

Effects of Shade-Tree Species and Crop Structure on the Winter Arthropod and Bird Communities in a Jamaican Shade Coffee Plantation¹

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ABSTRACT

I examined the effects of two farm management variables, shade-tree species and crop structure, on the winter (dry season) arthropod and bird communities in a Jamaican shade coffee plantation. Birds and canopy arthropods were more abundant in areas of the plantation shaded by the tree *Inga vera* than by *Pseudalbizia berteriana*. The abundance of arthropods (potential pests) on the coffee crop, however, was unaffected by shade-tree species. Canopy arthropods, particularly psyllids (Homoptera), were especially abundant on *Inga* in late winter, when it was producing new leaves and nectar-rich flowers. Insectivorous and nectarivorous birds showed the strongest response to *Inga*; thus the concentration of birds in *Inga* may be a response to abundant food. Coffee-tree arthropod abundance was much lower than in the shade trees and was affected little by farm management variables, although arthropods tended to be more abundant in dense (unpruned) than open (recently pruned) areas of the plantation. Perhaps in response, leaf-gleaning insectivorous birds were more abundant in dense areas. These results underscore that although some shade coffee plantations may provide habitat for arthropod and bird communities, differences in farm management practices can significantly affect their abundances. Furthermore, this study provides evidence suggesting that bird communities in coffee respond to spatial variation in arthropod availability. I conclude that *I. vera* is a better shade tree than *P. berteriana*, but a choice in crop structures is less clear due to changing effects of prune management over time.

Key words: birds; coffee plantations; food; *Inga*; insects; Jamaica; migratory birds; seasonality; shade; shade coffee.

CHANGES IN TROPICAL LAND USE are due largely to the rapid expansion of area devoted to agriculture. Although increasing agricultural area may contribute to a developing country's economy, it usually results in deforestation and a loss of biodiversity (Leonard 1987; reviews in Wilson 1988). By managing agricultural areas in ways that provide suitable habitat for wild species without relinquishing economic potential, the loss of biodiversity typically associated with development and deforestation can be reduced (Pimentel *et al.* 1992, Mitra & Sheldon 1993, Rice & Ward 1996). Thus, long-term plans to preserve tropical biodiversity must incorporate the use of agricultural management practices that integrate economic profits with wildlife needs.

Recently, shade coffee has been heralded as an agricultural crop that provides the potential for economic revenue and suitable habitat for many forest species, especially arthropods (Celedonio-Hurtado *et al.* 1995, Perfecto & Snelling 1995, Perfecto *et al.* 1996) and birds (Wunderle & Waide

1993, Greenberg *et al.* 1994, Vannini 1994, Wille 1994, Wunderle & Latta 1994, Greenberg 1996, Greenberg *et al.* 1996, Rice & Ward 1996; Greenberg, Bichier, Angon *et al.* 1997). However, all coffee plantations are managed differently with respect to shade-tree species, pruning frequency, use of insecticides, and myriad other variables that potentially affect biodiversity and animal abundance. To assess the suitability of shade coffee plantations for wild species, we must understand how different management variables affect their populations (Petit *et al.* 1993, Wunderle & Latta 1994, Rice & Ward 1996). In this study, I examined the effects of two management variables, shade-tree species and crop structure, on the arthropod and bird communities in a Jamaican shade coffee plantation.

METHODS

The study site was a coffee plantation managed by the Jamaican Coffee Industrial Board in James Hill, Westmoreland, Jamaica. The 48-ha plantation was located along a north–south ridgeline at an elevation of 620 m. The surrounding landscape was a mosaic of fragmented wet limestone forest, small family plots and gardens of sugarcane and fruit

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TABLE 1. *Bird species encountered during point counts and included in the analyses. Diet classifications from Lack (1976) and personal observations: AI = aerial (flycatching) insectivore; LI = leaf-gleaning insectivore; BI = bark-/twig-gleaning insectivore; GI = ground-level insectivore; N = nectarivore; F = frugivore; G = granivore; O = omnivore (fruits/nectar and insects contributing significantly to diet). Total number of detections (N = 40 point counts) provided in parentheses.*

