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Avian Community Density and Distribution Patterns among Nicaraguan Conventional and Organic Shade-Coffee Plantations

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Abstract

We used a distance-sampling survey method and multivariate statistics to obtain a unique estimate of bird species density and seasonal variation in shade-coffee plantations. Our aim was to determine which cultivation practices among plantations contribute most to bird abundance. We conducted avian species counts at 200 points distributed across 10 shade-coffee plantations bordering the lower slopes of the Mombacho Volcano Natural Reserve, in western Nicaragua. We measured vegetation structure (coffee plants and overstory). We used principal components analysis (PCA) among 14 habitat variables to derive a single phyto-geoclimate summary measure (PGSM). We also used PCA to derive an avian abundance summary measure (AASM) from three bird survey variables, which proved to be a good predictor of bird density. We found higher bird species densities (AASM) in organic and traditional polyculture shade coffee plantations whose structurally complex and diverse overstory could be verified by PGSM. However, this finding was true only for birds that were habitat specialists. Our results provide further evidence for promoting organic coffee cultivation practices that maintain a structurally diverse overstory and help retain avian species richness and abundance in coffee plantations.

Keywords

Bird Density, Coffee Cultivation Practices, Monoculture, Organic, Polyculture, Spatial Distribution, Species Richness

1. Introduction

Elevated species richness, abundance and spatiotemporal use of traditional and diverse shade-coffee plantations by resident and migratory birds have been reported throughout the Neotropics [1]-[11]. However, not all coffee plantations provide similar quantities of food, shelter, and anti-predator benefits [12]. Prior research suggests that more diverse and structurally complex organic and traditional polycultures provide for a greater species diversity, abundance, reproduction, survivorship, and dispersal compared to newer, monocultural systems [5] [7] [13]-[18]. Coffee cultivation techniques that affect the structural and floristic diversity of the vegetation (e.g. pruning, application of chemicals) affect faunal populations [8]. Density, basal area and diversity of overstory trees in shade coffee and cacao plantations affect avian diversity and abundance and are often significantly correlated with numbers of forest specialist species [8] [19] [20]. Avian species richness is often the highest in low-intensity management sites near natural forest and forest remnants, and the lowest in high-intensity management sites far from natural forest and forest remnants [7] [21]-[27]. The size of forest remnants and coffee plantations also influences avian species richness, composition and site persistence [7] [19] [28] [29] [30] [31]. Broad-leaf and natural pine forest harbor more habitat specialists and endemics, especially insectivores, relative to coffee plantations [4]. However, shade-coffee plantations often harbor more forest and overwintering generalists, especially insectivores and nectarivores, owing to flowering overstory trees such as *Inga* spp. with their extrafloral nectaries and their ancillary insects, as well as species of open habitats such as pastures and grasslands [4] [20] [30] [32] [33].

In this study, we replicated several previous, mostly qualitative studies (but see exception [34]) to corroborate their results. But our primary goal was to better quantify the link between vegetational and avian ecological parameters due to coffee cultivation practices. To this end, we derived a phyto-geoclimate summary response measure (PGSM) and an avian abundance summary measure (AASM). These two novel metrics quantify vegetation structure and complexity in association with geoclimate variables, and bird density estimates from species richness and abundance measures, respectively. We predicted higher bird species richness and density in the more vegetatively complex organic and traditional polyculture shade coffee plantations than in coffee plantation monocultures and used PGSM and AASM to test this prediction. Our study objectives were, therefore, to: 1) use of multivariate statistics to characterize vegetation structure and complexity, as well as bird density estimates from species richness and abundance measures among organic, conventional, and transitional from coffee plantations; 2) test the statistical model prediction that bird species density/abundance is a positively increasing function of vegetation complexity and 3) determine which of the three coffee cultivation practices contributes most to bird species biodiversity.

2. Materials and Methods

2.1. Study Area and Site Selection

We conducted our study within the Mombacho Natural Reserve, Grenada, Nicaragua (**Figure 1**), by surveying 10 highland shade-grown coffee plantations located between 400 and 800 m.a.s.l. (mean elev. = 558.4 m ± 124.89 SD) within a 7-km radius inside a 6644-ha buffer zone on the lower slopes of the volcano bordering the Reserve (physical, topographical, edaphic, and vegetational characteristics of the volcano are summarized in [35]). All four organic farms studied were certified under the same standards established by the Organic Crop Improvement Association (OCIA International) under a project implemented by the Cooperative League of the United States of America (CLUSA) [35]. The four conventional and two transitional plantations were under a "commercial polyculture" management system (management types, tree species, physiognomy, and husbandry activities are summarized in Philpott *et al.* [10]).

2.2. Habitat Measurements

From each avian survey point (hereafter "plot" as described below), we ran four 25-m transects to the north, south, east, and west to establish a 25-m plot radius encompassing ≈ 0.2 ha in which 14 vegetation-habitat (phyto-geoclimate) variables were measured (**Table 1**). Because the average plantation was about 62 ha in size, the average number of points was 20 per plantation and the overstory was homogeneous in each plantation, our sampling area is representative of the area used by the birds.

Elevation was measured using an altimeter into four strata (≤10 m, 11 - 20 m, 21 - 30 m, >30 m); we weighted each stratum by tree density to estimate total leaf volume (≤10 m = density × 1; 11 - 20 m = density × 2; 21 - 30 m = density × 3; >30 m = density × 4) [10]. We measured maximum coffee plant height with a telescopic meter stick and height of the four tallest coffee plants measured along each of the four cardinal transects. We estimated coffee plant density by counting all vertical coffee stems within an approximate 1.5-m lateral distance along the length of each transect [7]. We measured percent overstory cover with an ocular tube at 12 locations along each transect, starting 1 m from center point and then every 2 m along transects. We pointed the tube vertically into the shade overstory at the center of each point. We measured diameter of all stems ≥ 3 cm 1.3 m from the base (DBH); and counted the number of stems < 3 cm in 1.7-m wide belt transects in the four cardinal directions from the plot center. We recorded the total number of species of overstory trees within the plot; trees were

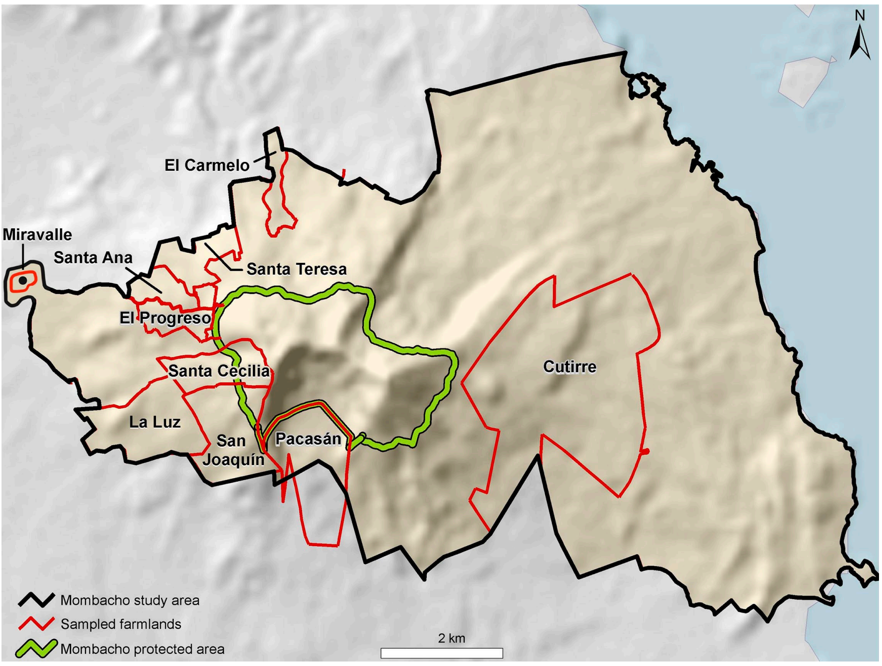


Figure 1. Ten, mid-elevation (mean = 558.4 m.a.s.l.), shade coffee plantations bordering the lower slopes of the Mombacho Volcano Natural Reserve in western Nicaragua.

Table 1. Results of principal components analysis of geo-climate and vegetation structure in 10 shade-coffee plantations bordering the lower slopes of the Mombacho Volcano Natural Reserve, Nicaragua (1998-1999). Coefficients for the 1st three principal components (eigenvectors) are given (n = 200 survey plots).

