Management effects on hummingbird abundance and ecosystem services in a coffee landscape

By

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Abstract

Birds provide critical ecosystem services to farmers including pollination and biological control. Yet, birds are sensitive to the habitat degradation that often results from agricultural intensification. Given this, we aim to understand the ecological role of hummingbirds on coffee farms and how they are affected by coffee management practices. Hummingbird abundance was measured across a gradient of coffee production intensity in Chiapas, Mexico and we investigated how their density was affected by a range of management practices, including shade cover, agrochemical use, flower abundance and vegetation complexity. We also observed hummingbird foraging behavior to gauge their role in pollination and pest control. Hummingbirds were significantly more abundant on shade coffee sites compared to sun coffee sites, though sun coffee production did not present a significant barrier to hummingbird movement across the landscape. Floral availability, and specifically the abundance of a single species in the *Bignonia* genus, was the best predictor of hummingbird abundance. Available flowers were often lianas or epiphytes found growing on upper canopy trees scattered throughout the coffee farms. The resident hummingbird community was dominated by a single generalist species, the blue-tailed hummingbird (*Amazilia cyanura*), with low densities of three other species. Blue-tailed hummingbirds were observed foraging for insects within the coffee layer, as well as visiting the flowers of native, ornamental and crop species. Given the high overall density of hummingbirds in the landscape, it is possible that hummingbirds play a significant role in both pollination and pest control. To promote hummingbirds and their associated ecosystem services, we suggest coffee farmers retain some upper canopy trees in their coffee plots and allow them to accumulate flowering lianas and epiphytes. This low-cost, low-effort management recommendation could enhance coffee yield in low intensity systems with benefits to hummingbird conservation, and forest bird conservation in general.

2. Background

Agriculture covers approximately 36% of the world's arable land surface (Food and Agriculture Organization [FAO] 2002). The conventional approach to farming in the United States is environmentally destructive and often promotes injustice to farm laborers and the surrounding rural community (Altieri et al., 2012; Chappell and LaValle, 2011). This industrial model is characterized by monocultures, petroleum-powered equipment and external agrichemical inputs. An agroecological approach, like an industrial approach, aims to be highly productive and efficient, yet it does so by leveraging biological processes and by minimizing off-farm inputs. Nearly one billion small-holder farmers around the globe utilize agroecological approaches to grow upwards of 50% of the world's consumed food (Altieri & Nicholls, 2012). This approach can produce diverse, quality food while often supporting a better quality of life for farmers. In addition, an agroecological approach can also act as a biodiversity conservation strategy (Kremen, 2018; Perfecto et al., 2009).

Coffee agroforestry is arguably the most well-studied example of agriculture as a biodiversity conservation strategy (Buechley et al., 2015; Perfecto et al., 1996; Perfecto and Vandermeer, 2015; Philpott et al., 2008). The broad distribution, associated biodiversity, and economic importance of coffee all motivate a deep understanding of this agroecosystem. Coffee production supports the livelihoods of 25 million farmers and is grown in over 60 countries (O'Brien and Kinnaird, 2003). Coffee plants (*Coffea arabica*) are understory shrubs native to the African tropics. Given the plants' ability to thrive under shade, coffee is traditionally planted under a tree canopy. The native understory shrub layer is removed, but much of the remaining forest structure and composition is left intact. Consequently, local ecosystem processes and biotic interactions can also remain and following an agroecological approach, be leveraged to support coffee production without the use of outside inputs. Also contributing to its conservation value, arabica coffee requires high-elevation, tropical climates for ideal growth and thus, coffee growing regions often overlap with biodiversity hotspots (Moguel and Toledo, 1999).

In the past decade, much work has documented the economic and ecological value of birds in coffee systems and agroforestry systems more broadly (Karp and Daily, 2014; Maas et al., 2016; Perfecto et al., 2004; Sekercioglu, 2006). The importance of coffee systems to migratory birds is particularly notable. Shaded coffee serves as a critical refuge during bird migration through landscapes dominated by agriculture (Greenberg et al., 1997). Some coffee farms can even support higher bird richness than nearby forest (Philpott et al., 2008).

Here, we focus on a particular group of birds in coffee, hummingbirds (Family: Trochilidae). Hummingbirds tend to be abundant in neotropical agroforestry systems and can provision agriculturally-relevant ecosystem services (Dietsch, 2005). Given this, we aim to understand the ecological role of hummingbirds on coffee farms and further, to understand how they are affected by coffee management. To date, the taxa has not been thoroughly examined in any agricultural system. Therefore, we also aim to provide foundational data regarding hummingbird ecology in coffee agroecosystems, to be built upon in future studies on pollination, biological control or conservation management.

1.1 Hummingbird Foraging Ecology and Ecosystem Services

Hummingbirds are well known for their role in pollination, where more than 7,000 New World plant species are dependent on them for this function (Abrahamczyk and Kessler, 2015). Their morphology is strongly driven by floral traits and accordingly, floral abundance and diversity have been the strongest predictors of hummingbird abundance and richness at the local level (Feinsinger et al., 1988; Peters, 2014; Rodrigues and Rodrigues, 2015). It is unknown whether hummingbirds successfully pollinate coffee, but they do visit coffee and other typically bee-pollinated agroforestry crops, including citrus and almonds (Barney, pers. obvs). They are the primary pollinators of many native plants in the coffee landscape, as well as popular ornamentals, such as *Heliconia* species. Lastly, they frequently visit intercropped species on coffee farms, such as cardamom, plantains and bananas (Barney, pers. obvs.), though the latter two do not require pollination. These direct interactions could be valuable to coffee growers, as pollination increases yield in coffee (Stein et al., 2017) and cardamom (Sinu and Shivanna, 2007), and is necessary for reproduction in many native ornamentals including *Costus* spp. (Kay et al., 2005) and *Heliconia* spp. (Stiles, 1975).

While hummingbirds are primarily nectivores, the dearth of essential nutrients in nectar, including protein and fat, also make them obligate insectivores (Chavez-Ramirez and Dowd, 1992; Powers et al., 2010; Remsen et al., 1972; Stiles, 1995). Thus, hummingbirds could contribute to biological pest control services on coffee farms, by consuming pests such as the coffee berry borer (*Hypothenemus hampei)* or coffee leaf miner (*Leucoptera coffeella*). We know very little about insectivorous behavior in most hummingbird species, including their preferred arthropod prey, foraging strategy or frequency of insectivory. Gut content collection by Remsen et al. (1972) revealed arthropods in the stomachs of 95% of observed hummingbird species (133/145 species) and 79% (1,279/1,629) of all individuals. Those stomachs with any arthropods were often packed full of them (Remsen et al., 1972). Additionally, Wagner (1946) observed some species of Mexican hummingbirds feeding primarily on arthropods. Again, the stomachs of some species were consistently packed with arthropods, while others contained primarily nectar (Wagner, 1946).

Limited time-budget case studies further elucidate insectivorous behavior in hummingbirds. For example, Chavez-Ramirez et al. (1992) observed purple-throat caribs (*Eulampis jugularis*) for 19 hours and found they spent ~20% of their foraging time catching arthropods, even in the presence of abundant flowers. In the Santa Catalina Mountains in Arizona, a nesting broad-tailed hummingbird (*Selasphorus platycerus*) consumed only arthropods for at least 14 days when no flowers were in bloom nearby (Montgomerie and Redsell, 1980). Still, Gass and Montgomerie (1981) posit most hummingbird species satisfy their energetic demands by spending 85% to 90% of their foraging time acquiring nectar.