Migrants		Residents
Prairie Warbler <i>Dendroica discolor</i> (LI, 14)	Jamaican Mango <i>Anthracothonax mango</i> (N, 1)	European Starling <i>Sturnus vulgaris</i> (O, 3)
Northern Parula <i>Parula americana</i> (LI, 17)	Streamertail <i>Trochilus polytmus</i> (N, 15)	Jamaican Vireo <i>Vireo modestus</i> (LI, 1)
American Redstart <i>Setophaga ruticilla</i> (LI, 12)	Vervain Hummingbird <i>Mellisuga minima</i> (N, 3)	Arrow-headed Warbler <i>Dendroica phareta</i> (LI, 1)
Cape May Warbler <i>Dendroica tigrina</i> (O, 1)	Jamaican Tody <i>Todus todus</i> (LI, 14)	Bananaquit <i>Coereba flaveola</i> (N, 14)
Magnolia Warbler <i>Dendroica magnolia</i> (O, 2)	Jamaican Woodpecker <i>Meleanerpes radiolatus</i> (BI, 3)	Jamaican Euphonia <i>Euphonia jamaica</i> (F, 5)
Yellow-throated Warbler <i>Dendroica dominica</i> (BI, 3)	Jamaican Peewee <i>Contopus jamaicensis</i> (AI, 1)	Stripe-headed Tanager <i>Spindalis zena</i> (F, 1)
Black-thr. Green Warbler <i>Dendroica virens</i> (LI, 10)	Sad Flycatcher <i>Myiarchus barbirostris</i> (AI, 2)	Black-faced Grassquit <i>Tiaris bicolor</i> (G, 3)
Black-thr. Blue Warbler <i>Dendroica caerulescens</i> (O, 1)	Stollid Flycatcher <i>Myiarchus stolidus</i> (AI, 1)	Yellow-faced Grassquit <i>Tiaris olivacea</i> (G, 14)
Black and White Warbler <i>Mniotilta varia</i> (BI, 7)	Rufous-tailed Flycatcher <i>Myiarchus validus</i> (AI, 1)	Gr. Antillean Bullfinch <i>Loxigilla violacea</i> (F, 1)
Ovenbird <i>Seiurus aurocapillus</i> (GI, 18)	Jamaican Becard <i>Pachyrhamphus niger</i> (O, 1)	Orangequit <i>Euneornis campestris</i> (N, 13)
Swainson's Warbler <i>Limnithlypis swainsonii</i> (GI, 1)	Loggerhead Kingbird <i>Tyrannus caudifasciatus</i> (AI, 4)	Gr. Antillean Grackle <i>Quiscalus niger</i> (O, 3)
Worm-eating Warbler <i>Helmitheros vermivorus</i> (LI, 1)	Rufous-throated Solitaire <i>Myadestes genibarbis</i> (O, 1)	Jamaican Oriole <i>Icterus leucopteryx</i> (BI, 5)
Common Yellowthroat <i>Geothlypis trichas</i> (LI, 2)	White-chinned Thrush <i>Turdus aurantius</i> (O, 1)	
Northern Waterthrush <i>Seiurus noveboracensis</i> (GI, 1)		
Palm Warbler <i>Dendroica palmaris</i> (LI, 6)		

trees, and narrow plantings of Caribbean pine (*Pinus caribaea*).

Coffee trees (*Coffea arabica* var. *typica*) were planted in rows and pruned periodically to maximize fruit production, as is typical among Jamaican coffee plantations (Budhlall 1986; distances between rows and adjacent trees within a row [$\bar{x} \pm 1$ SD] were 3.0 ± 0.06 m and 1.8 ± 0.03 m, $N_s = 30$, respectively). Most trees were *ca* 30 years old, although dead or dying trees were replaced periodically with young saplings. Banana trees (*Musa* sp.), planted to provide shade when the coffee trees were young, still grew between rows in portions of the plantation. Basudin and Thiodan, insecticides for the control of white coffee leaf miner (*Leucopota coffeella*) and coffee berry borer (*Hypothenemus hampei*), respectively, were applied directly to infested coffee trees (*ca* 75% of the plantation) with handheld pump dispensers twice yearly (April–May and June–July). A compatible fungi-

cide (Bayleton) was applied simultaneously to combat coffee leaf rust, *Hemileia vastatrix* (A. Palmer, pers. comm.).

Two tree species, *Pseudalbizia berteriana* (sometimes placed in the genus *Albizia*; Adams 1972) and *Inga vera*, were planted about 30 years ago to provide shade for the coffee trees. *Pseudalbizia* averaged 21.8 m in height (± 1.9 m SD) and 17.1 m in crown diameter (± 1.0 m, $N = 21$), while the slower growing *Inga* averaged 10.7 m in height (± 0.9 m) and 8.9 m in diameter (± 0.8 m, $N = 20$). Other less frequent trees, found especially along plantation roads, included Otaheite apple (*Syzygium malaccense*), oilnut (*Ricinus communis*), and African tulip tree (*Spathodea campanulata*). Thus, the plantation corresponded most closely to a "specialized shade" management system (Rice & Ward 1996). *Pseudalbizia berteriana* and *I. vera* are the two most commonly used species of shade trees throughout Jamaica (Budhlall 1986; M. Johnson,

TABLE 2. *Multivariate profile analysis (one-way MANOVA) of arthropod community in shade trees (canopy) versus coffee trees (understory), showing mean arthropod abundance¹ (± 1 SE, between subjects) and relative proportions of arthropod guilds (percentages, within subjects). Between-subject tests reveal differences in absolute abundance between shade and coffee trees, whereas within-subject tests reveal differences in relative abundances of different arthropod guilds. Polynomial guild contrasts are shown for significant between-subjects main effects (under F column). See text for details.*

Test group	Main effect tree type			
	Shade trees	Coffee trees	$F_{1, 192}$	
Between subjects	4.90 \pm 0.69	1.08 \pm 0.11	39.16***	
Walkers ²	0.69 \pm 0.09	0.29 \pm 0.05	***	
Hiders ³	0.14 \pm 0.04	0.04 \pm 0.01	*	
Homoptera	2.75 \pm 0.54	0.06 \pm 0.02	***	
Flyers ⁴	0.31 \pm 0.06	0.23 \pm 0.04	NS	
Formicidae	1.02 \pm 0.35	0.45 \pm 0.09	NS	
	Guild effect	Guild * tree type		
	F	Shade trees	Coffee trees	$F_{4, 768}$
Within subjects	15.05***			18.03***
Walkers		14.10	26.90	
Hiders		2.90	3.70	
Homoptera		56.10	5.60	
Flyers		6.30	21.30	
Formicidae		20.80	41.70	
N^5		97	97	

¹ Mean number of arthropods per gram of clipped and inspected vegetation ($\times 10$).

² Includes Aranae, Hemiptera, and Coleoptera.

³ Includes Orthoptera, Dictyoptera, and Lepidoptera.

⁴ Includes Diptera and non-formicid Hymenoptera.

⁵ Number of branch clip samples.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = no significant difference.

pers. obs.), suggesting that the James Hill Plantation was representative of other mid-elevation shade coffee farms on the island.

