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Bird Populations in Rustic and Planted Shade Coffee Plantations of Eastern Chiapas, México[1]

Russell Greenberg, Peter Bichier, and **John Sterling**

Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC 20008

ABSTRACT

Much of the remaining "forest" vegetation in eastern Chiapas, Mexico is managed for coffee production. In this region coffee is grown under either the canopy of natural forest or under a planted canopy dominated by *Inga* spp. Despite the large differences in diversity of dominant plant species, both planted and rustic shade coffee plantations support a high overall diversity of bird species; we recorded approximately 105 species in each plantation type on fixed radius point counts. We accumulated a combined species list of 180 species on repeatedly surveyed transects through both coffee plantation types. These values are exceeded regionally only by moist tropical forest. Of the habitats surveyed, shade coffee was second only to acacia groves in the abundance and diversity of Nearctic migrants. The two plantation types have similar bird species lists and both are similar in composition to the dominant woodland—mixed pine-oak. Both types of shade coffee plantation habitats differ from other local habitats in supporting highly seasonal bird populations. Survey numbers almost double during the dry season—an increase that is found in omnivorous migrants and omnivorous, frugivorous, and nectarivorous resident species. Particularly large influxes were found for Tennessee warblers (*Vermivora peregrina*) and northern orioles (*Icterus galbula*) in *Inga* dominated plantations.

Key words: Chiapas; coffee plantations; Inga; *migratory birds; seasonality; shade coffee.*

Ornithologists in tropical countries have long recognized that coffee farms often are excellent birding spots (Griscom 1932). In particular, shade coffee and cacao plantations are noted for their high diversity and density of migratory birds (Robbins *et al.* 1992, Petit *et al.* 1993, Wunderle & Waide 1993, Vannini 1994). Evidence for the importance of shade coffee plantations for all forest-dwelling birds (resident and migrant) was found in two studies. Aguilar-Ortiz (1982) conducted surveys of mixed shade coffee plantations, and several dominant forest types in the coffee zone of Veracruz, Mexico. Wunderle and Latta (1996) compared shade coffee plantations to remnant pine forest in the Dominican Republic. Both studies found that species richness of shade coffee plantations compared favorably with other natural forest habitats with which most species were shared.

Shade coffee varies as a habitat for birds in accordance with different cultivation systems. Coffee cultivation systems fall along a continuum, ranging from "traditional" to "modern" (*e.g.*, see Fuentes-Flores [1982] for a classification of Mexican systems). Modern systems have reduced or no shade and when a shade canopy exists it is often a monoculture. Traditional plantations are quite varied. In some areas the practice of inserting coffee into the existing natural vegetation (rustic coffee) has led to a closed canopy system exhibiting a highly diverse plant community. More commonly, plantings of leguminous, nitrogen-fixing trees, particularly, *Inga* spp., as well as *Erythrina* spp. and *Gliricidia sepium* (Jacq.) Kunth ex Walp., form an important component of many coffee farms. Throughout northern Latin America, it is common to find a variety of other trees, including fruit trees, mixed in with the coffee, creating multi-strata systems in which coffee itself forms the shrub layer. We refer to these mixed systems as "traditional planted plantations."

Rustic coffee plantations are relatively rare. However, they remain common in certain areas of eastern Chiapas (Marquez 1988). In addition, the Ocosingo area has numerous traditional planted plantations. The presence of both cultivation types in the same region allows for direct comparisons of their associated bird communities. The purpose of this paper is to present comparative data on the abundance and diversity of birds in the two coffee plantation types, in terms of the avifaunal composition, seasonality, and similarity to other habitats in the region. The comparison is not experimental and therefore not without potential confounding variables. However, the comparison should delineate some patterns that can be tied to the cultivation type with more thoroughly controlled studies in the future.

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STUDY SITES

Research was conducted in the vicinity of Ocosingo—including the Ocosingo Valley and the roads to Yajalon and Sibaca. Ocosingo receives a relatively low amount of rainfall (1800 mm per year) and experiences a lengthy dry season (February–May, Garcia 1988). The study area is in the lower elevational range (800–1600 m in elevation) of the pine-oak belt of eastern Chiapas. Most of the remaining natural vegetation is disturbed (grazed and periodically burned) pine-oak woodland. On moist slopes one can find pine-oak *Liquidambar* and lower montane tropical forest along ridges. See Breedlove (1981) for a botanical description of the major habitats in the region.

The valley floors are covered primarily with cattle pastures held in large (100–600 ha) holdings. Ejidos (community-owned lands) are situated in the surrounding hills, which are covered with degraded pine-oak woodland and pine or oak savanna, corn fields and corn field fallows, and coffee plantations. Coffee plantations are found primarily along arroyos, and are of two distinct origins (Marquez 1988). Rustic coffee is planted primarily in the shade of semi-deciduous tropical broad-leaved forest—a relatively uncommon community in eastern Chiapas (Breedlove 1981), and one that is presently found in the Ocosingo region only in coffee plantations. Typical canopy trees include *Spondias mombin, Bursera simaruba* (L.) Sarg. Bursuraceae, *Dendropanax arborea* (L.) Planch & Decne (Araliaceae), *Cupania dentata* DC. (Sapindaceae), *Quercus* spp., *Trichilia havanensis* Jacq. (Meliaceae). "*Inga*" plantations are dominated by species of *Inga* which produce a large crop of flowers used by birds in late March–early May, as well as *Croton glabellus* L. Euphorbiaceae and *Heliocarpus Donnell-Smithii* Rose (Tiliaceae), as well as small numbers of fruit trees (Zapotaceae, *Citrus,* Mango *Mangifera indica* L.).

At least until the early 1990s, coffee plantation has been a rapidly expanding habitat type in Chiapas, increasing from 71,000 ha in 1950 to 140,000 ha in 1970 and 214,000 ha in 1990 (Rice pers. comm.). Much of the impetus for the increase in coffee production in the region came from the effects of the decline of corn prices and the advent of INMECAFE, a government agency which provided credit and assistance in marketing to farmers in the coffee sector, as well as high coffee prices. The plantations in the Ocosingo area are generally old and traditional, with a tall and well developed canopy. High technology plantations with reduced or no shade (sun coffee) are virtually unknown in the study area, but plantations grown under heavily pruned monocultures are common to the south and west.

