization, as posited in Dalsgaard et al. (2009) and Maglianesi et al. (2014). While I excluded species with less than five feeding observations, increasing the number of feeding observations for all species may improve the statistical power of these relationships. Additionally, using actual bill length and curvature measurements

obtained by mist-netting may increase the statistical power, compared with binary categorizations.

### **Limitations and Sources of Error**

The most significant limitation of this study is the short temporal duration of observation, as tropical hummingbird-plant communities interact year-round. Similar studies have all included repeated sampling efforts throughout the year to quantify the impacts of seasonality on hummingbirds (Bustamante-Castillo et al., 2018; Dalsgaard et al., 2009; Gonzalez & Loiselle, 2016; Hadley et al., 2017; López-Segoviano et al., 2021; Maglianesi et al., 2014; Maglianesi et al., 2015; Marayuma et al., 2013; Marayuma et al., 2019; Marín-Gómez et al., 2021; Morrison & Mendenhall, 2020; Partida-Lara et al. 2018). This temporal sampling method is especially important considering that flowering phenology for different species are dispersed throughout the year in tropical highland communities (Sheldon & Nardkani, 2015). While Sheldon & Nardkani report some flowering peaks throughout the year, there is still a constant source of nectar from overturning flowers. This flowering phenology pattern has been suggested to be the primary driver of hummingbird-plant network structure (Gonzalez & Loiselle, 2016).

Another clear limitation in the applicability of these results is the small spatial area sampled for both hummingbirds and flowers. Montane forest environments are heterogenous, and can differ by topography and watershed (Monro et al., 2017a). Observationally, I noticed that floral density in the forest often was higher near streams, exemplifying this heterogeneity. Consequently, these findings from Mount Totumas and the Rio Colorado watershed may not be expandable even to nearby areas of similar elevation in the Western Highlands.

Regarding potential sources of error, one looming uncertainty is the relative role of hummingbird feeders in attracting hummingbirds to the Garden area, and potentially away from the forest. During informal observations, I saw 11 of the 14 hummingbird species in the study at the hummingbird feeders, with many species feeding on the sugar-water feeders extensively. While I did not observe flower feeding behavior from the Long-billed Starthroat (*Helimaster longirostris*), I saw it regularly at feeders. I attempted to alleviate the conflating effects of the feeders by removing them during Garden watches. This decision was based on the findings of Sonne et al. (2016) that hummingbird feeders locally inflate abundance and floral visitation within 75 meters. However, removal only for sampling did not fully account for the impact of feeders. The observed high abundance of hummingbirds within the Garden could be due to the long-term presence of the feeders, as they provide predictable high quantities of sugar-water to sustain and attract a large population of hummingbirds (Avalos et al., 2012). Behaviorally, I observed numerous hummingbirds at Garden plots G01 and G04, positioned adjacent to feeding stations, that were clearly looking for the absent hummingbird feeders. Additionally, faced with an absence of the regular energy source of the feeders, hummingbirds in the Garden may have inflated their visitation rates to nearby flowers. In Costa Rica, Avalos et al. (2011) found decreased hummingbird abundance up to 3 km from a feeding station. If the attractive effects of feeders extend this far at Mount Totumas, then there may have been decreased abundance and visitation in the forest sites because of feeders. Consequently, my decision to only remove the feeders during Garden watches may have biased the results, especially in the Cloud Forest. While my experimental design is not able to address the confounding effects of the feeders on

the observed trends, further quantitative study could untangle this complex topic by quantifying visitation at various distances from feeders when they were both available and unavailable.

Another potential bias within this study was the non-random plot placement in areas of high floral density, as well as the reduced number of plots in the Garden site. I decided to place plots non-randomly (1) because published studies (Partida-Lara et al., 2018) have made similar decisions, and (2) because I wanted to maximize the likelihood of observing hummingbirds and interactions during the short study period. I maintained spatial independence by keeping plots 100 meters apart. While I made sure that I watched all potential ornithophilous flower species at least once in each site, my biased choices of plot by perceived floral density may have skewed visitation averages. Additionally, this plot placement method raises the potential that I missed hummingbirds with different habitat preferences or that visited inconspicuous flowering plants that I missed. While I believe that comparisons between sites are still possible with this sampling method, I did not attempt to quantify absolute hummingbird abundance or density due to the pitfalls of this method.