I estimated bird abundance at 40 "bird survey points" distributed at 75 to 100-m intervals along parallel transects (100 m apart) passing through the plantation, and sampled arthropods from the canopy and understory at 97 "arthropod sampling points" separated from each other by at least 10 m and haphazardly distributed among the bird survey points. All points were at least 50 m from the nearest farm edge, and no two adjacent arthropod samples were taken from the same tree. I labeled each point with respect to shade-tree species (*Inga* or *Pseudalbizia*) and crop structure ("dense" or "open"). A point was labeled *Inga*- or *Pseudalbizia*-dominated if at least 75 percent (visual estimation) of its canopy cover (excluding that contributed by banana) was comprised of that species. Dense areas were defined operationally as those rows of the plantation that had not been pruned within one calendar year, and were quantitatively distinct from open areas. Coffee trees were significantly taller in dense than in open areas (3.7 vs. 2.9 m total

height; $t = 4.04$ on 57 df, $P < 0.01$) and also had wider crowns (2.2 vs. 1.6 m; $t = 6.31$ on 57 df, $P < 0.01$).

I sampled the abundances of foliage arthropods using branch-clipping, a sampling technique modified from Schowalter (1994). I positioned a collapsible bag in the understory or canopy (up to 9 m with the aid of extension poles), quickly enclosed the end of a branch, tightened the mouth of the bag around the branch with a drawstring, clipped the branch free with a telescoping tree pruner, then lowered the bag and visually inspected the clipped branch for arthropods. Trapped arthropods were identified to order (except $< 2\%$ left unidentified), or family in the case of Formicidae (ants). At each arthropod sampling point, I took two branch-clip samples: one from a shade tree (sample height $\bar{x} \pm 1$ SD = 6.7 ± 0.15 m) and one from a coffee tree (1.5 ± 0.03 m). Although the top of the *Pseudalbizia* canopy was inaccessible, samples from lower regions did not differ significantly with respect to sample height (ANOVA: $F_{1,51} = 1.34$, $P = 0.25$, $N = 53$). Therefore, I assumed the area sampled in this study was repre-

TABLE 3. *Multivariate profile analysis (three-way MANOVA) of canopy arthropod community, showing mean arthropod abundance¹ (± 1 SE, between subjects) and relative proportions of arthropod guilds (percentages, within subjects). Between-subject tests reveal the effects of grouping factors (shade-tree species, crop structure, winter period) and their interactions on absolute arthropod abundance. Within-subject tests reveal effects of grouping factors and their interactions on relative abundances of different arthropod guilds. Polynomial guild contrasts are provided for significant between-subjects main effects (under F column). See text for details.*

Test group	Main effect Shade-tree species (ST)			Main effect Crop structure (CS)			
	<i>Inga</i>	<i>Pseudalbizia</i>	$F_{1, 85}$	Dense	Open	$F_{1, 85}$	
Between subjects	8.37 \pm 1.16	2.03 \pm 0.57	13.57***	5.85 \pm 1.09	4.09 \pm 0.86	3.82†	
Walkers ²	1.10 \pm 0.12	0.36 \pm 0.12	***	0.74 \pm 0.14	0.65 \pm 0.12	NS	
Hiders ³	0.17 \pm 0.05	0.10 \pm 0.06	NS	0.21 \pm 0.08	0.08 \pm 0.03	NS	
Homoptera	5.03 \pm 0.99	0.85 \pm 0.04	**	2.65 \pm 0.08	2.83 \pm 0.07	NS	
Flyers ⁴	0.39 \pm 0.07	0.25 \pm 0.10	NS	0.40 \pm 0.12	0.23 \pm 0.05	NS	
Formicidae	1.68 \pm 0.75	0.47 \pm 0.14	NS	1.85 \pm 0.73	0.30 \pm 0.13	*	
	Guild effect (G)	G*ST		G*CS			
	$F_{4, 340}$	<i>Inga</i>	<i>Pseudalbizia</i>	$F_{4, 340}$	Dense	Open	$F_{4, 340}$
Within subjects	12.47***			4.94***			1.26
Walkers		13.10	17.70		12.60	15.90	
Hiders		2.00	4.90		3.60	2.00	
Homoptera		60.10	41.80		45.30	69.20	
Flyers		4.70	12.30		6.80	5.60	
Formicidae		20.10	23.20		31.60	7.30	
N^5		44	53		45	52	

¹ Mean number of arthropods per gram of clipped and inspected vegetation ($\times 10$).

² Includes Aranae, Hemiptera, and Coleoptera.

³ Includes Orthoptera, Dictyoptera, and Lepidoptera.

sentative of the overall *Pseudalbizia* canopy. I sampled arthropods during three periods corresponding to early, middle, and late winter (12–18 Nov 1995; 7–13 Jan 1996; 25 Feb–2 Mar 1995 and 17–26 Feb 1996, respectively). The late winter samples were taken in two years to assess annual consistency of arthropod abundances during that period.