Hummingbird foraging behavior (nectivory and insectivory) has the potential to provide ecosystem services for coffee farmers, through pollination and pest control, though the composition of the local hummingbird community should impact the outcome of these behaviors. For example, the specific plants that will benefit from pollination should largely depend on body size and bill morphology of the local hummingbirds. Specifically, hummingbirds tend to visit flowers more frequently when the corolla matches the length and shape of their bill (Abrahamczyk and Kessler, 2015). Foraging strategy, and not morphology, is likely to be a better predictor of preferred arthropod prey (Remsen et al., 1972). For example, hummingbirds that establish territories should impact a hyper-localized arthropod community around its home flowers. Hummingbirds also utilize different behaviors to capture insects, such as gleaning from foliage or hawking insects from a perch, and this should impact the types of arthropods they consume.

1.2 Hummingbird Habitat Preferences

While hummingbirds have the potential to contribute to pollination and biological control services on coffee farms, the magnitude of these effects depends on their abundance and distribution in the landscape. This motivates our work to understand hummingbird habitat preferences and specifically, how coffee management decisions impact hummingbird abundance and distribution in the coffee landscape.

In general, forest birds are negatively affected by forest fragmentation and degradation (Philip C. Stouffer and Bierregaard, 1995). Alternatively, forest hummingbird abundance and diversity is largely unaffected by forest fragmentation and degradation and the taxa is often more abundant in secondary forest (Philip C Stouffer and Bierregaard, 1995). Hummingbirds seem to face little barrier in moving across open, pasture habitats while most forest insectivores can face difficulty moving across small gaps (Powell et al., 2015; Philip C Stouffer and Bierregaard, 1995). Additionally, light gaps and edges are often associated with a greater density of flowering plants (Borges, 2007). This may explain why hummingbirds tend to be abundant in coffee systems, especially in the coffee layer itself (Dietsch, 2005). For example, Dietsch (2005) caught blue-tailed hummingbirds (*Amazilia cyanura*) 1.5

times more often than the next most common bird species in mist nets on coffee farms in Chiapas, Mexico.

Hummingbirds could be impacted by a variety of coffee management decisions. The use of toxic fungicides and herbicides may directly affect hummingbird health or have cascading effects on other resources such as ground layer flowering plants (Boatman et al., 2004). The frequency or intensity of pruning to coffee shrubs and surrounding trees could affect the reliability of nesting and perching locations or food resources (Philpott and Bichier, 2012). The diversity of flowering plants could affect the consistency of floral availability throughout the year (Peters, 2014). Canopy structure could impact hummingbirds in a variety of ways. For example, canopy density could hinder movement when high or promote predation when low.

Little is known about the habitat preferences of hummingbirds on coffee farms or how agricultural management affects them. Given the potential value that hummingbird communities could contribute to ecosystem function and agriculturally-relevant services, it is critical to understand how farm managers can promote and retain hummingbirds at the local and landscape level.

1.3 Research Questions

We aimed to explore the ecosystem service potential of hummingbirds in coffee agroecosystems and understand how agricultural management affects their abundance and distribution in the landscape. We also aimed to produce management recommendations for coffee managers to facilitate the occupancy of hummingbirds on coffee farms and to promote agriculturally-relevant services. Specifically, we asked: (1) How do coffee management practices affect hummingbird abundance and distribution? (2) Does local hummingbird behavior support their role as pollinators and pest consumers? (i.e. Are they directly interacting with coffee plants? What other vegetative strata are they interacting with? How and where are they foraging for arthropods and nectar?).

2. Methods

2.1 Study Site

All observations and collections took place in the Soconusco region of Chiapas, Mexico from May – August (dry season) 2016. The region is dominated by coffee production and is 1000 m asl with 4500 mm of annual rainfall (Philpott and Bichier, 2012). Field research was based in a 300-hectare, certified organic shade coffee farm, Finca Irlanda, where coffee agroecology research has been conducted for over two decades. Additional sampling sites were in an adjacent 300-hectare intensively managed low-shade coffee farm, Finca Hamburgo, and an adjacent secondary forest fragment. This region is ideal to study hummingbird interactions in agroecosystems due to its richness of hummingbird species and landscape/management heterogeneity.

Management differs significantly between our three sites. On Finca Hamburgo, newer varieties of coffee are grown under full sun or a sparse monoculture of shade from *Inga micheliana*. *Inga*, a nitrogen fixing tree in the Fabaceae family, is the most common shade tree in coffee farms across Mexico. Finca Hamburgo (from now on called “sun coffee” for simplicity) also utilizes a variety of synthetic pesticides including herbicides on the herbaceous layer, insecticides for the coffee berry borer and fungicides for the coffee rust.

On Finca Irlanda (from now on called “shade coffee”), no synthetic pesticides are used, except for copper sulfate for the control of the coffee rust. Coffee shrubs are in general older but are quickly being replaced with newer varieties. The canopy is quite heterogeneous and more diverse than the sun coffee farm. *Inga* spp. are the most common shade trees, though there are other planted, and some native trees dispersed throughout. A previous study recorded 91 species of shade trees in a 45-hectare plot within the shade coffee farm (Vandermeer et al., 2008). Most obviously different, the canopy in shade coffee has multiple vertical layers, including very tall, emergent canopy trees. Thus, from afar, the shade coffee farm appears like surrounding forest. The size and age of these tall trees allows the accumulation of epiphytes and some lianas. Additionally, the weedy ground layer is permitted to grow for some time, before being manually chopped. This results in an overall more diverse and vegetatively complex system.

In addition to coffee production, there are many patches of forest throughout the landscape. Here, we focus on a secondary forest fragment separating the sun and shade coffee farms. Much of this has been left as forest because it is surrounding a network of streams and is very steep. Within this forest fragment, there is one portion of abandoned coffee where secondary growth has taken over. At the time of this study, remnants of previous coffee production were almost undetectable.

2.2 Hummingbird Community Survey

Standard avian point-count methodology was used to survey the hummingbird community across a management gradient following (Bibby et al., 1992). Survey points were placed on a 200 m x 200 m grid using Google Earth, and GPS Essentials Android application (Schollmeyer 2009) was used to locate the points in the field. A randomized grid was chosen to best capture the heterogeneity of the landscape and prevent over-estimation of hummingbird abundance. There could be strong bias if only roadways and trails were surveyed, as these areas are dominated by ornamental flowers that are frequented by hummingbirds. If a point was completely inaccessible (i.e. in a body of water or on extremely steep terrain), the closest traversable point was used instead. In a few instances, a point was thrown out altogether and the grid was expanded with an additional point. 27 and 25 points were surveyed in shade coffee and sun coffee, respectively. No point counts were conducted in the forest fragment because a much lower probability of detection would make comparisons between sites unreliable. Points were surveyed by the same individual between 7 and 11 EST in fair weather conditions in June and July 2017. Upon arriving at the designated point, the surveyor allowed a three-minute buffer before counting to give birds the opportunity to resume normal activity. All hummingbirds heard or seen within a period of ten minutes were recorded, as well as the distance from the observer.

2.3 Habitat Survey

To assess the effects of coffee management practices on hummingbird abundance and community composition, habitat characteristics were quantified within a 25-meter radius of each hummingbird survey point. The characteristics measured at each of the 52 points are described in Table 1. While we recorded all flowers at each point, we refer to floral availability as the sum of all blooms on plant species that we confirmed are visited by hummingbirds.

Table 1. Habitat characteristics measured at each hummingbird point count location, methodology used and our expectation of the potential effect of each management variable on hummingbird habitat. Methods refer to measurements taken at the point location or within a 25 m^2 radius where appropriate.

