

AVIAN ABUNDANCE IN SUN AND SHADE COFFEE PLANTATIONS AND REMNANT PINE FOREST IN THE CORDILLERA CENTRAL, DOMINICAN REPUBLIC

Joseph M. Wunderle, Jr., & Steven C. Latta¹

International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 490, Palmer,
Puerto Rico 00721, U.S.A.

Resumen. Se usaron conteos en puntos y redes ornitológicas para censar aves en plantaciones de café de sol y de sombra y en remanentes de bosques de pinos en una región agrícola de la Cordillera Central de la República Dominicana durante enero y febrero de 1992, 1993 y 1994. Los análisis de la técnica de enrarecimiento indican que la riqueza de especies fue mayor en los pinares y menor en las plantaciones. La diversidad de las especies (H') fue similar en los conteos en puntos en los tres hábitaculos, pero un "sobrepredominio" se hizo evidente en las muestras con redes en las plantaciones de café de sombra donde las dos especies más comunes constituyeron el 51% de todas las capturas en contraste de 37% en pinos y el 27% en las plantaciones de café al sol. Los bosques de pinos tienen más especialistas para ese tipo de hábitaculo y aves endémicas (en comparación con los cafetales) y una mayor abundancia de insectívoros. El café de sombra tiene más nectarívoros (debido al florecimiento de *Inga vera* en el dosel), una razón de sexo que favorece a los machos de dos especies de aves migratorias nearcticas (*Dendroica caerulescens* y *Setophaga ruticilla*), y a un mayor número de especies comunes en los bosques latifoliados. Por el contrario, el café de sol tiene más frugívoros, una razón de sexo que favorece a las hembras de las mismas especies de aves migratorias, y especies típicas de un ambiente de matorral y de sotobosque latifoliado en los pinares. De las 37 especies encontradas en las plantaciones de café, el 46% se encontró en las dos plantaciones. Las diferencias en la composición de la avifauna entre el café de sol y el de sombra se espera que sean más claras en un continente que en una isla debido a una mayor especialización en los hábitats ocupados por las especies continentales. El café de sombra contribuye a la biodiversidad en las regiones agrícolas, proveyendo hábitat para las especies de bosques latifoliados; en contraste al café de sol, que puede proveer hábitat para las especies de matorral.

Abstract. Point counts and mist nets were used to sample birds in sun and shade coffee plantations, and remnant pine forests in an agricultural region of the Cordillera Central, Dominican Republic from Jan.–Feb. 1992 to 1994. Rarefaction analysis indicated that species richness was highest in pine and lowest in plantations. Species diversity (H') was similar in point counts in the three habitats, but an "overdominance" was evident in net samples in shade coffee where the two most common species constituted 51% of all captures in contrast to 37% in pine and 27% in sun coffee. Pine forest had more habitat specialists and endemics (relative to coffee), and an abundance of insectivores. Shade coffee had more nectarivores (due to a flowering *Inga vera* overstory), male-biased sex ratios in two nearctic migrants (Black-throated Blue Warblers, *Dendroica caerulescens*; American Redstarts, *Setophaga ruticilla*), more permanent residents (relative to sun coffee), and species common in broadleaf forest. In contrast, sun coffee had more frugivore/seed eaters, female-biased sex ratios in the two migrants, and species of open brushland ("matorral") or broadleaf understory of pine. Of the 37 species found in coffee plantations, 46% were found in both plantations. The differences in avian assemblages between sun and shade coffee are expected to be more distinct on a continent than an island, due to the more restricted habitat breadth of continental species. Shade coffee contributes to biodiversity in agricultural regions by providing habitat for some broadleaf forest species; in contrast to sun coffee, which may provide habitat for some "matorral" species. Accepted 6 November 1995.

Key words: Avian abundance, coffee plantations, pine, Cordillera Central, Dominican Republic.

INTRODUCTION

Coffee plantations with an overstory of shade trees may be used by some species of forest dwelling birds (Wetmore 1916, Griscom 1932, Beehler *et al.* 1987, Terborgh 1989, Askins *et al.* 1990,

Greenberg 1994, Wille 1994). Brash (1987) suggested that shade coffee plantations served as a refugia for many forest species during a period of extreme deforestation on the island of Puerto Rico, thereby limiting the expected loss of

¹ *Current Address:* Department of Biological Sciences, 110 Tucker Hall, University of Missouri, Columbia, MO 65211, U.S.A.

species due to deforestation. However despite these claims and findings from one Asian study (Beehler *et al.* 1987), few workers have studied avian abundance in shade coffee plantations in the neotropics and most have concentrated on overwintering nearctic migrants (Robbins *et al.* 1992, Petit *et al.* 1993, Vannini 1994, Wunderle & Waide 1993, Greenberg *et al.* 1995), with few studies including residents (Aguilar-Ortiz 1982, Greenberg *et al.*, in press).

Recently, several authors have expressed concern regarding the ecological effects of the conversion of traditional shade coffee plantations into a newer, high intensity form of cultivation in which coffee is grown in full sunlight in the absence of a shade overstory (Borrero 1986, Greenberg 1994, Vannini 1994, Wille 1994, Wunderle and Waide 1994, Perfecto *et al.* in press). These sun coffee plantations require higher inputs of pesticides, and combined with the elimination of the shade overstory, may contribute to a reduction in biodiversity (Greenberg 1994, Vannini 1994, Wille 1994, Perfecto *et al.* in press). Given the large area devoted to coffee cultivation in the Neotropics, the conversion to sun coffee is likely to have a major effect on regional biodiversity. Despite the potential negative effect of the conversion of shade to sun coffee, only Borrero (1986) has summarized the effect on avian diversity, but without providing census data from the two plantations he sampled.

The objective of this study is to compare the abundance of individual bird species and the characteristics of the avian assemblages in sun and shade coffee plantations and remnant pine forest. The three habitats were sampled with mist nets, which provide a sample of birds in the coffee or pine understory, and point counts, which sampled birds in both understory and canopy. Here we examine the importance of shade coffee for providing broadleaf habitat in an agricultural landscape where the remaining native habitat is pine with broadleaf understory. We expected that avian diversity and abundance would be greatest in the most structurally and floristically diverse habitat (pine forest) and least in the habitat with the simplest structure and flora (sun coffee). Furthermore, we expected that shade coffee plantations would have a high proportion of forest dwelling species in contrast to

sun coffee which would have a high proportion of species from structurally similar brushland or "matorral". Comparisons of bird populations in sun and shade coffee may enable us to predict some of the expected changes in avian abundance as conversion to sun coffee proceeds in Hispaniola and elsewhere in the Caribbean.

STUDY SITES AND METHODS

In the Cordillera Central of the Dominican Republic, coffee is cultivated in areas which were originally pine forest (*Pinus occidentalis*). Pine forests, many of which have been selectively logged, remain in scattered patches on the steeper slopes, with variable amounts of broadleaf understory which may be degraded by fire, cutting, or grazing. Within this region, broadleaf trees are restricted primarily to shade coffee plantations, fruit and ornamental trees along fence rows and around homes, and in arroyos lined primarily with the exotic *Syzygium jambos*. Broadleaf forest or woodland are absent while pasture and cultivated fields of ground crops are the predominant cover type.

Shade coffee plantations were sampled in the vicinity of Manabao (19° 6' N, 70° 48' W) and Jarabacoa (19° 9' N, 70° 39' W), La Vega province, at an altitude of 540–850 m. A total of 32 plantations were sampled by point counts of which 14 plantations were also sampled by mist netting. The shade plantations here are characterized by a predominate overstory of *Inga vera* (Mimosoideae), although mango (*Mangifera indica*), avocado (*Persea americana*), various citrus species (*Citrus* sp.), and banana or plantains (*Musa* sp.) are also scattered throughout some plantations where they provide an intermediate layer above the coffee. In a few plantations, an occasional pine (*Pinus* sp.) or palm (*Roystonea* sp.) extend into the overstory. The predominant variety of coffee (*Coffea arabica*) in the shade plantations is the traditional "típica" variety, although "catorra" predominates in some of the larger plantations and is used to replace "típica" in some of the smaller plantations. Most of the shade coffee plantations sampled were relatively small (mean = 1.2 ha, range 0.1–8.7 ha for point counts; mean = 1.9 ha, range 0.1–9.7 ha for mist netting). One hundred meter transects run in the four major cardinal direc-

tions from each plantation (Wunderle & Latta, unpublished data for 14 plantations where netting was conducted) indicate that 75 % of the land area surrounding the plantations is non-forest (67 % pasture and 8 % cultivation). Tree canopies cover 20 % of the surrounding area (13 % arroyo; 5 % coffee plantations; 2 % pine) and the remaining 5 % of the land area contains a miscellaneous mix of roads, buildings, rivers, etc.