To quantify the abundance of birds in the plantation, I conducted a 10-min fixed-radius count (Hutto *et al.* 1986) at each bird survey point, recording all individuals seen or heard within a 25-m radius. Because the plantation was fairly open and sound traveled well, I included in the analyses only those species I considered adequately sampled by point counts; I excluded especially loud or wide-ranging species that could be double counted, such as parrots, crows, and large cuckoos, as suggested by Hutto *et al.* (1986; Table 1). Sliwa and Sherry (1992) demonstrated that augmenting point counts with broadcast playbacks of songs and calls can increase greatly the detectability of secretive and/or vocally inconspicuous birds, such as wintering migratory warblers, which can be notoriously difficult to census but are critical components of

coffee bird communities (Greenberg 1996). Unfortunately, playbacks can lure some birds away from their territories and potentially inflate abundance estimates (Johnson *et al.* 1981). Bird territories in coffee plantations, however, tend to be relatively small (<1 ha; Greenberg, Bichier, Angon *et al.* 1997); for American Redstarts (*Setophaga ruticilla*), the only species for which data are available, individuals occupy territories tenaciously, rarely leaving them, even when playbacks are broadcast nearby (Sliwa & Sherry 1992; M. Johnson, pers. obs.). Therefore, playback-augmented point counts were chosen to provide the most accurate estimation of bird abundance possible within the constraints of the study. Although using playbacks of all relevant species is impossible within a reasonable point count duration, multiple species are attracted to the vocalizations of warbler songs and chip notes (Sliwa & Sherry 1992). Therefore, I chose to broadcast the songs and chips of three of the most common but potentially overlooked warblers: American Redstart, Northern Parula, and Prairie Warbler (see Table 1 for scientific names). Each point count consisted of an initial 5-min playback period (100 sec of songs and chip notes of each species in a

TABLE 3. *Extended.*

Main effect Winter period (WP)			ST*CS	ST*WP	CS*WP	ST* CS*WP	
Early	Middle	Late	$F_{2, 85}$	$F_{1, 85}$	$F_{2, 85}$	$F_{2, 85}$	
3.47 ± 1.14	5.09 ± 1.47	5.80 ± 1.03	2.97	2.11	6.20**	1.31	
0.48 ± 0.09	0.89 ± 0.23	0.72 ± 0.14				1.04	
0.11 ± 0.04	0.20 ± 0.13	0.11 ± 0.04					
0.37 ± 0.20	2.76 ± 1.24	4.42 ± 0.90					
0.20 ± 0.07	0.47 ± 0.19	0.29 ± 0.06					
2.32 ± 1.11	0.77 ± 0.27	0.26 ± 0.11					
G*WP				G*ST *CS	G*ST *WP	G*CS *WP	GS*ST* CS*WP
Early	Middle	Late	$F_{8, 340}$	$F_{4, 340}$	$F_{8, 340}$	$F_{8, 340}$	$F_{8, 340}$
			9.92***	1.24	11.20***	1.53	1.08
13.80	17.50	12.40					
3.20	3.90	1.90					
10.70	54.20	76.20					
5.80	9.20	5.00					
66.90	15.10	4.50					
29	27	41					

⁴ Includes Diptera and non-formicid Hymenoptera.

⁵ Number of branch clip samples.

† $P = 0.06$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = no significant difference.

randomized order), during which many birds were detected visually; this was followed by a 5-min silent period, during which visually inconspicuous but vocal birds were detected. All point counts were conducted during the late winter period of 1995.

Community-level patterns of abundance can be partitioned into two components: patterns of absolute (total) abundance and patterns of relative abundance. Absolute abundance measures actual numbers (or density) of taxonomic units in a community and can be conceptualized as the “size” of a community, whereas relative abundance measures proportional representation of taxonomic units and can be conceptualized as community “shape” (Boecklen & Price 1989). In this study, I employed multivariate profile analyses (MPA, an application of MANOVA) to examine the effects of shade-tree species, crop structure, winter period (for arthropods only), and their interactions on the arthropod and bird communities using SYSTAT 5.2.1 for the Macintosh (Wilkinson 1989). Multivariate profile analyses simultaneously evaluate differences in absolute community abundances (via between subjects tests) and differences in relative abundances of taxonomic units within communities (via within subjects tests; Tabachnick & Fidell 1996). In MPA terminology, the former corresponds to the “levels hypothesis,” and in this study addresses the ques-

tion, “Does arthropod (or bird) community abundance differ with respect to shade-tree species, crop structure, and winter period?” The latter corresponds to the “parallel hypothesis,” and addresses the question, “Do the relative abundances of taxonomic units differ within communities with respect to shade-tree species, crop structure, and winter period?”

The use of profile analyses necessitated a reduction in the number of dependent variables to retain statistical power (Tabachnick & Fidell 1996). Thus, I quantified arthropod community profiles by partitioning the 11 taxonomic groups into 5 “guilds.” Because I was interested in any effects the arthropod community might have upon the food resources available to the bird community, arthropod guilds were chosen to correspond to classes of prey types available to different types of avian insectivores (Sherry 1984): “walkers” (Araneae, Hemiptera, and Coleoptera) moved relatively slowly and were typically found on leaf or twig surfaces; “hidiers” (Orthoptera and Lepidoptera) included nocturnal species and often were found within curled leaves or beneath cover; Homoptera were classified into a single guild because they were very common and represented a unique prey class (small jumping insects usually found on new leaves); “flyers” (Diptera and Hymenoptera) often flew near vegetation, occasionally landing on leaves and

TABLE 4. *Multivariate profile analysis (three-way MANOVA) of understory arthropod community, showing mean arthropod abundance¹ (± 1 SE, between subjects) and relative proportions of arthropod guilds (percentages, within subjects). Between-subject tests reveal the effects of grouping factors (shade-tree species, crop structure, winter period) and their interactions on absolute arthropod abundance. Within-subject tests reveal effects of grouping factors and their interactions on relative abundances of different arthropod guilds. Polynomial guild contrasts are shown for significant between-subjects main effects (under F column). See text for details.*

