

# Canopy tree preference by insectivorous birds in shade-coffee farms: Implications for migratory bird conservation

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## Abstract

Land converted to coffee agriculture occupies >5 million hectares of what was once prime overwintering natural habitat in the American Neotropics for migrating birds. When tree canopy is retained or restored (i.e., shade-grown), coffee farms can serve as habitat refuge for wildlife. Yet few studies have examined whether canopy tree identity impacts habitat quality for biodiversity. Specifically, whether or not certain tree species are disproportionately important for foraging insectivorous birds remains unclear. In this study, we quantified bird foraging activity on 22 tree species in two Latin American Bird Friendly<sup>®</sup> coffee farms. Specifically, we conducted timed observations on focal trees to determine 1) tree preferences, 2) foraging bird abundance, 3) foraging time, and 4) species richness of birds using each canopy tree species. We found that birds did not forage randomly, and instead exhibited preferences for particular native tree species. Nitrogen-fixing Fabaceae were consistently used more frequently, supported more resident and migratory birds for longer periods of time, and supported more bird species than trees in other families. We posit that the potential mechanism contributing to tree preferences is the increase in insect abundance and diversity that provide high-quality food for insectivores but do not present pest problems for coffee. Thus, tree species that support insects may provide multiple benefits for farmers in the form of bottom-up soil fertilization and top-down pest control. This study provides evidence that agroforestry land can be improved for birds of conservation concern by prioritizing canopy tree species that help birds and farm productivity.

Abstract in Spanish is available with online material.

## KEYWORDS

coffee agroforestry, Colombia, foraging, Nicaragua, pest control, plant-animal interactions, tropical conservation

## 1 | INTRODUCTION

In over 5.2 million hectares of Mexico, central and South America (Food and Agriculture Organization Of The United Nations (FAO), 2016), coffee farms have replaced the diverse forests that once supported much of new world biodiversity. This has impacted South American resident birds, as well as North American migratory

species, including numerous species of conservation concern such as Cerulean (*Setophaga cerulea*) and Golden-winged warblers (*Vermivora chrysoptera*) (Bakermans, Vitz, Rodewald & Rengifo, 2009; Bennett, Rothman, Rosenberg & Rodriguez, 2016). At present, at least 200 species of North American breeding warblers, orioles, flycatchers, swallows, vireos, tanagers, hummingbirds, buntings, and thrushes winter in the Neotropics and are impacted by the management

decisions that affect habitat quality on human-dominated land (Smithsonian Migratory Bird Center 2018). Most of these migrants are primarily insectivorous and for seven months of the year rely on insects produced in forests at altitudes ideal for coffee production. Greenberg (1995) hypothesized that migrant birds exploit a seasonal peak in soft-bodied arthropods in the tropics, and documented high abundances of Lepidoptera caterpillars, as well as Hemipterans, Orthopterans, and spiders in both temperate and tropical ecosystems during the season that Neotropical migrants were present.

Shade-grown coffee is promoted as a superior alternative to sun-grown varieties because of its potential to provide habitat for wintering migrants (Perfecto, Rice, Greenberg, Voort & Van, 1996). However, within agroforestry, it is commonly assumed that shade trees are equal in their ability to support the abundance and diversity of insects required by overwintering birds. Moreover, there is a lack of studies on whether choice of canopy tree species for shade is relevant to the success of wintering migrants. Most studies to date have compared avian biodiversity metrics across broad habitat categories (Greenberg, Bichier, Angon & Reitsma, 1997; Greenberg, Bichier & Sterling, 1997; Mcdermott & Rodewald, 2014; Perfecto et al., 2004), plant structure, diversity or biomass gradients (Bakermans, Rodewald, Vitz & Rengifo, 2012; McDermott et al. 2015; Colorado, Mehlman & Valencia, 2018), or compared farms dominated by one or two tree species (Johnson & Sherry, 2001; Johnson, Sherry, Holmes & Marra, 2006) and thus are unable to directly test for effects of tree species on bird preferences (but see Johnson, 2000 and Bakermans et al., 2012).

Excluding predatory taxa, many of the arthropods on which birds depend are largely herbivores that are particularly sensitive to the phytochemistry of their host species (Bernays & Graham, 1988; Forister et al., 2015). Recent research in both temperate (Tallamy & Shropshire, 2009; Burghardt, Tallamy, Phillips & Shropshire, 2010; Burghardt & Tallamy 2013, Narango, Tallamy & Marra, 2017) and tropical ecosystems (Carlo, Aukema & Morales, 2007; Faria & Baumgarten, 2007) has demonstrated that tree species differ markedly in their contributions to plant-animal interactions. Analyses of pollination and seed-dispersal networks, for example, have repeatedly shown that a few tree species support the majority of local interactions and serve as “foraging hubs” for frugivores and pollinators (Bascompte & Jordano, 2014; Carlo et al., 2007; Peters et al., 2016). Moreover, within agroforestry, several studies have found that *Inga*-dominated farms tend to support high abundance and diversity of migratory birds (Bakermans et al., 2012; Greenberg, Bichier & Sterling, 1997; Johnson & Sherry, 2001; Mcdermott, Rodewald & Matthews, 2015), while low numbers are found in monocultural *Eucalyptus* (Calviño-Cancela, 2013) or *Citrus* (Johnson et al., 2006) farms. Yet, we still know little about the degree to which foraging insectivorous birds discriminate among tree species on the basis of the availability of insect food on shade-coffee farms information that is necessary to design agroforestry systems with high bird conservation value.

Because some tree species produce orders of magnitude more insect herbivores than others (Tallamy & Shropshire, 2009; Janzen

1987), we predict that such productive species serve as bird foraging hubs in both wintering and breeding grounds. Most insect herbivores evolve elaborate physiological, behavioral, and life history adaptations to circumvent the defenses of particular host lineages (Bernays & Graham, 1988; Tallamy, 2004); thus, foraging hubs are most often trees that evolved within local food webs. Ironically, coffee growers seeking Bird Friendly® certification increasingly are using introduced shade trees such as *Eucalyptus*, *Mangifera indica*, and *Citrus* (Calviño-Cancela, 2013; Méndez, Gliessman & Gilbert, 2007) because of the additional sources of income provided by lumber (Rice, 2008) and fruit crops (Ambinakudige & Sathish, 2009; Rice 2011). However, these non-native species are predicted to support few nutritionally valuable insects required by insectivorous birds (e.g., Lepidopteran larvae) because they are evolutionarily novel within tropical ecosystems and thus lack coevolutionary relationships with local insects. Management strategies that promote nutrient-rich foraging hubs within shade coffee should enable birds wintering on such farms to have higher rates of survival, be able to return to breeding grounds earlier and in better condition, and have higher reproductive success than birds that are food-stressed on wintering grounds (Marra et al. 1998; Norris et al. 2004; Brown & Sherry, 2006). High bird densities within coffee farms may also provide top-down control of coffee pests (Karp et al., 2013).