METHODS

Birds were censused using two complementary techniques: fixed radius point counts designed to provide broad coverage of numerous sites, and repeatedly censused, fixed-width transects (Greenberg 1992) to determine seasonality of habitat use. Fixed distances were used to assure homogeneity of habitat surveyed (Hutto *et al.* 1986, Petit *et al.* 1994) since the surveys were conducted in characteristically patchy habitats. A total of 222 point counts were conducted in rustic and planted plantations from January–March 1993 for 10 min each during the period 06:45–10:00, therefore nocturnal birds are not included in these analyses. Points were located at least 25 m from the edge of the woodlots and 200 m from the nearest point. All birds detected within 25 m were recorded. In this analysis we exclude individuals that flew over the point. In addition, the surveyor recorded the number of trees, the estimated canopy height, as well as the aerial extent of the plantation, the number of tree morphospecies, and the average coffee plant height for the 25 m radius circle. Differences in both bird and habitat data were tested between plantation types by averaging results from multiple points within plantations and using each plantation as an independent observation.

We also compare results of coffee plantations with data from other major habitats in the region. Point counts were conducted from January–March 1991–1993 in the following major habitats (lowland sites < 500 m, mid-elevation 900–1500 m, and high-elevation $> 2,000$ m): lowland tropical forest, lowland second growth, lowland pasture, mid-elevation pine-oak *Liquidambar* forest, montane forest, mid-elevation pine forest, mid-elevation farm and garden, mid-elevation second growth, mid-elevation coffee plantation (both under diverse forest canopy and under a monoculture of planted trees, *e.g., Inga*), high elevation farm, high elevation pine-oak woodland, high elevation second growth, and high elevation pine forest.

Transects were 1 km long by 40 m wide and flagged each 50 m. Each 1 km transect was surveyed weekly during the winters of 1992–3 and 1993–4 from October to late March (N = 18 weeks). It should be noted that most coffee plantations in the Ocosingo area are small and it is

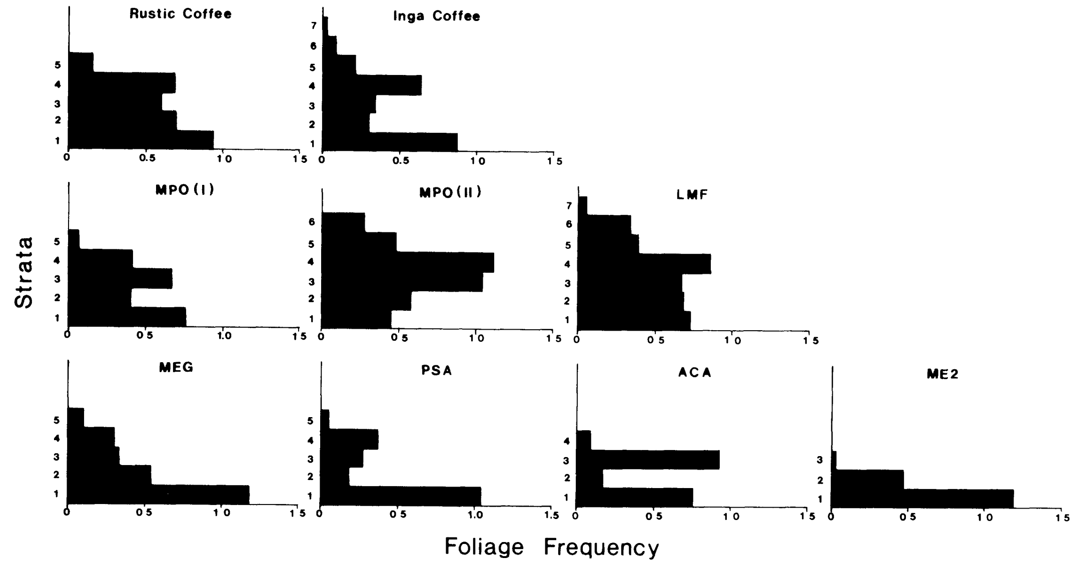

FIGURE 1. Foliage height profiles for habitat transects in the Ocosingo, Chiapas region. Strata are as follows: 1 = 0–2 m, 2 = 2.1–5 m, 3 = 5.1–8 m, 4 = 8.1–12 m, 5 = 12.1–15 m, 6 = 15.1–20 m, 7 = 20.1–30 m. Foliage frequency is the mean number of foliage "hits" per stratum per point.

difficult to find ones large enough in which to place a 1 km transect. To the degree there is an area effect, results from the transects will portray a best case scenario for the diversity of birds in plantations. We will use the data from transects primarily to examine seasonal changes in the detection and presumably the abundance of birds. Data presented here were collected as a more general assessment of migratory bird distribution in southern Mexico. For this paper we analyze the seasonal pattern of occurrence of birds in mid-elevation habitats. The following is a brief description of the habitats surveyed: pine-oak woodland (2 transects), riparian trees in pasture, rustic coffee plantation (under forest trees), planted coffee plantation, scrubby second growth, acacia woodland, and pine-oak savanna.

To compare gross vegetative structure of the major habitats surveyed near Ocosingo, foliage height profiles were recorded at 100 points (every 10 m) along these transects. The frequency of foliage "contacts" per point in different strata is presented in Figure 1. The foliage distribution of both plantation types is more similar to other forest habitats than to the secondary habitats. *Inga* plantations clearly show the high density of foliage in the *Inga* and coffee layers. Based on the correlation of foliage frequency per strata, rustic coffee is most similar to lower montane forest (r = 0.923), low-elevation pine-oak woodland (MPOI, 0.899), and gallery forest (0.851), and is slightly less similar to *Inga* coffee (0.774). *Inga* coffee is most similar to pine-oak savanna (0.827), rustic coffee (0.774), and lower montane forest (0.743).

To investigate further the ecological underpinnings of the patterns presented, we have classified the species into broad guilds. For many of the species, we have no quantitative data on foraging behavior or diet. Rather, the guild classifications are based on our impressions of the species based on our collective observations. In addition, we used information on diet presented in Stiles and Skutch (1989). The classification is presented for species occurring in coffee plantations. The guild classification for all species encountered in the study will be published elsewhere. This scheme should be improved with more quantitative studies. In addition, the system is typological (*i.e.,* one class per species despite seasonal, individual, and other types of variation) and some species are not easily classified. Nevertheless, we believe this first effort at classification is adequate for the broad patterns we described. Species are categorized into strata of occurrence which include: canopy (birds that forage in the crowns of trees), understory (birds that forage in shrubbery under trees), scrub (birds that forage in shrubbery in open areas), trunk (birds that occur on trunks or branches at all levels), ground (birds that forage on the ground or in leaf litter). Species are also classified by diet: insectivores (spe-

TABLE 1. *The number of individual and species of migrants per point and overall species richness in coffee plantations and other habitats in Chiapas based on point counts.*