Vegetation-Habitat Variable	PC1	PC2	PC3
Elevation (m)	−0.1303	0.7819	0.126
Average wind speed	−0.2298	0.5954	0.0033
Arcsine-square root (% cloud cover)	0.2381	0.5725	0.1328
Number of trees/plot	−0.135	0.0578	−0.6766
Mean tree height	0.7419	−0.04	0.582
SD tree height	0.9111	−0.2329	−0.0348
Maximum tree height	0.9106	−0.1537	−0.0646
Mean (No. of tree-height strata per plot)	0.6639	−0.0368	0.6264
Number of tree species per point	0.0657	−0.5402	−0.5014
Arcsine-square root (% canopy cover)	0.2584	−0.6037	0.1203
Mean height of coffee plants/plot	0.1062	−0.3513	0.5144
Mean (total leaf volume)	−0.3305	0.2508	0.6085
Arcsine-square root (% flowering)	−0.0634	0.3289	−0.1422
Arcsine-square root (% with fruit)	0.0412	−0.3638	0.0277

identified to species where possible, whereas 17 were classified simply as "morpho" species. We calculated the maximum height of overstory shade trees 100-m from their base with a clinometer. We measured total leaf volume of trees separated to determine if foliage (leaves only) was present or absent at a point. To meet the criteria of foliage present, at least 25% of the tube's sighting area had to be covered by foliage. We calculated average percent overstory cover for each of the two-hundred 0.2-ha plots ([(3.14 × 25 m^2)] × 0.0001). We recorded fruit and flower abundance of overstory trees on a scale from 0 to 4, representing percentages (0%, 25%, 50%, 75%, 100%) within four imaginary quadrants superimposed on the tree's canopy, *i.e.*, 0% fruit when all four quadrants were empty, 100% when fruit was observed in all four quadrants; these measures enabled a comparison of avian density in relation to seasonal variation.

2.3. Avian Surveys

We conducted 10-min, unlimited radius surveys at 200 points that were spaced ca.100 m apart and distributed randomly across the 10 shade-coffee plantations. Only detections from within a plantation were recorded. We surveyed 83, 63 and 54 plots in 4 organic, 4 conventional, and 2 transitional plantations, respectively (described and tabular summaries in [35]). Each point was surveyed between sunrise and 1030 hr (CST: Central Standard Time) in good weather conditions (no rain or excessive wind) once in each of four periods: 1) 25 February - 1 March 1998; 2) 22 July - 5 August 1998; 3) 10 November - 21 November 1998; and 4) 16 March - 14 April 1999. Two to four observers surveyed different points in each period. To eliminate double-counting of vociferous species such as parrots and jays, we conducted a means comparison test [7] by comparing mean detections per point at 100 vs. 200 m (results were: $P = 0.874$). Data were truncated in the outer bins, further eliminating the possibility of double counting highly vocal species. Observers recorded the number of individuals of all species detected during the count, estimated distance to detected birds or to the center of the cluster, *i.e.*, groups of two or more [36], and categorized the observation as occurring in the coffee plants within the understory or the shade-tree overstory. The chronological order of plot visits was randomized to minimize temporal bias in bird detectability throughout the morning. Aerial birds were not recorded unless they alighted in vegetation during the 10-min count. Because cloud cover can be a major hindrance to avian surveys at high elevation cloud forest sites, we estimated percent cloud cover on a scale from 0 - 100 in increments of 25 (0 = clear skies, 100 = overcast). Similarly, high winds can drown out bird vocalizations on exposed slopes. Therefore, we recorded wind speed using the Beaufort scale (http://www.spc.noaa.gov/faq/tornado/beaufort.html).

2.4. Avian Species Richness, Abundance and Density Estimation

We compared species richness and abundance by ANOVA statistical methods among plantations grouped by the three coffee cultivation practices: Conventional, Organic and Transitional. We estimated bird density per hectare using distance models [37] for species with ≥30 observations in program Distance 6.0 [36]. This method accounts for birds present but not detected by fitting a detection function, P, to observed counts for a given distance from the observer. We filtered the data by species and distances ≥ 0 to account for missing distance values. We truncated data to detections with distances ≤ 40 m and grouped observations by 0 - 10 m, 10 - 20 m, 20 - 40 m, and 40 - 60 m, except for raucous species that were audible at long distances: Yellow-throated Euphonia (*Euphonia* *hirundinacea*) and Hoffmann's Woodpecker (*Melanerpes hoffmannii*) (truncated at 85 m) and Keel-billed Toucan (*Ramphastos sulfuratus*) (truncated at 100 m). The truncation distance for each species was determined by the maximum distance at which the species was audible, except for the toucan, which, although audible at distances greater than 100 m, was truncated at our designated maximum distance of 100 m. We did not include birds detected more than 40 m in the direction of points behind us as not to count the same individuals in areas of overlap. We used a half-normal detection function with a cosine series expansion to fit the data. Because each point was visited four times, we included survey effort as a multiplier, which allowed us to divide density by effort. Because some species, e.g., parrots, were often detected in groups, designated as clusters, we included the total number of individuals detected per point at each distance and specified the size-bias regression method to estimate group size. For species with >50 detections, we compared support for the global model internal to the Distance 6.0 software, with models including observer, period, and observer + period as covariates in the multiple covariate distance sampling (MCDS) engine. The most supported model had the lowest Akaike's Information Criterion (AIC_c) value (tabulated as $\Delta AIC_c = 0$). We report ΔAIC_c from models evaluated for each species (**Table 2**). For species with fewer than 50 detections, we estimated density per hectare using a global detection function. We report detection probability (*P*), effective detection radius (EDR), cluster size, and density for each management type based on the top model (**Table 3**).

Table 2. Support for candidate models for 14 species with >50 detections from point counts in Nicaragua, 1998-1999. Shown here are number of parameters (K) and ΔAIC_c (difference in AICc from the most supported model to the evaluated model; ΔAIC_c for top model is 0) for each model. The global model derived a global detection function; observer, period, and observer + period models derived the detection function using the respective covariate (see text). Species codes are defined in the Appendix.

	Global		Observer		Period		Observer + Period	
Species	K	ΔAICc	K	ΔAICc	K	ΔAICc	K	ΔAICc
CALFOR	1	21.72	4	6.70	4	9.17	7	**0.00**
CANMOD	1	7.50	5	**0.00**	4	11.48	8	2.44
CHILIN	2	15.47	4	**0.00**	4	17.46	7	2.23
EUPHIR	1	5.27	5	1.62	4	9.12	8	**0.00**
HYLDEC	1	**0.00**	4	1.88	4	4.37	7	7.85
HYLELI	1	16.45	4	**0.00**	4	15.82	8	0.63
MELHOF	2	43.66	5	14.17	5	32.26	8	**0.00**
MYITUB	2	7.20	4	**0.00**	5	10.40	7	1.82
OREPER	1	**0.00**	4	4.57	3	2.59	6	7.31
PSAMON	1	22.92	5	0.02	4	21.76	7	**0.00**
RAMSUL	1	2.17	4	**0.00**	4	5.62	-	-
SETPET	1	14.44	4	1.18	3	6.14	6	**0.00**
THRPLE	2	27.05	5	12.05	5	17.21	8	**0.00**
TOLSUL	2	8.65	4	4.09	4	5.01	6	**0.00**

Table 3. Number of observations (N), detection probability (*P*), effective detection radius (EDR), mean cluster size, and density per hectare by management system (95% CI) from point counts in Nicaragua, 1998-1999. We surveyed 372, 332, and 96 points in conventional, organic, and transitional farms, respectively.