Increasing the habitat quality of land used for coffee production by favoring shade trees that support insects important in bird diets will have implications for bird conservation in general and coffee certification programs in particular. However, a lack of knowledge regarding which tree species in various coffee regions are best at supporting insects is preventing action by growers. Our understanding of shade trees that produce fruit important to wintering and resident birds is comprehensive (Peters, Mordecai, Ronald, Cooper & Greenberg, 2010; Peters & Nibbelink, 2011), but little work has been done to compare various candidate tree species in terms of their ability to support insect prey and attract birds for pest control (Staver, Guharay, Monterroso & Muschler, 2001). Here, we begin this process by comparing the foraging activity of non-breeding resident and Neotropical migrant birds on tree species commonly used in shade coffee while controlling for canopy volume and fruiting phenology. Our objective was to determine whether foraging among shade trees within a diverse polyculture is random or whether there are distinct functional or taxonomic patterns in bird use. Specifically, we were interested in whether trees preferred by birds provide certain benefits to farmers, or belong to specific families.

## 2 | METHODS

### 2.1 | Sites

We conducted this study on two Bird Friendly® certified, shade-grown coffee farms, one in Nicaragua in years 2015 & 2016, and one in Colombia in 2016. *Gaia Estate* is a 36-hectare farm located in southwestern Nicaragua at 575-m elevation, within dry-forest habitat in the department of Carazo. *Agroberlin* is a 188-hectare farm in

**TABLE 1** Planted tree species used in foraging observations in each country

Scientific name	Common name	Family	Origin*	Purpose	Country
<i>Albizia</i> sp.	Genízaro, Carbonero	Fabaceae	Native	Nitrogen-fixing	Both
<i>Anacardium excelsum</i>	Caracoli	Anacardiaceae	Native	Fruit	Colombia
<i>Annona muricata</i>	Soursop, Guanabana	Annonaceae	Native	Fruit	Colombia
<i>Bursera simaruba</i>	Gumbo-limbo	Burseraceae	Native	Lumber	Nicaragua
<i>Cedrela odorata</i>	Spanish Cedar	Meliaceae	Native	Lumber	Nicaragua
<i>Ceiba</i> sp.	Kapok tree	Malvaceae	Native	Lumber	Colombia
<i>Citrus nobilis</i>	Citrus	Rutaceae	Non-native	Fruit	Both
<i>Cordia alliodora</i>	Nogal cafetero	Boraginaceae	Native	Lumber	Colombia
<i>Enterolobium cyclocarpum</i>	Guanacaste	Fabaceae	Native	Nitrogen-fixing	Nicaragua
<i>Eucalyptus</i> sp.	Eucalyptus	Myrtaceae	Non-native	Lumber	Colombia
<i>Ficus</i> sp.	Fig	Moraceae	Native	Lumber	Nicaragua
<i>Gliricidia sepium</i>	Madero Negro	Fabaceae	Native	Nitrogen-fixing	Nicaragua
<i>Inga</i> sp.	Guamo	Fabaceae	Native	Nitrogen-fixing	Both
<i>Mangifera indica</i>	Mango	Anacardiaceae	Non-native	Fruit	Both
<i>Persea americana</i>	Aguacate	Lauraceae	Native	Fruit	Both
<i>Pouteria sapota</i>	Zapote/sapote	Sapotaceae	Native	Fruit	Nicaragua
<i>Psidium guajava</i>	Guayaba, guava	Myrtaceae	Native	Fruit	Colombia
<i>Quercus humboldtii</i>	Roble	Fagaceae	Native	Lumber	Colombia
<i>Simarouba glauca</i>	Acetuno, Olive	Simaroubaceae	Native	Lumber	Nicaragua
<i>Spondias mombin</i>	Jacote	Anacardiaceae	Native	Fruit	Nicaragua

Note. \*Native or non-native to the country observed in.

northeastern Colombia on the western slope of the Sierra Nevada within cloud-forest habitat at 1250-m elevation. Both farms contain shade from overstory and understory trees. Under Bird Friendly® certification criteria, both farms had organic certification, contain >10 native woody plant species, could be categorized as “traditional polyculture,” and have vegetation composed of at least three vertical strata providing at least 40 percent foliage cover (Smithsonian Migratory Bird Center 2018).

## 2.2 | Tree selection

To measure bird foraging preferences, 13 and 11 target tree species were chosen for study in Nicaragua and Colombia, respectively (Table 1). Species were chosen because of their popularity and use as canopy trees on shade-coffee farms in the region and their abundance within each farm. Because of differences in climate and farmer preferences, different species were chosen at each farm. All trees were either planted or specifically retained by farmers and, thus, have been filtered according to characteristics that promote high coffee yields, such as deciduous leaves, preferred foliage densities, and impacts on coffee pests or disease (Soto-Pinto et al., 2007). The trees we selected included those that provide additional benefits to farmers such as nitrogen fixation, fruit production or lumber provisions (Soto-Pinto et al., 2007). In Nicaragua, we chose *Albizia* sp. (nitrogen), *Inga* sp. (nitrogen), *Enterolobium cyclocarpum* (nitrogen), *Gleditsia sepium*, (nitrogen), *Mangifera indica*

(fruit), *Citrus nobilis* (fruit), *Persea americana* (fruit), *Spondias mombin* (fruit), *Pouteria sapota* (fruit), *Cedrela odorata* (lumber), *Simarouba glauca* (lumber) and *Bursera simaruba* (lumber). In Colombia, we chose *Albizia* sp. (nitrogen), *Inga* sp. (nitrogen), *Persea americana* (fruit), *Mangifera indica* (fruit), *Citrus nobilis* (fruit), *Annona muricata* (fruit), *Psidium guajava* (fruit), *Eucalyptus* sp. (lumber), *Cordia alliodora* (lumber), *Quercus humboldtii* (lumber), *Anacardium excelsum* (lumber), and *Ceiba* sp., (lumber).

To be included in our study, trees had to be mature, healthy, and not producing fruits that could be eaten by birds. We randomly selected three individuals of each tree species located in different regions of the farm. All trees were in the interior of the coffee farm and not on the edge of adjacent forest. Despite our initial selection, some target species could not be included within our analyses. In Nicaragua, *Inga* trees became inaccessible in 2016 for observation during the full study period because of human disturbance; therefore, we only used 2015 observations in our analysis. We also excluded *B. simarouba* in both years because most individual trees produced small edible fruits which confounded our goal of assessing bird use for insect foraging on our focal species. We acknowledge that fruiting bodies can also attract insects that are important for insectivorous birds; however, we chose to remove this species due to our limited ability to discern diet based on visual observations, and that foraging observations appeared to be dominated primarily by frugivorous species (DLN personal observation). In Colombia, two of our target tree species (*A. muricata* and *A. excelsum*) did not have

multiple suitable individuals available for observation during the study and were removed from analyses.