Test group	Main effect Shade-tree species (ST)			Main effect Crop structure (CS)			
	<i>Inga</i>	<i>Pseudalbizia</i>	$F_{1, 85}$	Dense	Open	$F_{1, 85}$	
Between subjects	1.18 \pm 0.19	1.00 \pm 0.12	0.06	1.28 \pm 0.18	0.93 \pm 0.12	3.72†	
Walker ²	0.31 \pm 0.10	0.28 \pm 0.06		0.27 \pm 0.05	0.32 \pm 0.09	NS	
Hiders ³	0.04 \pm 0.02	0.04 \pm 0.02		0.05 \pm 0.02	0.04 \pm 0.02	NS	
Homoptera	0.04 \pm 0.02	0.08 \pm 0.04		0.03 \pm 0.02	0.09 \pm 0.04	NS	
Flyers ⁴	0.27 \pm 0.06	0.20 \pm 0.05		0.30 \pm 0.07	0.17 \pm 0.04	†	
Formicidae	0.52 \pm 0.18	0.40 \pm 0.08		0.63 \pm 0.18	0.31 \pm 0.07	†	
	Guild effect (G)	G*ST		G*CS			
	$F_{4, 340}$	<i>Inga</i>	<i>Pseudalbizia</i>	$F_{4, 340}$	Dense	Open	$F_{4, 340}$
Within subjects	8.36***			0.10			2.28
Walkers		26.30	28.00		21.10	34.40	
Hiders		3.40	4.00		3.90	4.30	
Homoptera		3.40	7.90		2.30	9.60	
Flyers		22.90	20.00		23.40	18.20	
Formicidae		44.10	40.10		49.2	33.30	
N^5		44	53		45	52	

¹ Mean number of arthropods per gram of clipped and inspected vegetation ($\times 10$).

² Includes Aranae, Hemiptera, and Coleoptera.

³ Includes Orthoptera, Dictyoptera, and Lepidoptera.

twigs; and Formicidae, which also were classified as a single guild because they were common and represented a unique prey class (poorly digestible, walking prey typically found on twigs and branches). Rare miscellaneous groups (*e.g.*, Neuroptera, Psocoptera) and unidentified arthropods were excluded from analyses (<3% of all individuals). The abundance of each guild was calculated as the number of trapped arthropods per gram of clipped and inspected vegetation in a branch-clip sample. All arthropod data were transformed ($\log Y + 0.5$) to normalize for analyses (Sokal & Rohlf 1995).

Similarly, the bird community was partitioned into five guilds based on foraging strategies: leaf-gleaning insectivores (LI), bark-/twig-gleaning insectivores (BI), ground-level insectivores (GI), fly-catching or aerial-feeding insectivores (AI), nectarivores (N), and frugivores, granivores, and omnivores pooled together (FGO; see Table 1 for species classifications). All bird data also were transformed ($\log Y + 0.5$) to normalize for analyses.

First, a one-way MPA was performed to examine differences in arthropod communities in the canopy (shade trees) versus the understory (coffee trees). Next, two three-way MPAs (one for the can-

opy, one for the understory) were run to examine the effects of shade tree species, crop structure, winter period, and their interactions on arthropod communities. Lastly, a two-way MPA was completed to examine the effect of shade-tree species and crop structure on the bird community. In cases in which there were significant main effects between subjects, I subsequently ran polynomial contrasts to compare guild means (Wilkinson 1989).

RESULTS

OVERALL ARTHROPOD COMMUNITY.—Pooling all farm management variables, the arthropod community in the canopy (shade trees) was very different from that in the understory (coffee trees; Table 2). Overall, arthropods were over four times more abundant in the canopy than in the understory. Polynomial contrasts demonstrated that the difference in absolute arthropod abundance was most pronounced for hiders, walkers, and above all, Homoptera. The profiles, or “shapes,” of the arthropod communities were also different between the two regions. Although Formicidae and walkers were relatively important in both communities

TABLE 4. *Extended.*

Main effect Winter period (WP)			ST*CS	ST*WP	CS*WP	ST* CS*WP
Early	Middle	Late	$F_{2, 85}$	$F_{1, 85}$	$F_{2, 85}$	$F_{2, 85}$
1.12 ± 0.25	0.73 ± 0.12	1.32 ± 0.15	2.50	1.04	0.07	0.45
0.16 ± 0.05	0.15 ± 0.06	0.48 ± 0.11				0.15
0.00	0.05 ± 0.03	0.10 ± 0.05				
0.01 ± 0.01	0.05 ± 0.02	0.10 ± 0.05				
0.20 ± 0.07	0.17 ± 0.07	0.30 ± 0.06				
0.75 ± 0.26	0.31 ± 0.09	0.34 ± 0.10				
G*WP			G*ST *CS	G*ST *WP	G*CS *WP	G*ST* CS*WP
Early	Middle	Late	$F_{8, 340}$	$F_{4, 340}$	$F_{8, 340}$	$F_{8, 340}$
			3.18**	0.40	1.01	2.27*
14.30	20.50	36.40	*			0.29
0.00	6.80	7.60	NS			
0.90	6.80	7.60	NS			
17.90	23.30	22.70	NS			
67.00	42.50	25.80	†			
29	27	41				

⁴ Includes Diptera and non-formicid Hymenoptera.

⁵ Number of branch clip samples.

† $P = 0.06$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = no significant difference.

(proportionately slightly more so in the understory), Homoptera comprised 56.1 percent of all canopy arthropods, but only 5.6 percent of those in the understory. Lastly, there was a significant main effect of guilds (corresponding to the “flatness hypothesis” in MPA terminology), demonstrating that different types of arthropods were more abundant than others, an intuitive result of relatively little importance to this study.