Regarding the plot-sampling method, there were also potential sources of error due to observer mistakes and missed species or interactions. During observational watches, I stood in the center of the radial plot. This prevented me from viewing flowers in front and behind me simultaneously, and also reduced the visibility of flowers further from plot center. In forest sites, visibility was often hindered by undergrowth and trees, especially in comparison to the Garden, which was quite open. On numerous occasions, I heard hummingbirds in the forest sites but was unable to identify them or see if they were feeding. In the Oak Forest, I observed the Scintillant Hummingbird (*Selasphorus scintilla*) feeding on flowers in the canopy, but was unable to ID the flowers or keep a count of the number of visits because of poor visibility. Additionally, there is always the chance that I misidentified species, as hummingbirds were often fast moving and I had limited exposure to these species before starting the study. In the Garden, hummingbird activity was often very high, with many individuals feeding simultaneously. I certainly missed visitation while counting other individuals' visits.

In all sites, I only counted visits when I observed the hummingbird fully contact floral reproductive structures. Even so, visitation does not always result in actual pollen collection or transfer. It was impossible to concretely verify pollination efficiency through observation alone. These limitations are inherent to the observational radial plot sampling protocol detailed in Bustamente-Castillo et al. (2018) and López-Segoviano et al. (2021). Other authors have reduced the error associated with floral observation by conducting focal plant species watches (Dalsgaard et al., 2009; Gonzalez & Loiselle, 2016;), mist-netting hummingbirds and sampling the pollen on them (Gonzalez & Loiselle, 2016; Maglianesi et al., 2014; Maglianesi et al., 2015; Morrison et al., 2020) and setting up video cameras on specific plant species (Maglianesi et al., 2014; Maglianesi et al., 2015; Sonne et al., 2019). Given more resources and time, I believe that a combination of mist-netting/pollen analysis and videoing would provide the least biased quantification of hummingbird-plant interactions possible.

Finally, these methods do not account for observed parasitic nectar robbing behaviors by hummingbirds and flowerpiercers in the study area. I viewed numerous hummingbird species feeding from flowers by using holes poked through external flower structures, especially in the garden. Common nectar robbing species included the Stripe-tailed Hummingbird (*Eupherusa*



*eximia*), Talamanca Hummingbird (*Eugenes spectabilis*), Magenta-throated Woodstar (*Philodice bryante*), and the Slaty Flowerpiercer (*Diglossa plumbea*). Flowering plants that experienced robbing included *Abutilon spp.*, *Hibiscus spp.*, *Canna indica*, *Tecoma capensis*, and *Streptosolen jamesonii*. While I observed *Diglossa plumbea* on numerous plant species, I could not determine if it facilitated hummingbird nectar-robbing as detailed in Gonzalez & Loiselle (2016). I did not count these interactions in the field or in analysis, as they don't represent a mutualism. However, these feeding events do represent one way that hummingbirds obtain energy, and certainly deplete flower nectar rewards.

## Conclusions

These data serve as a preliminary study of hummingbird community composition and hummingbird-plant interactions in the understudied biodiversity hotspot of the Western Highlands of Panamá. Based on 40 hours of observation on Mount Totumas, I observed clear differences in hummingbird richness, diversity, abundance, and visitation between the Cloud Forest, Oak Forest, and Garden sites. The Garden fostered significantly higher richness, abundance, and floral visitation rates compared to the forest sites. However, increased evenness in the forest sites gave the Cloud Forest a slight edge in Shannon diversity over the Garden. These differences in hummingbird community composition were best explained by the high floral density in the Garden site; however, elevation and available habitat space also seem to play a role. Hummingbird-plant interactions were generally specialized, creating a modular network with low connectance and nestedness. Network-level specialization was higher in Cloud Forest and Oak Forest than in the Garden, supporting the idea that mutualistic interactions are more generalized in human-impacted environments. Hummingbird specialization differed at a species-specific level between sites, indicating that different hummingbirds may exercise behavioral feeding flexibility in different environments. These conclusions are limited by the small spatial extent and short temporal duration of the study, as hummingbird-plant networks are dynamic and may change over time and space due to hummingbird migration and flowering phenology. Additionally, the unexplained role of feeders in attracting hummingbirds and nectar-robbing requires further study.