Metric	Method	Expectation
Shade Cover	Average densiometer reading five steps in each cardinal direction	Tree structure allows flowering epiphyte growth, but too much shade may inhibit flower density
Canopy Structure	Presence/absence of mid- and upper-canopies	Upper canopy trees support more flowering lianas and epiphytes
Flower Abundance and Composition	Number of blooms on bird- visited species in 25 m^2 radius	Nectar availability should increase with flower abundance
Weed Height	Average height of weed layer five steps in each cardinal direction	Weeding removes flowers and indicates recent human disturbance
Weeding Frequency	Qualitative score (1 – 3) based on the growth of the weed layer	Branch, epiphyte and liana pruning co-occurs with weeding, resulting in flower loss in the canopy
Coffee Height	Average height of four	Coffee height typically

	random coffee plants	increases with age. Coffee age informs surrounding shrubbery age.
Stream	Presence/absence within 25 m^2 radius	Native vegetation is usually left around streams
Herbicide Use	Presence/absence of bare ground with algae or moss	Herbicides could directly deter hummingbirds or result in loss of flowering weeds and shrubs

2.4 Hummingbird Mark - Recapture

Hummingbirds were captured and individually marked with nontoxic nailpolish to allow for reidentification of captured individuals, allowing a look into hummingbird movement across the landscape. We also took morphological measurements so that we could better characterize this understudied hummingbird community. Note that we did not design a true mark-recapture study (i.e. resulting in a probability of recapture) and that our analysis of hummingbird movement was an unintended outcome of marking birds for another project.

Trapping stations were set up in the sun coffee site, the shade coffee site and the forest fragment, in specific locations where hummingbird activity had been previously observed. At each trapping site, we placed a nectar feeder filled with 25% sucrose solution. After a waiting period, we set up a mesh bonnet trap over the feeder and placed it on a PVC pipe stand (Figure 1). During a trapping session, birds were actively caught by lowering the mesh cage around an individual at the feeder. We immediately removed the bird, took standard measurements including bill and keel lengths, and applied a unique color marking. Fecal samples were also collected for another study. All animals were handled according to standards set by the University of Michigan’s Institutional Animal Care and Use Committee (Protocol #: PRO00007632) and approved by the Secretary of Environment and Natural Resources of Mexico (SEMARNAT) under permit SGPA/DGVS/04787/17.

Figure 1. A hummingbird trapping station: standard hummingbird feeder with 25% sucrose solution surrounded by a mesh Hall trap hung from a painted PVC pipe stand. The string shown is a fishing line used to manually open and close the trap.

2.5 Hummingbird Behavioral Observations

We observed hummingbird behavior to better understand what flora and fauna birds were interacting with and how they budget their time in this system. Specifically, we wanted to know how much time they spent foraging for nectar and arthropods, what plants they were potentially pollinating, what foraging strategies they used for arthropods and where in the vegetative strata they were consuming arthropods.

Blue-tailed hummingbirds were the only species observed for time budgets, as they are consistently territorial, and it is nearly impossible to track a trap-lining hummingbird over a large area. Hummingbird territories were identified during slow walks at dawn by visually searching for birds or listening for songs. Once a hummingbird was located, it was observed for as long as we could keep track of it, up to thirty minutes. All behaviors were recorded including: perching, singing, preening, foraging, and defending. Specific arthropod foraging strategies used were also recorded. We defined the foraging strategies as follows: (1) hover-hawk: flying insects are captured during a sustained foraging bout; (2) sally-glean: arthropods on foliage are captured in flight before returning to a perch; (3) sally-hawk: flying arthropods captured in flight before returning to a perch; (4) hover-glean: arthropods on foliage are captured during a sustained foraging bout. When possible, we recorded the identity of the perches and consumed flowers and arthropods. To summarize blue-tailed hummingbird behavior, we averaged the number of minutes spent doing each behavior across all observation eight trials and present these as means ± standard error.

In addition to territory-centric observations, we observed focal plants for hummingbird activity. For every flowering plant species recorded in the habitat survey, at least one individual was observed as a focal plant. We also recorded every plant-hummingbird interaction we saw in the field, whether or not it was during a plant observation trial. This allowed us to observe species beyond the blue-tailed hummingbird and determine whether flower species counted in our habitat survey were visited by hummingbirds (i.e. whether they were legitimate nectar resources). Each focal plant was observed for 30 minutes and all hummingbird visits were recorded. If a plant had no hummingbird visits, another individual in a different location was observed before concluding that hummingbirds did not utilize the species.

2.6 Statistical Approach

All statistical analyses were carried out in R version 3.4.1. Hummingbird abundance per point was averaged within each farm to obtain mean birds per point ± standard error and a t-test was used to test for a significant difference between the mean hummingbird abundance on the sun coffee site and the shade coffee site. The density of hummingbirds on each farm was calculated according to Bibby et al. (1992): Equation 1. $density = \log_e\left(\frac{n1}{n2}\right) * n/m(\pi r^2)$ where n = total number of birds counted; n_1 = the number of birds within the radius; n_2 = the number of birds beyond the fixed radius; m = total number of point counts; and r = fixed radius of the survey area. We chose the survey radius based on our ability to confidently observe all hummingbirds within that distance. Therefore, we assume our detection probability is very close to one and consider it to be one in our calculations for simplification.

To visualize which habitat variables were driving trends in hummingbird abundance, we did a principle component analysis (PCA) using R's built-in function prcmp(), including loadings for each habitat variable. Linear regressions were also done between hummingbird abundance and each habitat variable. Regression lines and R^2 values are presented for statistically significant relationships ($p < 0.05$).

To understand the total effects of coffee management on hummingbird abundance, we built generalized linear models using the glm() function and a Poisson error distribution. Based on the outcomes of regressing all habitat variables against hummingbird abundance, we built six different models that we thought could plausibly predict hummingbird abundance at a given point. The model of best fit was selected based on the ecological interpretation of the variables and AIC values. All models are shown in Table 2 including the formula, difference in AIC between each model and the best model, degrees of freedom, and residual deviance.

Time-budgets were computed by taking each territory-centric observation trial and summing the time the focal hummingbird spent doing each behavior. Each value was divided by the total observation time to get the proportion of time spent engaging in each behavior. Proportions were then averaged across trials and presented as mean proportion ± standard error for each behavior. We also calculated the proportion of arthropod foraging time spent utilizing each arthropod foraging strategy (e.g. sally-hawk, hover-glean, etc.). A one-way ANOVA tested for differences in average time spent utilizing each foraging strategy.

The distance between capture events for recaptured hummingbirds was determined by connecting the trapping locations where the bird was caught and recaptured on Google Earth. We report the mean distance ± standard error between capture events of the same individual. This does not consider those birds that were recaptured at the same location. Morphological measurements (keel and bill lengths) of captured birds were averaged and reported as mean ± standard error for each species. A one-way ANOVA was used to test for differences in the mean bill and keel lengths between species and a post-hoc Tukey test tested for differences between every pair of species.

3. Results

3.1 Hummingbird Morphology and Community Composition

The blue-tailed hummingbird, *Amazilia cyanura*, was the most commonly encountered hummingbird species throughout the coffee landscape. It was observed on all three types of habitats. The blue-tailed hummingbird is medium-sized (average keel length: 20.4 ± 0.26 mm) with a short and straight bill (average bill length: 20.1 ± 0.16 mm). Three other hummingbird species were identified at our sites including: the cinnamon hummingbird (*Amazilia rutila*), violet sabrewing (*Campylopterus hemileucurus*) and long-billed starthroat (*Heliomaster longirostris*), although their distribution was much patchier than the blue-tailed hummingbird. Cinnamon hummingbirds tended to be in the riparian zone of streams throughout the coffee or utilized ornamental shrubs along roadways. Long-billed starthroats were observed trap-lining (foraging along a fixed long-distance route) at epiphytes in all three habitat types. Female violet sabrewings were also observed in all three habitat types, though always near the forest fragment, while males were only observed in the forest fragment. Additional hummingbirds species are likely present during the dry season (Dietsch, 2005).