In this region, sun coffee is found at higher altitudes on steeper slopes and in larger plantations than shade coffee. We sampled one sun plantation at La Ciénaga (1,240 m altitude; 28 ha) and two plantations at El Montaso (980 m altitude, 34 ha; and 1,050 m altitude, 84 ha). All sun coffee plantations were planted with the variety "catorra" which appeared to be of similar height and density among the three plantations.

Remnant pine forest was sampled with point counts and mist nets on slopes above Manabao (905–1,050 m) and Jarabacoa (643–779 m). Mist netting was also conducted at an additional site on a slope below Jarabacoa (433 m). Although the area of the pine forest was not measured, the remnant patches surveyed were all considerably larger than the largest sun coffee plantation.

We used two to seven 16 m diameter circular plots in each habitat to characterize the foliage distribution in the three habitats. At least two plots were placed in vegetation representative of areas in which point counts and mist netting were conducted. In shade coffee plantations, plots were placed in the middle of the plantation centered on the point count locations in plantations where mist netting was conducted ($n = 30$ plots). Only two plots were placed in the sun coffee plantations (at La Ciénaga) because the other two plantations had been thinned of coffee trees by the time of vegetation sampling and therefore were no longer representative of the habitat originally sampled by nets and point counts. Eight plots were sampled in pine.

Foliage-height profiles were determined at 20 points located at 1.6 m intervals along the north, south, east, and west radii of the circular plot (following the methods of Schemske and Brokaw 1981). A 3 m pole (2.0 cm diameter) marked at 0.5 m intervals was placed vertically at each sample point. We recorded the presence or absence of foliage touching the pole within each

height class. Foliage was classified as coffee or shade overstory in the plantations or as broadleaf or pine in the pine forest. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following height intervals: 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, and 20–25 m. For each height interval, percent cover was calculated by dividing the number of points in which foliage was present in that height interval by the total number of sample points and multiplying by 100.

We sampled shrub layer invertebrate abundance with a version of the visual leaf sampling ("leaf turning") method developed by Holmes *et al.* (1986) as modified by Askins & Ewert (1994). To allow comparison among sites with different size leaves, we standardized observations in terms of time (no. of invertebrates per 2 min) rather than in terms of number of leaves sampled (no. of invertebrates per leaf). We believe that invertebrate prey per unit time is a relevant measure of comparison as it measures the rate at which a foraging insectivore encounters prey in the different habitats, regardless of leaf size. Both upper and lower surfaces of leaves at 1–1.5 m above ground were inspected for invertebrates during a two-minute period at a station in which the observer followed a north-south transect. A total of 20 stations were sampled at a site, with each station located 3 m apart along a transect line. To sample sufficient stations in small shade coffee plantations it was necessary to run several parallel north-south transects, each separated by 4 m. In larger habitat, such as pine or sun coffee, transects were located in the center of the habitat. A total of 11 shade coffee plantations, 3 sun coffee plantations, and 3 pine sites were sampled in this manner. Invertebrates were categorized as spiders, snails, or insects. The latter category was broken down by order, and each egg cluster and aggregation recorded as a single individual.

Birds were censused with point counts during the winters of 1992–1993 and 1993–1994, as follows: shade coffee (12–26 Jan. 1993); pine (11 Jan.–9 Feb. 1994); sun coffee (14–20 Feb. 1994). We used fixed-radius point counts (Hutto *et al.* 1986) in which an observer recorded all birds seen and heard during a ten-minute period at each point. Each point was at least 100 m from

all others. Only in the 10 largest shade coffee plantations was it possible to conduct more than one point count. Counts were initiated at sunrise and terminated before 11:00, with most counts completed before 10:30. The three habitats were sampled during similar time intervals in the morning. All counts were made by the same observer who estimated the minimum distance to each bird detected during a count within a 25 m radius. We calculated the mean number of detections for each species per 25 m radius plot. To verify the independence of samples from each point we compared mean detections per 25 m radius plot at ≥ 200 m intervals with those at 100 m intervals and found no significant differences. Our analysis excludes aerial foragers and raptors detected during the counts, although the latter are listed in the Appendix along with additional species detected outside of the count period and missed during the netting periods.

Mist nets were used in Jan.—Feb. 1994 to sample birds in shade coffee (11–28 Jan. 1994), sun coffee (13–27 Feb. 1994) and pine forest understory (8–28 Feb. 1994). We used 12- and 6-m nets with 30 mm mesh and four shelves set to a height of 2.5 m. Nets were set in continuous lines in both pine forest and sun coffee plantations. However, this was not possible in most shade coffee plantations and hence nets were scattered throughout the plantations to obtain even coverage. The number of nets run at a site was variable depending on the size of the site and ranged from 3 to 23 nets. Size of shade coffee plantations had no effect on the composition of birds captured in mist nets and there was no evidence of an edge effect in the shade plantations (Wunderle & Latta, unpubl. data). Nets were set during the early afternoon and opened until sunset and then opened at sunrise on the following day. Therefore each site received net coverage during the late afternoon until sunset and again from sunrise until mid-day. Capture rates are reported as captures per net hour $\times 100$, where a net hour is equivalent to one 12 m net set open for one hour. We cut a small piece of the outer primary feather from each captured resident bird and banded all migrants for identification of recaptures. Sex was determined for residents according to descriptions in Bond (1979) and Dodd (1987), and Pyle *et al.* (1987) for Nearctic migrants.

We did not systematically analyze local variation in bird populations or vegetation within a given habitat type; although this was done elsewhere for shade coffee (Wunderle, in prep.). Instead we pooled samples from different sites for each habitat type. Species richness was determined by the technique of rarefaction (Simberloff 1972, 1978) to compare species richness in different sites obtained from point counts and netting samples of different sizes. Species diversity was characterized using the Shannon-Weiner index (H') where

$$H' = \sum_{i=s} p_i \log p_i$$

Here s is the number of species and p_i is the proportion of the total number of individuals consisting of the i th species (Krebs 1989). This index takes into account both relative species abundance and the number of species in a community.

All statistical tests and their assumptions are described by Sokal & Rohlf (1981). Homogeneity of variances was established with Bartlett's test before Analysis of Variance (ANOVA) was used. A two-level nested ANOVA (mixed model) was used to compare invertebrate abundance among habitats and among sites within a habitat. Non-parametric tests were used to compare abundance of species detected in point counts among habitats, because sample distributions were non-normal, based on skewness and kurtosis. For example, the Mann-Whitney U-test was used to compare the abundance of individual species in point counts between sun and shade coffee plantations. The Kruskal-Wallis test was used to compare abundance in point counts among the three habitat types. The diet of each species was classified as either nectar, fruit/seeds, or insects on the basis of Faaborg (1985). This information was analyzed in a row \times column test of independence with a G-statistic to test for significant heterogeneity in number of individuals in a diet category among habitats. The natural habitat of each species was classified as forest, matorral, or generalist (common in both forest and matorral) on the basis of mist net and point count surveys conducted previously in a variety of habitats in the Dominican Republic (Wunderle & Waide 1993, Wunderle & Waide, unpubl. data). This information was tested with

a row x column test of independence with Yates' corrected χ^2 to test for significant heterogeneity in species' natural habitat category (forest or matorral) between sites of highest count (sun or shade coffee). Yates' correction for continuity was used to correct for small sample sizes. A G-test was used to analyze for significant heterogeneity in sex ratios among habitats. Spearman's rank correlation coefficient was used to quantify the association between two variables which were not linearly related. This included a comparison of the ranked order of abundance of species in one habitat with another, and is designated as relative abundance of species in a habitat. In all statistical analyses a probability of Type I error rate of 0.05 or less was accepted as significant.