					Density		
Species	N	*P*	EDR	Cluster Size	Conventional	Organic	Transition
AMAALB	26	0.30	32.67	2.38 (1.56 - 3.64)	0.05 (0.02 - 0.12)	0.05 (0.02 - 0.12)	0.02 (0.00 - 0.09)
AMARUT	32	0.04	12.52	1.06 (1.00 - 1.15)	0.23 (0.13 - 0.43)	0.17 (0.08 - 0.35)	0.21 (0.08 - 0.57)
AMASAU	44	0.05	12.85	1.23 (1.06 - 1.43)	0.28 (0.16 - 0.48)	0.33 (0.19 - 0.58)	0.16 (0.05 - 0.49)
CALFOR	210	0.24	29.14	1.68 (1.52 - 1.86)	0.43 (0.32 - 0.59)	0.57 (0.42 - 0.76)	0.55 (0.33 - 0.90)
CANMOD	230	0.34	35.08	1.18 (1.12 - 1.24)	0.16 (0.12 - 0.23)	0.26 (0.20 - 0.35)	0.25 (0.16 - 0.40)
CHILIN	235	0.37	36.43	1.34 (1.24 - 1.44)	0.18 (0.13 - 0.25)	0.34 (0.26 - 0.44)	0.29 (0.17 - 0.51)
EUPHIR	139	0.11	28.64	1.88 (1.65 - 2.13)	0.33 (0.17 - 0.65)	0.35 (0.19 - 0.64)	0.18 (0.06 - 0.54)
HYLDEC	121	0.23	28.52	1.27 (1.16 - 1.40)	0.20 (0.13 - 0.30)	0.22 (0.15 - 0.30)	0.18 (0.09 - 0.36)
HYLELI	67	0.04	12.66	1.15 (1.03 - 1.28)	0.48 (0.28 - 0.80)	0.43 (0.24 - 0.79)	0.28 (0.07 - 1.04)
MELHOF	265	0.51	60.96	1.15 (1.11 - 1.21)	0.08 (0.06 - 0.10)	0.07 (0.06 - 0.10)	0.09 (0.06 - 0.16)
MOMMOM	33	0.65	48.30	1.21 (1.05 - 1.40)	0.02 (0.01 - 0.03)	0.02 (0.01 - 0.05)	---
MYITUB	108	0.19	26.13	1.34 (1.15 - 1.57)	0.22 (0.14 - 0.34)	0.29 (0.18 - 0.46)	0.18 (0.07 - 0.50)
OREPER	105	0.10	19.26	3.11 (2.58 - 3.76)	1.25 (0.85 - 1.84)	0.66 (0.41 - 1.06)	1.48 (0.82 - 2.65)
PSAMON	282	0.40	38.15	1.97 (1.55 - 2.51)	0.43 (0.34 - 0.54)	0.38 (0.29 - 0.49)	0.13 (0.06 - 0.29)
PTETRO	37	0.24	29.24	1.97 (1.32 - 2.94)	0.10 (0.05 - 0.19)	0.08 (0.04 - 0.17)	0.08 (0.03 - 0.23)
RAMSUL	55	0.38	61.32	1.31 (1.17 - 1.46)	0.02 (0.01 - 0.03)	0.03 (0.02 - 0.05)	---
SETPET	285	0.09	18.17	1.56 (1.39 - 1.75)	1.15 (0.87 - 1.52)	1.58 (1.21 - 2.05)	1.62 (1.04 - 2.52)
THRPLE	587	0.27	31.43	1.25 (1.21 - 1.30)	0.72 (0.60 - 0.86)	0.72 (0.60 - 0.86)	0.84 (0.62 - 1.16)
TOLSUL	66	0.42	38.93	1.08 (1.01 - 1.14)	0.05 (0.02 - 0.10)	0.06 (0.02 - 0.14)	0.01 (0.00 - 0.11)
TROMEL	31	0.28	31.91	1.39 (1.01 - 1.90)	0.06 (0.03 - 0.11)	0.04 (0.02 - 0.09)	0.01 (0.00 - 0.07)
VIRFLD	36	0.17	24.96	2.08 (1.34 - 3.23)	0.13 (0.06 - 0.24)	0.13 (0.06 - 0.26)	0.15 (0.06 - 0.38)

2.5. Statistical Design and Modeling

To examine patterns of seasonal bird density per hectare, we report density estimates for each species by period (Table 4), which are explained below.

Habitat variables not otherwise quantified on a measurement scale, but estimated as percentages (e.g., canopy cover and trees with flowers or fruits) were normalized via the arcsine-square root transformation, a common variance-stabilizing technique.

From the bird species observation data, we selected only those species with >= 30 detections for further analysis. These species were considered to have sufficient sample size for comparison. The intent of the design was to estimate the effects of shade-coffee cultivation practice (management system) and sampling period on a bird species diversity-richness response measure using simple linear regression (SLR) [38]. Species with a larger number (≥50) of detections allowed us to model the co-variation in this response with phyto-geoclimate variables per cultivation practice as well using the method of analysis of covariance (ANCOVA) [38].

Table 4. Bird density (95% CI) per hectare estimated using distance-based models to account for imperfect detection for each survey period (Period 1: 25 February - 1 March 1998; Period 2: 22 July - 5 August 1998; Period 3: 10 November - 21 November 1998; and Period 4: 16 March - 14 April 1999) from point counts in Nicaragua, 1998-1999. We surveyed 200 points per period.

		Density			
Species	N	Period 1	Period 2	Period 3	Period 4
AMAALB	26	0.06 (0.03 - 0.14)	0.02 (0.01 - 0.07)	0.03 (0.01 - 0.09)	0.08 (0.04 - 0.19)
AMARUT	32	0.18 (0.08 - 0.40)	0.23 (0.10 - 0.50)	0.15 (0.07 - 0.36)	0.26 (0.12 - 0.54)
AMASAU	44	0.18 (0.08 - 0.40)	0.10 (0.04 - 0.28)	0.08 (0.03 - 0.23)	0.78 (0.48 - 1.28)
CALFOR	210	0.84 (0.65 - 1.09)	0.36 (0.26 - 0.51)	0.32 (0.21 - 0.46)	0.49 (0.36 - 0.65)
CANMOD	230	0.25 (0.19 - 0.34)	0.27 (0.20 - 0.38)	0.21 (0.16 - 0.29)	0.12 (0.08 - 0.19)
CHILIN	235	0.36 (0.27 - 0.48)	0.40 (0.30 - 0.52)	0.12 (0.08 - 0.19)	0.16 (0.11 - 0.24)
EUPHIR	139	0.06 (0.03 - 0.14)	0.50 (0.29 - 0.84)	0.40 (0.24 - 0.68)	0.31 (0.18 - 0.54)
HYLDEC	121	0.07 (0.03 - 0.13)	0.23 (0.14 - 0.37)	0.36 (0.25 - 0.53)	0.15 (0.10 - 0.25)
HYLELI	67	0.96 (0.62 - 1.49)	0.16 (0.07 - 0.35)	0.23 (0.10 - 0.54)	0.39 (0.22 - 0.70)
MELHOF	265	0.09 (0.07 - 0.11)	0.08 (0.06 - 0.10)	0.07 (0.05 - 0.09)	0.08 (0.06 - 0.10)
MOMMOM	33	0.06 (0.03 - 0.12)	0.00 (0.00 - 0.01)	---	0.01 (0.00 - 0.02)
MYITUB	108	0.21 (0.12 - 0.36)	0.27 (0.16 - 0.44)	0.31 (0.20 - 0.49)	0.18 (0.11 - 0.29)
OREPER	105	0.94 (0.58 - 1.53)	---	2.64 (1.82 - 3.83)	0.55 (0.30 - 1.01)
PSAMON	282	0.52 (0.41 - 0.66)	0.28 (0.20 - 0.38)	0.30 (0.23 - 0.40)	0.38 (0.29 - 0.50)
PTETRO	37	0.16 (0.08 - 0.30)	0.06 (0.02 - 0.16)	0.02 (0.00 - 0.07)	0.13 (0.07 - 0.25)
RAMSUL	55	0.03 (0.02 - 0.05)	0.03 (0.02 - 0.05)	0.01 (0.00 - 0.03)	0.01 (0.00 - 0.02)
SETPET	285	1.53 (1.20 - 1.96)	---	2.13 (1.69 - 2.69)	1.86 (1.47 - 2.36)
THRPLE	587	0.53 (0.42 - 0.67)	1.04 (0.88 - 1.23)	0.65 (0.53 - 0.79)	0.71 (0.59 - 0.85)
TOLSUL	66	---	0.10 (0.06 - 0.20)	0.04 (0.02 - 0.08)	0.04 (0.02 - 0.09)
TROMEL	31	0.03 (0.01 - 0.09)	0.06 (0.03 - 0.14)	0.01 (0.00 - 0.05)	0.09 (0.04 - 0.17)
VIRFLD	36	0.03 (0.01 - 0.11)	0.19 (0.09 - 0.38)	0.17 (0.08 - 0.36)	0.13 (0.06 - 0.29)

The multivariate method of principal components analysis (PCA) [39] was used as a dimensionality reduction tool among the 14 phyto-geoclimate variables (*i.e.* dimensions). Each of the 14 principal components is ordered in magnitude (PC1, PC2, …, PC14) in accounting for the largest to the smallest percentage of total variation explained among the 14 original variables. We employed the first principal component (PC1) exclusively as a univariate summary measure. It characterizes in one dimension the largest amount of environmental information at each of the 200 avian sampling plots among the 10 coffee plantations. This method partitions the information in a correlation matrix comprising ${}_{14}C_2 = 91$ combinations of pairwise correlations among the phyto-geoclimate variables [40]. The first eigen value of that matrix is also an indication of the number of dimensions represented in our phyto-geoclimate summary response measure (PGSM) or PC1. Unlike the foliage height diversity (FHD) measure of MacArthur and MacArthur [41], PGSM characterizes the habitat on a more continuous scale instead of just 2 to 4 height classes.