The local hummingbird community varied greatly in their overall morphology (Figure 2a,b). Mean bill length significantly varied between species, even with sexual dimorphism in some species (ANOVA, $F(3, 53) = 345$, $p < 0.001$). A post-hoc Tukey test confirmed significant differences between the mean bill length of every combination of all four hummingbird species at $p < 0.05$ (Figure 2a). Keel length, a proxy for body size, was significantly different between the blue-tailed hummingbird and the three other observed species (ANOVA, F(3,50) = 13, $p < 0.001$), with the keel length of the blue-tail hummingbird being smaller than the other three species (Figure 2b).

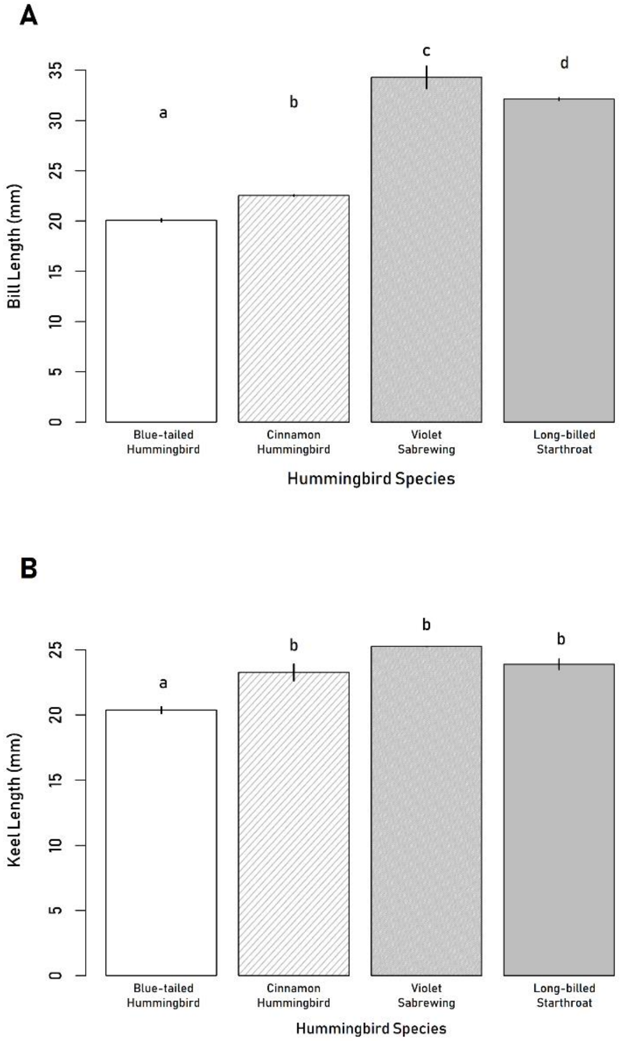

Figure 2. Bill (panel A) and keel (panel B) lengths of the hummingbird community captured across all sites. Averages are from 33 blue-tailed hummingbirds, 3 cinnamon hummingbirds, 3 long-billed starthroats and 5 violet sabrewings. Standard error bars with different letters are significantly different from each other according to a post-hoc Tukey test.

3.2 Effects of Coffee Management on Hummingbird Abundance

Hummingbird abundance counted per point varied significantly by site, where on average the sun coffee site had 0.08 ± 0.055 birds per point over 10 minutes and the shade coffee site had 1.23 ± 0.22 birds per point over 10 minutes (t-test, t = -5.1, df = 28, 95% CI [-1.6, -0.69], p < 0.0001). Given this, the density of hummingbirds on each coffee management type, according to Equation 1, is 0.41 hummingbirds per hectare on sun coffee and 6.27 hummingbirds per hectare on shade coffee. Only two hummingbirds were ever recorded during our point counts on the sun coffee site (Figure 3). Observed hummingbirds were distributed randomly throughout shade coffee, with no obvious clustering within the farm (Figure 3).

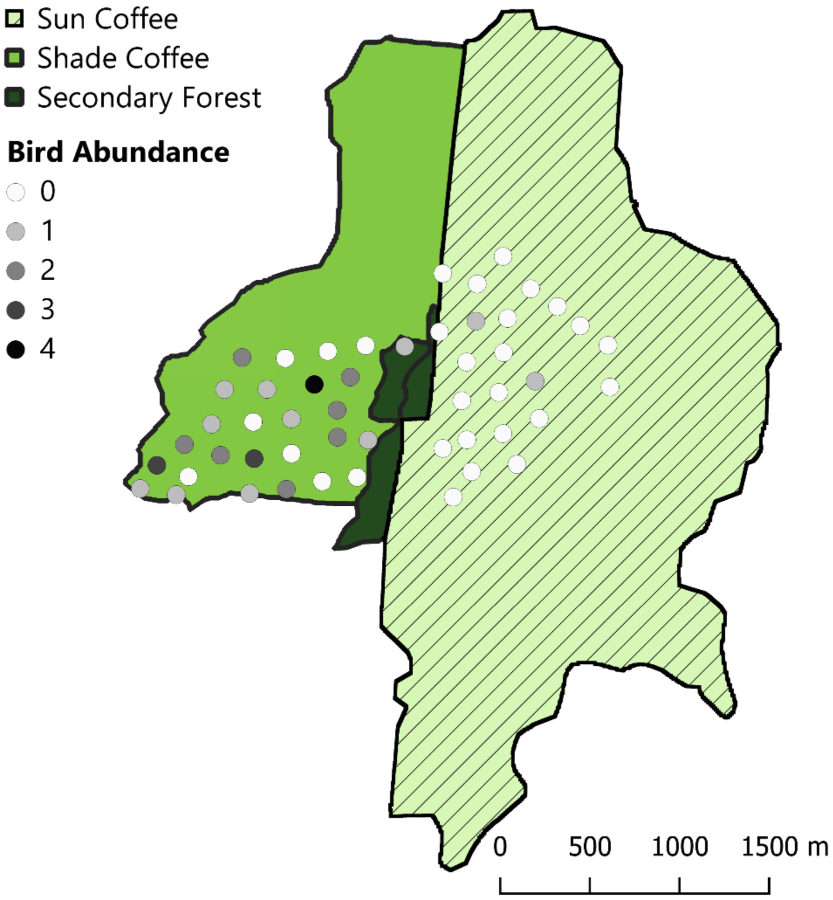

Figure 3. A map of the study site in Chiapas, Mexico with hummingbird abundance at each point count.

Farm-level differences in hummingbird abundance were driven by differences in management practices and associated changes in habitat structure and complexity. Clustering of points by farm in a principle component analysis (PCA) confirmed our qualitative descriptions of the management differences between the two farms (Figure 4). Principle component axis 1 explained 25% of the variance between points and was positively correlated with herbicide use and total flower abundance. PC1 was negatively correlated with all other habitat variables. Principle component axis 2 explained 16% of the variance and was positively correlated with shade cover, number of canopy layers, weed height and stream presence. PC2 was negatively correlated with ornithophilous flower abundance, coffee height and time since last weeding.