RESULTS

Foliage Height Profiles. Sun coffee had the lowest maximum height of vegetation, but the highest percentage of foliage cover in a height category, for foliage at 0.5–1.0 m, 1.0–1.5 m, and 1.5–2.0 m (Figure 1). In contrast, coffee in shade plantations was taller than sun coffee, but with less cover in a foliage height category (Figure 1). *Inga vera* provided most of the shade overstory cover (81–97% foliage cover in a height category), with greatest cover in the 10–12 m height category in shade coffee plantations. Compared with the two types of coffee plantations, pine forest had the highest canopy, but with sparse foliage cover within the different height categories, except near the ground at 0–0.5 m and 0.5–1.0 m (Fig. 1). Within the pine forests,

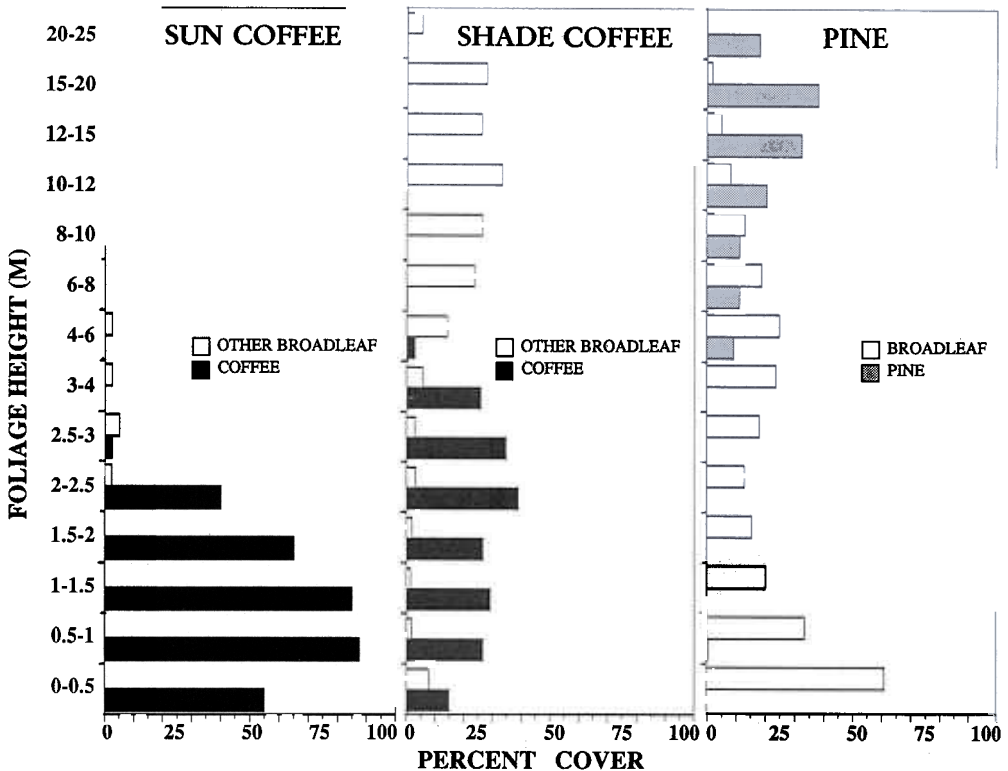


FIG. 1. Representative foliage height profiles for sun and shade coffee plantations and pine forest in the Cordillera Central of the Dominican Republic. Twenty vertical transects were run in 16-m diameter plots in sun ($N = 2$ plots), shade ($N = 30$ plots), and pine ($N = 8$ plots). Percent cover (X-axis) represents the percentage of vegetation touches in a given height interval in meters (Y-axis). Height intervals increase with height on Y-axis.

pine foliage predominated in the canopy, but scattered broadleaf trees extended into the canopy.

Shrub Layer Invertebrate Abundance. Significant differences were found among habitats in average number of invertebrates per station (mixed model, nested ANOVA, $F_{1, 324} = 13.63$, $P < 0.001$) with the highest counts in sun coffee and lowest count in pine (Fig. 2). Moreover, significant heterogeneity in average number of invertebrates per station was found among sites within a habitat (mixed Model, nested ANOVA, $F_{14, 324} = 4.41$, $P < 0.001$).

Significant differences were found among habitats in average number of insects per station (mixed model, nested ANOVA, $F_{1, 324} = 14.90$, $P < 0.001$) with the highest counts in sun coffee and lowest counts in pine, as found with the total invertebrate count (Fig. 2). In addition, significant heterogeneity in average number of insects per station was found among sites within a habitat (mixed model, nested ANOVA, $F_{14, 324} = 5.93$, $P < 0.001$). However, no significant differences were found among habitats in average number of spiders per station (mixed model, nested ANOVA, $F_{1, 324} = 0.01$, $P = 0.91$), although significant heterogeneity was found among sites within a habitat (mixed model, nested ANOVA, $F_{14, 324} = 3.83$, $P < 0.001$). Thus invertebrate abundance in the shrub layer was greatest in sun coffee and least in pine, due primarily to the greater abundance of insects in sun coffee than elsewhere.

Point Counts. A total of 144 point counts (44 in pine, 47 in sun coffee, 53 in shade coffee) were conducted. Mean total birds per point was highest in pine forest, which was only slightly higher than the mean for shade coffee, which in turn, was significantly (Mann-Whitney $U = 505$, $P < 0.001$) higher than the mean in sun coffee (Table 1). These differences are attributable to permanent residents which were most abundant in pine and shade coffee and least abundant in sun coffee; the difference in mean number of permanent residents per point found in the two types of coffee was significant (Mann-Whitney $U = 241.5$, $P < 0.001$). In contrast, counts of nearctic migrants were highest in sun coffee, followed by shade coffee, then pine, although

TABLE 1. Occurrence of birds in sun and shade coffee plantations and pine forest in the Cordillera Central of the Dominican Republic. Occurrence is based on the average number of detections per point (x100) in fixed-radius point counts where each species was encountered (P.C.) and capture rate in mist-nets (C.R.). C.R. = 100 x no. of individuals captured per net hour. P-values for sun-shade comparison of point count distributions based on Mann-Whitney U Test, and F-values for sun-shade-pine comparison of point counts based on Kruskal-Wallis Test. Letter in parenthesis following name represents habitat: F, broadleaf forest; M, matorral; G, generalist, forest & matorral. Letters for diet indicate: F/S, fruit or seed; N, nectar; I, insects.

SPECIES	DIET		SUN		SHADE		PINE		SUN-SHADE		SUN-SHADE	
			P. C.	(C. R.)	P. C.	(C. R.)	P. C.	(C. R.)	P	P	P	P
Bananaquit, <i>Coereba flaveola</i> (G)	N								<0.001			<0.001
Bl.-thr. Blue Warbler, <i>Dendroica caerulescens</i> (G)	I								0.02			0.05
Vervain Hummingbird, <i>Melissaga minima</i> (F)	N								<0.001			<0.001
American Redstart, <i>Setophaga ruticilla</i> (G)	I								0.39			<0.001
Stripe-headed Tanager, <i>Spindalis zena</i> (M)	F/S								0.002			0.002
Hispaniolan Emerald, <i>Chlorostilbon swainsonii</i> (G)	N								0.008			0.025
Cape May Warbler, <i>Dendroica tigrinum</i> (G)	N								<0.001			<0.001
Antillean Mango, <i>Anthracoceros viridis</i> (G)	N								<0.001			<0.001
Hispaniolan Woodpecker, <i>Melanerpes striatus</i> (F)	I								0.01			<0.001