## 2.3 | Bird foraging

We determined bird foraging preferences by conducting timed observations on each focal tree species within the month of January in 2015 (Nicaragua) and 2016 (both countries). A trained observer conducted observations at focal trees for 10-min periods during which they identified every bird using the tree canopy for foraging. The observer was at a fixed location approximately 15-m from the target tree in an area that maximized their ability to observe foraging birds in the canopy of the tree. To calculate time spent foraging, the observer recorded the time each bird was first observed entering the tree and the time the bird left the tree. Foraging times were truncated to the 10-min survey period, thus, if a bird began foraging in the tree before the survey period, we started its foraging time at zero. Likewise, we concluded a foraging bout at the end of the 10-min period, regardless if the bird continued foraging in the focal tree. Only actual time spent foraging (as opposed to preening or resting) was recorded. Observations were conducted for each tree species twice per day; once during morning hours (sunrise–1200) and once in the afternoon (1300 to sunset). Individual trees were alternated so that each tree was observed for equal times in the morning and the afternoon time periods.

Observations were made on days without precipitation or high wind that would affect the ability to observe birds or bird foraging itself. During each observation period, the observer also recorded the phenological status of each tree, that is, whether it was fruiting, flowering or growing leaves. At the end of the season, we measured the total height (m), height to lowest canopy (m), diameter-at-breast-height (cm), and canopy size (width and depth in m) of each focal tree to derive basal area and canopy volume. We subtracted the height of the lowest canopy from the total height to get “canopy height.” We then used canopy height, width and depth to calculate canopy volume ( $m^3$ ) using a modified equation for cylindrical canopies (Thorne et al., 2002).

## 2.4 | Statistical analysis

We compared relative tree use by foraging birds in three ways. First, to determine whether birds exhibited tree preferences, we calculated the extent that observed foraging frequency (i.e., pooled number of birds observed in each tree species) deviated from expected frequency with a chi-square test for count data using the function “chi-square test” in R (R Core Team, 2017). In this analysis, each tree species was a sample unit. Expected frequencies were calculated as the number of observations if the total observations observed were distributed evenly among all trees. We calculated the 95% confidence interval (CI) of proportional differences by performing an exact binomial test using the function “binomial test.”

Second, to test the hypothesis that particular tree species supported more foraging bird activity than others, we used bird

abundance and foraging time from our focal tree observations as response variables and each individual tree observation as the sample unit. Bird abundance was the total number of individuals per 10-min observation and foraging time was the total time spent foraging (in seconds) per ten-minute period, per individual bird. For bird abundance, we used a generalized linear model (GLM) with Poisson distribution because our bird abundance dataset was non-normally distributed count data with zeros.

For foraging time, our response was the time in seconds spent foraging in a tree for each individual bird (excluding zeros). Because foraging time had both a lower and upper bound, we converted our response into a proportion by dividing by the maximum time (600 sec) and used a beta distribution to model differences in the mean proportion of time spent foraging among the tree species. To conform to the requirements of the model function, we subtracted 0.5 s from each observation so that no sample had a value of exactly 1 (i.e., 10 min of foraging). Some birds may have been foraging both before and after the observation, thus our measurements should be considered an index to make relative comparisons among the tree species, and not “true” foraging times, *per se*.

We were specifically interested in the ability of these trees to support habitat for non-breeding insectivorous migratory birds from North America. We separated the data into total number of primarily insectivorous Neotropical migrants (*Parulidae* and *Vireonidae*), and total foraging time of migrants. In Nicaragua, insectivorous migrants observed in focal trees consisted of Yellow Warbler (*Setophaga petechia*), Tennessee Warbler (*Leiothlypis peregrina*), Philadelphia Vireo (*Vireo philadelphicus*), Warbling Vireo (*Vireo gilvus*), and Yellow-throated Vireo (*Vireo flavifrons*). In Colombia, American Redstart (*Setophaga ruticilla*), Black-throated Green Warbler (*Setophaga virens*), Blackburnian Warbler (*Setophaga fusca*), Yellow Warbler, Tennessee Warbler, Black-and-white Warbler (*Mniotilta varia*), Mourning Warbler (*Geothlypis philadelphia*), Bay-breasted Warbler (*Setophaga castanea*), Cerulean Warbler (*Setophaga cerulea*), Philadelphia Vireo, and Yellow-throated Vireo represented the Neotropical migrants.

We constructed models with tree species as our fixed factor of interest and tree canopy volume (in  $m^3$ ) as a covariate to account for plant biomass. We constructed separate models for Nicaraguan and Colombian trees. We did not consider date or time as covariates because trees were evenly sampled across the season and time of day for all species, and these covariates did not improve model predictions. We assessed how well our covariate improved the fit of our models using the “Anova” test from package “car” (Fox & Weisberg, 2011). We reported  $\beta$ -coefficients,  $p$ -values, and 95% CI for our covariate term, and  $F$  tests for both terms to assess whether they improved model fit. We also performed pairwise comparisons of tree species with least square means adjusted for a Tukey's comparison using the function “cld” from package “lsmeans” (Lenth, 2016).

Finally, we were interested in whether there were differences in the species richness of birds supported on each canopy tree species. Because of the large differences in total observed individual birds between the trees (see foraging observation results), we estimated species richness by calculating individual-based estimates of species

richness per tree species and rarefaction curves. All individuals were pooled for each tree species to calculate estimates of mean species richness and bootstrap standard error. Prior to analysis, we excluded birds that were not identified to species (“unknown”) and birds identified only to genus (i.e., *Turdus* sp.) unless those observations were the only samples of that bird genus for that tree. To ensure the accuracy of species identifications, we only included 2016 data for Nicaragua. We calculated species richness estimates, extrapolated rarefaction curves and 95% CI using Chao estimators (Chao, Chiu & Jost, 2014) via the package “iNext” (Hsieh, Ma & Chao, 2016). All statistical analyses were performed in program R 3.3.3 (R Core Team 2017).