Habitat	Number of points	Common migrant species[a]	Migrant individuals per point $\bar{x}$ (SE)	Resident individuals per point $\bar{x}$ (SE)	Estimated species[b] total (SD)
Acacia woodlot	73	18	9.0 (1.1)	3.2 (1.2)	50.8 (1.8)
Low elevation pasture	70	3	1.2 (0.6)	2.1 (1.3)	38.1 (1.2)
Low elevation, 2nd growth	100	6	2.5 (0.7)	4.5 (2.2)	68.1 (3.7)
Low elevation gallery	187	13	4.7 (0.7)	7.4 (2.5)	68.7 (3.0)
Low elevation forest	102	5	1.2 (0.5)	7.0 (2.6)	81.6 (3.7)
Mid-elevation pasture	70	5	1.2 (0.6)	1.9 (2.0)	46.4 (1.2)
Mid-elevation 2nd growth	100	4	2.1 (0.7)	1.8 (1.0)	49.9 (2.3)
Mid-elevation milpa	70	8	2.3 (0.9)	2.8 (1.5)	56.0 (2.4)
Inga coffee	125	11	5.3 (1.1)	4.7 (1.8)	64.7 (3.6)
Rustic coffee	97	11	4.3 (1.3)	5.8 (2.5)	68.7 (3.7)
Mid-elevation gallery	52	13	4.6 (1.3)	2.5 (1.2)	56.8 (2.8)
Mid-elevation Pine-Oak *Liquidambar*	100	3	1.2 (0.5)	1.1 (0.8)	56.0 (2.5)
Mid-elevation Pine-Oak	82	7	3.4 (0.6)	6.7 (2.5)	68.1 (3.3)
Mid-elevation Pine	70	3	1.3 (0.5)	1.9 (2.0)	37.0 (1.6)
Lower montane forest	80	3	1.1 (0.4)	3.2 (1.8)	75.2 (3.2)
High elevation milpa	70	3	1.1 (0.4)	2.8 (1.5)	29.8 (1.5)
High elevation 2nd growth	100	2	1.3 (0.3)	1.3 (0.7)	39.5 (1.4)
High elevation Pine	70	4	1.8 (0.7)	2.3 (1.0)	27.0 (1.6)
High elevation Pine-Oak	50	4	1.4 (0.5)	0.8 (0.6)	40.0 (1.7)

[a] Includes only those species with mean > .10 per point.
[b] Estimated number of species in a sample of 250 individuals.

cies that feed almost exclusively on arthropods or small vertebrates), frugivores (birds that feed more than half the time on fruit or on the seeds of fruit while on trees, *e.g.,* parrots), nectarivores (birds that feed more than half the time on nectar), omnivores (birds that feed on a mixed diet of arthropods, fruit, nectar, or seeds), granivores (birds that feed more than half the time on seeds).

RESULTS

COMPARISON OF HABITAT VARIABLES BETWEEN PLANTATION TYPES.—Planted versus rustic plantations were classified on the basis of overall canopy composition. Plantations that were dominated (> 50% cover) by *Inga* were classified as planted plantations. Those showing no clear dominance by a single tree genus or species and having a canopy consisting of forest trees common to the region were classified as rustic. Other than this fundamental difference, we detected few other distinctions between the two plantation types. We found no significant difference in plantation size (3.7 ha ± 1.3 SEM versus 5.7 ± 1.1 in rustic and *Inga* respectively), average canopy height (12.3 m ± 0.6 versus 13.4 ± 0.4), coffee height (2.2 m ± 0.1 versus 2.4 ± 0.1), or tree density (108 ± 6.5 versus 111 ± 6.0 trees per ha). Despite the overall difference in dominance by a single genus of trees, local species diversity (species found within 25 m circle) was also similar (5.2 ± 0.2 versus 4.8 ± 0.2).

COMPARISON OF SPECIES NUMBER AND ABUNDANCE ON POINT COUNTS.—Point counts in shade coffee plantations averaged 5.3 (0.2 SEM) migrants, 5.0 (0.2) residents and a total of 10.1 total birds per point (Table 1). The migrant value is high, similar to gallery woods and exceeded only by acacia groves. The two plantation types are strikingly similar in these summary statistics: rustic and planted plantations had 4.3 (0.6 SE) and 5.3 (0.3) migrants per point, respectively (NS) and 5.8 (0.6) and 4.7 (0.3) resident individuals per point (*t*-test, NS), respectively (Table 1). The cumulative number of species detected on point counts for coffee plantations was 140, with 104 in *Inga* and 107 in rustic coffee (for analyses we excluded raptors). The species total for transects through coffee plantations was somewhat higher (180). Both habitats had similar diversity as estimated in a rarefaction analysis (James & Rathbun 1981; Table 1). Both were significantly more diverse than other habitats except lowland tropical forest, lowland second growth, mid-elevation pine-oak woodland, and mesophilous lower montane forest.

INDIVIDUAL SPECIES.—We found significant differences between coffee plantation types for the mean numbers for individual bird species (Table 2). Rustic coffee had more individuals of seven species and *Inga* had higher numbers of five species. The species found more commonly in rustic coffee tended to be frugivorous or omnivorous species that eat a quantity of fruit (ochre-bellied flycatcher, gray silky-flycatcher, acorn woodpecker, masked tityra, brown jay see Table 2 for Latin names). There is no clear pattern for *Inga*; two of the species showing a large difference in abundance are the omnivorous migrants which feed largely on flower nectar (Tennessee warbler and Baltimore oriole). There is a tendency for the rustic plantations to have greater representation from more specialized tropical groups. For example, on point counts we found a total of seven species of woodcreepers, furnariids, and antbirds totalling 0.16 individuals per point, compared to four species totalling 0.04 individuals in the traditional planted plantations. On the other hand, *Inga* had a greater number of hummingbird species (10 vs. 4) and individuals (0.39 vs. 0.20 per point), as well as more icterids (0.97 vs. 0.20 per point). These groups are the most frequent users of *Inga* flowers.

FAUNAL SIMILARITY OF POINT COUNT SAMPLES.—We examined faunal similarity in two ways: using Dice's index (Dice 1945), $2a/(2a + b + c)$, where a is the number of species present in both habitats, and b and c are the number of unshared species in the two habitats, we can calculate the shared species in the point count samples, and using Pearson's correlation coefficient we can examine the similarity in numbers detected for the overall species pool. Both types of indices show similar patterns (Table 3). The two types of coffee plantations are most similar primarily to each other and then to other managed forest patches (acacia woodlots and gallery forest) and mid-elevation woodlands (pine-oak, pine-oak *Liquidambar*). The similarity values between *Inga* and rustic and other habitats are highly correlated ($r = 0.99$ for both Dice's and Pearson's correlation coefficients).