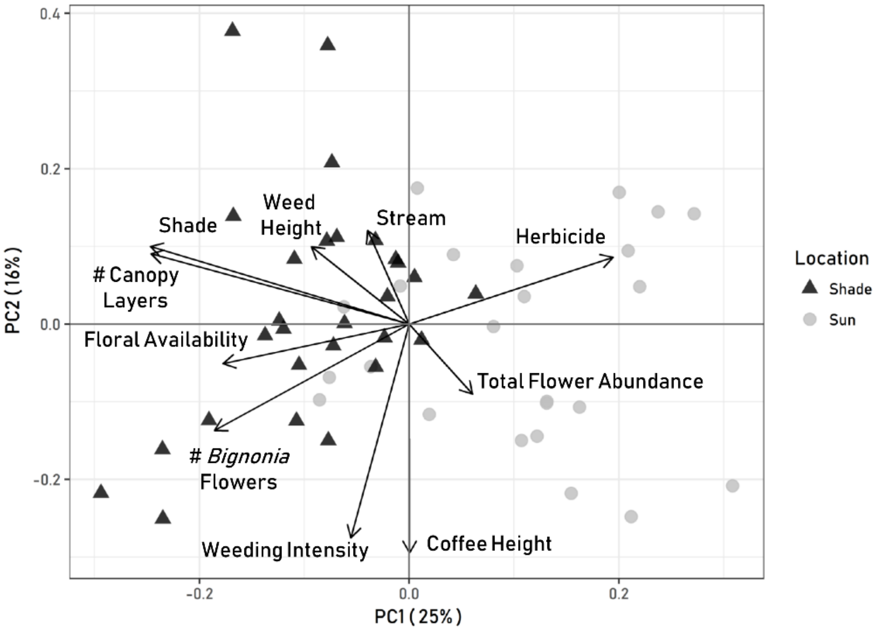

Figure 4. A principle components analysis showing clustering of points by farm and habitat variable vectors.

Compared to shade coffee, sun coffee had less shade cover, a shorter weed layer, fewer canopy layers, a lower abundance and diversity of flowers including fewer ornithophilous flowers, and widespread herbicide use. The average shade cover at a point in the shade coffee sites was 69.7 % ± 3.0 %, while it was 33.6 % ± 5.3 % in sun coffee sites. Additionally, the average floral availability at a point in shade coffee was 49 ±13 blooms, while it was 18 ± 6 blooms in sun coffee.

While there were pronounced differences in hummingbird abundance at the farm level, abundance also correlated with habitat variables within farms. Within shade coffee, hummingbird density was driven by a positive relationship between hummingbird abundance and floral availability (Figure 5). The positive relationship between hummingbirds and flowers on shade coffee was statistically significant ($R^2 = 0.35$, $p < 0.001$). Notably, the majority of ornithophilous flowers across all sites belonged to a single species in the *Bignonia* genus (Figure 5). It is a liana with many large, pink blooms that usually grows up emergent canopy trees. There was also a slightly positive relationship between hummingbird abundance and canopy cover in shade coffee ($R^2 = 0.09$, $p = 0.07$). These within farm variations in abundance that were observed in shade coffee did not occur in sun coffee, where few hummingbirds were ever recorded in point counts.

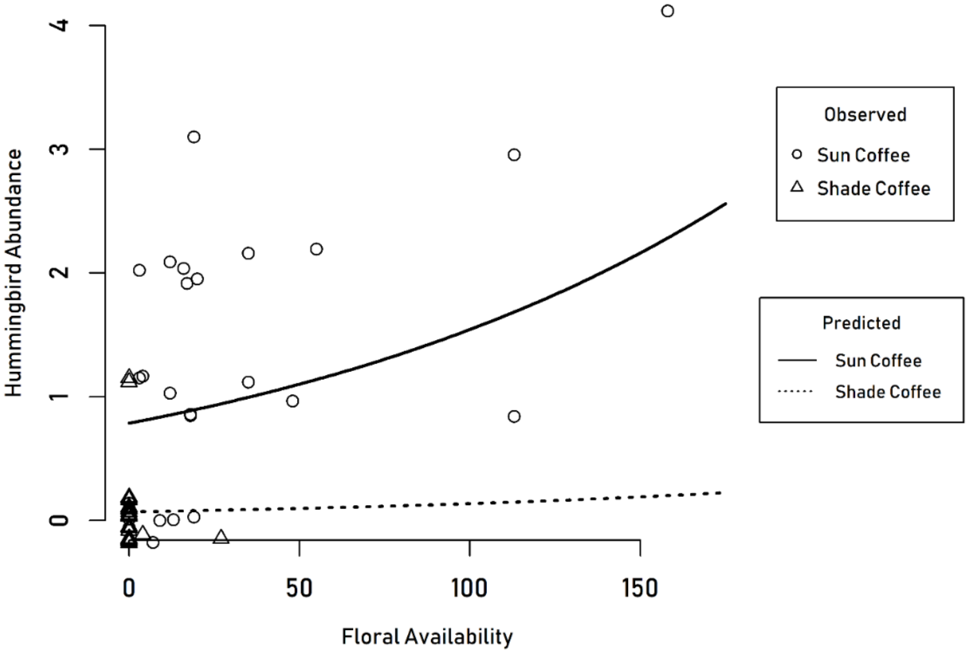

Figure 5. The observed relationship between hummingbird abundance and floral availability at each point. Predictions from the model of best fit (Model 3 - hummingbird abundance as a response to farm identity and floral availability) are also shown for each farm. See Supplementary Figure 2 for additional plots between hummingbird abundance and habitat variables.

After visualizing the relationship between each habitat variable and hummingbird abundance, we fit the data to six generalized linear models with varying explanatory variables (Table 2). Model 3 was selected as the model of best fit as it captures much of the explanatory power available with our dataset and is parsimonious. Hummingbird abundance at a single point is best predicted by a strong effect of farm-level management intensity and a positive effect of floral availability (Figure 5). While we recorded habitat variables that captured large differences in the two farms, the effect of farm identity (or overall management intensity) was a better predictor of hummingbird abundance than the sum of all measured habitat variables.

Table 2. A summary table of the models compared during the model selection process with hummingbird abundance as the response variable. Here, *flowers* refers to hummingbird-visited flowers only.

	Model	dAIC	df	Weight	Residual Deviance
1	~ farm	7.5	2	0.011	40.5
2	~ # flowers	18.2	2	< 0.001	51.18

3	~ farm + # flowers	0.0	3	0.462	31.01
4	~ farm + # flowers + shade	1.7	4	0.195	30.73
5	~ farm + # flowers + shade + weed height	1.3	5	0.242	28.3
6	~ farm + # flowers + shade + weed height + pruning	3.3	6	0.090	28.29

3.3 Hummingbird Movement in the Coffee Landscape

In addition to our point count survey, mark and recapture data gave us another perspective of how coffee management affected hummingbirds. 18% of capture events (11/60) were recaptures of the same individual in different locations. The distance between these captures ranged from 48 to 1171 m with an average distance of 540 m ± 128 m for blue-tailed hummingbirds, the only predominantly territorial hummingbird at our sites (Supplementary Figure 1).

3.4 Hummingbird Behavior

Individual hummingbirds were observed for a total of 2.89 hours over eight trials. Birds spent the greatest proportion of their time perching (56.9% ± 7.5%) or away from their territory (31.5% ± 7.2%), usually chasing off another hummingbird. Birds foraged for nectar 7.1 % ± 2.0 % of the time and for arthropods 1.8% ± 0.7% (Supplementary Figure 3). Hummingbirds utilized four arthropod foraging strategies relatively evenly (i.e. hover-hawking, hover-gleaning, sally-hawking, sally-gleaning) (Supplementary Figure 4). Additionally, hummingbirds were observed arthropod foraging on a diversity of vegetative strata, including gleaning from coffee bushes, fly-catching from lower canopy perches or catching bees and other arthropods from flowers in their territory.

Hummingbirds were observed visiting a diversity of flowers, including some non-ornithophilous flowers. Agricultural plants were visited, including: two species of cardamom (*Elattaria cardamomum*; *Amomum* sp.) and bananas and plantains (*Musa* spp.) (Figure 6). Coffee was not in bloom during our surveys, so we are not able to say if it is visited by hummingbirds. Ornamental plants were also visited including *Heliconia* spp., *Sanchezia nobilis*, and a variety of gingers. On coffee farms in the Soconusco region, these ornamentals are often planted along roadways, paths and streams, as well as intentionally left to grow within coffee patches. A full list of the documented interactions between hummingbirds and flowers is included in the supplemental materials (Supplemental Figure 5). Beyond our observations presented in Figure 6, hummingbirds likely visit many other native flowering plants that are in bloom during the dry season (i.e. peak flowering season), as well as rarer flower species that we failed to observe during the wet season.