### 3 | RESULTS

#### 3.1 | Summary

In Nicaragua, we conducted 774 focal observations on 12 tree species ( $64.5 \pm 7.28$  SD observations per tree) resulting in 129 hr of observation. The mean height of our focal trees was  $19 \pm 9$  SD meters and the mean canopy volume was  $2500 \text{ m}^3 \pm 4613$  SD. In total, we observed 612 birds of 25 different species (10 sp. of Neotropical migrants, Table S1) foraging in our focal trees with a mean of  $0.79 \pm 2.85$  SD birds per observation. The most frequently encountered bird species, which comprised 81.70 percent of all observations, included Tennessee Warbler (57 observations, 344 individuals), Yellow Warbler (95 observations, 122 individuals), and Yellow-throated Vireo (16 observations, 18 individuals) (Table S3).

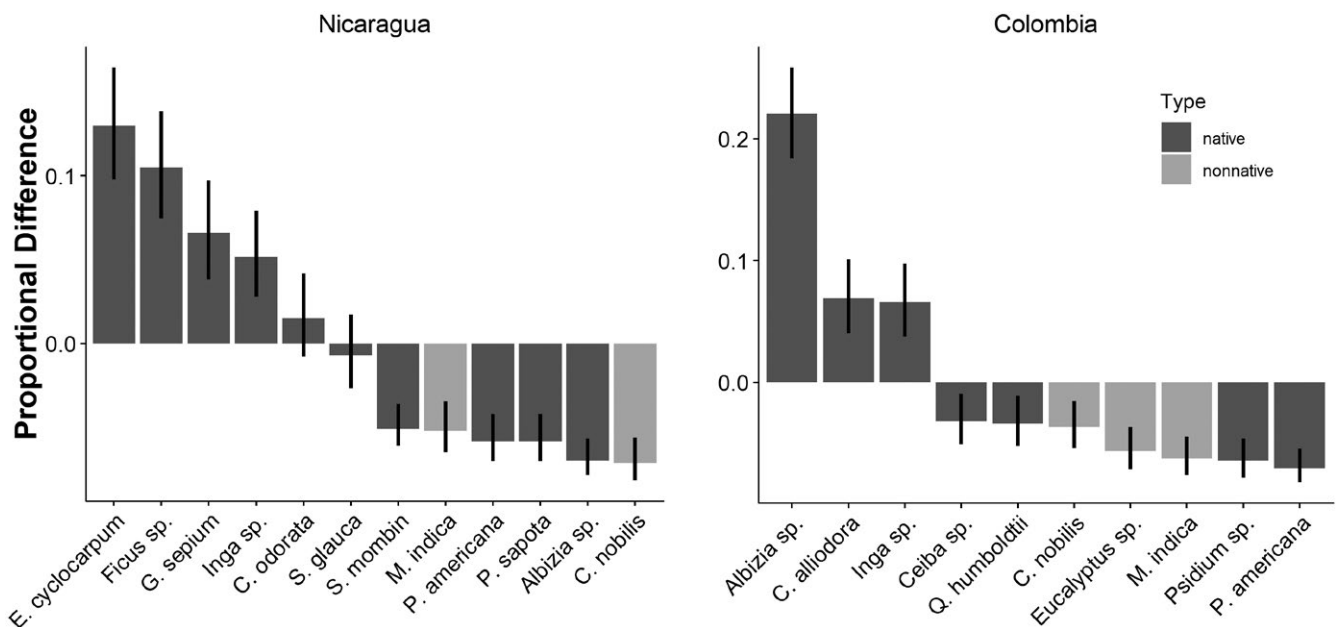
In Colombia, we conducted 207 focal observations on 10 tree species ( $20.70 \pm 0.48$  SD observations per tree) in 2016 resulting in 34.50 hr of observation. The canopy was shorter in Colombia

than in Nicaragua ( $12 \pm 7$  SD), with smaller mean canopy volume ( $320 \text{ m}^3 \pm 925$  SD). In total, we observed 622 birds of 48 different species (13 sp. of Neotropical migrants, Table S2) foraging in our focal trees with a mean of  $3.00 \pm 3.68$  SD birds per observation. The most frequently encountered bird species, which comprised 39.07 percent of all observations, included Tennessee Warbler (61 observations, 111 individuals), Blue-gray Tanager (*Thraupis episcopus*, 35 observations, 69 individuals), and Blackburnian Warbler (42 observations, 63 individuals) (Table S3).