In addition, multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) [39] were used to discriminate differences among the vegetation-habitat characteristics of shade-coffee plantations grouped by organic, conventional, and transitional coffee cultivation practices. MANOVA determined the strength of evidence in favor of the hypothesis that the multivariate phyto-geoclimate measurement response vectors differ significantly among the three coffee cultivation practices [39]. DFA also identifies those phyto-geoclimate variables that contribute most to the discrimination among these three groups of measurements, that is, among their multivariate mean vectors called centroids [42].

DFA was conducted via a stepwise forward-selection procedure [42]. Tree species richness and diversity estimates were obtained using EstimateS 8.2 software [43].

To summarize bird abundance at each of the 200 sampling plots, we performed a similar PCA using three bird abundance variables: total bird count, mean distance to detection, and the standard deviation of detection distance. This PC1 is referred to as the avian abundance summary measure (AASM). Density estimates using the Distance 6.0 software [36] for each of 21 species were also calculated for each of the four sampling periods, for each coffee cultivation practice. Shannon-Wiener and Simpson's diversity indices [44] were used to compare species diversity among management types.

We used SLR by the standard least squares method to compare the AASM scores for bird abundance to the calculated bird density measurements among the four sampling periods for all bird species. SLR was also used to determine the dependence, if any, of AASM on PGSM. Since there is measurement error in both, an orthogonal regression [45] was also performed for an alternate and perhaps more accurate explanation of the relationship between the two summary measures.

The AASM was further aggregated by sampling plot for each of two species groups—one group with relatively steep (large valued) SLR slopes between AASM vs bird density and another group with relatively shallow (small valued) SLR slopes.

We used an analysis of covariance (ANCOVA) model [38] to discover the effects of coffee cultivation practices on the AASM after accounting for its expected relation with the PGSM. All statistical analyses were performed using the JMP® [46].

3. Results

3.1. Vegetation and Habitat Analysis

We found that tree species diversity is higher under organic and transitional management types compared to conventional. The Shannon-Wiener diversity index was highest in organic farms (organic = 2.44, conventional = 2.28, and transitional = 2.29). Although the Simpson's Diversity index was higher in transitional farms, it is more similar in magnitude to organic than conventional farms (organic = 5.54, conventional = 5.01, and transitional = 5.67). All reported diversity values are average calculations among census plots within management types.

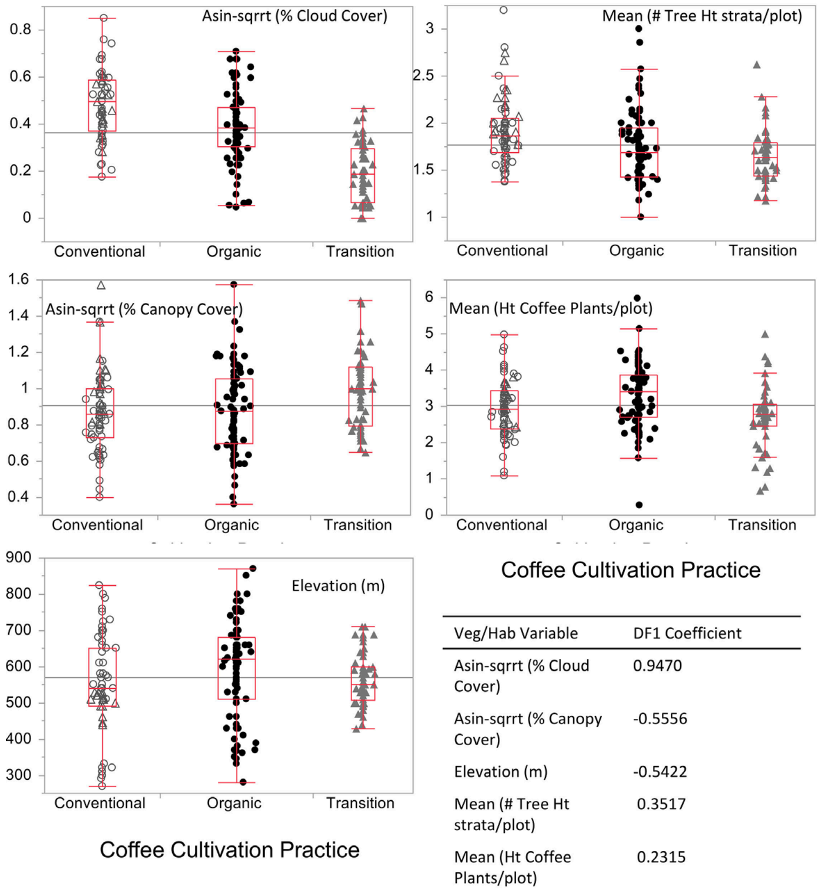
PCA of the 14 phyto-geoclimate variables showed that PC1 (PGSM hereafter) accounted for 27% of the total variation among these variables while PC2 and PC3 each explained an additional 18% and 9.4%, respectively (**Table 1**). The four variables in PC1 with the largest eigenvector coefficients and therefore greatest contributing information to the PGSM were mean tree height, SD tree height, maximum tree height, and mean number of tree-height strata per plot (**Table 1**). The cumulative magnitude of the three largest and corresponding eigen values was 7.6 indicating that almost 8 of the 14 phyto-geoclimate measurement dimensions could be summarized from the 1st three PCs, approximately 4 dimensions in the 1st PC (PGSM) alone.

A subset of five phyto-geoclimate variables were selected by the stepwise DFA modeling method that account for the statistically significant ($P < 0.001$) MANOVA differences among the three coffee cultivation practices. *These variables are* percent cloud cover, percent canopy cover, elevation, mean number of tree height strata per plot, and mean height of coffee plants per plot. Measurement data for these five variables are summarized in **Figure 2** by coffee cultivation practice.

MANOVA showed a significant difference (Wilk's lambda = 0.338, $\sim F_{28,368} = 9.46$, $P < 0.001$) among the three coffee cultivation practices corresponding to differences among the 14 phyto-geoclimate variables. The concomitant DFA results indicate significant group (cultivation practice) separation among the 200 avian sample locations. This is illustrated in a scatter-plot of the 1st vs. 2nd discriminant functions (DF1 or DF2), or canonical variate scores for each group (**Figure 3**). The most important variables that contribute to the discrimination among the coffee cultivation practices (group centroids) in DF1 were percent cloud cover (0.9192), mean number of tree-height strata per plot (0.7208), percent canopy cover (−0.5302), and elevation (−0.4640). Those contributing most to DF2 were mean coffee plant height (−0.8404), SD of tree height (−0.6510), mean total leaf volume/tree height stratum (−0.6340), and elevation (0.6257).

3.2. Bird Species Density vs. Coffee Cultivation Practice

We documented 6110 audio-visual detections of 98 bird species, of which 13 were identified only to genera (Appendix). The average number of species (richness) among the two transitional plantations (avg. = 57) and the four organic plantations (avg. = 51) was greater than that of the four conventional plantations (avg. = 47), although not significantly significant ($p > 0.05$) (**Table 5**). All bird species were more abundant in the overstory than in coffee plants, except for two species of wren, *Cantorchilus modestus* and *Thryophilus pleurostictus*.



Veg/Hab Variable	DF1 Coefficient
Asin-sqrrt (% Cloud Cover)	0.9470
Asin-sqrrt (% Canopy Cover)	-0.5556
Elevation (m)	-0.5422
Mean (# Tree Ht strata/plot)	0.3517
Mean (Ht Coffee Plants/plot)	0.2315

Figure 2. Boxplots for 5 of the 14 vegetation/habitat variables with the largest (absolute value) 1st Discriminant Function (DF1) coefficients in order of entry to a stepwise DF analysis, which show the relative importance of each to the discrimination among groups of sampling plots corresponding to the three shade-coffee cultivation methods.

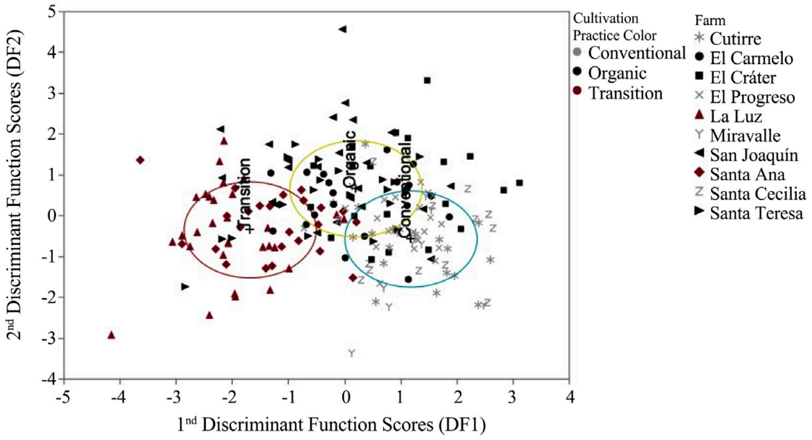


Figure 3. A scatterplot of the scores of the first two discriminant functions (DF1 and DF2) obtained by the stepwise DFA method. This figure distinguishes the groups of farms that use each of the three coffee cultivation practices (marker color) as well as the farms themselves (marker symbols)—see legends. In addition, the group centroids (DF1 mean coordinate, DF2 mean coordinate) is signified by the + marker. The ellipses represent the areas containing 50% of the scores for each DF group.