Further research on hummingbirds and hummingbird-plant interaction networks in the Western Highlands of Panamá should focus on expanding both the spatial area and temporal duration of study. Understanding these interactions is especially important given the deficit of hummingbird-plant network studies in Panamá, the speciose hummingbird community, as well as the importance of the biodiversity held within the La Amistad Biosphere Reserve. Future research should also attempt to separate the role of elevation and land use change on hummingbird-plant interactions, as a more intentional and replicated experimental design could glean an interesting understanding of the drivers behind hummingbird communities and interactions. To mitigate observer bias and error, future studies could also utilize different methodologies incorporating mist netting, pollen analysis, and video recording. While the scope of this study is limited to Mount Totumas during the end of the wet season, these observations form a solid basis for further investigation into hummingbird-plant interactions in Panamá.

## Appendix

**Table 1.** Plot UTM coordinates, elevation, and vegetative characteristics.

Transect	Plot #	UTM	Elevation (m)	Under-growth	Epiphyte	Mean Canopy Height (m)	Mean Canopy Density
<b>Cloud Forest</b>	CF01	17 P 0314789 0982968	1975	4	3	27.8	0.88
	CF02	17P 0314805 0982851	1961	4	3	15.4	0.85
	CF03	17P 03141865 0982878	1968	2	2	17.8	0.90
	CF04	17P 0314872 0982755	1946	4	2	25.6	0.87
	CF05	17P 0314831 0982663	1934	2	3	18.8	0.89
	CF06	17P 0314843 0982581	1923	2	2	18.8	0.88
	CF07	17P 0314786 0982322	1875	3	1	7.4	0.79
	CF08	17P 0314748 0982217	1854	4	1	9.2	0.87
	CF09	17P 0314704 0982123	1838	2	2	20.2	0.86
	CF10	17P 0314678 0982038	1817	2	2	17.2	0.88
<b>Garden</b>	G01	17P 0314879 0982299	1875	1	1	NA	0.07
	G02	17P 0314861 0982392	1891	3	1	NA	0.35
	G03	17P 0314864 0982481	1905	1	1	NA	0.10
	G04	17P 0314776 0982482	1906	2	2	NA	0.08
	G05	17P 0314730 0982393	1896	2	1	NA	0.18
<b>Oak Forest</b>	O01	17P 0316800 0983226	2072	2	4	19.2	0.86
	O02	17P 0316841 0983298	2078	4	3	24.2	0.88
	O03	17P 0316882 0983392	2101	3	3	23.4	0.94
	O04	17P 0316831 0983473	2105	4	3	14.4	0.92
	O05	17P 0316933 0983566	2133	2	4	21.6	0.93
	O06	17P 0317041 0983641	2130	3	4	23.4	0.93
	O07	17P 0317189 0983694	2142	4	4	20	0.88
	O08	17P 0317297 0983746	2153	3	4	28.4	0.93
	O09	17P 0317397 0983784	2161	4	4	27.2	0.91
	O10	17P 0317692 0983996	2223	4	4	21.6	0.92

**Table 2.** Hummingbird species observed in the study area. Abundance is the proportion of individual records from the entire study site. Body length measurements are published values in Angehr & Dean, 2010).