The overall similarity values are much greater for migrants than they are for residents when the two species pools are analyzed separately (Table 4). Pearson's coefficients average 0.31 and 0.30 for migrants in *Inga* and rustic plantations respectively, but 0.17 for residents for both plantation types (Wilcoxon T, $P < 0.0001$). Within the migrant-resident status category the Pearson's coefficients for the two plantation types compared with other habitats are very high (0.99 for migrants and 0.90 for residents).

ECOLOGICAL SIMILARITY.—Proportional guild composition was compared for each habitat surveyed. Since proportions based on numbers of species and numbers of individuals are highly correlated ($Y = -0.18 + 1.0$ x, $r = 0.83$. $P < 0.001$), we present data based only on proportion of individuals. Based on the between-habitat Pearson r of the proportion of individuals found in different feeding-strata guilds ($N = 17$ guilds), we found that coffee plantations are most similar to each other ($r = 0.925$, Table 5), and then both are most similar to other mid-elevation forest habitats.

SPECIES RICHNESS IN DIET GUILDS.—Both coffee plantation types showed particularly high species richness for omnivorous species, 45 and 48 species for rustic and *Inga,* respectively. These values are based on a variable number of point counts per habitat (Table 1), and can only define broad patterns. However, they are closely approached only by lowland tropical forest, lower montane forest, and lowland second growth. In particular, rustic coffee had high species numbers of canopy insectivores, frugivores, and omnivores and *Inga* coffee had high species numbers of canopy insectivores and omnivores. *Inga* coffee plantations had an exceptionally high number (12) of nectarivores, a number approached only by lowland second growth and lower montane forest. Rustic coffee had a high number of frugivore species (12), a number exceeded only by lowland tropical forest. These comparisons are influenced by different sampling effort, but most of the differences are quite large.

NUMERICAL DOMINANCE OF CANOPY OMNIVORES AND FRUGIVORES.—The most striking attribute of the composition of coffee plantation bird assemblages is the relative density of canopy omnivores and frugivores. Canopy omnivores and frugivores comprise 40 and 45 percent of the total numbers of individuals recorded on point counts for *Inga* and rustic plantations, respectively. This value is significantly greater (X^2, $P < 0.05$) than for lower montane forest (33%) and high elevation pine forest (30%)—the only two habitats that approach the proportion of omnivores and frugivores found in coffee plantations.

SEASONALITY OF MIGRANTS IN RUSTIC VERSUS *INGA* PLANTATIONS.—We used the repeated transect sur-

TABLE 2. *The number of birds per point detected on point counts in planted and rustic coffee plantations.*

Species	Status[a]	Guild[b]	Rustic[d]	*Inga*[c,d]
Little tinamou *Crypturellus soui*	R	o/g	+	
Slate-breasted tinamou *Crypturellus boucardi*	R	o/g	+	
White-breasted hawk *Accipiter striatus*	R			0.01
Roadside hawk *Buteo magnirostris*	R		0.05	0.02
Plain chachalaca *Ortalis vetula*	R	f/c	0.03	
Pale-vented pigeon *Columba cayennensis*	R	f/c	0.08	
Red-billed pigeon *Columba flavirostris*	R	f/c	0.16	
White-tipped dove *Leptotila verreauxi*	R	g/g	+	
Red-lored parrot *Amazona autumnalis*	R	f/c	0.01	
White-crowned parrot *Pionus senilis*	R	f/c	0.02	+
Squirrel cuckoo *Piaya cayana*	R	i/c	0.06	0.02
Groove-billed ani *Crotophaga sulcirostris*	R	i/s	0.01	
Long-tailed hermit *Phaethornis superciliosus*	R	n/u		0.01
Little hermit *Phaethornis longuemareus*	R	n/u	0.01	0.03
Violet sabrewing *Campylopterus hemileucurus*	R	n/c		0.04
Fork-tailed emerald *Chlorostilbon canivetii*	R	n/s	0.01	
White-eared hummingbird *Hylocharis leucotis*	R	n/u		0.02
Azure-crowned hummingbird *Amazilia cyanocephala*	R	n/s		0.02
Rufous-tailed hummingbird *Amazilia tzacatl*	R	n/u	0.12	0.09
Green-throated mountain-gem *Lampornis viridipallens*	R	n/u		0.03
Amethyst-throated hummingbird *Lampornis amethystinus*	R	n/u		0.01
Magnificent hummingbird *Eugenes fulgens*	R	n/u		0.03
Long-billed starthroat *Heliomaster longirostris*	R	n/c	+	
Ruby-throated hummingbird *Archilochus colubris*	M	n/s		0.02
Unidentified hummingbird	?		0.06	0.09
Violaceous trogon *Trogon violaceus*	R	o/c	0.05	0.02
Collared trogon *Trogon collaris*	R	o/c	0.01	0.01
Blue-crowned motmot *Momotus momota*	R	o/u	0.02	0.02
Emerald toucanet *Aulacorhynchus prasinus*	R	f/c	0.01	
Acorn woodpecker *Melanerpes formicivorus*	R	o/t	0.10	0.03*
Golden-fronted woodpecker *Melanerpes aurifrons*	R	o/t	0.10	0.12
Yellow-bellied sapsucker *Sphyrapicus varius*	M	o/t	0.03	0.05
Golden-olive woodpecker *Piculus rubiginosus*	R	i/t	0.09	0.01
Lineated woodpecker *Dryocopus lineatus*	R	i/t	+	
Pale-billed woodpecker *Campephilus guatemalensis*	R	i/t	+	+
Rufous-breasted spine-tail *Synallaxis erythrothorax*	R	i/s	0.02	
Strong-billed woodcreeper *Xiphocolaptes promeropirhynchus*	R	i/t	0.02	
Ivory-billed woodcreeper *Xiphorhynchus flavigaster*	R	i/t	0.07	
Spotted woodcreeper *Xiphorhynchus erythropygius*	R	i/t	0.01	0.01
Streak-headed woodcreeper *Lepidocolaptes souleyetii*	R	i/t	0.02	0.01
Spot-crowned woodcreeper *Lepidocolaptes affinis*	R	i/t		0.01
Barred antshrike *Thamnophilus doliatus*	R	i/s	0.01	0.01
Black-faced antthrush *Formicarius analis*	R	i/g	0.01	
Ochre-bellied flycatcher *Mionectes oleaginus*	R	f/u	0.09	0.02*
Yellow-olive flycatcher *Tolmomyias sulphurescens*	R	o/c	0.18	0.13*
Tufted flycatcher *Mitrephanes phaeocercus*	R	i/c	0.01	0.01
Greater pewee *Contopus pertinax*	R	i/c	0.05	0.08*
Tropical pewee *Contopus cinereus*	R	i/c	0.02	0.01
Yellow-bellied flycatcher *Empidonax flaviventris*	M	i/c	0.04	0.02
Least flycatcher *Empidonax minimus*	M	i/s	0.23	0.06*
Hammond's flycatcher *Empidonax hammondi*	M	i/c	0.01	0.02
Dusky-capped flycatcher *Myiarchus tuberculifer*	R	o/c	0.12	0.07
Great crested flycatcher *Myiarchus crinitus*	M	o/c	0.01	
Brown-crested flycatcher *Myiarchus tyrannulus*	R	o/c	0.05	
Boat-billed flycatcher *Megarynchus pitangua*	R	o/c	0.07	0.05
Social flycatcher *Myiozetetes similis*	R	o/c	0.23	0.20
Sulphur-bellied flycatcher *Myiodynastes luteiventris*	M	o/c	0.01	
Tropical kingbird *Tyrannus melancholicus*	R	o/c	0.01	0.01
Couch's kingbird *Tyrannus couchii*	R	o/c	0.02	0.02
Rose-throated becard *Pachyramphus aglaiae*	R	o/c	0.08	0.06
Masked tityra *Tityra semifaciata*	R	o/c	0.32	0.11*