Table 5. Total number of species, detections, and relative abundance of birds per farm and management type.

Cultivation Practice	Conventional				Transitional		Organic			
Farm	Cutirre	El Progreso	Miravalle	Santa Cecilia	La Luz	Santa Ana	El Carmelo	Pancasán	San Joaquín	Santa Terresa
Total Detections	940	465	213	538	851	683	679	679	546	516
Total Species	68	40	35	43	58	56	57	50	47	48
Relative Abundance (avg. detects./species)	13.82	11.63	6.09	12.51	14.67	12.20	11.91	13.58	11.62	10.75

The PC1 (AASM hereafter) from this PCA explained 82% of the variation among its three constituent variables, viz., bird count, mean distance to the detected individual/cluster, and the standard deviation of that detection distance. The AASM also summarized ~2.5 of the 3 dimensions (see Methods above). The summarized information constituting this dimensionality-reduced latent variable (AASM) positively correlated with the bird species density estimates obtained by the DISTANCE 6.0 software. SLR examined this relationship between species density and AASM among periods. Of the 21 most frequently detected (≥50) bird species, five have similar and more steeply (large) positive SLR slopes in the graph of bird density against AASM (**Figure 4(A)**) when compared to the remaining 16 species (**Figure 4(B)**) with less steep (small) but positive slopes. SLR slopes of both species groups were statistically significant ($P < 0.001$). After examination of these two species groups, the former comprises five habitat generalists, whereas the latter comprises 16 habitat specialists.

Bird densities (per hectare) for the subset of 21 species with ≥50 detections varied among dietary guilds (**Figure 5(A)**) and in relation to vegetation strata, seasonality, and tree reproductive phenology (spring and fall flowering and fruiting peaks) (**Figure 5(B)**).

The entire data set was then re-aggregated to produce a new response vector from three variables, viz., total count, mean detection distance, and the standard deviation of detection distance, for each of the two species groups defined in **Figure 4**. A different PCA was performed to produce a separate AASM for each species group (habitat generalist and specialist, or AASM$_g$ and AASM$_s$) among sampling plots, plantations, and periods. The AASM$_g$ and AASM$_s$ coefficients of the three variables that comprise them were similar for each species group (0.4435, 0.6473, 0.6200 and 0.3745, 0.6711, 0.6398, respectively). Each of these two new response variables also explained 75% and 69% of the total variation and summarized 2.5 and 2.1 of the 3 response dimensions for each species group, respectively.

A 2-way ANOVA model was fit to the surrogate density estimate AASM$_g$ or AASM$_s$ as a function of coffee cultivation practice and period main effects, and included an interaction effect. For the generalist species group, the results showed no effect due to cultivation practice, but a significant period effect ($P <$

0.001) due to low bird counts for these species in period 2 (**Figure 6(A)**). Neither was there a significant cultivation practice by period interaction effect. In contrast, the specialist species group showed a significant ($P < 0.001$) cultivation practice effect (**Figure 6(B)**), but no period or interaction effect.

Subsequent ANCOVA models were also fit separately for $AASM_g$ and $AASM_s$ to test for a cultivation practice effect after accounting for the relationship with the covariate (*i.e.*, the PGSM). Results showed no significant regression relation between the $AASM_g$ vs. PGSM scores, or any evidence that the slope of this relation differs from zero among cultivation practices (**Figure 7(A)**). However, results for the habitat specialists showed a significantly ($P = 0.008$) positive overall regression relation between the $AASM_s$ vs. PGSM. In addition, at the average value of the covariate (vertical dotted line at zero **Figure 7(B)**), the least squares mean bird abundance/density was significantly higher in organic coffee plantations, than in either conventional or transitional coffee plantations ($P = 0.07$ and $P = 0.005$, respectively). Note that we regard a 7% chance of Type I error as indistinguishable from 5%.

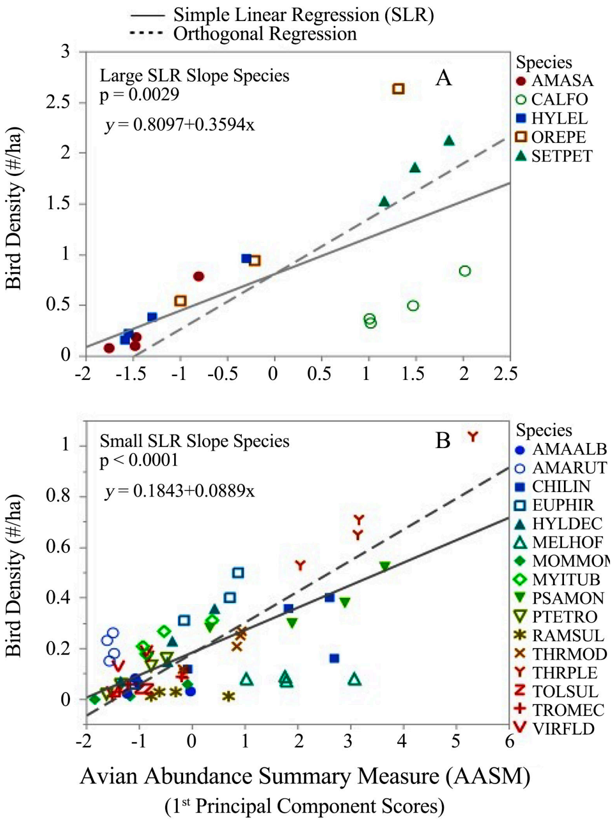


Figure 4. Regression analyses showing the statistically significant and positive relationship between bird density per hectare (sensu DISTANCE 6.0 software calculation) and the Avian Abundance Summary Measure (AASM) or 1st principal component scores (PC1) from 3 bird abundance measures (see text). Five species (A) have a larger SLR slope than the remaining 16 species (B). Orthogonal fits assume measurement error in both variables.

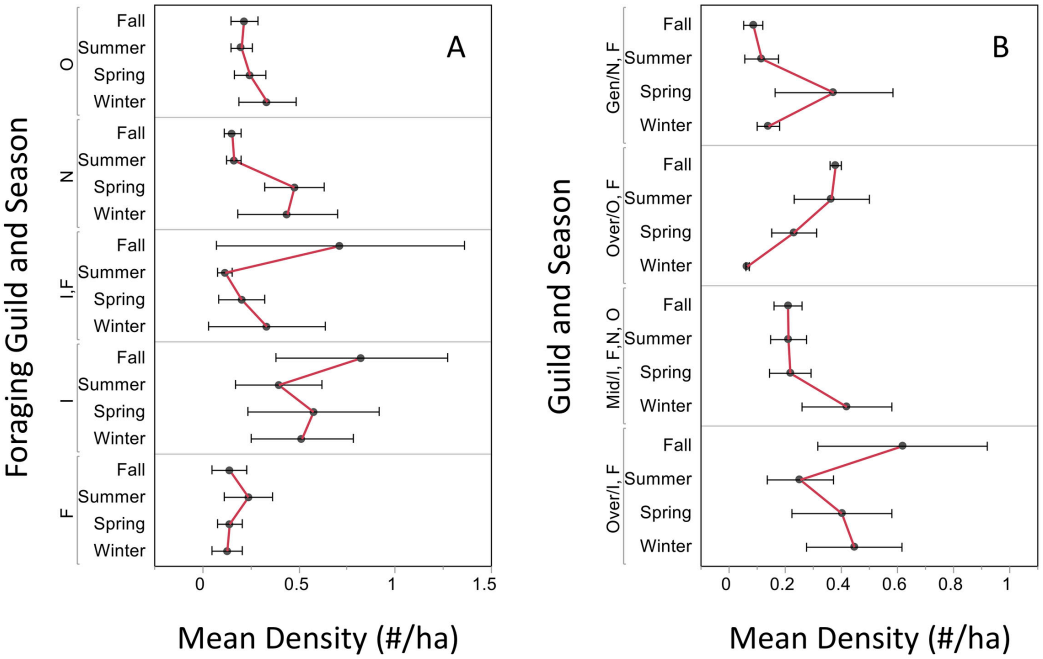


Figure 5. Density of birds per hectare by: (A) dietary guild; and (B) habitat strata in relation to spring and fall flowering and fruiting peaks in Mombacho shade-coffee overstory. Habitat strata: understory, shrub, mid-canopy and trunk specialists (Mid), overstory specialists (Over), strata generalists (Gen). Dietary guilds: frugivore (F); insectivore (I); nectarivore (N); ominivore (O). "Winter" (25 February - 1 March 1998); "spring" (16 March - 14 April 1999) "summer" (22 July - 5 August 1998); "fall" (10 November - 21 November 1998).