Common Name	Species name	Garden	Cloud Forest	Oak Forest	Abundance	Visits Observed	Length (cm)	Bill Length	Bill Curve
Green Hermit	<i>Phaethornis guy</i>	x	x	x	0.022	66	15	long	curve
Brown Violetear	<i>Colibri delphinae</i>	x			0.002	0	12	short	straight
Lesser Violetear	<i>Colibri cyanotus</i>	x	x		0.251	1296	11	long	straight
Green-crowned Brilliant	<i>Heliodoxa jacula</i>	x	x		0.033	11	13	long	straight
Talamanca Hummingbird*	<i>Eugenes spectabilis</i>	x	x	x	0.201	581	15	long	straight
Long-billed Starthroat	<i>Helioaster longirostris</i>	x			0.006	0	11	long	curve
Fiery-throated Hummingbird*	<i>Panterpe insignis</i>	x			0.004	10	11	short	straight
White-throated Mountain Gem*	<i>Lampornis castaneiventris</i>	x		x	0.018	63	11	long	straight
Magenta-throated Woodstar*	<i>Philodice bryantae</i>	x			0.030	6	8	short	straight
Scintillant hummingbird*	<i>Selasphorus scintilla</i>	x	x	x	0.161	2028	8	short	straight
Violet Sabrewing	<i>Campylopterus hemileucurus</i>	x	x	x	0.159	244	15	long	curve
White-tailed Emerald*	<i>Elvira chionura</i>		x		0.002	4	8	short	straight
Stripe-tailed hummingbird	<i>Eupherusa eximia</i>	x	x	x	0.061	174	10	short	straight
Snowy-bellied hummingbird	<i>Saucerottia edward</i>	x	x		0.052	50	10	short	straight

\* Indicates Western Highland endemic species (Angehr & Dean, 2010).

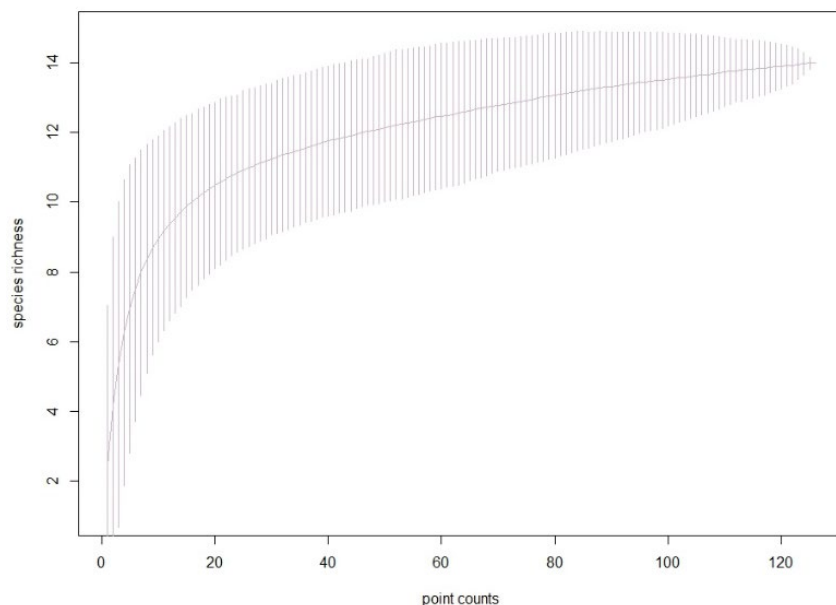
**Table 3.** Plant species observed in all sites with location and visitation information.