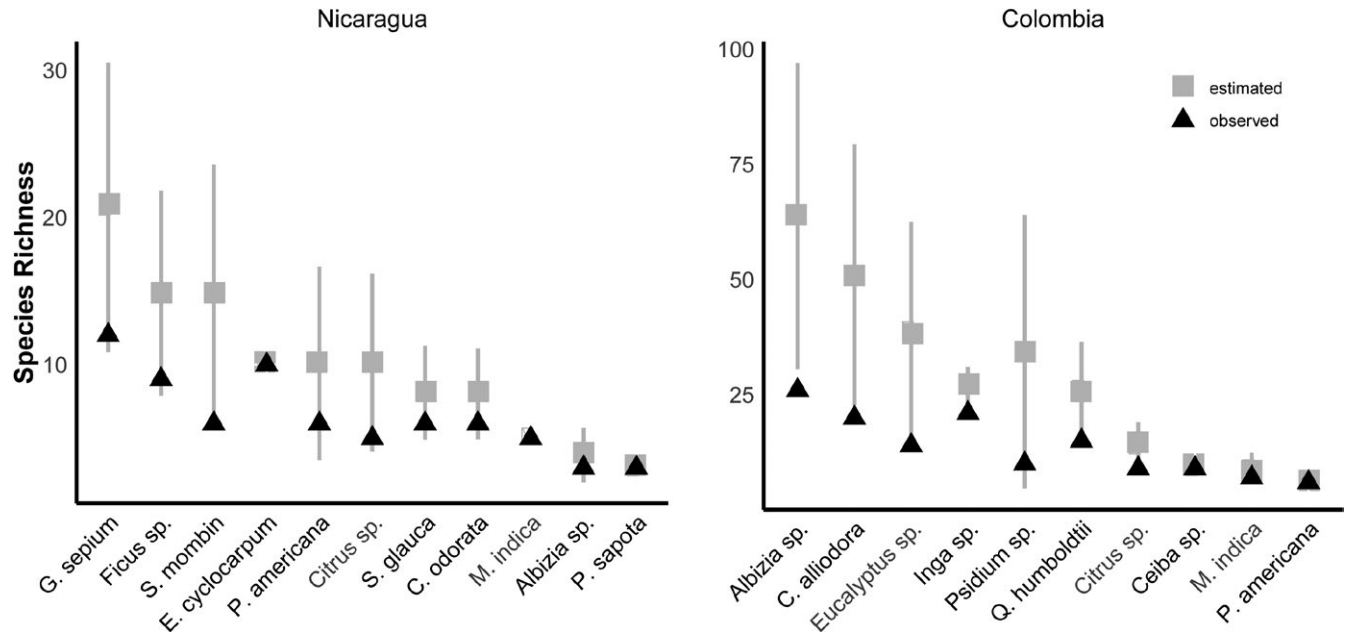
#### 3.2 | Tree preference

In Nicaragua, frequency of birds varied among tree species with 56.21 percent of our observations occurring in *E. cyclocarpum*, *Ficus* sp. and *G. sepium*. In our study site, birds did not forage randomly; instead, they preferentially foraged in some tree species while avoiding others ( $\chi^2 = 413.72$ ,  $df = 11$ ,  $p < 0.001$ ). *Ficus* sp., *E. cyclocarpum*, *G. sepium*, and *Inga* sp. were preferred, while all other species were either avoided (six species), or foraging frequency was consistent with random foraging (two species) (Figure 1). For Neotropical migrant insectivores, frequency of birds also varied among tree species with 54.81 percent of our observations occurring in *E. cyclocarpum*, *Ficus* sp., and *G. sepium*. Migratory birds preferentially foraged in some trees over others ( $\chi^2 = 376.88$ ,  $df = 11$ ,  $p < 0.001$ ). *Enterolobium cyclocarpum*, *Ficus* sp., *G. sepium*, *Inga* sp., and *C. odorata* were preferred relative to availability, while most other species were avoided (six species), or foraging frequency was consistent with random foraging (one species) (Figure S1).

In Colombia, frequency of foraging birds varied among tree species with 49.04 percent of our observations occurring in *Albizia* sp., and *C. alliodora*. Birds preferentially foraged in trees more or less than what



**FIGURE 1** Proportional difference ( $\pm$  95% CI) between expected and observed percent frequency of bird observations on the 12 focal tree species in Nicaragua, and 10 focal tree species in Colombia. In Nicaragua, *E. cyclocarpum*, *Ficus* sp., *G. sepium* and *Inga* sp. were all foraged in more than expected by chance. In Colombia, *Albizia* sp., *C. alliodora* and *Inga* sp. were all foraged in more than expected by chance



**FIGURE 2** Observed (black triangles) and estimated (gray squares) species richness of foraging birds on 11 species of Nicaraguan canopy trees and 10 species in Colombia. Estimated species richness is the asymptotic estimate via Chao (1984) and vertical lines are the estimated bootstrap standard error. Tree species native to the country observed are shown in blank font and non-native species are shown in gray

was expected by chance ( $\chi^2 = 482.94$ ,  $df = 9$ ,  $p < 0.001$ ). *Albizia* sp., *Inga* sp., and *C. alliodora* were preferred relative to availability, while all other species were avoided (seven species) (Figure 2). For Colombian Neotropical migrant insectivores, frequency of bird observations also varied among tree species with 59.60 percent of our observations occurring in *Albizia* sp., and *Inga* sp. Birds preferentially foraged in trees more or less than what was expected by chance ( $\chi^2 = 351.28$ ,  $df = 9$ ,  $p < 0.001$ ). *Albizia* sp., *Inga* sp., and *C. alliodora* were preferred relative to availability, while all other species were avoided (six species) or foraging was consistent with random frequencies (one species) (Figure S1).

### 3.3 | Bird abundance

In Nicaragua, the number of birds observed was not related to the canopy volume of the tree (scaled canopy volume:  $\beta -0.03 \pm 0.04$ ,  $p = 0.44$ , 95% CI  $-0.11$ ,  $0.05$ ), and canopy volume did not improve the model fit ( $F_{1, 809} = 0.08$ ,  $p = 0.77$ ). The number of birds foraging was significantly different among the trees ( $F_{11, 809} = 5.35$ ,  $p < 0.001$ ). *Ficus* sp., and *E. cyclocarpum* had significantly more foraging birds than all other tree species except *Inga* sp. and *G. sepium* ( $p < 0.05$ , Figure S1, Table 2). The number of foraging migratory birds observed was negatively related to canopy volume ( $\beta -0.19 \pm 0.06$ ,  $p < 0.001$ , 95% CI  $-0.31$ ,  $-0.09$ ), but inclusion of this variable did not improve model fit ( $F_{1, 811} = 1.87$ ,  $p = 0.17$ ). The number of migratory birds was significantly different among the canopy tree species ( $F_{11, 812} = 5.08$ ,  $p < 0.001$ ). Here, *E. cyclocarpum* and *Inga* sp. had significantly more foraging migrants on average than all other tree species except *Ficus* sp. and *G. sepium* ( $p < 0.05$ , Figure S3, Table 2).

In Colombia, the number of foraging birds was positively but weakly related to the canopy volume of the tree ( $\beta 0.06 \pm 0.03$ ,

$p = 0.02$ , 95% CI  $0.01$ ,  $0.11$ ), but including this variable did not improve model fit ( $F_{1, 592} = 2.09$ ,  $p = 0.15$ ). The mean number of birds per observation was significantly different among the trees ( $F_{9, 593} = 16.71$ ,  $p < 0.001$ ). This was driven by *Inga* spp., *Albizia* spp. and *C. alliodora* having significantly more foraging birds than all other trees ( $p < 0.05$ , Figure S2, Table 2). For migratory birds, the number of foraging birds was positively related to canopy volume ( $\beta 0.15 \pm 0.04$ ,  $p < 0.001$ , 95% CI  $0.08$ ,  $0.22$ ) and this variable did improve model fit ( $F_{8, 533} = 9.58$ ,  $p = 0.002$ ). When accounting for canopy volume, the mean number of migrants per observation was significantly different among the trees ( $F_{9, 533} = 15.42$ ,  $p < 0.001$ ). Again, this was driven by *Inga*, *Albizia*, and *C. alliodora* having significantly more foraging birds than all other trees ( $p < 0.05$ , Figure S4, Table 2).