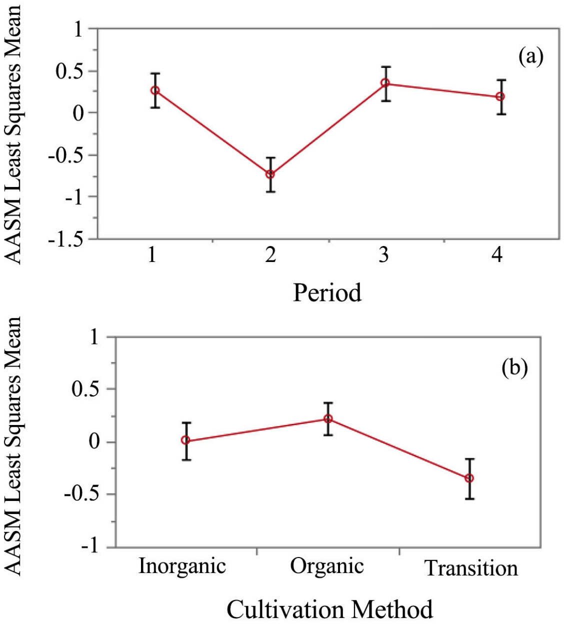


Figure 6. Least squares means (with standard error bars) for the AASM measure of bird density (see text) as a function of a 2-way ANOVA model using sampling period and coffee cultivation method as main effects, with interaction. Statistically significant ($p < 0.05$) main effect results are presented for the large SLR slope (A) and small SLR slope (B) bird species. See **Figure 4** for SLR slope illustration.

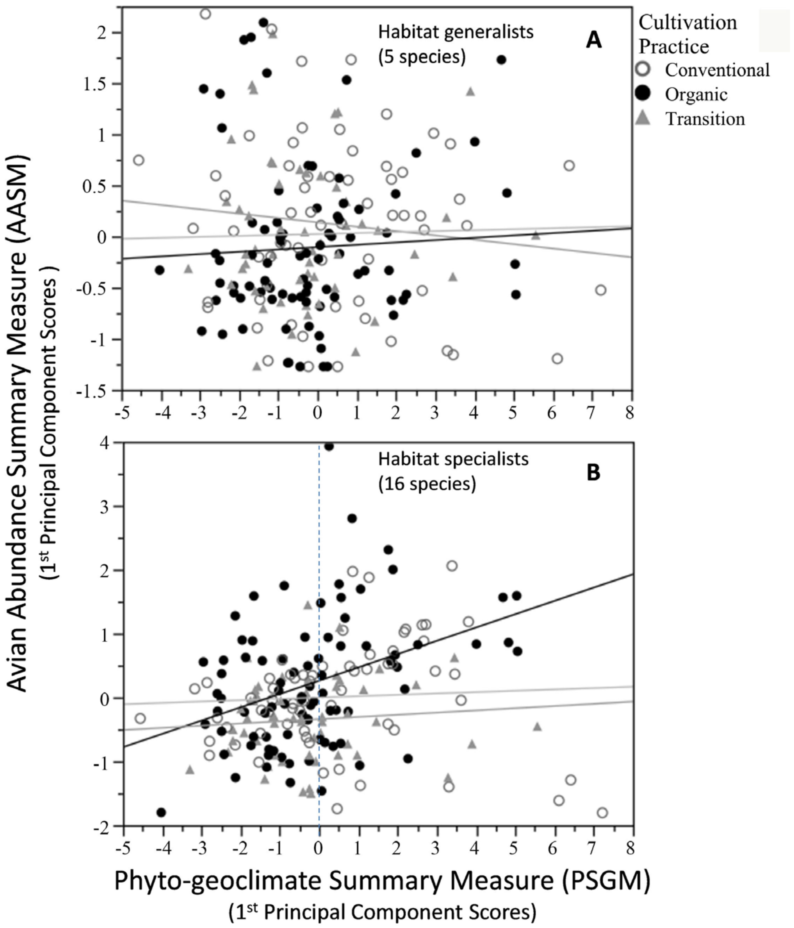


Figure 7. Simple linear regression fit of the dimensionality reduced summary measures (PC1 scores) for bird abundance (AASM) vs vegetation/habitat (PGSM) variables. (A) Habitat generalist species show no significant slopes regardless of cultivation practice. (B) Habitat specialist or discriminating species show significant ($P < 0.001$) and positive slope in organically cultivated coffee farms.

4. Discussion

4.1. Habitat Factors Affecting Avian Communities

We have shown by the methods of PCA and DFA, that diverse vegetation and complex native canopy structure in organic shade-coffee plantations result in greater avian species diversity, richness, abundance, and composition as reported in previous studies [15] [18] [47]. More importantly, we have added to the contemporary collective knowledge of bird abundance in coffee plantations by deriving two novel metrics (PGSM and AASM) that quantify species densities among coffee management systems, seasonally and under disparate climatic conditions. The phyto-geoclimate summary measure or PGSM represents the aspects of vegetation structure and canopy composition that are positively related to greater avian habitat stratification and demonstrates that coffee overstory is similar to natural forest harbors of greater bird diversity, abundance [10] [26] [27] [35] [47] [48] [49] [50] and density [51] [52].

DF1 represents a measure of bird habitat type "positioning" (**Figure 2**). Positive DF1 coefficients meant that as percent cloud cover and mean number of tree height classes increased, the DF scores increased. But there is much overlap in a large range of DF1 scores among farms with organic and conventional practices (**Figure 3**). This figure shows that farms under transitional practices separate from organic and conventional farms by their lower DF1 scores. In both cases, these multivariate summary measures indicate that the organic farms were intermediate to the transitional and conventional farms. Originally, we expected that these phyto-geoclimate results from transitional farms would be intermediate between organic and conventional farms. This is somewhat puzzling and suggests there are possibly additional, unstudied, "lurking" variables contributing to the significant and positive relation between the AASM and PGSM among farms under organic cultivation practices,

4.2. Factors Affecting Bird Species Richness, Abundance and Density

Bird density estimation using methods that incorporate detection probability, such as the distance sampling method [37], is generally viewed with preference to relative abundance measurement only; albeit, results are dependent on meeting strict model assumptions, which are often hard to achieve. Also, by our not including birds detected more than 40 m in the direction of already surveyed plots behind us, our bird densities (per hectare) may be slightly lower.

However, our use of PCA produced a dimensionality reduced measure (AASM) of bird abundance per sampling plot that also yielded predictive information about bird density estimates from distance sampling calculations. Although this relationship has only moderate precision ($R^2 \cong 0.50$), it is nonetheless significantly positive. The slope of this relation was bird species, dependent as illustrated in **Figure 4**, and was markedly different between two groups of bird species, which groups corresponded to habitat generalists and specialists.

Among the five species with steep slopes for bird density vs. AASM, two are Nearctic-Neotropical migrant warblers, Yellow Warbler *Setophaga petechia* (SETPET) and Tennessee Warbler *Oreothlypis peregrina* (OREPER) wintering in Nicaragua. A third is a resident corvid, the White-throated Magpie Jay *Calocitta formosa* (CALFOR). All three species are well known habitat and resource generalists on their breeding grounds and, especially, throughout their wintering ranges (the two migrants) where they often occur from sea level to over 2000 m.a.s.l. (1250 m.a.s.l. for the jay) [53] [54] [55].

The two migratory species (SETPET, OREPER) had higher densities than any of the resident birds as expected because the study site lies within the Central Americas Flyway used by Nearctic-Neotropical migrants, many of whose numbers greatly increase during fall and spring passage through Nicaragua.

Note that the greater percentage of detections for SETPET and OREPER in conventional, rather than either organic or transitional plantations (~50% in conventional, ~30% in organic, and ~20% in transitional) was not consistent with our expectation. It is likely due to the concentration of "bird friendly" extrafloral nectaries and associated insects of the leguminous dominated overstory, e.g., *Inga, Gliricidia* and *Erythrina* spp., in conventional plantations [5] [8] [20] [31] [32] [33] [56] [57] [58].

The remaining two species of habitat generalists are hummingbirds: Steely-vented Hummingbird *Amazilia saucerrottei* (AMASAU) and Blue-throated Goldentail *Hylocharis eliciae* (HYLELI). Both are principally nectarivores that forage in diverse habitats ranging from open areas, e.g., agricultural lands and forest edge, to cloud and dry forests from sea level to 1200 m.a.s.l. [59] [60]. Not surprisingly, these species were in great abundance among sampling plots as well all sampling periods.