TABLE 2. *Continued.*

Species	Status[a]	Guild[b]	Rustic[d]	*Inga*[c,d]
Green jay *Cyanocorax yncas*	R	o/c	0.03	0.10
Brown jay *Cyanocorax morio*	R	o/c	0.35	0.14*
Band-backed wren *Campylorhynchus zonatus*	R	i/s	0.06	0.06
Plain wren *Thryothorus modestus*	R	i/s	0.25	0.11
Spot-breasted wren *Thryothorus maculipectus*	R	i/s	0.04	0.04
House wren *Troglodytes aedon*	R	i/s		0.01
White-breasted wood-wren *Henicorhina leucostita*	R	i/u	0.01	
Blue-gray gnatcatcher *Polioptila caerulea*	M/R	i/c	0.46	0.48
Eastern bluebird *Sialia sialis*	R	o/c		0.02
Brown-backed solitaire *Myadestes obscurus*	R	f/c	0.05	
Slate-colored solitaire *Myadestes unicolor*	R	f/c	0.02	0.02
Orange-billed nightingale-thrush *Catharus aurantiirostris*	R	o/u		0.02
Spotted nightingale-thrush *Catharus dryas*	R	o/u		0.01
Swainson's thrush *Catharus ustulatus*	M	f/u	0.03	0.02
Wood thrush *Hylocichla mustelina*	M	o/u	0.02	0.08
Clay-colored robin *Turdus grayi*	R	o/c	0.13	0.26
White-throated robin *Turdus assimilis*	R	o/c		0.02
Rufous-collared robin *Turdus rufitorques*	R	o/c	0.01	
Gray catbird *Dumetella carolinensis*	M	o/s	0.20	0.26
Blue-and-white mockingbird *Melanotis hypoleucus*	R	o/u	0.03	
Cedar waxwing *Bombycilla cedrorum*	M	f/c	0.25	
Gray silky-flycatcher *Ptilogonys cinereus*	R	f/c	0.51	*
White-eyed vireo *Vireo griseus*	M	o/c	0.04	0.05
Solitary vireo *Vireo solitarius*	M	o/c	0.22	0.11
Yellow-throated vireo *Vireo flavifrons*	M	o/c	0.05	0.02
Warbling vireo *Vireo gilvus*	M	i/c	0.02	
Philadelphia vireo *Vireo philadelphicus*	M	o/c	0.03	0.07
Rufous-browed peppershrike *Cyclarhis gujanensis*	R	i/s		0.02
Blue-winged warbler *Vermivora pinus*	M	i/c	0.01	0.05
Nashville warbler *Vermivora ruficapilla*	M	o/c	0.06	0.09
Tennessee warbler *Vermivora peregrina*	M	o/c	0.07	0.49*
Northern parula *Parula americana*	M	o/c		0.02
Crescent-chested warbler *Parula superciliosa*	R	i/c	+	
Yellow warbler *Dendroica petechia*	M	i/s	0.02	0.02
Magnolia warbler *Dendroica magnolia*	M	i/u	0.49	0.75*
Chestnut-sided warbler *Dendroica pensylvanica*	M	o/c		0.08
Black-throated blue warbler *Dendroica caerulescens*	M	o/u		0.01
Townsend's warbler *Dendroica townsendi*	M	i/c	0.01	
Hermit warbler *Dendroica occidentalis*	M	i/c	0.01	
Black-throated green warbler *Dendroica virens*	M	i/c	0.73	1.03*
Black-and-white warbler *Mniotilta varia*	M	i/t	0.23	0.21
American redstart *Setophaga ruticilla*	M	i/c	0.24	0.34
Worm-eating warbler *Helmitheros vermivorus*	M	i/u	0.01	
Ovenbird *Seiurus aurocapillus*	M	i/g	0.14	0.07
Northern waterthrush *Seiurus noveboracensis*	M	i/g		0.02
Kentucky warbler *Oporornis formosus*	M	i/g	0.03	0.06
Macgillivray's warbler *Oporornis tolmei*	M	i/u	0.09	0.09
Common yellowthroat *Geothlypis trichas*	M	i/s	0.01	
Gray-crowned yellowthroat *Geothlypis poliocephala*	R	o/s	0.01	
Hooded warbler *Wilsonia citrina*	M	i/u	0.02	+
Wilson's warbler *Wilsonia pusilla*	M	i/u	0.47	0.66
Slate-throated redstart *Myioborus miniatus*	R	i/c	0.01	0.02
Yellow-breasted chat *Icteria virens*	M	o/s	0.07	0.03
Red-legged honeycreeper *Cyanerpes cyaneus*	R	o/c		0.01
Blue-crowned chlorophonia *Chlorophonia occipitalis*	R	f/c		0.02
Yellow-throated euphonia *Euphonia hirundinacea*	R	f/c	0.33	0.15
Blue-hooded euphonia *Euphonia elegantissima*	R	f/c	0.22	0.44
Blue-gray tanager *Thraupis episcopus*	R	o/c		0.02
Yellow-winged tanager *Thraupis abbas*	R	o/c	0.04	0.18*
Red-throated ant-tanager *Habia fuscicauda*	R	o/u	0.26	0.13
Red-crowned ant-tanager *Habia rubica*	R	o/u	0.03	
Summer tanager *Piranga rubra*	M	o/c	0.09	0.06