CANOPY ARTHROPODS.—Within the canopy, the arthropod community differed in absolute and relative guild abundances with respect to shade-tree species, crop structure, and winter period (Table 3). Total canopy arthropod abundance (between subjects test) was influenced strongly by shade-tree species; *Inga* supported over four times more arthropods than *Pseudalbizia*. This was due largely to a high abundance of Homoptera on *Inga* leaves, although walkers were also most common on *Inga*. Dense areas tended to support more abundant arthropods (particularly Formicidae) than did open areas, but this difference was not significant. Winter period did not show a significant main effect on arthropod abundance. The higher abundance of arthropods on *Inga* than on *Pseudalbizia* canopy leaves, however, was especially pronounced in late winter, as evidenced by a significant interaction between shade-tree species and winter period. This

marked increase in the abundance of arthropods in the *Inga* canopy during the late winter period was due largely to dense concentrations of psyllids (Homoptera: Psyllidae), which comprised 81.5 percent of all arthropods from *Inga* samples at that time ($N = 1062$; Fig. 1).

Shade-tree species and winter period both had significant effects on the relative abundances of guilds within the canopy arthropod community (within subjects tests), as did their interaction (Table 3). Walkers, and especially Homoptera, increased in relative abundance from early to late winter, particularly on *Inga* trees, whereas the importance of Formicidae in the community steadily declined over the winter.

UNDERSTORY ARTHROPODS.—The understory arthropod community was affected less strongly by shade-tree species, crop structure, and winter period than was the canopy community (Table 4). Although *Inga* harbored many more canopy arthropods than *Pseudalbizia*, all coffee trees had similar arthropod abundances regardless of the shade-tree species under which they grew (between subjects). Similarly, total coffee tree arthropod abundance was not significantly affected by winter period. As in the canopy, arthropods tended to be more abundant in dense than open areas of the plantation (mainly as a result of slightly higher

TABLE 5. *Multivariate profile analysis (three-way MANOVA) of bird community, showing mean arthropod abundance¹ (± 1 SE, between subjects) and relative proportions of bird guilds (percentages, within subjects). Between-subject tests reveal the effects of grouping factors (shade-tree species, crop structure) and their interactions on absolute bird abundance. Within-subject tests reveal effects of grouping factors and their interactions on relative abundances of different bird guilds. Polynomial guild contrasts are shown for significant between-subjects main effects. See text for details.*

Test group	Main effect Shade-tree species (ST)			Main effect Crop structure (CS)			ST*CS	
	<i>Inga</i>	<i>Pseudalbizia</i>	$F_{1, 36}$	Dense	Open	$F_{1, 36}$	$F_{1, 36}$	
Between subjects	7.90 \pm 0.71	3.35 \pm 0.47	27.26***	6.65 \pm 0.92	4.60 \pm 0.56	4.26*	2.08	
Leaf-gleaning insectivores	3.00 \pm 0.42	0.90 \pm 0.24	***	2.65 \pm 0.46	1.25 \pm 0.29	*		
Bark insectivores	0.75 \pm 0.20	0.15 \pm 0.11	*	0.60 \pm 0.20	0.30 \pm 0.15	NS		
Aerial insectivores	0.20 \pm 0.09	0.25 \pm 0.10	NS	0.30 \pm 0.11	0.15 \pm 0.08	NS		
Ground-level insectivores	0.60 \pm 0.18	0.40 \pm 0.13	NS	0.60 \pm 0.18	0.40 \pm 0.13	NS		
Nectarivores	1.70 \pm 0.26	0.60 \pm 0.13	**	1.35 \pm 0.26	0.95 \pm 0.21	NS		
Frugivores, Granivores, and Omnivores	1.65 \pm 0.34	1.05 \pm 0.26	NS	1.15 \pm 0.28	1.55 \pm 0.33	NS		
	Guild effect (G) <i>F</i>	G*ST		G*CS		G*ST *CS		
		<i>Inga</i>	<i>Pseudalbizia</i>	$F_{5, 180}$	Dense	Open	$F_{5, 180}$	$F_{5, 180}$
Within subjects	16.40***			3.48**			2.04	0.39
Leaf-gleaning insectivores		38.00	26.90		39.80	27.20		
Bark insectivores		9.50	4.50		9.00	6.50		
Aerial insectivores		2.50	7.50		4.50	3.30		
Ground-level insectivores		7.60	11.90		9.00	8.70		
Nectarivores		21.50	17.90		20.30	20.70		
Frugivores, Granivores, and Omnivores		20.90	31.30		17.30	33.70		
N^2		20	20		20	20		

¹ Abundance is the mean number of individual birds detected per point count (see Table 1 for species list and group classification).

² Number of point counts.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = no significant difference.

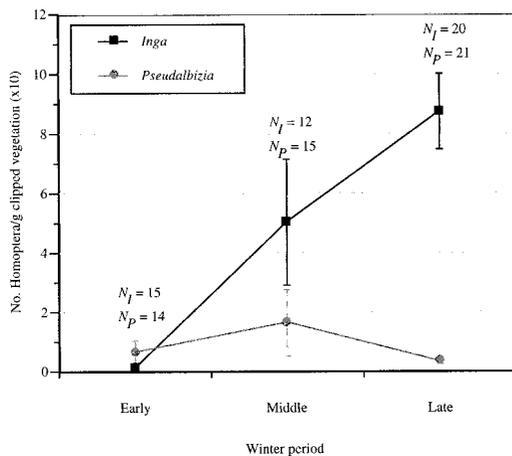


FIGURE 1. Interaction between shade-tree species and winter period on homopteran abundance in the canopy ($\bar{x} \pm 1$ SE, N_I and N_P are the number of *Inga* and *Pseudalbizia* branch clip samples, respectively).

abundances of flyers and Formicidae), but this difference was not statistically significant. With respect to the relative proportions of understory arthropod guilds, walkers and Homoptera showed a slight increase in relative abundance over the winter, much like in the canopy, but on a less dramatic scale. Formicidae showed a strong decline over the winter, especially from the early to middle winter periods; however, this decline in ants was present only in dense areas of the plantation, resulting in a significant interaction between crop structure and winter period.