Bl-cr. Palm Tanager, <i>Phaenictophilus palmarum</i> (G)	14.6 (1.1)	20.8 (0.7)	31.1 (1.1)	0.40	0.42
Common Yellowthroat, <i>Geothlypis trichas</i> (M)	56.3 (1.8)	0.0 (0.1)	4.4 (0.2)	<0.001	<0.001
Yellow-rumped Warbler, <i>Dendroica coronata</i> (M)	20.8 (1.1)	0.0 (0.0)	37.8 (0.4)	0.001	0.004
Rufous-collared Sparrow, <i>Zonotrichia capensis</i> (M)	31.3 (1.4)	0.0 (0.0)	22.2 (0.0)	<0.001	0.001
Narrow-billed Tody, <i>Todus angustirostris</i> (G)	27.1 (1.6)	9.4 (0.2)	13.3 (0.6)	0.001	0.003
Hispaniolan Parrot, <i>Amazona ventralis</i> (F)	0.0 (0.0)	0.0 (0.0)	48.9 (0.0)	1.00	<0.001
Pine Warbler, <i>Dendroica pinus</i>	0.0 (0.0)	0.0 (0.0)	44.4 (0.0)	1.00	<0.001
Rufous-throated Solitaire, <i>Myadestes genibarbus</i> (F)	0.0 (0.0)	0.0 (0.1)	42.2 (0.9)	1.00	<0.001
Greater Antillean Elaenia, <i>Elaenia jalax</i> (F)	0.0 (0.5)	0.0 (0.0)	37.8 (1.0)	1.00	<0.001
Greater Antillean Pewee, <i>Contopus caribaea</i> (F)	0.0 (0.0)	13.2 (0.2)	22.2 (0.4)	0.01	<0.001
Broad-billed Tody, <i>Todus subulatus</i> (F)	6.3 (0.2)	5.7 (1.0)	15.6 (0.6)	0.57	0.34
Black-and-white Warbler, <i>Mniotilta varia</i> (F)	0.0 (0.1)	3.8 (0.6)	20.0 (0.6)	0.18	0.002
Hispani, Lizard Cuckoo, <i>Saurothera longirostris</i> (F)	0.0 (0.0)	7.5 (0.0)	6.7 (0.0)	0.05	0.16
Ground Warbler, <i>Microgilia palustris</i> (G)	0.0 (1.3)	0.0 (0.0)	13.3 (0.9)	1.00	0.03
Ovenbird, <i>Seiurus aurocapillus</i> (F)	2.1 (1.5)	9.4 (1.7)	0.0 (1.1)	0.12	0.05
Mourning Dove, <i>Zenaidura macroura</i> (G)	0.0 (0.0)	0.0 (0.0)	11.1 (0.0)	1.00	0.003
Black-faced Grassquit, <i>Tiaris bicolor</i> (M)	10.4 (3.7)	0.0 (0.5)	0.0 (0.4)	0.07	0.05
Palmchat, <i>Dulus dominicus</i> (F)	0.0 (0.0)	5.7 (0.1)	4.4 (0.0)	0.18	0.41
Loggerhead Kingbird, <i>Tyrannus caudifasciatus</i> (F)	0.0 (0.0)	7.5 (0.0)	2.2 (0.0)	0.09	0.21
Greater Antillean Bullfinch, <i>Loxigilla violacea</i> (M)	6.3 (3.4)	0.0 (0.0)	2.2 (0.4)	0.07	0.16
Smooth-billed Ani, <i>Crotophaga ani</i> (M)	0.0(0.0)	5.7 (0.0)	2.2 (0.0)	0.09	0.21
Yellow-faced Grassquit, <i>Tiaris olivacea</i> (M)	4.2 (1.3)	0.0 (0.0)	2.2 (0.0)	0.14	0.34
Northern Mockingbird, <i>Mimus polyglottus</i> (M)	6.3 (0.0)	0.0 (0.0)	0.0 (0.0)	0.07	0.05
Antillean Euphonia, <i>Euphonia musica</i> (F)	0.0 (0.0)	3.8 (0.0)	2.2 (0.0)	0.18	0.41
Black-cowled Oriole, <i>Icterus dominicensis</i> (F)	0.0 (0.0)	5.7 (0.0)	0.0 (0.0)	0.18	0.17
Black-whiskered Vireo, <i>Vireo atiloqueus</i> (F)	0.0 (0.0)	5.7 (0.1)	0.0 (0.1)	0.09	0.07
Prairie Warbler, <i>Dendroica discolor</i> (M)	2.1 (0.0)	0.0 (0.0)	2.2 (0.0)	0.29	0.56
Yellow-throated Warbler, <i>Dendroica dominica</i> (F)	0.0 (0.0)	1.9 (0.0)	2.2 (0.0)	0.34	0.61
Red-legged Thrush, <i>Mimotichla plumbeus</i> (F)	0.0 (0.1)	0.0 (0.1)	2.2 (0.7)	1.00	0.33
Scaly-naped Pigeon, <i>Columba squamosa</i> (F)	0.0 (0.0)	0.0 (0.0)	2.2 (0.0)	1.00	0.33
Stolid Flycatcher, <i>Myiarchus stolidus</i> (F)	0.0 (0.0)	1.9 (0.2)	0.0 (0.0)	1.00	0.33
Ruddy Quail-Dove, <i>Geotrygon montana</i> (F)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.34	0.42
Worm-eating Warbler, <i>Helminthophila vermivorus</i> (F)	0.0 (0.1)	0.0 (0.0)	0.0 (0.1)	1.00	1.00
Antillean Piculet, <i>Neocittes micromega</i> (F)	0.0 (0.0)	0.0 (0.0)	0.0 (0.1)	1.00	1.00
Bicknell's Thrush, <i>Catharus bicknelli</i> (F)	0.0 (0.0)	0.0 (0.0)	0.0 (0.1)	1.00	1.00
Antillean Siskin, <i>Carduelis dominicensis</i>	0.0 (0.1)	0.0 (0.0)	0.0 (0.0)	1.00	1.00
MEAN TOTAL RESIDENTS PER POINT	2.16 (25.0)	4.52 (12.4)	5.76 (22.6)	0.001	0.001
MEAN TOTAL MIGRANTS PER POINT	2.02 (11.9)	2.00 (8.4)	1.78 (7.9)	0.28	0.45
MEAN ALL	4.18 (36.9)	6.52 (20.7)	7.53 (30.4)	0.001	0.001

these differences were not significant (Kruskal Wallis statistic = 1.61, $P = 0.45$).

Of the 41 species detected in point counts, approximately half the species (24 species) showed significant heterogeneity in abundance in counts among habitats (Table 1). Of these species, 12 were most abundant in pine, 6 most abundant in sun coffee, and 6 most abundant in shade coffee. Only 1 species was found exclusively in sun coffee, 3 species exclusively in shade coffee, and 9 species exclusively in pine. Thus the native pine forest had more habitat specialists than either coffee habitat.

Of the 14 species which showed significant differences in abundance between the two types of coffee, 8 species were more abundant in shade coffee, 6 species were more abundant in sun coffee. Species which were significantly more abundant in sun than shade coffee include Narrow-billed Tody, Black-throated Blue Warbler, Common Yellowthroat, Yellow-rumped Warbler, Stripe-headed Tanager, and Rufous-collared Sparrow (scientific names listed in Table 1). Suggestive, but not statistically significant ($P \geq 0.06$ but ≤ 0.10), higher abundance in sun than shade coffee was found in Northern Mockingbird, Black-faced Grassquit, and Greater Antillean Bullfinch. Five of the species which were significantly more abundant in shade than sun coffee were nectarivorous, including Hispaniolan Emerald, Vervain Hummingbird, Antillean Mango, Cape May Warbler, and Bananaquit. Other species which were also significantly more abundant in shade coffee include Hispaniolan Woodpecker, Hispaniolan Lizard Cuckoo, and Greater Antillean Pewee. Greater abundance in shade coffee was suggested for Black-whiskered Vireos and Loggerhead Kingbirds, but the differences were not significant.

Estimated species richness, as determined by rarefaction of point count results, was considerably higher in pine forest than in either type of coffee which were both similar (Fig. 3). The Shannon-Weiner index values were all relatively low, with the highest value in pine forest ($H' = 1.35$) followed by shade coffee ($H' = 1.17$) and sun coffee ($H' = 1.11$). Despite the similarity in species richness and diversity in the two types of coffee, the correlation of relative abundance of species between the two coffee habitats was relatively low, although statistically significant

(Spearman $r = 0.44$, $df = 38$, $P = 0.001$). The highest correlation of relative abundance occurred between pine and sun coffee samples (Spearman $r = 0.52$, $df = 43$, $P = 0.0001$) and the lowest correlation occurred between pine and shade coffee samples (Spearman $r = 0.41$, $df = 46$, $P = 0.003$).

The three habitats differed in the proportion of individuals in each diet category. For example, nectarivores were most common in samples from shade coffee, where they accounted for 67 % of the 353 individuals detected there, in contrast to 25 % of the 88 individuals detected in sun coffee and 25 % of the 327 individuals detected in pine. However, fruit/seedeaters constituted 48 % of the individuals detected in sun coffee versus 26 % of those detected in pine and 3 % of those detected in shade coffee. Insectivores accounted for 49 % of the individuals detected in pine versus 30 % of those detected in shade coffee and 27 % of those detected in sun coffee. The distribution of detections among the three diet categories varied significantly among the habitats ($G = 205.0$ $df = 4$, $P < 0.001$). Thus, nectarivores predominated in point counts in shade coffee, fruit/seedeaters in sun coffee, and insectivores in pine forest.