We believe it is unlikely that coffee cultivation practices would affect all birds in the same way. We found, in fact, no relation between AASM and PGSM for 5 habitat generalist species of the 21 species most frequently counted among farms. The same finding was also true for the remaining 16 habitat specialists among farms in transition or using conventional coffee cultivation practices. Only among farms using organic cultivation practices, was bird abundance/density (AASM) significantly and positively related to PGSM among habitat specialists.

The ANCOVA results substantiate our hypothesis that SETPET, OREPER, CALFOR, AMASAU and HYLELI are generalists that do not necessarily discriminate among habitats, and also explain the lack of statistical evidence of a relationship between PGSM and AASM. However, among the remaining 16 species wherein no migrants were represented, these behaved as habitat specialists in organic shade-coffee plantations, meaning that there was substantial value in PGSM as a predictor AASM and a positive correlation between them. This may be interpreted ecologically much like MacArthur and MacArthurs' [41] and Morton *et al.*'s [61] findings identifying, respectively, foliage height density and stem orientation as measures of habitat structure. Birds in these cases, *i.e.*, those that visually discriminate the structure of the vegetation may perceive a greater potential as refugia from predation and the possibility of greater niche partitioning of 3-dimensional spatial resources including foraging strata and favorable sites for nesting within a given physical location of the forest and within particular vegetation types.

5. Conclusion

Benefits of Organic Farms and Other "Biodiversity-Friendly" Coffee Systems

Our study demonstrates that bird abundance and density per hectare are higher within farms using organic shade-coffee cultivation practices. We assert that this is due to their incorporation of more mature (e.g., taller, structurally complex) tropical forest ecosystems, especially among habitat specialists. Our results confirm that shaded organic coffee plantations, which are most similar to surrounding forests in respect to overstory tree diversity and configuration, have more trophic structure and therefore support a greater variety of habitat specialists. Agricultural profit among the farm management types was not part of the present study. However, our results further substantiate that there is greater merit in organic farming over other coffee cultivation practices in preserving greater bird species richness, abundance and density. Increased crop revenue would be expected from reduced plant pest damage, owing to increased bird species richness and dietary/strata guild abundance and density. This applies especially to species that rely on particular habitat features that parallel those of the tropical forest ecosystem with its diverse and complex forest canopy and shrubby understory.

Author Contributions

All of the authors contributed to the conception and design of the study, acquisition of data, or analysis and interpretation of data. Martínez-Sánchez and Zolotoff assisted in summarizing coffee management strategies among the farms: organic and traditional polyculture shade coffee plantations. Zolotoff assisted Arendt (among others—see Acknowledgments below) in collecting the field data. Arendt wrote most of the ms. and conducted some of the traditional statistical analysis (parametric, non-parametric). Tuckfield, Thompson, and Reidy performed specialized statistical procedures (modelling, Distance Sampling, R, among others). Tuckfield derived the PGSM and AASM metrics, two novel ways to quantify vegetation parameters and avian species densities per unit area sections, wrote the related sections, and made numerous edits, adding wording and constructive comments throughout the manuscript's entirety. All authors provided editorial suggestions on various sections and drafts.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Appendix

Table A1. Species codes, scientific and common name, residency status (R = resident; M = migrant), foraging guild (C = carnivore; F = frugivore; G = granivore; I = insectivore; N = nectarivore; O = omnivore; S = scavenger) and strata (O = overstory; G = ground; S = shrub; T = trunk; U = understory), number of observations (total number of points at which a species was detected), and total detections (total detections of individuals of a species) and detections by period and overstory and coffee at 200 count points visited four times inshade coffee plantations on Mambacho Volcano, Nicaragua, 1998-1999. Seasons correspond to the boreal seasons including winter (25 February - 1 March 1998), spring (16 March - 14 April 1999), summer (22 July - 5 August 1998), and fall (10 November - 21 November 1998). Symbol * after the species code refers to 16 species of habitat discrminators (small slope species) and symbol ^ refers to the five habitat generalist species (large slope species) as explained in text.

								Winter (25 Feb. - 1 Mar. 1998)		Summer (22 Jul. - 5 Aug. 1998)		Fall (10 - 21 Nov. 1998)		Spring (16 Mar. - 14 Apr. 1999)	
Species Code	Scientific Name	Common Name	Status	Guild	Strata	Number of Observation	Number of Detections	Over-story	Coffee	Overstory	Coffee	Overstory	Coffee	Overstory	Coffee
AMAALB*	*Amazona albifrons*	White-fronted Parrot	R	f	o	30	77	34	1	5	0	16	0	21	0
AMAAUR	*Amazona auropalliata*	Yellow-naped Parrot	R	f	o	26	85	23	0	22	0	33	0	7	0
AMAFAR	*Amazona farinosa*	Mealy Parrot	R	f	o	1	1	0	0	0	0	0	0	1	0
AMARUT*	*Amazilia rutila*	Cinnamon Hummingbird	R	n	o,s	30	32	8	1	7	1	4	2	9	0
AMASAU	*Amazilia saucerrottei*	Steely-vented Hummingbird	R	n	o,s	42	52	10	2	4	0	3	0	32	1
Amazona sp.	*Amazona* sp.	parrot sp.				23	55								
ARACAN	*Eupsittula* (*Aratinga*) *canicularis*	Orange-fronted Parakeet	R	f	o	20	57	34	0	6	0	17	0	0	0
ARANAN	*Eupsittula* (*Aratinga*) *nana*	Olive-throated Parakeet	R	f	o	6	54	35	0	19	0	0	0	0	0
Aratinga sp.	*Eupsittula* sp.	parakeet sp.				24	75								
ARCCOL	*Archilochus colubris*	Ruby-throated Hummingbird	M	n	o,s	7	8	3	1	0	0	0	0	4	0
BROJUG	*Brotogeris jugularis*	Orange-chinned Parakeet	R	f	o	25	106	3	0	57	0	36	0	10	0
BUTNIT	*Buteo nitidus*	Gray Hawk	R	c	o	8	13	2	0	4	0	3	0	4	0
CALFOR	*Calocitta formosa*	White-throated Magpie-Jay	R	o	o,s,u	400	402	155	5	104	0	52	0	86	0
CAMGUA	*Campephilus guatemalensis*	Pale-billed Woodpecker	R	i	t	1	1	0	0	1	0	0	0	0	0
CAMRUN	*Campylorhynchus rufinucha*	Rufous-naped Wren	R	i	s	22	30	2	4	8	3	3	1	9	0
CHILIN*	*Chiroxiphia linearis*	Long-tailed Manakin	R	f	o,s,u	199	361	111	20	115	34	30	0	51	0
CHLCAN	*Chlorostilbon canivetii*	Canivet's Emerald	R	n	o,s	16	19	9	8	0	0	0	0	2	0
Colibri sp.	*Colibri* sp.	hummingbird sp.				73	102								
COLINC	*Columbina inca*	Inca Dove	R	g	g	23	27	17	3	2	2	0	0	3	0
Columbina sp.	*Columbina* sp.	dove sp.				4	4								
CONALB	*Conopias albovittatus*	White-ringed Flycatcher	R	i	o	1	1	0	0	0	0	0	0	1	0
CONSOR	*Contopus sordidulus*	Western Wood-Pewee	M	i	o,s	1	1	0	0	0	0	0	0	1	0
Contopus sp.	*Contopus* sp.	pewee sp.				11	11								
CONVIR	*Contopus virens*	Eastern Wood-Pewee	M	i	o,s	17	17	2	0	0	0	11	0	4	0
CORATR	*Coragyps atratus*	Black Vulture	R	s	o,g	2	2	0	0	1	0	1	0	0	0