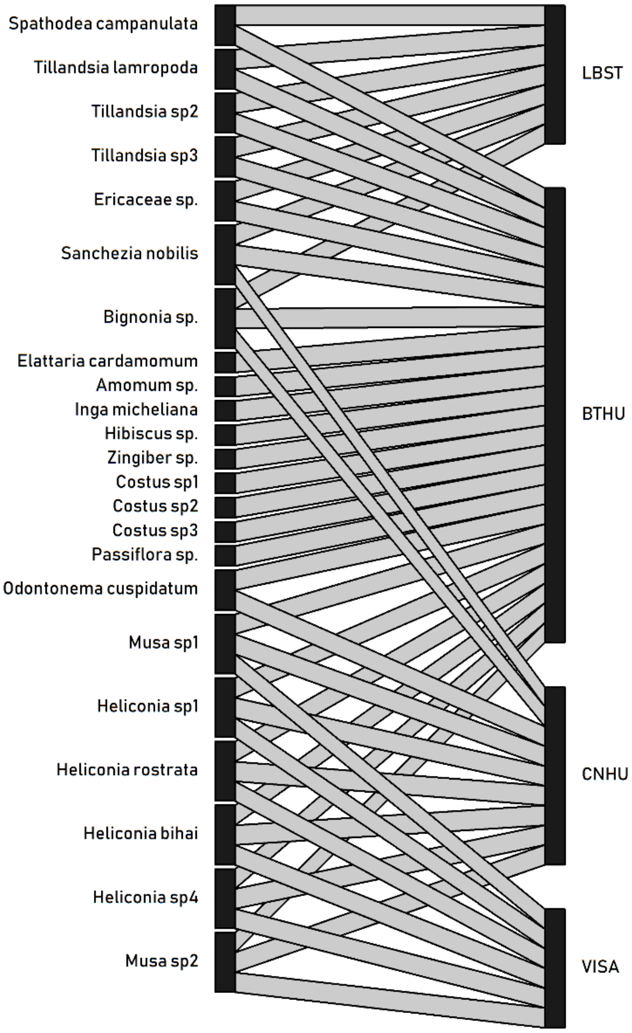

Figure 6. A bipartite network of all interactions observed between flowering plants (left) and hummingbirds (right) in all sampled sites. This list is not exhaustive, and it is likely that additional hummingbird species visit each plant beyond what we observed here. More information about these plant species are provided in Supplemental Figure 5.

5. Discussion

5.1 Hummingbird Abundance and Distribution in the Coffee Landscape

Hummingbirds were more abundant on a lower intensity, shaded organic coffee farm (shade coffee) compared to a neighboring high-intensity coffee farm (sun coffee), with 1.23 and 0.08 birds per point, respectively. This density of hummingbirds on the shaded coffee farm is relatively high when compared to 0.20 and 0.39 hummingbirds per point that were identified in a broad avian survey on coffee farms in the Ocosingo region of Chiapas (Greenberg et al., 1997). Given that the Ocosingo survey was conducted in the dry season, during peak bloom, we suggest that hummingbirds could have been more dispersed across the landscape (i.e. with a lower density) than at our sites. Hummingbirds facing major resource limitations during the wet season should be more concentrated around patches of dense flowers, as was seen in our survey. Nonetheless, the density of hummingbirds on the sun coffee farm was shockingly low. Though, we assume it would be somewhat higher when the scattered *Inga* trees are in bloom, as these are a favorite of some hummingbird species (Greenberg et al., 1997).

The stark contrast in hummingbird abundance between farms can be explained, in part, by known differences in management practices. Most strongly, it can be explained by a higher floral availability in shade coffee. As seen in many other systems (Feinsinger and Colwell, 1978; Maruyama et al., 2013; Montgomerie and Gass, 1981; Tinoco et al., 2017) and supported here, hummingbird communities are largely structured by floral availability While our finding is not surprising, what is notable is most blooms on the shade coffee site belonged to a single species, a liana in the *Bignonia* genus (Family: Bignoniaceae). The plant grew throughout the shade coffee farm and whenever present, there was likely a blue-tailed hummingbird defending it. The liana was only found growing on the trunks of large, emergent canopy trees which towered above the lower *Inga* canopy, most of which had no leaves during the wet season. At a time of year when floral resources are relatively scarce, the existence of this liana was critical to the resident hummingbird population. Within coffee patches, hummingbirds were seen frequenting other flowering epiphytes on emergent canopy trees, including a variety of bromeliads and a common Ericaceae species.

While flower density was the single best predictor of hummingbird abundance, farm identity (i.e. management intensity) explained another significant portion of the variability in hummingbird abundance. We attempted to quantify all the habitat characteristics that we thought could be impacting hummingbirds and that also varied between farms. Yet, farm identity was a better predictor of hummingbird abundance than the sum of all habitat characteristics. A possible explanation for this is that hummingbirds can tolerate some level of management intensification but that there is a threshold after which the habitat becomes completely unsuitable. For example, high intensity farms could have exceptionally low densities of preferred arthropod prey, such as spiders, due to frequent pesticide use and vegetational simplicity. If this was the case, hummingbirds may not be able to meet their nutritional needs, even if there was a patch with adequate nectar resources.

Though our data suggests that hummingbirds do not occupy sun coffee farms (i.e. establish territories or nest in them), they do move through them and stop to utilize resources when available. This is evidenced by our recapturing of hummingbirds over 1000 m apart on different farms. In fact, the feeder trap where we caught the most hummingbirds in one day was in the sun coffee site. Captures included trap-lining hummingbirds, such as female violet sabrewings and long-billed starthroats, as well as territorial blue-tailed hummingbirds. This suggests that while hummingbirds are sensitive to changes in habitat features at the local level, they are less sensitive to changes at the landscape level. Nonetheless, when small patches of flowers were present in sun coffee, we still did not record hummingbirds during point counts. If hummingbirds are just passing through, it is possible that it is not energetically lucrative to stop and visit isolated flower resources. Our feeders represent a very high-quality resource, and this could explain why so many birds were attracted to our feeders in the sun coffee site.

The ability of hummingbirds to move through low-quality habitat could be quite important to maintaining ecosystem function in the coffee landscape. If hummingbirds are providing agriculturally-relevant ecosystem services, then high-intensity farms are likely indirectly benefiting from their proximity to low-intensity farms or forest patches due to hummingbird stop-overs. Though this interaction may cease to exist during peak flower season, when hummingbirds may not have to leave their ideal habitat in search of flowers. Conversely, low-intensity farms may benefit from their proximity to high-intensity farms, if the low-quality farm forces hummingbirds to transport pollen long distances from high-quality patch to high-quality patch. This more distant outcrossing should increase the fitness of both native and naturalized ornamental plants species in coffee farms.

5.2 Potential for Hummingbird-Mediated Ecosystem Services in Coffee

Hummingbirds are important pollinators in the tropics. But are they providing agriculturally-important pollination services to coffee farmers? We cannot say whether or not they visit or pollinate coffee. They do visit *Inga* trees, the most common shade tree across all coffee farms in the region. Farms growing their own *Inga* seedlings would rely on this pollination for quality seeds. Hummingbirds also visit the most commonly used ornamental plants in the region. While coffee farmers may initially buy these plants from a nursery, they are often naturalized throughout the farm and spread via seeds or cuttings. Some neighboring coffee farms have started to diversify their operations with cut flowers from these ornamentals or have switched over entirely to flower production. Beyond this direct economic gain, ornamental flowers provide important biodiversity and vegetative complexity that likely have cascading effects on coffee production. They are also quite beautiful and may enhance the agritourism that is popular along the “Coffee Route” in the region.