Family	Scientific Name	Cloud Forest	Oak Forest	Garden	Visits Observed	Hours Observed	Visits/ Hour
Acanthaceae	<i>Dicliptera iopus</i> *	x	x		0	12.0	0.0
Alstroemeriaceae	<i>Alstroemeria spp.</i>			x	2	2.7	0.8
Amaryllidaceae	<b>Unknown Amaryllis</b>			x	11	2.7	4.1
Apiaceae	Unknown Apiaceae			x	0	2.7	0.0
Apocynaceae	<i>Asclepias curassavica</i>			x	33	2.7	12.4
Asteraceae	<i>Gaillardia spp.</i>			x	44	2.7	16.5
Asteraceae	<i>Gazania spp.</i>			x	0	2.7	0.0
Asteraceae	<i>Ratibida spp.</i>			x	0	2.7	0.0
Asteraceae	<i>Unknown Aster 1</i>	x			0	1.3	0.0
Asteraceae	<b>Unknown Aster 2</b>			x	3	2.7	1.1
Asteraceae	<b>Zinnia spp.</b>			x	27	2.7	10.1
Balsaminaceae	<i>Impatiens spp.*</i>			x	0	2.7	0.0
Begoniaceae	<i>Begonia spp. 1</i>	x			0	2.7	0.0
Begoniaceae	<i>Begonia spp. 2</i>	x			0	0.0	0.0
Begoniaceae	<i>Begonia spp. 3</i>	x	x		0	5.3	0.0
Bignoniaceae	<b><i>Tecoma capensis</i>*</b>			x	12	2.7	4.5
Campanulaceae	<b><i>Centropogon congestus</i>*</b>	x	x		3	8.0	0.4
Campanulaceae	<b><i>Centropogon granulatus</i>*</b>	x	x		8	12.0	0.7
Cannaceae	<b><i>Canna indica</i>*</b>			x	57	2.7	21.4
Commelinaceae	<i>Commelina spp.</i>	x	x		0	8.0	0.0
Costaceae	<b><i>Costus spp.*</i></b>			x	4	8.0	0.5
Costaceae	<i>Costus wilsonii*</i>			x	0	5.3	0.0
Crassulaceae	<b><i>Kalanchoes spp. 1</i>*</b>			x	1	2.7	0.4
Crassulaceae	<b><i>Kalanchoes spp. 2</i>*</b>			x	5	2.7	1.9
Ericaceae	<b><i>Cavendishia spp.*</i></b>		x		23	5.3	4.3
Ericaceae	<i>Unknown Ericaceae*</i>	x			0	1.3	0.0
Fabaceae	<b><i>Erythrina spp.*</i></b>			x	13	1.3	9.8
Fabaceae	<b><i>Inga spp.</i></b>	x			50	1.3	37.5
Fabaceae	<b><i>Trifolium spp.</i></b>			x	127	2.7	47.6
Gesneriaceae	<i>Besleria solanoides*</i>	x			0	1.3	0.0
Gesneriaceae	<b><i>Columnea chiricana*</i></b>		x		237	12.0	19.8
Heliconiaceae	<b><i>Heliconia lankasterii*</i></b>		x		17	2.7	6.4
Heliconiaceae	<b><i>Heliconia spp.*</i></b>	x		x	0	1.3	0.0
Hydrangeaceae	<i>Hydrangea spp.</i>			x	0	2.7	0.0
Iridaceae	<b><i>Crocsmia spp.*</i></b>			x	9	2.7	3.4
Lamiaceae	<b><i>Salvia involucrata*</i></b>			x	279	5.3	52.3
Lamiaceae	<i>Salvia spp. 1</i>	x			0	0.0	0.0
Lamiaceae	<i>Salvia spp. 2*</i>		x		0	9.3	0.0
Lamiaceae	<b><i>Salvia spp. 3*</i></b>			x	18	2.7	6.8
Lamiaceae	<b><i>Salvia spp. 4*</i></b>			x	4	2.7	1.5
Loasaceae	<i>Nasa Tryphylla</i>		x		0	1.3	0.0
Loranthaceae	<b><i>Psittacanthus schiedeanus*</i></b>		x		33	2.7	12.4