We expected that matorral species would have their highest point count detection rates in sun coffee in contrast to forest species which were expected to have their highest counts in shade coffee. These predictions were tested by tallying the number of matorral species that had their highest counts in sun versus shade coffee, and the number of forest species that had their highest counts in either plantation type. Habitat generalists, common in both matorral and forest were excluded from the analysis (see Table 1 for habitat classification of each species). Our analysis indicates that 90 % of the matorral species ($n = 10$) had their highest counts in sun coffee in contrast to 93 % of the forest species ($n = 14$) which had their highest counts in shade coffee. Matorral and forest species differed significantly in the distribution of highest detections between the two types of plantations (Yates corrected $\chi^2 = 13.24$, $df = 1$, $P < 0.001$). Thus, matorral species are likely to be more abundant in sun than shade coffee, whereas the inverse applies for forest species.

Mist Netting. Netting and point count results were not expected to be strongly correlated, because the two methods do not always sample

equivalent vertical zones of vegetation and a species' detectability during a count may not be related to its likelihood of mist net capture. As expected relative species abundance as sampled by point counts was most strongly correlated with relative species abundance obtained by netting in the sun coffee where nets sampled the entire vertical foliage profile (Spearman $r=0.55$, $df=25$, $P < 0.01$). However in shade coffee and pine, where birds in the overstory had a lower likelihood of net capture, a weaker correlation was found between the relative abundance of species in the net sample compared with the point count sample in shade coffee (Spearman $r=0.37$, $df=26$, $P=0.07$) and in pine (Spearman $r=0.33$, $df=40$, $P=0.05$).

Nets were operated for a total of 4,149.4 net hours (1,002 net h in sun; 1,748.4 net h in shade; 1,399 net h in pine). Net capture rates were highest in sun coffee and lowest in shade coffee (Table 1), in contrast to point counts in which counts were highest in pine and shade coffee. The higher net capture rates in sun coffee also

included higher capture rates of both permanent residents and migrants compared with pine or shade coffee which had the lowest capture rates. Despite the lower capture rates in shade coffee, migrants made up the highest percentage of captures (41 % of 358 total captures) there compared with sun coffee (32 % of 370 total captures) and pine (26 % of 423 total captures). These differences in composition among the three habitats were significant ($G=20.03$, $df=2$, $P < 0.001$). Thus the netting data coincides with the point counts by indicating the relative importance of coffee plantations to migrants in contrast to pine.

Estimated species richness as determined by rarefaction of net captures was highest in pine and lowest in shade coffee, which differed only slightly from sun coffee (2 species more in a sample of 220 individuals, Fig. 3). Despite the similarity in species richness in the two types of coffee, the correlation of relative abundance of species between captures in the two coffee habitats was very low, although statistically

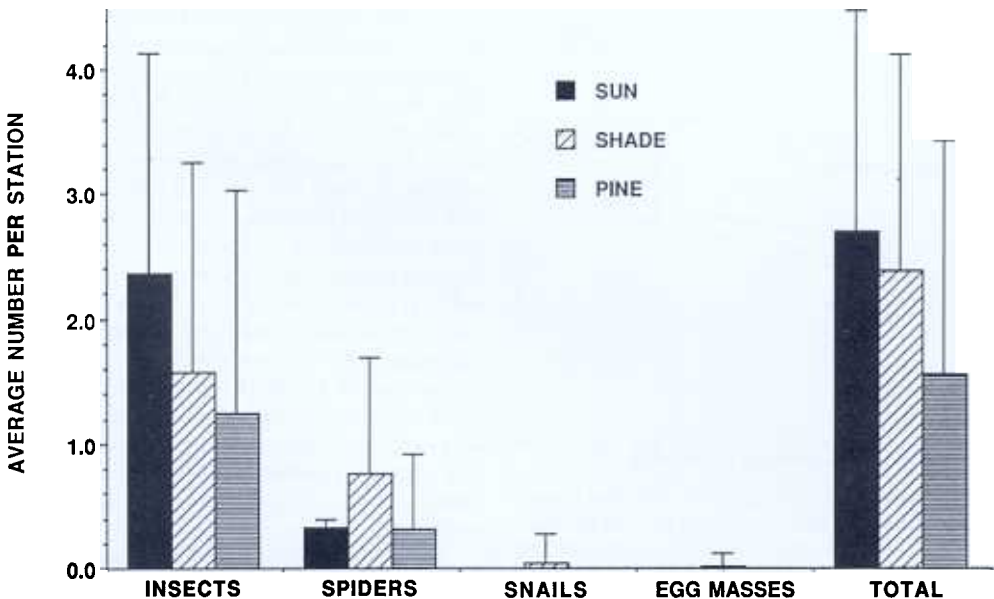


FIG. 2. Average (\pm SD) number of invertebrates per 2-min. station in the shrub-layer of sun and shade coffee plantations and pine forest in the Cordillera Central of the Dominican Republic. Leaf inspections were made in the shrub layer (1–1.5 m) during 2-minute intervals at 20 stations located three meters apart along north-south transects. Transects with 20 stations each were sampled in 3 sun coffee plantations, 11 shade coffee plantations, and 3 sites in pine forest.

significant (Spearman $r=0.33$, $df=29$, $P=0.05$). The highest correlation of relative abundance occurred between captures in pine and sun coffee (Spearman $r=0.52$, $df=29$, $P=0.006$) and the correlation between captures in pine and shade coffee were intermediate (Spearman $r=0.37$, $df=30$, $P=0.02$).

The habitats differed in numerical dominance of species and composition of the predominant species in the net samples. This was evident in the Shannon-Weiner index values which were similar in net samples from sun coffee ($H' = 1.20$) and pine ($H' = 1.18$), but differed from the very low value for shade coffee ($H' = 0.82$). This low value is partially explained by the high numerical dominance of Bananaquits in shade coffee, where they constituted 31 % of the

captures, in contrast to sun coffee and pine where it was also the most common species, but constituted only 16 % and 17 % of captures respectively. The numerical dominance of species in captures in shade coffee is even more evident when considering the contribution of the two most abundant species which accounted for 51 % of all captures, in contrast to pine (31 %) and sun coffee (27 %). In shade coffee, the five most commonly captured species constituted 76 % of all captures and included the following species in order of decreasing abundance: Bananaquit, Black-throated Blue Warbler, Hispaniolan Emerald, Ovenbird, and American Redstart. In pine, the five most abundant species constituted only 63 % of all captures and included the following in order of decreasing abundance: Bananaquit, Black-throated Blue Warbler, Hispaniolan Emerald, Antillean Mango, and Stripe-headed Tanager. In sun coffee, the top five species constituted 52 % of all captures and included the following in order of decreasing abundance: Bananaquit, Black-faced Grassquit, Greater Antillean Bullfinch, Black-throated Blue Warbler, and Common Yellowthroat.

Sex ratios were compared among habitats in the two species with adequate captures and easily distinguishable sexes. Sex ratios of Black-throated Blue Warblers and American Redstarts varied significantly ($G=35.63$, $df=2$, $P=0.001$; $G=10.19$, $df=2$, $P=0.006$, respectively) among the three habitats. In both Black-throated Blue Warblers and American Redstarts, males predominated in shade coffee (64.4 % of 73 captures, 68.8 % of 32 captures respectively), were least abundant in sun coffee (11.1 % of 59 captures, 35.0 % of 20 captures, respectively) and had intermediate or equivalent levels of abundance in pine (47.5 % of 59 captures, 35.7 % of 14 captures, respectively). Thus males of these two species predominated in sites with broadleaf overstory and understory and females predominated in sites where broadleaf vegetation was confined to understory shrubs.

The habitats differed in the proportion of captured individuals in each diet category as found in the point counts, although the differences were not as marked. Nectarivores made up a higher percentage of the 358 captures in shade coffee (43 %) than in pine (38 % of 393 captures) or sun coffee (25 % of 370 captures).