TABLE 2. *Continued.*

Species	Status[a]	Guild[b]	Rustic[d]	*Inga*[c,d]
Western tanager *Piranga ludoviciana*	M	o/c	0.01	0.01
Flame-colored tanager *Piranga bidentata*	R	o/c		0.02
White-winged tanager *Piranga leucoptera*	R	o/c	0.02	
Crimson-collared tanager *Ramphocelus sanguinolentus*	R	f/s		0.01
Grayish saltator *Saltator coerulescens*	R	o/s	0.07	0.03
Buff-throated saltator *Saltator maximus*	R	o/c	0.06	0.17
Black-headed saltator *Saltator atriceps*	R	o/cs	0.14	0.17
Black-faced grosbeak *Caryothraustes poliogaster*	R	o/c		
Rose-breasted grosbeak *Pheucticus ludovicianus*	M	o/c	0.05	0.10
Indigo bunting *Passerina cyanea*	M	g/s	0.20	0.09
Yellow-faced grassquit *Tiaris olivacea*	R	o/s	0.02	
Green-backed sparrow *Arremonops chloronotus*	R	o/g	0.03	0.01
White-faced-ground sparrow *Melozone leucotis*	R	o/s	0.01	0.06
Cinnamon-bellied flower-piercer *Diglossa baritula*	R	o/s		0.01
Rusty sparrow *Aimophila rufescens*	R	o/s	+	
Melodious blackbird *Dives dives*	R	o/s	0.05	0.33*
Great-tailed grackle *Quiscalus mexicanus*	R	o/g		0.02
Orchard oriole *Icterus spurius*	M	o/c	0.03	
Yellow-backed oriole *Icterus chrysater*	R	o/c		0.12
Yellow-tailed oriole *Icterus mesomela*	R	i/c	+	
Baltimore oriole *Icterus galbula galbula*	M	o/c	0.14	0.35
Bullock's oriole *Icterus galbula bullocki*	M	o/c	0.01	0.05
Yellow-billed cacique *Amblycercus holosericeus*	R	i/s	0.03	0.02
Chestnut-headed oropendola *Psarocolius wagleri*	R	f/c		0.06
Montezuma's oropendola *Psarocolius montezuma*	R	o/c	0.02	0.02
Black-headed siskin *Carduelis notata*	R	g/c		0.14
Lesser goldfinch *Carduelis psaltria*	R	g/c	0.03	0.02

[a] Status categories are R = tropical resident and M = temperate zone migrant.
[b] Guild categories are diet/strata. Diet categories are o = omnivore, n = nectarivore, i = insectivore, g = granivore, and f = frugivore; strata categories are c = canopy, u = understory, s = open scrub, t = trunk.
[c] * indicates significance at $P < 0.05$, Student's t-test.
[d] + indicates species detected in coffee plantation but not within 25 m count circle.

veys of rustic and *Inga* coffee to examine differences in overall seasonality of bird populations during the non-breeding season. An important feature of a coffee plantation is the high degree of seasonality of its use. Of the habitats surveyed in the Ocosingo region (mid-elevation), both *Inga* and rustic coffee were the only habitats showing strong monotonic increases between October (rainy) and April (late dry season).

Both plantation types show the same fundamental pattern. The numbers of all migrants are positively correlated with week number (Table 6), or, in other words, numbers increased with time. Other habitats in the region showed either no significant change or declines during the same period. The number of insectivorous migrants, however, is not significantly related to week number (showing a small negative slope in both habitats, Table 7). The pattern of seasonality is dominated by a small number of omnivorous species—species that feed largely upon fruit or nectar in the dry season (Table 7). An analysis of covariance was conducted to examine the homogeneity of slopes for the bird/week relationship in *Inga* and rustic coffee. The slopes for total migrants and insectivorous migrants were not significantly different. However, omnivorous species had a significantly greater slope for rustic than for *Inga* ($F_{1,20} = 4.6$, $P < 0.05$).

The importance of the seasonality of omnivorous species is underscored by the analysis of individual species. We conducted regressions between bird numbers and week numbers for all migratory species that were found at a minimum average abundance of 1 individual/week. On an individual species basis, both *Inga* and rustic coffee showed more significant increases than decreases in population over the winter (Table 8), which is in sharp contrast to other habitats sampled in the region. For rustic coffee this ratio was 6:1 in year 1 and 5:3 in year 2. For *Inga* coffee (year 2 only), the ratio was 7:0. The species showing increases were dominated by omnivorous migratory species in both plantation types (5/7 and 4/5 for rustic and 5/7 for *Inga*).

TABLE 3. *Similarity indices for species detected on point counts in* Inga *and rustic coffee compared with 16 habitats in eastern Chiapas.*

Index Habitat	Dice's		Pearson's	
	Inga	Rustic	*Inga*	Rustic
Low elevation (<500 m)				
Pasture	0.25	0.31	.09	.13
Second growth	0.51	0.51	.54	.45
Moist forest	0.36	0.39	.12	.10
Mid-elevation (900–1500 m)				
Pasture	0.28	0.29	.33	.29
Milpa	0.50	0.47	.48	.40
Second-growth	0.48	0.46	.55	.50
Gallery vegetation	0.50	0.51	.71	.66
Acacia woodlot	0.64	0.62	.67	.64
Pine	0.28	0.29	.33	.29
Pine-Oak	0.67	0.69	.54	.54
Pine-Oak *Liquidambar*	0.42	0.40	.65	.59
Lower montane forest	0.50	0.55	.47	.52
Inga coffee	—	0.71	—	.77
Rustic coffee	0.71	—	.77	—
High elevation (>2000 m)				
Milpa	0.21	0.17	.07	.04
Second growth	0.20	0.23	.22	.20
Pine	0.12	0.13	−.05	−.02
Pine-Oak	0.22	0.22	.01	.09

TABLE 4. *Comparison of similarity values (Pearson's r) for migrants and residents in two types of coffee plantations.*

Habitat	Migrant		Resident	
	Inga	Rustic	*Inga*	Rustic
Low elevation (<500 m)				
Pasture	0.10	0.20	0.06	0.06
Second growth	0.70	0.66	0.36	0.22
Moist forest	0.40	0.24	0.04	0.04
Mid-elevation (900–1500 m)				
Pasture	0.40	0.38	0.12	0.06
Milpa	0.59	0.58	0.02	0.08
Second growth	0.54	0.58	0.40	0.23
Gallery vegetation	0.78	0.78	0.40	0.37
Acacia woodlot	0.70	0.74	0.40	0.52
Pine	0.40	0.38	0.12	0.06
Pine-Oak	0.77	0.75	0.37	0.38
Pine-Oak *Liquidambar*	0.76	0.72	0.12	0.20
Lower montane forest	0.70	0.69	0.21	0.33
Inga coffee	—	0.87	—	0.55
Rustic coffee	0.87	—	0.55	—
High elevation (>2000 m)				
Milpa	−0.08	−0.07	−0.05	−0.04
Second growth	0.26	0.25	−0.04	−0.02
Pine	−0.08	−0.07	−0.05	−0.04
Pine-Oak	0.06	0.06	0.05	−0.01