Hummingbirds also visited non-focal crops within coffee farms. Hummingbirds visit bananas and plantains and we frequently observed interactions between the two, though neither plant requires pollination. This crop may not be sold at market by the farm owner, but instead consumed by farmers and farm workers. Cardamom is also visited by hummingbirds, though we do not know if it is effectively pollinated by them. In India, sunbirds commonly visit cardamom flowers, but it is unclear whether this results in effective pollination (Sinu and Shivanna, 2007). Cardamom pods are made into value-added products such as chocolate-covered cardamom and sold at gift shops in the area. Though our data is preliminary, hummingbird visitation behaviors suggest they are important to many auxiliary pieces of the coffee system.

While hummingbirds are considered agriculturally beneficial for their role in pollination, they could also be contributing to biological pest control services. Our time budget data suggests that blue-tailed hummingbirds are not spending a large proportion of their time foraging for arthropods. Yet, they were observed gleaning arthropods from coffee and hawking flying insects within the coffee layer. Our ongoing work in molecular diet characterization should elucidate which arthropod taxa are primarily consumed by hummingbirds. In other regions, hummingbirds often consume web-building spiders. Trap-lining hummingbirds, such as the violet sabrewing and long-billed starthroat, tend to be especially keen on spider foraging. This intraguild predation could have a net positive effect on coffee pests or it could release a more effective predator from spider predation (Perfecto and Vandermeer, 2015).

Hummingbirds are also likely consuming small flying insects (Wagner, 1946) and flies and planthoppers were among the most commonly collected arthropods across farms. This strategy is more often used by territorial hummingbirds, like the blue-tailed and cinnamon hummingbirds, that look for insects flying past their perch. Small, flying arthropods could include the economically important, coffee berry borer or coffee leaf miner. Consumption of these pests is particularly relevant on organic coffee farms where synthetic insecticides are not used to minimize arthropod populations.

Whether or not hummingbirds are consuming arthropods that are directly important to coffee production, they are likely an important part of stabilizing the broader food web, which has cascading effects on other aspects of ecosystem function. The magnitude of their effects depends on the quantity and volume of arthropods consumed compared to floral nectar. While many researchers maintain that floral nectar is universally the most important food resource for hummingbirds (Montgomerie and Gass, 1981), others posit that it greatly varies between species (Wagner, 1946). Wagner (1946) observed some species of hummingbirds in Chiapas that chiefly consumed arthropods. He posits that these species hunt for arthropods at flowers (such as thrips, beetles, spiders and bees) and that this explains their frequent flower visits, as well as morphological matching with flowers. As descendants of swifts (Family: Apodidae), whom are voracious hawking insectivores, it seems evolutionarily plausible that hummingbirds have maintained some traits adapted to arthropod foraging (Ksepka et al., 2013).

5.3 Management Implications

Hummingbirds have the potential to provide ecosystem services to coffee farmers due to their abundance, mobility and behaviors (i.e. visiting flowers and consuming arthropods). Given this, how can farm managers promote and retain hummingbirds on their land? We suggest that hummingbird occupancy and abundance can be encouraged with a set of simple, feasible management strategies. First, emergent canopy trees, about 25 to 30 m in this system, should be permitted to grow at least sporadically throughout the coffee landscape. While farmers are often hesitant to provide too much shade, our data suggests that a minimal number of quality upper canopy trees could suffice. Additionally, these upper canopy trees often do not block much light from the coffee understory due to their height and low leaf density.

The quality of these trees is then determined by how much they are permitted to accumulate flowering epiphytes. While trimming *Inga* trees and clearing the herbaceous layer, farm workers usually cut the base of lianas on large trees and remove the lower branches covered in epiphytes. We believe the potential loss from shade created by large epiphytes is likely outweighed by the positive impact on hummingbird populations. This is supported by a study conducted in coffee in Veracruz, Mexico that found that epiphyte removal had a negative effect on bird abundance, including two resident hummingbird species (Cruz-Angón and Greenberg, 2005). The beauty of this management recommendation is that it is quite feasible, no matter the current management regime of the coffee farm. It requires less labor (i.e. time saved weeding and pruning) and no additional inputs (i.e. using only naturally-occurring trees/plants). Integrated and steady flower production within the coffee layer should also support insect pollinators of coffee.

In addition to epiphyte-covered upper canopy trees, we recommend farmers continue or begin to grow ornamental flowering plants, such as heliconias, gingers, and fire spikes, where appropriate. Ornamentals can be grown in parts of the landscape that are unsuitable to grow coffee, such as along roads, paths and streams. This can support the local hummingbird community, as well as provide a higher-quality corridor across the landscape. A potential drawback is that hummingbirds may be deterred from consuming large volumes of arthropods if they have access to abundant flowers. While this is quite plausible, we do know that hummingbirds are obligated to consume some level of arthropods even if their energetic needs are met by floral nectar. Additionally, hummingbirds in this region are known to migrate seasonally, especially altitudinally. Thus, if they are deprived of adequate nectar resources, they may leave the system entirely, instead of switching to a diet of mostly arthropods.

6. Conclusions

To summarize, hummingbirds have the potential to be quite ecologically and economically important to coffee production. They are relatively common in the coffee landscape and exhibit behaviors that could contribute to both pollination and biological pest control ecosystem services. The magnitude of their role depends on habitat quality as mediated by coffee management intensity. Specifically, hummingbirds flourish where farm management allows vegetative complexity to increase beyond a monoculture coffee layer. The quantity of blooms from flowering lianas and epiphytes was the best predictor of hummingbird abundance, and these flowers tended to grow on emergent canopy trees.

Because so little is known about this particular community of hummingbirds and hummingbirds in agricultural systems more generally, we aimed to take a broad sweep at understanding their ecological role on coffee farms. We hope this foundational data will inspire future targeted experiments that quantify the services provided by hummingbirds. In addition to the field observations presented here, we have ongoing work that aims to characterize the diet of hummingbirds at our sites using fecal samples and a metabarcoding approach. Again, this could set the stage for more detailed investigation into the biological control and pollination services provided by hummingbirds.

While much research has conveyed the importance of birds in general on coffee farms, it can be impractical for coffee growers to manage for the entire bird community. By identifying the specific birds which play the greatest role in providing bird-mediated ecosystem services, farmers can take simple and practical steps to promote and retain desired services. While the focus may be on a subset of birds, it is likely that altered management practices will impact the broader community and thus, promote biodiversity conservation in general.