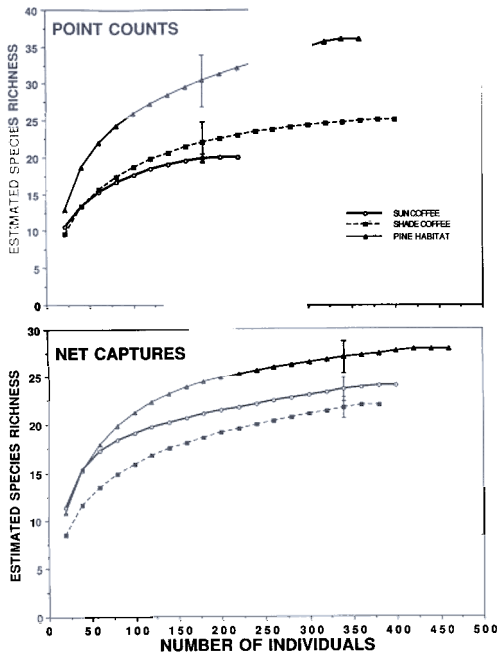


FIG. 3. Rarefaction curves for point count data (upper) and mist-net data (lower), showing the rate at which species richness increases as a function of the number of individuals sampled. The vertical line at $n=180$ individuals in point count sample (upper) and $n=340$ individuals in mist-net sample (lower) represents 2 standard deviations of the projected mean species richness. The curves are based on samples made in sun and shade coffee and pine forest in the Cordillera Central of the Dominican Republic.

Fruit/seedeaters constituted 30 % of the captures in sun coffee compared with 17 % of pine captures and 7 % of shade coffee captures. Insectivores predominated in all samples, and constituted 50 % of the captures in shade coffee, 46 % of the captures in pine and 44 % of the captures in sun coffee. The distribution of captures among the three diet categories varied significantly among the habitats ($G=79.12$, $df=4$, $P < 0.001$). Thus as found in the point counts, nectarivores were more commonly captured in shade coffee than elsewhere, and fruit/seedeaters more commonly captured in sun coffee.

The mist net and point count results were also similar by indicating that matorral species were likely to be most abundant in sun relative to shade coffee in contrast to forest species in which the inverse applied. For example, 100 % of the captured matorral species ($n=7$) had higher capture rates in sun than shade coffee, in contrast to 82 % of the captured forest species ($n=11$) which had higher capture rates in shade than sun coffee. These differences were significant (Yates corrected $\chi^2=8.42$, $df=1$, $P=0.004$) and consistent with the point count results.

DISCUSSION

Some of the differences in avian distribution among the three habitats may result from the fact that the habitats were not equivalent in area and altitude, both of which can affect avian distribution. For instance, habitat area can influence both the number of species and individuals present in an isolated habitat with most studies demonstrating an increase in species number with area (e.g., MacArthur & Wilson 1967), although in some habitats an inverse relation with area may exist (Loman & von Schantz 1991). These factors may contribute to some of the differences among habitats found in this study, although we suspect that the effects may be small relative to intrinsic characteristics of the habitats.

The larger fragment size and greater altitudinal range over which pine forest was sampled, likely contributed to some differences in species abundance compared to coffee plantations. However, these were minor factors relative to the importance of the vegetation diversity of these forests and the fact that pine forest was the

native habitat which was converted for plantations. Moreover, the structural and taxonomic diversity of the pine forest undoubtedly contributes to higher avian species richness. This vegetation diversity includes not only the obvious structural differences between pine and broadleaf understory, but more importantly, the taxonomic diversity of the broadleaf understory which provides a variety of food resources. The understory may serve as a source of colonists given that only a few species appeared to be pine specialists (e.g., Pine Warbler, Greater Antillean Elaenia; Antillean Siskin and White-winged Crossbill were found outside our surveys as listed with scientific names in Appendix), and some species foraged in both pine and broadleaf understory (e.g., Greater Antillean Pewee, Black-crowned Palm Tanager) or only in the broadleaf understory (Ground Warbler, Rufous-throated Solitaire, Stripe-headed Tanager, Rufous-collared Sparrow, Greater Antillean Bullfinch). Thus, although the higher avian species richness of pine forest compared to coffee plantations may be partially attributed to its greater area and altitudinal range, the fact that pine forest is the native habitat of the region (i.e., a source) and its higher vegetation diversity are all likely to be important contributing factors to the native forest's higher species richness than the cultivated habitats.

Area undoubtedly contributed to differences in avian abundance in shade coffee, but the effect may have been small. Shade coffee occurred in the smallest habitat patches and preliminary analysis (Wunderle, in prep) has suggested that the number of resident (but not migrant) species increases with plantation size. This analysis also shows that species such as Hispaniolan Woodpecker, Rufous-throated Solitaire, Hispaniolan Lizard Cuckoo, and Narrow-billed Tody are more abundant in large than small shade plantations and therefore these species may have been even more abundant in our samples had larger plantations been censused. Nevertheless, despite their sensitivity to area effects, woodpeckers and cuckoos were still more common in our relatively small shade coffee plantations than in the larger sun coffee plantations.

The larger size and higher altitude of our sun coffee plantations relative to shade plantations

may have contributed to some of the differences in species abundance. Sun coffee plantations were confined to higher altitudes which probably affected species such as todies in which distribution is partially related to altitude (Kepler 1977). For example, Narrow-billed Todies, which are most abundant at higher altitudes, were most common in sun coffee while Broad-billed Todies (the lowland species), were most common in point counts in pine or net samples in shade coffee, both of which were sampled at lower altitudes. However except for todies, we suspect that the effects of altitude and plantation size on species abundance in coffee plantations were relatively small in comparison to the obvious structural differences between the two plantation types.

Our diet classification scheme (i.e., Faaborg 1985) is limited by the fact that it does not allow for variation among individuals and habitats, and ignores the fact that some species are not easily classified. Nonetheless, we believe that this scheme adequately describes most of the broad patterns found among our habitats. Even taking diet variation into account, most patterns found in this study still persist. For example, our foraging observations (Wunderle & Latta, in prep.) indicate that our scheme underestimates the number of individuals feeding on nectar in shade coffee as several "non-nectarivores" opportunistically fed on *Inga* flowers (e.g., Hispaniolan Woodpecker, Black-throated Blue Warbler, Black-cowled Oriole, Stripe-headed Tanager). However, this is unlikely in our sun coffee plantations where flowers were absent during our sampling and coffee flowers, when in bloom, are only infrequently visited by avian nectarivores and therefore the incidence of nectarivory there is unlikely to change. Only in pine would we expect the predominant diet type to shift (i.e., from a predominance of insectivory to frugivory) with increased fruit production in the understory when insectivores opportunistically take fruit (e.g., Greater Antillean Elaenia and Hispaniolan Woodpeckers). Thus despite the weakness of our diet classification scheme we expect the predominance of nectarivores in shade coffee and fruit/seed eaters in sun coffee to persist, while the importance of frugivory would increase in pine with an increase in understory fruit production.

Besides the shade overstory, the two types of coffee plantations differed structurally in the density of coffee foliage, composition of coffee varieties, and the diversity of plants interspersed between the coffee. However, the shade overstory undoubtedly contributed to most of the variation in avian assemblage composition and species abundance observed between plantations. This was evident in the greater abundance of Hispaniolan Woodpeckers, Hispaniolan Lizard Cuckoos, and Greater Antillean Pewees in shade plantations, and also more Black-whiskered Vireos had March–April censuses been included (Wunderle, unpubl. data). However, it was the presence of *Inga vera* flowers which contributed substantially to avian differences between the plantations. This was evident in the variety and abundance of nectarivores found in the shade plantations where they fed on the *Inga* flowers throughout the winter months (October–April). Because flowering of *Inga* was asynchronous, at least some *Inga* flowers were present in shade plantations throughout the winter and nectarivores were observed through this period (Wunderle & Latta, unpubl. data). Greenberg (in press) has similarly found *Inga* nectar to be an important food source in his Mexican shade coffee plantations where he found 12 species of nectarivores and a variety of omnivores, including some which invade the plantations in the dry season to feed on *Inga* flowers. In addition to the *Inga* flowers, the seed pods also attracted Hispaniolan Parakeets and Parrots. Thus, the shade overstory and specifically *Inga vera* accounted for much of the variation between shade and sun plantations.

The influence of the shade canopy extended down into the coffee understory as evident in the differences in relative abundance and composition of avian assemblages in net samples from shade and sun coffee. For example, even though very little floral nectar was available in the coffee understory, nectarivores had higher capture rates and constituted a higher proportion of birds captured in shade than sun coffee. Evidently, some canopy nectarivores (particularly Bananquits) descend into the coffee understory, as did most insectivores which were also more commonly observed in the canopy than in coffee (Wunderle & Latta, in prep.). One exception to this pattern was the ground-foraging insectivore.

tivorous Ovenbird, which was most abundant in shade coffee, as expected for a species known from woodlands with a broadleaf canopy (Wunderle & Waide 1993). Thus even though the coffee in sun and shade plantations might offer similar resources, the presence of an overstory canopy affects the composition of the avian assemblage in the coffee. This occurs mostly because the canopy initially attracts some foragers which subsequently descend into the coffee understory.