TABLE 5. *Ecological similarity, based on Pearson's* r, *comparing proportions of individuals in different guilds.*

Habitat	Rustic	*Inga*
Low elevation (<500 m)		
Pasture	0.23	0.24
Second growth	0.68	0.77
Moist forest	0.67	0.71
Mid-elevation (900–1500 m)		
Pasture	0.22	0.27
Milpa	0.48	0.61
Second growth	0.60	0.64
Gallery vegetation	0.76	0.84
Acacia woodlot	0.60	0.62
Pine	0.64	0.69
Pine-Oak	0.81	0.89
Pine-Oak *Liquidambar*	0.82	0.87
Lower montane forest	0.80	0.83
Inga coffee	0.93	—
Rustic coffee	—	0.93
High elevation (>2000 m)		
Milpa	0.32	0.43
Second growth	0.69	0.72
Pine	0.77	0.84
Pine-Oak	0.65	0.67

A unique feature of shade coffee plantations was the large influx of a few migratory omnivores during the dry season. For *Inga* $5/7$ of the omnivorous and only $2/9$ of the insectivorous species showed positive trends; for rustic coffee these values were $9/12$ of the omnivorous species (different years for different species are counted separately) and $3/23$ insectivorous migrants. Two species in particular are involved in the dry season influx, Tennessee warblers and Baltimore orioles. The transect data graphically demonstrate the numbers that arrive just prior to and remain for the flowering of the *Inga* canopy (late March–April). For example, the four surveys in early March to early April averaged 27.0 Baltimore orioles and 13.3 Tennessee warblers per transect in *Inga* and 12.1 and 8.5 for rustic coffee respectively. These numbers are considerably higher than gallery forest (4.3 and 4.3 respectively), the only other habitat that has a high abundance of flowering *Inga*. Other habitats for southeastern Mexico ranged from 0–2 for each species. The only exceptions are for rustic cacao plantation, which averaged 4 and 1.8 for the two species.

SEASONALITY OF RESIDENT SPECIES IN PLANTATIONS.—Resident species showed a similar pattern of seasonality. In fact, there is a strong correlation between the percentage weekly change in migrant and resident numbers across the different habitats ($r = 0.90$). For residents, we found a strong positive slope in the bird vs. week regression for both years in rustic and *Inga* coffee (Table 6). As in the migrants, the relationship was positive when we examined only omnivorous, granivorous, and nectarivorous species (Table 7), but was not significant for insectivores. These results are based on number of individuals. The analysis of total species numbers reveals a similar pattern with a significant slope of 0.8 ($r = 0.57$, $P < 0.02$) and 0.66 ($r = 0.56$, $P < 0.02$) for rustic coffee in years 1 and 2, respectively and 0.8 for *Inga* ($r = 0.646$, $P < 0.005$).

DISCUSSION

SIMILARITY OF THE TWO PLANTATION TYPES.—Despite large differences in the floristics of the two types of coffee plantations, we found they were similar in almost every parameter compared. The two plantation types had similar abundances of resident and migrant birds, numbers of resident and migrant species, species and guild composition, dominance of canopy omnivores, and seasonal pattern of abundances between early and late "winter" months. These results suggest that much of the value of shade coffee plantations for conserving bird diversity can be found in planted as well as rustic coffee, provided that the planted plantations are of comparable stature.

COMPARISON TO OTHER HABITATS IN THE REGION.—With respect to avian composition, *Inga* and rustic coffee are not only each others most similar habitats, but their similarity coefficients for the other 17 habitats are also extremely well correlated (Table 4). The high diversity of birds in coffee plantations is a result of their mixed composition; plantations support species characteristic of more open agricultural habitats, as well as a diversity of forest generalists and forest edge species. Some of the more specialized forest species are not found in coffee plantations, particularly those associated with the understory of mesophilous forest. The following species are those commonly associated with mid-elevation broadleafed forests that we have not detected in our surveys of coffee plantations: streaked foliage-gleaner (*Anabacerthia variegaticeps*), buff-throated foliage-gleaner (*Automolus ochrolaemus*), golden-crowned warbler (*Basileuterus culicivorus*), and common bush–tanager (*Chlorospingus ophthalmicus*).

COFFEE PLANTATIONS AS A DRY SEASON REFUGE.—Although numerous authors have discussed the topic

TABLE 6. *Regression statistics for relationship between abundance of birds and week of census for repeatedly surveyed transects in the Ocosingo area.*

Transect		Constant	% Slope[a]	*r*	Significance
Year 1					
Rustic coffee total	Total	63	+13.2	0.586	$P = 0.013$
	Residents	34	+12.0	0.493	$P = 0.04$
	Migrants	32	+9.1	0.605	$P = 0.008$
Pine-Oak I	Total	96	−1.7	0.345	NS
	Residents	57	−1.9	0.237	NS
	Migrants	55	−2.4	0.459	NS
Pine-Oak II	Total	103	+1.6	0.278	NS
	Residents	52	+1.0	0.128	NS
	Migrants	43	−1.6	0.156	NS
Gallery vegetation	Total	124	+2.0	0.053	NS
	Residents	50	0	0.007	NS
	Migrants	77	+12.9	0.109	NS
Second growth scrub	Total	97	−2.0	0.445	$P = 0.06$
	Residents	47	−2.0	0.359	NS
	Migrants	48	−1.9	0.465	$P = 0.05$
Pine-Oak savanna	Total	47	−4.9	0.086	NS
	Residents	29	−1.2	0.216	NS
	Migrants	17	+1.3	0.143	NS
Milpa	Total	112	−5.4	0.640	$P = 0.004$
	Residents	63	−5.3	0.610	$P = 0.004$
	Migrants	25	−5.7	0.821	$P < 0.001$
Acacia woodlot	Total	194	−2.5	0.543	$P < 0.01$
	Residents	57	−2.2	0.550	$P < 0.01$
	Migrants	144	−2.6	0.589	$P < 0.01$
Year 2					
Inga coffee	Total	128	+6.8	0.811	$P = 0.001$
	Residents	65	+8.6	0.797	$P = 0.005$
	Migrants	65	+3.7	0.459	NS
Rustic coffee	Total	130	+5.5	0.640	$P = 0.001$
	Residents	63	+8.2	0.602	$P = 0.01$
	Migrants	66	+3.6	0.510	$P < 0.05$
Pine-Oak I	Total	123	−2.3	0.236	NS
	Residents	47	+4.4	0.177	NS
	Migrants	78	−2.0	0.604	$P < 0.01$
Gallery forest	Total	126	+2.3	0.426	NS
	Residents	45	+4.4	0.396	NS
	Migrants	78	+1.9	0.481	NS
Second growth scrub	Total	150	−1.3	0.308	NS
	Residents	73	+1.6	0.279	NS
	Migrants	59	−1.2	0.541	$P < 0.05$
Pine-Oak savanna	Total	55	−1.4	0.225	NS
	Residents	32	−6.3	0.080	NS
	Migrants	22	−2.7	0.358	NS
Acacia woodlot	Total	136	0.09	0.024	NS
	Residents	25	1.31	0.446	$P = 0.07$
	Migrants	110	−1.18	0.372	NS

[a] % slope = slope/constant × 100.