BIRD COMMUNITY.—Forty bird species were detected on the plantation (Table 1), including 15 migrant warbler species dominated by insectivores (12 species) and a more diverse group of 25 resident species that included 5 nectarivores and 3 frugivores. Overall, 50.2 percent of all individuals detected with point counts ($N = 225$) were migrant warblers. Correspondingly, the bird community was dominated by insectivores (55.6%), especially leaf gleaners (34.7%), although resident nectarivores also constituted a large proportion (20.4%). Exclusively granivorous and frugivorous individuals were rare (7.6 and 3.1%, respectively), although omnivores, most of which eat some fruit, comprised 13.3 percent of all birds detected.

The bird community was influenced by both shade-tree species and crop structure (Table 5). Those areas of the plantation that had *Inga* as the dominant shade tree supported significantly greater abundances of birds than those areas with *Pseudal-*

bizia. Leaf-gleaning insectivores, bark-gleaning insectivores, and nectarivores were attracted especially to *Inga*; the other guilds showed no significant preference. There was also a significant main effect of crop structure, with more birds detected in dense than in open areas of the plantation. As evidenced by polynomial contrasts, this result was due largely to high abundances of leaf-gleaning insectivores in dense areas; crop structure did not significantly affect the abundance of other guilds.

The relative abundances of bird guilds also was affected by shade-tree species (within subjects; Table 5). Leaf- and bark-gleaning insectivores were proportionately more common in *Inga*-shaded areas, while aerial insectivores, ground-level insectivores, and non-insectivores were proportionately slightly more important in *Pseudalbizia*-shaded areas. Crop structure and its interaction with shade-tree species did not significantly affect relative bird abundances.

DISCUSSION

Previous comparisons of “sun” and “shade” coffee have shown that farm management practices can alter greatly the capacity for agricultural habitats to support biodiversity (Perfecto & Snelling 1995; Greenberg, Bichier, Angon *et al.* 1997). Yet a strict dichotomy of “shade vs. sun” or “traditional vs. intensified” coffee management systems is too simplistic (Rice & Ward 1996). The recognition of a broad spectrum of management practices is critical to understand the suitability of coffee plantations as habitat for tropical organisms (Rice & Ward 1996, Greenberg, Bichier, Angon *et al.* 1997, Greenberg, Bichier, & Sterling 1997, Wunderle & Latta 1998).

This study suggests that even within a single management system (*i.e.*, “specialized shade”), subtle differences in shade-tree species and crop structure can have significant effects on the communities present. Those areas of the plantation with *I. vera* as the dominant shade tree and, to a lesser extent, a dense crop structure, supported the most abundant arthropod and bird communities. This pattern was especially true during late winter. Greenberg, Bichier, Angon *et al.* (1997) and Greenberg, Bichier, and Sterling (1997) found as high or higher bird abundances on plantations shaded by trees of the genus *Inga* compared to those shaded by *Gliricidia* (Guatemala) or a canopy of natural forest species (Mexico). Although they lacked comparative data, the authors suggested that these patterns may have been due to high arthropod abundances on *Inga* leaves, a hypothesis sup-

ported by the results of this study. Wunderle and Latta (1998) described the foraging behavior of birds in Dominican coffee plantations shaded mainly by *I. vera* and *Citrus* spp., demonstrating that many birds, particularly insectivores and nectarivores, foraged predominantly in the shade tree canopy. Although no arthropod sampling was conducted, they, like Greenberg, Bichier, Angon *et al.* (1997), also implicated the importance of differential arthropod abundance. This study provides the first evidence linking observed differences in bird abundance to variation in arthropod abundance on a coffee plantation, and provides an ecological mechanism for the growing body of evidence suggesting the preference of *Inga* by birds. It is important to note that although *Inga* trees supported high arthropod and bird abundances, the abundance of arthropods (potential pests) on the coffee crop growing below was not affected by shade-tree species. Coffee-tree arthropods may be maintained at low abundance (>7 times lower than in the *Inga* canopy during this study) by chemically well-defended leaves (Frischknecht *et al.* 1986) and the application of insecticides.

In this study, the concentration of insectivorous and nectarivorous birds in *Inga*-dominated areas and that of leaf-gleaning insectivores in dense areas of the plantation appear to be due to high food abundance. Large numbers of arthropods in branch-clip samples from *Inga*-dominated and dense coffee areas suggest that these places may be particularly attractive to insectivores. Moreover, the most dramatic arthropod preferences for *Inga* canopies were exhibited by Homoptera, and for dense areas by flying arthropods and ants. These arthropod groups often comprise significant portions of insectivorous bird diets, particularly for leaf gleaners (Nolan 1978, Moldenhauer & Regelski 1996, Sherry & Holmes 1997). Psyllids (Homoptera) were present in Prairie Warbler, Northern Parula, and American Redstart emetic (regurgitation) samples obtained from this study site and other Jamaican *Inga*-dominated plantations (M. Johnson, pers. obs.), suggesting that at least some leaf gleaners were capitalizing on the abundant insect resource. With its food-rich flowers and extrafloral nectaries, *Inga* also provides abundant non-insect food (Koptur 1994, Celedonio-Hurtato *et al.* 1995), especially for nectarivores (Greenberg, Bichier, Angon *et al.* 1997, Wunderle & Latta 1998). Thus, the fact that nectarivores (but not granivores, frugivores, and omnivores) were more abundant in areas shaded by *Inga* than by *Pseudalbizia* further suggests the importance of food.