### 3.4 | Foraging time

In Nicaragua, foraging time was marginally positively related to canopy volume ( $\beta 0.17 \pm 0.09$ ,  $p = 0.07$ , 95% CI  $-0.01$ ,  $0.34$ ) and this variable only modestly improved model fit ( $F_{1, 407} = 3.34$ ,  $p = 0.07$ ); it was not included in the final model. Foraging time was significantly different among trees ( $F_{11, 414} = 3.38$ ,  $p < 0.001$ ). However, given the variation and uncertainty in the mean predictions, the only clear difference was that birds foraged significantly longer in *Ficus* sp. compared to *E. cyclocarpum*, *C. odorata*, *G. sepium*, and *S. glauca* ( $p < 0.05$ , Figure S5, Table 3). When considering only migrant foraging time, there was a positive effect of canopy volume ( $\beta 0.39 \pm 0.10$ ,  $p < 0.001$ , 95% CI  $0.19$ ,  $0.588$ ), and this variable improved model fit ( $F_{1, 277} = 14.46$ ,  $p < 0.001$ ). Accounting for canopy, foraging times of migrants were significantly different among trees ( $F_{11, 277} = 4.56$ ,  $p < 0.001$ ). For migratory insectivores, birds foraged significantly

**TABLE 2** Mean ( $\pm$  SD) abundance of all foraging birds and migratory insectivorous birds in the 12 Nicaraguan and 10 Colombian focal trees on shade-coffee farms\*

Country	Tree species	All birds	Migratory insectivores
Nicaragua	<i>Albizia</i> sp.	0.15 ( $\pm$ 0.40) e	0.10 ( $\pm$ 0.31) d
	<i>Cedrela odorata</i>	0.93 ( $\pm$ 3.09) bc	0.85 ( $\pm$ 3.07) bc
	<i>Citrus</i> sp.	0.19 ( $\pm$ 0.43) e	0.08 ( $\pm$ 0.28) d
	<i>Enterolobium cyclocarpum</i>	<b>1.99 (<math>\pm</math> 4.02) a</b>	<b>1.57 (<math>\pm</math> 4.02) a</b>
	<i>Ficus</i> sp.	<b>1.75 (<math>\pm</math> 4.47) a</b>	<b>1.39 (<math>\pm</math> 4.22) ab</b>
	<i>Gliricidia sepium</i>	<b>1.38 (<math>\pm</math> 3.10) ab</b>	<b>1.03 (<math>\pm</math> 2.86) ac</b>
	<i>Inga</i> sp.	<b>2.98 (<math>\pm</math> 12.90) ab</b>	<b>2.98 (<math>\pm</math> 12.90) a</b>
	<i>Mangifera indica</i>	0.31 ( $\pm$ 0.99) de	0.21 ( $\pm$ 0.86) d
	<i>Persea americana</i>	0.25 ( $\pm$ 0.72) e	0.16 ( $\pm$ 0.37) d
	<i>Pouteria sapota</i>	0.25 ( $\pm$ 0.70) e	0.13 ( $\pm$ 0.39) d
	<i>Simarouba glauca</i>	0.75 ( $\pm$ 2.11) cd	0.63 ( $\pm$ 2.04) c
	<i>Spondias mombin</i>	0.23 ( $\pm$ 0.47) e	0.16 ( $\pm$ 0.37) d
Colombia	<i>Albizia</i> sp.	<b>9.48 (<math>\pm</math> 4.90) a</b>	<b>4.33 (<math>\pm</math> 2.18) a</b>
	<i>Ceiba</i> sp.	2.15 ( $\pm$ 2.16) c	0.00 ( $\pm$ NA)
	<i>Citrus</i> sp.	1.76 ( $\pm$ 1.30) cd	0.33 ( $\pm$ 0.58) b
	<i>Cordia alliodora</i>	5.30 ( $\pm$ 3.76) b	<b>2.65 (<math>\pm</math> 2.18) a</b>
	<i>Eucalyptus</i> sp.	1.33 ( $\pm$ 1.83) cd	0.05 ( $\pm$ 0.22) b
	<i>Inga</i> sp.	5.15 ( $\pm$ 2.41) b	<b>2.90 (<math>\pm</math> 1.74) a</b>
	<i>Mangifera indica</i>	1.10 ( $\pm$ 2.02) cd	0.29 ( $\pm$ 0.72) b
	<i>Persea americana</i>	0.81 ( $\pm$ 2.04) d	0.24 ( $\pm$ 0.89) b
	<i>Psidium guajava</i>	1.14 ( $\pm$ 1.46) cd	0.52 ( $\pm$ 0.87) b
	<i>Quercus humboldtii</i>	2.00 ( $\pm$ 2.05) cd	0.86 ( $\pm$ 1.01) b

\*Values with the same letter (a, b, c, d, e) are not significantly different ( $p < 0.05$ ) according to the Tukey's all-pair comparisons test. Tree species in bold were estimated to have the greatest abundance of foraging birds (a) for each country.

longer in *Albizia* compared to all other trees except *Ficus* sp. and *Citrus* ( $p < 0.05$ , Figure S7, Table 3).

In Colombia, the proportion of time spent foraging per individual was positively related to canopy volume ( $\beta 0.19 \pm 0.06$ ,  $p = 0.001$ , 95% CI 0.07, 0.30), and this variable improved model fit ( $F_{1, 618} = 10.30$ ,  $p = 0.001$ ). When accounting for canopy volume, the mean time spent foraging was significantly different among the trees ( $F_{9, 618} = 8.25$ ,  $p < 0.001$ ). This was driven by *Albizia* supporting birds that foraged significantly longer than in all other trees but *Inga* sp. ( $p < 0.05$ , Figure S6, Table 3). Foraging time of migrant birds was not related to canopy volume ( $\beta 0.02 \pm 0.10$ ,  $p = 0.88$ , 95% CI  $-0.18$ ,  $0.21$ ) which did not improve model fit ( $F_{1, 239} = 0.02$ ,  $p = 0.88$ ). The mean foraging time of migrant insectivores was significantly different among the trees ( $F_{8, 240} = 10.86$ ,  $p < 0.001$ ). Here, foraging times were more similar, except that *Albizia* had significantly more foraging birds than most other trees except *P. guajava* ( $p < 0.05$ , Figure S8, Table 3).

### 3.5 | Species richness

When comparing observed species richness, the trees with the most species were *G. sepium* (12 sp.), *E. cyclocarpum* (10 sp.) and *Ficus* (9 sp.) in Nicaragua and *Albizia* (28 sp.), *Inga* (23 sp.) and *C. alliodora*

(21 sp.) in Colombia. However, in our sample-based extrapolation, confidence intervals for estimated species richness were wide and overlapped for all tree species. For Nicaragua, the trees predicted to support the most foraging bird species were *G. sepium* (estimated  $20.69 \pm 9.84$  SE, CI: 13.47, 63.54, observed 12), *Ficus* sp. (estimated  $14.86 \pm 6.97$  SE, CI: 9.93, 45.89, observed 10) and *S. mombin* (estimated  $14.75 \pm 8.84$  SE, CI: 7.69, 51.29, observed 6) (Figure 2). For Colombia, the tree species predicted to support the most bird species were *Albizia* sp. (estimated  $63.81 \pm 33.23$  SE, CI: 35.64, 195.85, observed 28), *C. alliodora* (estimated  $50.96 \pm 28.38$  SE, CI: 27.24, 164.76, observed 21), and *Eucalyptus* sp. (estimated  $39.11 \pm 23.39$  SE, CI: 19.89, 133.98, observed 15) (Figure 2).