Malvaceae	<b><i>Abutilon spp.</i></b>			x	294	13.3	22.1
Malvaceae	<b><i>Hibiscus spp.</i></b>			x	163	13.3	12.2
Malvaceae	<b><i>Malvaviscus concinnus*</i></b>	x		x	73	10.7	6.8
Malvaceae	<i>Pavonia spp.</i>	x			0	1.3	0.0
Malvaceae	<i>Sida rhombifolia</i>		x		0	1.3	0.0
Melastomataceae	<i>Miconia spp.</i>	x			0	4.0	0.0
Melastomataceae	<i>Monochaetum spp.</i>	x	x	x	0	6.7	0.0
Myrtaceae	<b><i>Callistemon spp.</i></b>			x	143	2.7	53.6
Nyctaginaceae	<b><i>Bougainvillea spp.*</i></b>			x	63	2.7	23.6
Onagraceae	<b><i>Fuchsia paniculata</i></b>	x	x	x	1005	16.0	62.8
Onagraceae	<b><i>Fuchsia spp.</i></b>			x	2	2.7	0.8
Orchidaceae	<i>Graminifolia</i>			x	0	2.7	0.0
Orchidaceae	<i>Oncidium spp.</i>		x		0	1.3	0.0
Orchidaceae	<i>Unknown Orchid</i>	x			0	1.3	0.0
Piperaceae	<i>Piper spp.</i>	x			0	5.3	0.0
Rubiaceae	<b><i>Gonzalagunia rosea*</i></b>	x	x		14	5.3	2.6
Rubiaceae	<b><i>Palicourea spp.*</i></b>	x			1	16.0	0.1
Solanaceae	<i>Browallia americana*</i>	x	x		0	5.3	0.0
Solanaceae	<i>Brugmansia spp.</i>				0	0.0	0.0
Solanaceae	<b><i>Streptosolen jamesonii*</i></b>			x	1623	13.3	121.7
Verbenaceae	<i>Lantana spp.</i>			x	0	5.3	0.0
Unknown Family	<i>Unknown 1*</i>	x			0	1.3	0.0
Unknown Family	<i>Unknown 2</i>	x	x	x	0	6.7	0.0
Unknown Family	<i>Unknown 3</i>		x		0	1.7	0.0
Unknown Family	<b><i>Unknown 4</i></b>			x	132	2.7	49.5

**Bolding** indicates species that were visited by hummingbirds.

\* Indicates plants with ornithophilous flowers.

**Figure 9.** Hummingbird species accumulation curve for the entire study area.**Table 6.** Plant species with the highest average floral density in each site (flowers per hectare).

Cloud Forest	Garden	Oak Forest
<i>Malvaviscus concinnus</i> (547)	<i>Streptosolen jamesonii</i> (35472)	<i>Fuchsia paniculata</i> (2400)
<i>Fuchsia paniculata</i> (217)	<i>Fuchsia paniculata</i> (6561)	<i>Columnnea chiricana</i> (1517)
<i>Dicliptera iopus</i> (174)	<i>Abutilon spp.</i> (2544)	<i>Browallia americana</i> (1350)
Unknown Ericaceae (131)	<i>Hibiscus spp.</i> (1461)	<i>Salvia spp. 2</i> (719)
<i>Besleria solanoides</i> (131)	<i>Salvia involucrata</i> (1094)	<i>Psittacanthus schiedeanus</i> (217)
<i>Centropogon congestus</i> (103)	<i>Trifolium spp.</i> (894)	<i>Centropogon congestus</i> (211)
<i>Inga spp.</i> (75)	<i>Impatiens spp.</i> (711)	<i>Gonzalagunia rosea</i> (164)
<i>Palicourea spp.</i> (61)	Unknown red/orange aster (689)	<i>Centropogon granulatus</i> (133)
Unknown Orange Flower (53)	<i>Callistemon spp.</i> (622)	<i>Cavendishia spp.</i> (122)
<i>Gonzalagunia rosea</i> (44)	<i>Lantana spp.</i> (594)	<i>Dicliptera iopus</i> (103)

**Table 7.** Linear model outputs including Akaike's Information Criterion (AIC).

Model	Hummingbird Abundance			Hummingbird Richness		
	p-value	R <sup>2</sup>	AIC	p-value	R <sup>2</sup>	AIC
1. Y ~ Elevation + Site + Floral Density	2.2e-16	0.85	537.14	2.2e-16	0.76	374.04
2. Y ~ Elevation + Floral Density	2.2e-16	0.80	566.44	2.2e-16	0.66	416.80
3. Y ~ Elevation + Site	2.2e-16	0.57	658.56	2.2e-16	0.62	432.52
<b>4. Y ~ Site + Floral Density</b>	<b>2.2e-16</b>	<b>0.85</b>	<b>535.20</b>	<b>2.2e-16</b>	<b>0.77</b>	<b>372.10</b>
5. Y ~ Elevation	1.1e-05	0.1459	739.01	2.3e-05	0.14	527.40
6. Y ~ Floral Density	2.2e-16	0.786	574.59	2.2e-16	0.64	421.95
7. Y ~ Site	2.2e-16	0.576	656.93	2.2e-16	0.62	430.55

**Best fit model**

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