The abundance of insect and nectar food in coffee plantations may be especially important to birds in late winter. As the dry season progresses, many habitats exhibit winter declines in insect numbers (Janzen 1973, Wolda 1988, Von Schaik *et al.* 1993); yet bird food requirements rise as many resident species initiate breeding in anticipation of coming rains and migrants accumulate fat for spring migration to temperate breeding grounds (Berthold 1975). *Inga vera* begins to produce new leaves in late winter; flowering shortly follows, and insect populations, especially plant juice-feeding Psyllidae, appear to respond numerically (Adams 1972, Celedonio-Hurtato *et al.* 1995, Greenberg, Bichier, & Sterling 1997; Fig. 1). Although this study encompassed only one farm over two winters, increases in numbers of arthropods, especially psyllids, in the 1995–1996, 1996–1997, and 1997–1998 late winters were found in two additional Jamaican coffee farms dominated by *I. vera*, suggesting that this pattern may be more widespread in space and time (M. Johnson, pers. obs.). Thus, coffee plantations shaded by *Inga* or species with similar phenologies may serve as dry season refugia for birds by providing abundant food at a time when bird energetic demands are high and other habitats are food-poor. It is important to note, however, that although birds were more abundant in *Inga*-shaded areas of the plantation and Homopteran abundance increased nearly ninefold on *Inga* leaves over the winter, I did not quantify the seasonal use of different areas of the plantation by birds. Thus, before shade coffee is regarded as a safe harbor for birds, it is imperative that the seasonal use of plantations by birds be better understood. Namely, how do rates of over-winter site persistence (survival) of migrants and productivity of resident species in coffee plantations compare to those found in native forest?

Although food may play an important role in the use of coffee habitats by birds, other factors also may be operating. Flycatching insectivores, many of which have diets comprised largely of Diptera (Sherry 1984), did not show a significant preference for dense areas of the plantation containing disproportionately high abundances of flying arthropods. Dense areas might be avoided by flycatchers because they restrict visibility and maneuverability (and hence, food acquisition). Similarly, bark-gleaning insectivores, which are probably behaviorally well-adapted to feed on ants, were not more abundant in dense areas of the plantation, even though they supported many more ants than did open areas. This may be because ants are dif-

ficult to digest and probably provide relatively little nutrition compared to other insect groups (Zach & Falls 1978). Dense coffee areas, and to a lesser extent *Inga*-dominated areas, may provide protection from avian predators by providing increased cover, which could explain higher abundances of foliage-gleaning birds in those areas; however, it does not explain why other small bird groups did not show similar responses. Alternatively, increased cover in those areas could reduce sun exposure and help retain moisture, a potentially important consideration for tropical birds (Karr & Freemark 1983). These patterns suggest that other factors, such as habitat structural constraints, predation risks, and prey digestibility, interact with, and in some cases override, absolute arthropod abundance.

My results suggest that the abundance of arthropods significantly affected the bird community in the plantation, but the reverse also may have been operating (Holmes *et al.* 1979, Marquis & Whelan 1994). Bird and arthropod abundance covaried in this study; thus, any depression of arthropods by insectivorous birds would only act to *lessen* differences between treatment groups. Differences, however, were detected simply by measuring arthropod standing crop. Therefore, the potential operation of top-down effects would result in a conservative bias, and would not alter the significance of these findings. Avian insectivores in agricultural systems theoretically can regulate insect pest populations (Kirk *et al.* 1997) and furnish farmers with inexpensive biological control, which could in turn potentially enhance plant productivity (Marquis & Whelan 1994) and provide the critical economic incentive for farmers to retain management practices beneficial to birds (Greenberg, pers. comm.). Clearly, future research should focus on evaluating indirect effects of bird consumption on coffee productivity, as well as determining which, if any, bird species ingest coffee insect pests.

These results indicate that *Inga* is a better shade-tree species than *Pseudalbizia* from the perspective of maintaining arthropod and bird communities, but what about from a farmer's perspective? Both species are legumes, and provide nitrogen fixation; however, unlike *Pseudalbizia*, which has large brittle branches that occasionally fall and damage the crop, *Inga* grows more slowly and lives longer, making it a more profitable long-term choice as a shade-tree species. Therefore, *Inga* is more common on Jamaican farms (L. Campbell, A. Palmer, L. Barrett, and J. Minott, pers. comm.). Thus, *I. vera* may be a better choice for a shade

tree than *Pseudalbizia*, both biologically and economically.

Although dense (infrequently pruned) areas of the plantation supported more insectivorous birds, other crop structure considerations may be important in the management of arthropods and birds in coffee. Infrequent prunings temporarily create dense areas preferred by insectivores, but necessitate periodic and severe "resuscitational" prunings. At present, the effects of severe prunings on bird and arthropod communities have not been documented, but such disturbance could reduce temporarily the suitability of plantations for many species, especially understory arthropods and birds (Budhall 1986, Rice & Ward 1996). Future research should focus on examining the effects of farm management practices on the *long-term* suitability of coffee as habitat for forest organisms.

In summary, this study suggests that although some economically viable shade coffee plantations may provide a habitat that supports many arthropods and birds, differences in farm management practices can affect greatly the wild communities supported. In Jamaica, *I. vera* appears to be a better shade tree than *P. berteriana*, both biologically and from a farming perspective, but a choice in crop structure is less clear due its relatively small effects on communities and uncertainty with respect to changing effects of prune management over time. More work is needed to determine the generality of the preference by arthropods and birds for *Inga* in other regions, and to assess the relative suitability for wildlife of other potential shade-tree species, including potentially important synergistic benefits of a heterogeneous canopy. Lastly, negative effects of other management practices, such as heavy use of pesticides, may overwhelm any advantage accrued from a particular shade-tree species or crop structure, making shade management and pruning decisions secondary to more influential management practices.

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