TABLE 7. *Regression statistics for the components of the coffee plantation avifauna (statistics apply to number of individuals except where noted).*

	Constant	% Slope[a]	*r*	Significance
Rustic coffee Year 1				
Resident species	17	2.5	.496	$P = .04$
Resident omnivores and frugivores	50	6.7	.571	$P = .02$
Resident insectivores	18	−2.2	.214	NS
Resident nectarivores	2	17.7	.550	$P = .02$
Resident granivores	2	12.5	.620	$P = .002$
Migrant omnivores	−3	60.0	.730	$P < .001$
Migrant insectivores	40	1.9	.311	NS
Rustic coffee Year 2				
Resident species	27	0.7	.563	$P = .02$
Resident omnivores and frugivores	92.2	6.2	.711	$P = .001$
Resident insectivores	35	−0.8	.346	NS
Resident nectarivores	2.4	0.6	.782	$P = .001$
Resident granivores	3.4	0.6	.632	$P = .007$
Migrant omnivores	−6	68.0	.816	$P < .001$
Migrant insectivores	72	−2.1	.506	$P < .05$
Inga coffee Year 2				
Resident species	21	0.8	.646	$P = .003$
Resident omnivores	52	3.3	.585	$P = .02$
Resident insectivores	8.3	0.70	.487	NS
Resident nectarivores	2.1	1.3	.74	$P = .006$
Resident granivores	1.6	0.1	.218	NS
Migrant omnivores	14.3	19.5	.699	$P < 0.05$
Migrant insectivores	51.0	−10.3	.163	NS

[a] See Table 6.

of habitat seasonality with respect to bird use (for brief review see Levey & Stiles 1992), few papers examining habitat quality for migratory birds have evaluated the pattern of seasonality when comparing habitats (but see Lefebvre *et al.* 1994). Morton (1980) was one of the first to emphasize that many tropical bird species can move along a moisture gradient as a strategy for surviving the dry season in the Isthmus of Panama. Martin (1985) argued that birds move into young second-growth woods during the dry season to take advantage of the abundance of small bird-dispersed fruit. Karr and Freemark (1983) documented more local within-habitat movements of birds in response to seasonality within mature tropical forest. Altitudinal migration, primarily for frugivorous and nectarivorous species, has been inferred from marked changes in populations in a number of places in Mesoamerica (Ramos 1988, Loiselle & Blake 1991, Levey & Stiles 1994). From all of these studies it is apparent that seasonal movements are a common feature of tropical habitats, particularly within the period spanned by the temperate zone winter. Coffee plantations appear to act as a refuge for many species of omnivorous birds during the dry season in the Ocosingo area. In this way they differ from other habitats within the region. This is partly because it is a relatively mesic habitat, in an area that is dominated by relatively dry habitat, such as pine-oak woodland and its successional stages. In addition, fruit and nectar are more available in coffee plantations than in other habitats at that time (Vannini 1994).

TABLE 8. *The mean number (two years' data) of migratory species showing significant positive or negative seasonal trends ($P < 0.10$) in numbers on transect surveys.*

Transect	Negative trend	Positive trend
Rustic coffee	1	5
Inga coffee	0	8
Gallery vegetation	0.5	1.5
Acacia grove	2.5	0
Pine-Oak savanna	0.5	0.5
Milpa	3	0
Secondary scrub	3.5	0
Pine Oak I	7.5	0
Pine Oak II	5.5	0
Lower montane forest	6.0	0

Three Nearctic migrants depend heavily on the mass flowering of *Inga* during the dry season. It is interesting that the two orioles appear in large numbers in habitats with *Inga,* but partition the habitats in which they use the *Inga* resource. The orchard oriole occurs in large flocks in flowering *Ingas* in gallery vegetation along streams, both in forest and in pasture. Baltimore orioles are largely restricted to *Inga* in coffee and cacao plantations. Tennessee warblers can be found in large numbers in both habitat types. The mechanisms underlying the habitat partitioning of the two orioles are unknown at this time.

Shade coffee plantations support a high diversity and density of birds, particularly in the mid- to late dry season. However, the plantations of the Ocosingo region differ in a number of ways from other coffee growing areas we have visited. For one, both planted and rustic plantations had relatively tall and lightly trimmed canopy trees. In other areas, the canopy is often only 6–8 m and trees are heavily pruned, creating a much less continuous shade. Trimming also reduces resources for many common species in shade coffee plantations. For example, euphonias depend heavily upon fruits of hemiparasitic or epiphytic plants. The relatively arid conditions in the Ocosingo area may make coffee plantations a more important refuge during the dry season. Further research in different coffee growing areas is needed to determine the role that coffee plantations play in maintaining forest bird populations.

CONCLUSIONS

1. Shade coffee plantations in eastern Chiapas support a moderately high diversity of birds.
2. The plantations have among the highest densities and diversity of Nearctic migrants of all habitats surveyed in the region.
3. Unlike other habitats surveyed in the region, coffee plantations support a major influx of birds, almost doubling the density and diversity of birds between the early and late "winter". This increase is found primarily in omnivorous species, those that feed extensively on fruit and nectar. Two species of migrants, Baltimore oriole and Tennessee warbler, are found in particularly high numbers in the *Inga* coffee plantations. Flowering *Inga* may be a critical resource for these species.
4. We found a strong similarity between the rustic coffee plantations, with high diversity of canopy trees, and the modern plantations, with a few canopy species (primarily *Inga*).
5. Shaded coffee plantations play an important role in the maintenance of diverse bird populations in eastern Chiapas, and as a dry season refuge for mobile populations of omnivores, frugivores, and nectarivores. The role that such plantations play in other tropical ecosystems needs further study.

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