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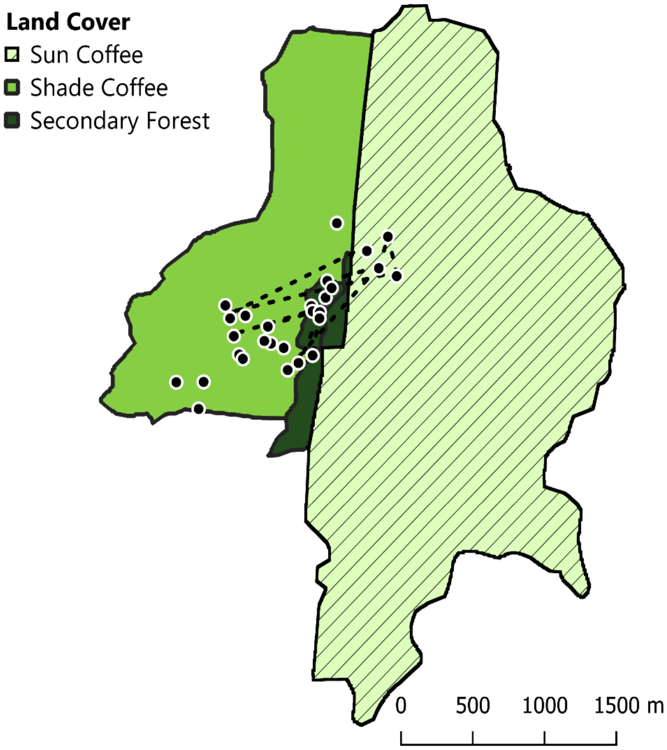
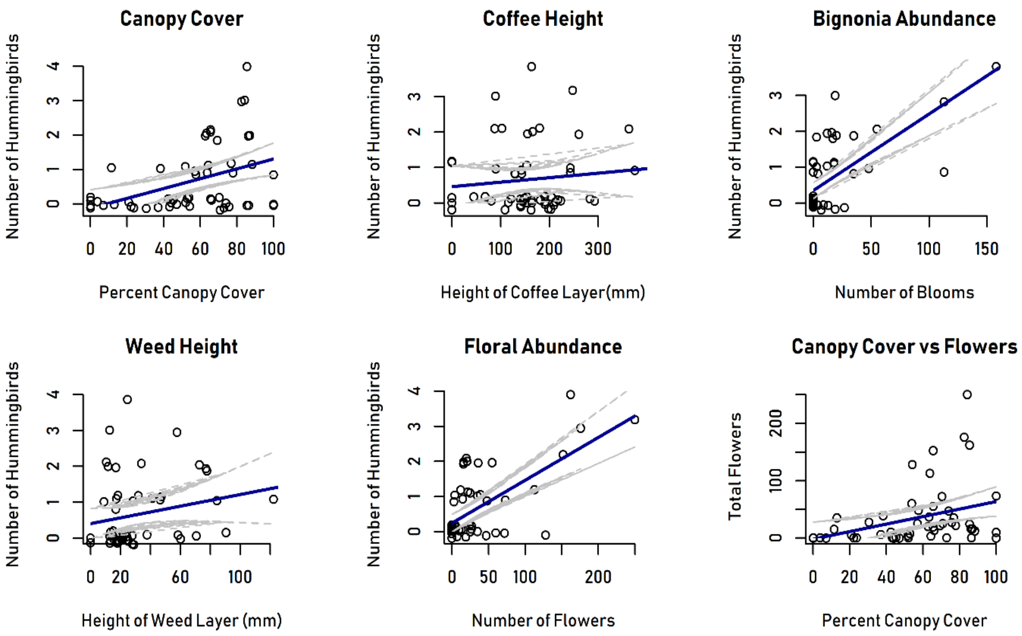
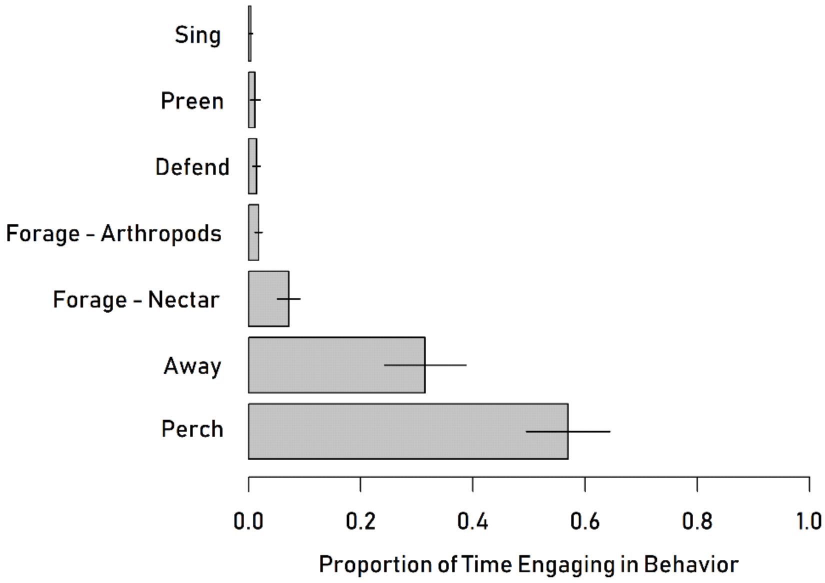
Supplementals



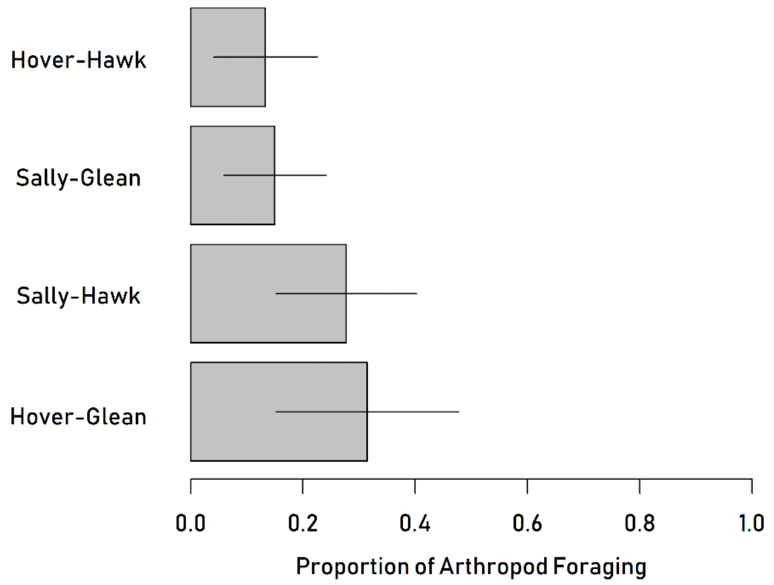
S1. A map of the study site with points representing the location of a hummingbird feeder trap and dashed lines between every pair of feeders where the same individual was caught.



S2. A multipanel plot with each panel showing the relationship between a habitat variable and hummingbird abundance with a linear regression (blue solid lines) and 95% confidence intervals (grey dashed lines).



S3. Proportional time budgets from behavioral observations of blue-tailed hummingbirds.



S4. Proportion of arthropod foraging time by blue-tailed hummingbirds spent utilizing four different foraging strategies.

S5. A list of all interactions observed between hummingbirds and flowering plants in sun coffee, shade coffee, and an adjacent secondary forest fragment (BTHU = blue-tailed hummingbird, CNHU = cinnamon hummingbird, VISA = violet sabrewing, LBST = long-billed starthroat). This list is not exhaustive, and it is possible and likely that additional hummingbird species visit each plant beyond what we observed here.

Plant Species	**Common Name**	**Use**	**BTHU**	**CNHU**	**VISA**	**LBST**
Musa sp1	banana	edible	X	X	X	
Musa sp2	plantain	edible	X	X	X	
Elattaria cardamomum	green cardamom	edible	X			
Amomum sp.	black cardamom	edible	X			
Inga micheliana		shade tree	X			
Spathodea campanulata	African tulip tree	shade tree	X			X
Sanchezia nobilis	zebra plant	ornamental	X	X		X
Odontonema cuspidatum	fire spike	ornamental	X	X		
Hibiscus sp.	perennial hibiscus	ornamental	X			

Heliconia sp1			X	X	X	
Heliconia rostrata	lobster claws	ornamental	X	X	X	
Heliconia bihai		ornamental	X	X	X	
Heliconia sp4		ornamental	X	X	X	
Zingiber sp.	beehive ginger	ornamental	X			
Costus sp1	spiral ginger	ornamental	X			
Costus sp2	spiral ginger	ornamental	X			
Costus sp3	spiral ginger	ornamental	X			
Tillandsia lamropoda	bromeliad	epiphyte	X			X
Tillandsia sp2	bromeliad	epiphyte	X			X
Tillandsia sp3	bromeliad	epiphyte	X			X
Bignonia sp.		epiphyte	X	X		X
Ericaceae sp.		epiphyte	X			X
Passiflora sp.	passion flower	epiphyte	X			