Continued

CROSUL	*Crotophaga sulcirostris*	Groove-billed Ani	R	o	s	10	18	1	0	11	1	0	0	5	0
CYACYA	*Cyanerpes cyaneus*	Red-legged Honeycreeper	R	n	o	9	22	2	0	9	0	7	0	4	0
Dendrocolaptes sp.	*Dendrocolaptes* sp.	woodcreeper sp.				1	1								
Elaenia sp.	*Elaenia* sp.	Elaenia sp.				2	2								
ELAFRA	*Elaenia frantzii*	Mountain Elaenia	R	o	o	12	18	1	4	9	0	0	0	4	0
EMPFLN	*Empidonax flaviventris*	Yellow-bellied Flycatcher	M	i	o	12	23	0	0	0	0	23	0	0	0
Empidonax sp.	*Empidonax* sp.	flycatcher sp.				4	4								
EMPMIN	*Empidonax minimus*	Least Flycatcher	M	i	s	2	2	0	2	0	0	0	0	0	0
EUCPEN	*Eucometis penicillata*	Gray-headed Tanager	R	o	u	2	2	1	0	0	0	0	0	1	0
EUPAFF	*Euphonia affinis*	Scrub Euphonia	R	f	o	2	7	0	0	4	5	0	0	0	0
EUPHIR*	*Euphonia hirundinacea*	Yellow-throated Euphonia	R	f	o	114	277	19	0	123	3	84	1	47	0
Euphonia sp.	*Euphonia* sp.	Euphonia sp.				18	28								
EUPLAN	*Euphonia laniirostris*	Thick-billed Euphonia	R	f	o	16	46	9	0	1	0	1	0	35	0
EUPLUT	*Euphonia luteicapilla*	Yellow-crowned Euphonia	R	f	o	3	6	1	0	0	0	5	0	0	0
EUMSUP	*Eumomota superciliosa*	Turquoise-browed Motmot	R	i	u	4	4	0	0	2	0	1	0	1	0
Geotrygon sp.	*Geotrygon* sp.	quail-dove sp.				6	9								
HELCON	*Heliomaster constantii*	Plain-capped Starthroat	R	n	o	1	1	0	0	0	0	0	0	1	0
HYLDEC*	*Hylophilus decurtatus*	Lesser Greenlet	R	o	o	99	170	17	0	55	6	60	3	28	1
HYLELI	*Hylocharis eliciae*	Blue-throated Goldentail	R	n	s,u	67	89	44	14	6	0	9	0	16	0
HYLMUS	*Hylocichla mustelina*	Wood Thrush	M	o	u	1	1	0	1	0	0	0	0	0	0
ICTGAL	*Icterus galbula*	Baltimore Oriole	M	o	o	10	21	4	3	0	0	6	0	8	0
LEPSOU	*Lepidocolaptes souleyetii*	Streak-headed Woodcreeper	R	i	t	1	1	0	0	1	0	0	0	0	0
LEPVER	*Leptotila verreauxi*	White-tipped Dove	R	g	g	15	18	11	3	1	0	0	0	3	0
MEGPIT	*Megarynchus pitangua*	Boat-billed Flycatcher	R	o	o	19	20	7	0	4	0	2	0	7	0
MELHOF*	*Melanerpes hoffmannii*	Hoffmann’s Woodpecker	R	o	t	263	345	106	0	96	2	66	0	75	0
MIOOLE	*Mionectes oleagineus*	Ochre-bellied Flycatcher	R	f	u	1	1	0	0	0	0	1	0	0	0
MNIVAR	*Mniotilta varia*	Black-and-white Warbler	M	i	t	1	1	0	0	0	0	0	0	1	0
MOMMOM*	*Momotus momota*	Blue-crowned Motmot	R	i	u	32	40	32	2	2	0	0	0	4	0
Myiarchus sp.	*Myiarchus* sp.	flycatcher sp.				11	15								
MYICRI	*Myiarchus crinitus*	Great Crested Flycatcher	M	o	o	7	10	6	1	0	0	3	0	0	0
MYIMAC	*Myiodynastes maculatus*	Streaked Flycatcher	R	i	o	1	1	0	0	0	0	0	0	1	0
MYITUB*	*Myiarchus tuberculifer*	Dusky-capped Flycatcher	R	i	o	93	153	31	1	50	0	50	0	20	1

Continued

MYOLUT	*Myiodynastes luteiventris*	Sulphur-bellied Flycatcher	M	i	o	4	5	0	0	1	0	0	0	4	0
OREPER	*Oreothlypis peregrina*	Tennessee Warbler	M	i	o	100	342	103	0	0	0	191	0	48	0
PACPOL	*Pachyramphus polychopterus*	White-winged Becard	R	f	o	1	1	0	0	1	0	0	0	0	0
PATFLA	*Patagioenas flavirostris*	Red-billed Pigeon	R	f	o	1	1	1	0	0	0	0	0	0	0
PHASTR	*Phaethornis striigularis*	Stripe-throated Hermit	R	n	u	5	6	2	1	1	1	0	0	2	0
PIACAY	*Piaya cayana*	Squirrel Cuckoo	R	i	o	28	29								
PIRLEU	*Piranga leucoptera*	White-winged Tanager	R	f	o	3	4	4	0	16	0	5	0	4	0
PIRLUD	*Piranga ludoviciana*	Western Tanager	M	f	o	1	2	3	0	0	0	1	0	0	0
PIROLI	*Piranga olivacea*	Scarlet Tanager	M	f	o	1	1	1	0	0	0	0	0	1	0
PIRRUB	*Piranga rubra*	Summer Tanager	M	f	o	25	27	0	0	0	0	0	0	2	0
PITSUL	*Pitangus sulphuratus*	Great Kiskadee	R	i	o	17	17	15	0	0	0	7	0	5	0
POLPLU	*Polioptila plumbea*	Tropical Gnatcatcher	R	i	o	1	1	2	0	6	0	7	0	2	0
PSAMON*	*Psarocolius montezuma*	Montezuma Oropendola	R	o	o	256	572	0	0	0	0	1	0	0	0
PTETOR*	*Pteroglossus torquatus*	Collared Aracari	R	o	o	42	80	250	0	81	4	109	0	127	1
QUIMEX	*Quiscalus mexicanus*	Great-tailed Grackle	R	o	g	1	1	42	0	16	0	3	0	19	0
RAMSUL*	*Ramphastos sulfuratus*	Keel-billed Toucan	R	f	o	59	76	1	0	0	0	1	0	0	0
SETFUS	*Setophaga fusca*	Blackburnian Warbler	M	i	o	1	1	22	0	33	0	10	1	10	0
SETPEN	*Setophaga pensylvanica*	Chestnut-sided Warbler	M	o	o	3	3	0	0	0	0	0	0	1	0
SETPET	*Setophaga petechia*	Yellow Warbler	M	i	s	245	462	0	0	0	0	1	0	2	0
SETPIN	*Setophaga pinus*	Pine Warbler	M	i	o	1	2	170	5	0	0	149	1	137	0
SETSAN	*Dendrocolaptes sanctithomae*	Northern Barred-Woodcreeper	R	i	t	1	3	2	0	0	0	0	0	0	0
SETVIR	*Setophaga virens*	Black-throated Green Warbler	M	i	o	1	1	0	0	0	0	0	0	3	0
THADOL	*Thamnophilus doliatus*	Barred Antshrike	R	i	u	1	1	1	0	0	0	0	0	0	0
THRMOD*	*Thryothorus modestus*	Plain Wren	R	i	s	179	284	0	1	0	0	0	0	0	0
THRPLE*	*Thryothorus pleurostictus*	Banded Wren	R	i	s	437	887	5	91	7	84	11	51	0	35
THRRUL	*Thryothorus rufalbus*	Rufous-and-white Wren	R	i	s	16	27	25	132	50	369	21	134	16	140
Thryothorus sp.	*Thryothorus* sp.	wren sp.				1	1	5	6	6	8	0	0	0	2
TITSEM	*Tityra semifasciata*	Masked Tityra	R	o	o	22	29	6	0	8	0	3	0	12	0
TOLSUL*	*Tolmomyias sulphurescens*	Yellow-olive Flycatcher	R	o	o	74	102	0	0	70	2	14	0	14	2
TROMEL*	*Trogon melanocephalus*	Black-headed Trogon	R	o	o	34	48	12	0	12	0	2	0	21	1
TROVIO	*Trogon violaceus*	Violaceous Trogon	R	o	o	3	4	0	0	3	0	1	0	0	0
TURGRA	*Turdus grayi*	Clay-colored Thrush	R	o	o	17	21	12	0	7	1	0	0	1	0

Continued

TYRFOR	*Tyrannus forficatus*	Scissor-tailed Flycatcher	M	i	s	5	5	2	0	0	0	0	0	3	0
VERCEL	*Vermivora celata*	Orange-crowned Warbler	M	o	o	1	1	1	0	0	0	0	0	0	0
Vireo sp.	*Vireo* sp.	vireo sp.				5	7								
VIRFLD*	*Vireo flavoviridis*	Yellow-green Vireo	R	o	o	37	77	2	0	24	1	39	0	11	0
VIRFLF	*Vireo flavifrons*	Yellow-throated Vireo	M	o	o	3	3	0	0	0	0	3	0	0	0
VIROLI	*Vireo olivaceus*	Red-eyed Vireo	M	o	o	2	4	0	0	0	0	2	0	2	0
VIRSOL	*Vireo solitarius*	Blue-headed Vireo	M	o	o	1	3	0	0	0	0	1	0	2	0
VOLJAC	*Volatinia jacarina*	Blue-black Grassquit	R	g	g	8	9	0	0	5	0	1	2	0	1
ZENASI	*Zenaida asiatica*	White-winged Dove	R	g	g	9	11	4	0	7	0	0	0	0	0