Insectivores were present in the coffee and pine understory and even predominated in net captures, although our counts of invertebrates in the shrub layer were relatively low. For example, our averages for total invertebrates per station (2.7 sun, 2.4 shade, 1.6 in pine) fell within or below the range (2.7–4.9) found by Askins & Ewert (1994) using the same methods as ours in dry forest on St John, USVI, which also had a low abundance of insectivorous nearctic migrants. These values were much lower than their counts in moist forest (6.6–12.0), where insectivorous nearctic migrants were abundant. Although our low invertebrate counts were not unexpected, given the abundance of secondary compounds in coffee leaves (Frischknecht *et al.* 1986) and those of pine understory shrubs (most of which were tough and aromatic), we did expect a correspondingly lower abundance of insectivores in these shrubs. While it is possible that we failed to sample the invertebrate prey taken by insectivores in the coffee or pine understory, we suspect that other reasons explain the relatively high abundance of insectivores in the shrub layer. These include the possibility that many of the insectivores wander through the habitat in search of food, or feed on other resources (e.g., fruit in pine understory), or forage primarily in the canopy and only occasionally descend into the understory. The latter was particularly common in shade coffee where we frequently observed insectivores feeding on caterpillars in the *Inga* overstory, suggesting that invertebrate densities were probably higher there than in the coffee (Wunderle & Latta, in prep.).

The avian assemblage in sun coffee was characterized by birds of open brushland (matorral) or shrubby understory of pine forests. Many of these species are fruit/seed eaters, which were more prevalent in sun than shade coffee. These

include Black-faced Grassquits and Rufous-colored Sparrows, which fed on seeds of grasses and herbs between coffee rows, and others such as Stripe-headed Tanagers and Greater Antillean Bullfinches which sometimes fed on ripe coffee fruit and/or seeds (Wunderle & Latta, unpubl data). Two wintering Nearctic migrants, characteristic of early successional stages in the Caribbean (Wunderle and Waide 1993), were abundant in sun coffee in contrast to shade coffee where they were rare (Common Yellowthroat) or absent (Yellow-rumped Warbler). Even among the rare species in sun coffee, in which significant differences were not detected between plantation types, some were characteristic of matorral (Northern Mockingbird, Yellow-faced Grassquit, Prairie Warbler) and the shrubby understory of pine (Ground Warbler). Thus given the similarity of sun coffee to shrubby habitats as found in the understory of pine, it is not surprising that a stronger correlation was found between relative abundance of species in sun coffee and pine forest than between sun and shade coffee.

The female-biased sex ratio of two nearctic migrant species in sun coffee in contrast to the male-biased sex ratio in shade coffee is consistent with previous findings of sexual habitat segregation by nearctic migrants on the wintering grounds (e.g., Lynch *et al.* 1985, Lopez Ornat & Greenberg 1990, Wunderle 1992, Parrish & Sherry 1994). Generally in the Nearctic migrants in which sexual habitat segregation occurs, males are more abundant in mature, tall-stature forest while females predominate in shrubby or second-growth sites. Apparently, for wintering Black-throated Blue Warblers and American Redstarts, shade coffee substitutes for tall-stature forest and sun coffee substitutes for shrubby second-growth. In redstarts, interference competition may cause this segregation in which male territoriality prevents females from settling in tall-stature sites (Marra *et al.* 1993), which may have more seasonally stable food supplies than the habitats to which female redstarts are relegated (Parrish & Sherry 1994). Whether this mechanism applies to habitat segregation between sun and shade coffee is unknown.

The higher net capture rates in sun than shade coffee are attributable mostly to the fact that the entire vertical profile of the vegetation was sampled, in contrast to the shade plantations

where the canopy was missed. Another contributing factor to the higher capture rates in sun coffee, which can not presently be eliminated, is the possibility that wandering, and the absence of site persistence, may be more common in birds in sun than shade coffee. This may occur in Black-throated Blue Warblers, in which overwinter site persistence has been found to be lower in sites where females predominate compared to sites where males predominate (Wunderle 1995), although this was not the case in American Redstarts (Parrish & Sherry 1994). Obviously, future studies using banded birds should document the extent of wandering or site persistence in sun versus shade coffee.

Site persistence may be characteristic of many species in shade coffee. For example, we have found relatively high levels of overwinter site persistence in Nearctic migrants including Black-throated Blue Warblers, American Redstarts, Black-and-white Warblers, and Ovenbirds (Wunderle & Latta 1994). Site persistence in shade coffee may also be relatively high for many resident species as supported by the presence of active nests (Antillean Mango, Hispaniolan Emerald, Broad-billed Tody, Palm Chat, Red-legged Thrush, Bananaquit, Antillean Euphonia, Black-crowned Palm Tanager) and the recapture of marked individuals in the same plantation at intervals of 3–5 months (Narrow-billed Tody, Broad-billed Tody, Antillean Mango, Bananaquit, Black-crowned Palm Tanager). This suggests that shade coffee plantations provide adequate resources for site persistence by some species.

Avian assemblage differences between sun and shade coffee plantations are likely to be more distinct on the mainland than on islands, and in regions where the predominate species source is native broadleaf forest rather than pine with broadleaf understory. Although species differed in abundance in the two plantation types, almost half the species observed or captured in coffee plantations were found in both plantation types (45.9% of 37 species). Some of this species sharing may be attributed to the broader habitat breadth of island species in contrast to the mainland where habitat specialization is more prevalent (e.g., Cox & Ricklefs 1977). In addition, the absence of extensive broadleaf forest in our study area may have limited the number of broadleaf forest specialists

(e.g., trogons, quail-doves) available to colonize the shade plantations. However, nearby pine forests with shrubby understory provided a source for forest generalists (e.g., Black-crowned Palm Tanager, Narrow-billed Tody) which utilize a range of successional stages, and thus are not necessarily restricted to sites with a broadleaf overstory. Thus we expect that shade coffee in regions with native broadleaf forest will have more forest specialists and consequently an avifauna more distinctive than sun coffee, particularly on continents where habitat specialization is more prevalent.

Sun coffee may contribute to regional biodiversity in agricultural regions by providing habitat for some shrub or matorral species. However, even assuming that sun coffee has adequate resources for some matorral species, the contribution of sun coffee to regional biodiversity will be limited given that it provides habitat for species already common in disturbed sites. Moreover, the species inhabiting sun coffee are not likely to be the species threatened with habitat loss, as are the forest species. Therefore, the greatest contribution to biodiversity in agricultural regions comes from forest fragments or plantations with tree canopy overstory, such as shade coffee which provides habitat for some forest species. This is evident in the Cordillera Central of the Dominican Republic where elimination of the shade overstory in coffee plantations will contribute to local declines in Hispaniolan Parrots, Hispaniolan Parakeets, Hispaniolan Woodpeckers, Hispaniolan Lizard Cuckoos, Vervain Hummingbirds, Hispaniolan Emeralds, Antillean Mangos, and Greater Antillean Pewees as well as some habitat generalists.

ACKNOWLEDGEMENTS

We gratefully acknowledge the fine assistance provided by Teodoro Lara, Esteban Terranova, and Eduardo Vazquez. We thank the numerous coffee plantation owners for permission to work in their plantations. The manuscript benefited from the constructive comments of Russell Greenberg, Lisa J. Petit, and two anonymous reviewers. Funding was provided by the National Fish and Wildlife Foundation and the John T. and Catherine C. MacArthur Foundation.