## 4 | DISCUSSION

The patterns of foraging we observed in both Central and South America suggest that, within a coffee agroforestry system, birds do not forage in shade trees indiscriminately. Even within farms, we found significant differences in the abundance of foraging birds, total time spent foraging, and species richness supported between tree species, suggesting that birds prioritize certain trees that

**TABLE 3** Mean ( $\pm$  SD) proportion of foraging time of all foraging birds and migratory insectivorous birds in the 12 Nicaraguan and 10 Colombian focal trees on shade-coffee farms\*

Country	Tree species	All Birds	Migratory insectivores
Nicaragua	<b>Albizia sp.</b>	<b>0.38 (<math>\pm</math> 0.37) ab</b>	<b>0.43 (<math>\pm</math> 0.41) a</b>
	<i>Cedrela odorata</i>	0.15 ( $\pm$ 0.21) b	0.14 ( $\pm$ 0.22) c
	<b>Citrus sp.</b>	<b>0.21 (<math>\pm</math> 0.25) ab</b>	<b>0.26 (<math>\pm</math> 0.36) abc</b>
	<i>Enterolobium cyclocarpum</i>	0.20 ( $\pm$ 0.24) b	0.21 ( $\pm$ 0.25) c
	<b>Ficus sp.</b>	<b>0.34 (<math>\pm</math> 0.33) a</b>	<b>0.35 (<math>\pm</math> 0.34) ab</b>
	<i>Gliricidia sepium</i>	0.14 ( $\pm$ 0.18) b	0.12 ( $\pm$ 0.15) c
	<b>Inga sp.</b>	<b>0.14 (<math>\pm</math> 0.19) b</b>	<b>0.14 (<math>\pm</math> 0.19) c</b>
	<b>Mangifera indica</b>	<b>0.31 (<math>\pm</math> 0.36) ab</b>	<b>0.17 (<math>\pm</math> 0.20) bc</b>
	<b>Persea americana</b>	<b>0.17 (<math>\pm</math> 0.26) ab</b>	<b>0.13 (<math>\pm</math> 0.17) bc</b>
	<b>Pouteria sapota</b>	<b>0.21 (<math>\pm</math> 0.25) ab</b>	<b>0.16 (<math>\pm</math> 0.27) c</b>
	<i>Simarouba glauca</i>	0.12 ( $\pm$ 0.14) b	0.10 ( $\pm$ 0.11) c
	<b>Spondias mombin</b>	<b>0.14 (<math>\pm</math> 0.16) ab</b>	<b>0.15 (<math>\pm</math> 0.18) bc</b>
Colombia	<b>Albizia sp.</b>	<b>0.48 (<math>\pm</math> 0.35) a</b>	<b>0.59 (<math>\pm</math> 0.34) a</b>
	<i>Ceiba</i>	0.25 ( $\pm$ 0.26) bc	0.00 ( $\pm$ NA)
	<i>Citrus sp.</i>	0.19 ( $\pm$ 0.19) bc	0.07 ( $\pm$ 0.03) bc
	<i>Cordia alliodora</i>	0.21 ( $\pm$ 0.21) c	0.21 ( $\pm$ 0.19) c
	<i>Eucalyptus sp.</i>	0.22 ( $\pm$ 0.25) bc	0.03 ( $\pm$ NA)
	<b>Inga sp.</b>	<b>0.34 (<math>\pm</math> 0.29) ab</b>	<b>0.39 (<math>\pm</math> 0.30) b</b>
	<i>Mangifera indica</i>	0.08 ( $\pm$ 0.06) c	0.07 ( $\pm$ 0.04) bc
	<i>Persea americana</i>	0.17 ( $\pm$ 0.23) bc	0.13 ( $\pm$ 0.11) bc
	<b>Psidium guajava</b>	<b>0.28 (<math>\pm</math> 0.34) bc</b>	<b>0.51 (<math>\pm</math> 0.40) abc</b>
	<i>Quercus humboldtii</i>	0.22 ( $\pm$ 0.16) bc	0.25 ( $\pm$ 0.19) bc

\*Values with the same letter (a, b, c, d, e) are not significantly different ( $p < 0.05$ ) according to the Tukey's all-pair comparisons test. Tree species in bold were estimated to have the greatest proportion of foraging times (a) for each country.

provide more food resources. Moreover, we found that, of our tree functional groups and families, nitrogen-fixing trees (Fabaceae) were estimated to support the greatest abundance and species richness of birds and this pattern held across farms in two distinct geographies. Non-legumes were also preferred by birds in both countries, such as *Ficus* (Nicaragua) and *C. alliodora* (Colombia). Non-native plant species tended not to support high numbers or diversity of foraging birds in any of our comparisons except for *Eucalyptus* which was estimated to support moderately high species richness, albeit with very low bird activity.

Our bird foraging observations on shade-coffee farms were dominated by migratory insectivores that breed in North America (see results and supplementary table 3). This result complements previous studies demonstrating that agroforestry can provide important wintering habitat for migratory birds. Top-down control of arthropods is much stronger during seasons when migratory birds are present in agroforestry systems and when bird species diversity is high (Bael et al., 2008). Migratory birds are also the primary predator of the coffee berry borer (*Hypothenemus hampei*), considered the most economically damaging coffee pest (Kellermann, Johnson, Stercho & Hackett, 2008). We uniquely show that not all trees are equal in their ability to attract migratory birds during the non-breeding season;

thus, farmers may be able to increase natural pest control by prioritizing particular native canopy trees that maximize bird diversity and abundance. However, in either country, no one tree species was preferred alone, highlighting that a diverse suite of food hubs is necessary to provide high-quality resources throughout the season and maximize the presence of predatory consumers (Greenberg, Bichier, Angon, et al., 1997; Nell, Abdala-Roberts, Parra-Tabla & Mooney, 2018; Perfecto et al., 2004).