REFERENCES

- Askins, R. A., & D. N. Ewert. 1994. Wildlife Research, 1993–94. Annual Letter, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico.
- Askins, R. A., Lynch, J. F., & R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7: 1–57.
- Aguilar-Ortiz, F. 1982. Estudio ecológico de las aves del cafetal. Pp. 103–128 in Avila Jimenez, E. (ed.). *Estudios Ecológicos en el agroecosistema cafetalero*. Insto. Nacional de Investigaciones sobre Recursos Bióticos (INIREB), México.
- Beehler, B. M., Krishna Raju, K. S. R., & S. Ali. 1987. Avian use of man-disturbed habitats in the eastern Ghats, India. *Ibis* 129: 197–211.
- Bond, J. 1979. *Birds of the West Indies*. London.
- Borrero, J. I., 1986. La substitución de cafetales de sombrero por caturrales y su efecto negativo sobre la fauna de vertebrados. *Caldasia* 15:725–732.
- Brash, A. R. 1987. The history of avian extinction and forest conversion on Puerto Rico. *Biol. Conservation* 39: 97–111.
- Cox, G. W., & R. E. Ricklefs. 1977. Species diversity and ecological release in Caribbean land bird faunas. *Oikos* 28: 113–122.
- Dodd, A. S. 1987. *Aves de la República Dominicana*. Museo Nacional de Historia Natural, Santo Domingo.
- Faaborg, J. 1985. Ecological constraints on West Indian bird distributions. *Ornithol. Monogr.* 36: 621–653.
- Frischknecht, P. M., Dufek, J. V., & T. W. Baumann. 1986. Purine alkaloid development in buds and developing leaflets of *Coffea arabica*: an expression of optimal defense strategy. *Phytochemistry* 25: 613.
- Greenberg, R. 1994. Coffee and birds. *Smithsonian Magazine*, November pp. 24–27.
- Greenberg, R., Salgado, J., Warkentin, I., & P. Bichier. 1995. Managed forest patches and conservation of migratory birds in Chiapas, Mexico. Pp. 178–189. in Wilson, M. H., & S. A. Sader (eds.). *Conservation of Neotropical migratory birds in Mexico*. Maine Agricultural and Forest Experiment Station, Orono, Maine.
- Greenberg, R., Bichier, P., & J. Sterling. In press. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. *Biotropica*.
- Griscom, L. 1932. The distribution of bird-life in Guatemala. *Bull. Amer. Mus. Nat. Hist.* 64.
- Holmes, R. T., Sherry, T. W., & F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. *Ecol. Monogr.* 56: 201–220.
- Hutto, R. L., Pletschet, S. M., & P. Hendricks. 1986. A fixed-radius point count method for non-breeding and breeding season use. *Auk* 103: 593–602.
- Kepler, A. K. 1977. Comparative study of todies (Todiidae): with emphasis on the Puerto Rican Tody, *Todus mexicanus*. *Nuttall Ornithol. Club*. No. 16.
- Krebs, C. J. 1989. *Ecological methodology*. New York.
- Loman, J., & T. von Schantz. 1991. Birds in a farmland – more species in small than large habitat island. *Cons. Biol.* 5: 176–188.
- Lopez Ornat, A., & R. Greenberg. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107: 539–543.
- Lynch, J. F., Morton, E. S., & M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). *Auk* 102: 714–721.
- MacArthur, R. H., & E. O. Wilson. 1967. *The theory of island biogeography*. Princeton, NJ.
- Marra, P. P., Sherry, T. W., & R. T. Holmes. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk* 110: 565–572.
- Parrish, J. D., & T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. *Auk* 111: 38–49.
- Perfecto, I., Rice, R., Greenberg, R., & M. Van der Voort. In press. Shade coffee: a disappearing refuge for biodiversity. *Bioscience*
- Petit, D. R., Lynch, J. F., Hutto, R. L., Blake, J. G., & R. B. Waide. 1993. Management and conservation of migratory landbirds overwintering in the Neotropics. Pp. 70–93. in Finch, D. M., & P. W. Stangel (eds.). *Status and management of Neotropical migratory birds*. USDA Forest Service, Gen. Tech. Rep. RM-229, Fort Collins, Co.
- Pyle, P., Howell, S. N. G., Yunick, R. P., & D. F. DeSante. 1987. *Identification guide to North American passerines*. Bolinas, Cal.
- Robbins, C. S., Dowell, B. A., Dawson, D. K., Colón, J. A., Estrada, R., Sutton, A., Sutton, R., & D. Weyer. 1992. Comparison of Neotropical migrant landbird populations wintering in tropical forest, isolated forest fragments, and agricultural habitats. Pp. 207–220 in Hagan, J. M., III, & D. W. Johnston (eds.). *Ecology and conservation of Neotropical migrant landbirds*. Washington, D.C.
- Schemske, D. W., & N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938–945.
- Simberloff, D. S. 1972. Properties of the rarefaction diversity measurement. *Am. Nat.* 106: 414–418.
- Simberloff, D. S. 1978. Use of rarefaction and related methods in ecology. Pp. 150–165 in Cairns, J., Livingston, R. J., & K. I. Dickson (eds.). *Biological*

- data in water pollution assessment: quantitative and statistical analyses. Am. Soc. Testing and Materials Spec. Tech. Publ. No. 652.
- Sokal, R. R., & F. J. Rohlf. 1981. Biometry. New York.
- Terborgh, J. 1989. Where have all the birds gone? Princeton.
- Vannini, J. P. 1994. Nearctic avian migrants in coffee plantations and forest fragments of south-western Guatemala. Bird. Cons. Internat. 4: 209–232.
- Wetmore, A. 1916. Birds of Porto Rico. U. S. Dept. Agric. Bull. No. 326.
- Wille, C. 1994. The birds and beans. Audubon 96: 58–64.
- Wunderle, J. M., Jr. 1992. Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico. Pp. 299–307 in Hagan, J. M., III, & D. W. Johnston (eds.). Ecology and conservation of Neotropical migrant landbirds. Washington, D. C.
- Wunderle, J. M., Jr. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. Auk 112: 931–946.
- Wunderle, J. M., Jr., & S. C. Latta. 1994. Population biology and turnover of Nearctic migrants wintering in small coffee plantations in the Dominican Republic. J. Orn. 135: 477.
- Wunderle, J. M., Jr., & R. B. Waide. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Condor 95: 904–933.
- Wunderle, J. M., Jr., & R. B. Waide. 1994. Future prospects for Nearctic migrants wintering in Caribbean forests. Bird Cons. Internat. 4: 191–207.

APPENDIX. Additional birds detected during the study, but not included in the analysis (*), or species detected outside the period summarized in the methods. Shade coffee also sampled in period Oct.—Nov., Jan.—Feb., Mar.—April in winters 1992–93; 1993–94; 1994–95. Sun coffee sampled only in Feb. 1994. Pine sampled Feb.—Mar. 1994, and 1995.

Shade coffee. Cattle Egret (*Bubulcus ibis*), American Kestrel (*Falco sparverius*)*, Sharp-shinned Hawk (*Accipiter striatus*)*, Scaly-naped Pigeon (*Columba squamosa*), Plain Pigeon (*Columba inornata*), Common Ground Dove (*Columbina passerina*), Hispaniolan Parrot (*Amazona ventralis*), Hispaniolan Parakeet (*Aratinga chloroptera*), Barn Owl (*Tyto alba*), Greater Antillean Elaenia (*Elaenia fallax*), Gray Kingbird (*Tyrannus dominicensis*), Stolid Flycatcher (*Myiarchus stolidus*), Northern Mockingbird (*Mimus polyglottos*), Catbird (*Dumetella carolinensis*), Bicknell's Thrush (*Catharus bicknelli*), Red-eyed Vireo (*Vireo olivaceus*), Magnolia Warbler (*Dendroica magnolia*), Black-throated Green Warbler (*Dendroica virens*), Prairie Warbler (*Dendroica discolor*), Palm Warbler (*Dendroica palmarum*), Northern Parula (*Parula americana*), Brewster's Warbler (*Vermivora chrysoptera x pinus*), Tennessee Warbler (*Vermivora peregrina*), Louisiana Waterthrush (*Seiurus motacilla*), Greater Antillean Grackle (*Quiscalus niger*), Summer Tanager (*Piranga rubra*), Greater Antillean Bullfinch (*Loxigilla violacea*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Indigo Bunting (*Passerina cyanea*).

Sun coffee. American Kestrel*

Pine. Cattle Egret, American Kestrel*, Sharp-shinned Hawk*, Red-tailed Hawk (*Buteo jamaicensis*), Common Bobwhite (*Colinus virginianus*), Barn Owl (*Tyto alba*), Hispaniolan Trogon (*Tamnotrogon roseigaster*), Zenaida Dove (*Zenaida aurita*), White-winged Dove (*Zenaida asiatica*), Common Ground Dove, Hispaniolan Parakeet, Gray Kingbird, Northern Mockingbird, Blue-winged Warbler (*Vermivora pinus*), Northern Parula, Magnolia Warbler, Black-throated Green Warbler, Palm Warbler, Black-cowled Oriole, Antillean Siskin, White-winged Crossbill (*Loxia leucoptera*), Indigo Bunting.