Nitrogen-fixing Fabaceae appear to be disproportionately important for birds in coffee agroforestry systems. Most Fabaceae were preferred species in both countries and supported the greatest abundance, longest foraging times, and greatest avian species richness. We posit that foraging birds prefer leguminous trees because they support more insect prey due to 1) foliage that is high in nitrogen and low in chemical defenses and 2) they support high insect diversity from coevolved herbivore host-plant specialization. Nitrogen fixation is an essential ecosystem service primarily provided by legumes that convert atmospheric nitrogen into a usable compound. As the leaves and fruit of nitrogen-fixing trees senesce, the decomposing organic material releases the usable nitrogen into the surrounding soil, enhancing fertility and structure. The high nitrogen content of foliage makes legumes a high-quality



resource for herbivorous insects, enhancing both herbivory and insect abundance (Mattson 1980). Moreover, when legumes fix nitrogen, large amounts of carbon are allocated to this process, reducing the carbon availability for defensive compounds that would deter phytophagous insects (Briggs, 1990). Therefore, leaves with fewer foliar defenses may be more susceptible to damage from a greater abundance and diversity of herbivores, and in turn, provide more food for insectivorous birds. In addition, most herbivorous insects are specialized to feed on particular host plants (Forister et al., 2015); in the Neotropics, Fabaceae are abundant, diverse, and support high numbers of specialized insects. This is particularly true for specialized Lepidoptera (Janzen 1987) which are important components of bird diets due to their high biomass and protein (Razeng and Watson 2015). Although we did not directly quantify insect diversity or abundance on our canopy trees, habitat occupancy by birds is positively related to arthropod biomass (Johnson & Sherry, 2001); it is reasonable to assume tree occupancy is positively related to foraging success as well. It remains unclear whether legumes generally support overall greater quantities of insect prey compared to other canopy trees (but see Johnson, 2000), or whether birds are targeting particular insects of superior nutritional quality that maximize condition and survival.

Increasing the abundance of legumes on shade farms could provide multiple services for farmers in the form of increased crop growth via nitrogen inputs and improved pest control from higher abundances of bird predators. Because of the host-plant specialization that characterizes most herbivorous insects (Forister et al., 2015), planting shade trees that support insects will not simultaneously increase the abundance of pests found on coffee plants (Johnson, 2000); Neotropical insect herbivores are unable to overcome the particular phenolic defenses in coffee foliage. This practice will, however, attract insectivorous birds which could improve pest control on coffee plants (Van Bael et al., 2008; Karp et al., 2013). The popularity of leguminous trees in shade polycultures (Soto-Pinto et al., 2007) may help explain why shade coffee has been documented as attractive habitat for migratory insectivorous birds over other land uses (Greenberg, Bichier, Angon, et al., 1997; Greenberg, Bichier & Sterling, 1997; Perfecto et al., 1996). We offer insect prey availability as a functional explanation for why Fabaceae species are frequently reported to be heavily used by insectivorous birds on coffee farms (e.g., *Enterolobium*: Nell et al., 2018, this study; *Erythrina*: Bakermans et al., 2012; *Inga*: Johnson, 2000; Johnson & Sherry, 2001; Bakermans et al., 2012; Newell et al., 2014; Tarbox, Robinson, Loiselle & Flory, 2018, this study; *Machaerium*: Tarbox et al., 2018). We suggest that wildlife conservation programs should prioritize high inclusion of Fabaceae biomass in coffee certification criteria to improve habitat quality for migratory and insectivorous birds.

Farmers tend to prioritize ecosystem services that enhance coffee production over biodiversity conservation (Cerdán, Rebolledo, Soto, Rapidel & Sinclair, 2012) and already recognize the economic benefits of planting leguminous trees because of their low foliage density, fast growth, and soil fertilization (Soto-Pinto et al., 2007). Moreover, many fast-growing, nitrogen-fixing trees are also

important sources of other commodities such as lumber and fuelwood (Soto-Pinto et al., 2007), and legume flowers attract important insect pollinators to coffee farms that may bolster coffee berry production (Gutteridge & Shelton, 1994). Our work highlights the notion that farmers who increase the prevalence of nitrogen-fixing leguminous trees will also support more habitat for insectivorous birds, which may increase benefits of pest control and maximize total crop yields by the farm. Although fruit trees provide additional crops to sell and thus resources for the community (Davis, Rice, Rockwood, Wood & Marra, 2017; Rice 2011), these short-term benefits, while potentially beneficial during times of low coffee prices or destructive bouts of weather or disease, may not outweigh the loss of long-term economic benefits of increased soil nitrogen and biological pest control provided by birds. Needed are studies that identify to what extent particular tree species, or combinations of tree species, influence pest control and subsequent coffee production, and at what scale such species must be used to supply meaningful gains for the farmer.

Our extrapolated species richness estimates revealed that tree identities that supported high abundance were also predicted to support high species richness, including both Fabaceae (Nicaragua: *G. sepium*, Colombia: *Albizia*) and non-Fabaceae trees (Colombia: *C. alliodora*, Nicaragua: *Ficus*). However, some trees that supported very low abundances were also predicted to support high richness (Nicaragua: *P. sapota*, Colombia: *Eucalyptus*), albeit with high uncertainty. The high turnover in species, but low sampled individuals, may be due, in part, to two factors that were outside the scope of this study. First, individual birds may explore new foraging patches and then revisit locations that maximize prey intake with minimal effort (i.e., optimal foraging, Grubb, 1979). That is, high turnover may be an artifact of exploration and not foraging preference *per se*. Thus, trees within a coffee polyculture may generally support similarly speciose, nested bird communities, albeit at different frequencies. Our study was not able to test whether some tree species supported bird species unique to the local community. Second, diverse polycultures tend to support a higher abundance and diversity of birds, and higher avian predation pressure, compared to monocultures of the same tree species (Nell et al., 2018). Thus, it is possible that birds foraging in low-quality patches (i.e., non-preferred trees), may result from foraging “spillover” (Blitzer et al., 2012; Karp et al., 2013) due to close proximity to high-quality tree species that support greater prey availability. Future research should identify the relative influence of tree diversity, identity and function, in driving direct and indirect tri-trophic interactions.

Going forward, management recommendations for shade-coffee farms, such as Bird Friendly© certification, need to balance both the needs of farmers, as well as local wildlife. Most recommendations have suggested that high floristic diversity (Perfecto et al., 2004), structural complexity (Johnson, Levy, Kellermann & Robinson, 2009), or landscape heterogeneity (Kellermann et al., 2008) drives bird richness. Recommendations for high floral diversity also increase the probability that highly productive food hubs

will be present to attract foraging birds. This may explain why farms dominated by, or solely planted with, productive genera (e.g., *Inga*) tend to support bird numbers similar to those found in diverse, rustic polycultures (Bakermans et al., 2012; Greenberg, Bichier & Sterling, 1997; Johnson, 2000; Johnson & Sherry, 2001; Johnson et al., 2006; Newell et al., 2014). Ecologists should take advantage of the variation of tree diversity within shade polycultures to further investigate the identity of tree species and scale necessary to provide ecological services that translate into meaningful economic gains for farmers and conservation value for resident and migratory birds (Wenny et al., 2011).

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## AUTHOR CONTRIBUTIONS

Conceptualization, DLN, DWT and RAR; Methodology, DLN, KJS and DWT; Investigation, DLN and KJS; Formal Analysis, DLN; Writing—Original Draft, DLN; Writing—Review & Editing, DLN, DWT, KJS and RAR; Funding Acquisition, RAR.

## DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c04k521> (Narango, Tallamy, Snyder & Rice, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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