

The Effects of Cropping Systems on Avian Communities in Cacao and Banana Agro-Forestry Systems of Talamanca, Costa Rica

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ABSTRACT

Multispecies agro-forestry is generally lauded for providing ecosystem services, especially in tropical environments. Avian communities contribute to services such as biodiversity and pest management. Characterizing and evaluating avian community composition in similar cropping systems will help optimize management for ecosystem services. We examined the relationship between cropping system vegetation and avian communities in four shaded agro-forestry systems common to the Limón province of Costa Rica: abandoned and managed systems of cacao, cacao with banana, and banana. During two field seasons, we detected 2605 birds from 106 species and identified 2791 trees and shrubs from 62 morphospecies. We compared vegetation and avian species richness across systems with mixed-effects linear models. Canopy, understory, and groundcover vegetation differed among agro-forestry systems. More ground- and understory-foraging forest species were detected in agro-forestry systems lacking banana, whereas richness of agricultural generalist species was highest in systems with banana. Richness of understory- and ground-foraging species correlated with understory tree species richness and leaf litter. Our results indicate that shaded cacao and banana systems can have similar canopy-foraging species richness that includes both agricultural and woodland generalist species, but that interspersing banana with cacao can adversely influence understory forest bird community composition. Agro-forests with diverse understory vegetation support more understory-foraging bird species that have proven valuable in pest management.

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Key words: ecosystem services; *Musa*; ordination; species richness; *Theobroma cacao*; tropical agriculture; vegetation covariates.

CONSERVATION IN HUMAN-DOMINATED LANDSCAPES often emphasizes agricultural practices, such as agro-forestry, that are both profitable and support native biodiversity (Pimentel *et al.* 1992). Agro-forests managed for multiple products and/or ecosystem functions may contain diverse structural elements that have been shown to correlate with high animal diversity. Studies in coffee and cacao systems have observed positive correlations between animal species diversity and habitat variables such as canopy height (Znajda 2000, Mas & Dietsch 2004, Harvey & González Villalobos 2007, Philpott *et al.* 2008), tree density, diversity and composition (Johnson 2000, Znajda 2000, Mas & Dietsch 2004, Harvey & González Villalobos 2007, Philpott *et al.* 2008), and clearing and pruning practices (Johnson 2000, Mas & Dietsch 2004, Philpott *et al.* 2008). Conversely, replacing rustic plantations shaded by a mature forest canopy with a planted monoculture leads to losses in plant and animal diversity (Gallina *et al.* 1996, Roberts *et al.* 2000, Goehring *et al.* 2002, Siebert 2002, Harvey & González Villalobos 2007, Philpott *et al.* 2008). The loss of shade trees, where many insects live (Johnson 2000, Philpott *et al.* 2008) and birds forage (Wunderle & Latta 1998, Van Bael *et al.* 2007b), is clearly an important driver of these changes. Furthermore, each agro-forestry system supports a unique animal community. For example, bird community composition differs between shaded cacao and coffee plantations (Greenberg *et al.* 2000a), shaded cacao and banana plantations (Harvey &

González Villalobos 2007), or shaded (Van Bael *et al.* 2007b) and abandoned (Reitsma *et al.* 2001) cacao plantations and forest. Taken as a whole, these descriptive studies demonstrate how species assemblages in forest and agricultural systems can be dynamic and responsive to changes in the composition and structure of vegetation (Roth & Perfecto 1994, Perfecto & Snelling 1995, Goehring *et al.* 2002, Philpott *et al.* 2008). Identifying those elements of cropping systems that influence animal diversity will provide further insight for producers and consumer certification programs seeking to encourage the provision of ecosystem services while maintaining economically profitable agricultural output.

Agro-forests based on cacao, *Theobroma cacao*, encompass large portions of tropical Africa (5.7 million ha), America (1.5 million ha), and Asia (1.0 million ha; Food and Agricultural Organization [FAO] 2009) and are located in humid lowlands known to be rich in biodiversity (Greenberg *et al.* 2000a, Rice & Greenberg 2000). Vegetation structure in shaded cacao is forest-like, often with multiple strata and diverse tree species (Greenberg *et al.* 2000a, Rice & Greenberg 2000, Suatunce 2002), and high insect (Leston 1970, Room 1971, Perfecto *et al.* 1996, Klein *et al.* 2002, Suatunce 2002), bird (Greenberg *et al.* 2000a, Reitsma *et al.* 2001, Harvey & González Villalobos 2007), and mammal (Guiracocha *et al.* 2000, Harvey & González Villalobos 2007) species diversity. Cacao production has been characterized by regional and global economic cycles of boom and bust (Ruf & Schroth 2004) resulting in some plantations being temporarily abandoned or converted to other agricultural land uses.

Banana plantations also occur throughout tropical Africa (1.7 million ha), America (1.2 million ha), and Asia (2.1 million ha),

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although they occupy 38 percent less area globally than cacao (FAO 2009). Animal communities in banana monocultures are either depauperate (Harvey & González Villalobos 2007) or nonexistent due to the intense use of pesticides and lack of vegetation complexity. Bananas are also interplanted within rustic coffee or cacao agro-forests as a means to diversify crop production (Moguel & Toledo 1999, Rice & Greenberg 2000), and recently shade-grown organic banana cultivation has become the focus of conservation groups (Rainforest Relief 2009). In comparison to coffee or cacao, few characterizations of animal communities in banana agro-forests exist (but see Guiracocha *et al.* 2000, Harvey & González Villalobos 2007) despite the similarity of all three systems.

The coastal plain of Talamanca, Costa Rica provides a unique setting to compare animal communities in cacao and banana agro-forests. During the 1900s, plantations often alternated between cacao and bananas or plantains, *Musa* spp., or a mixture of both (Palmer 1993, Somarriba 1993). In the past 20 yr, the production of organic shade-grown bananas increased among small farmers, some of whom joined together in 1993 to form the Association of Peasant Organic Producers (ACAPRO 2005). Many of these producers either converted abandoned cacao plantations to shaded banana or simply planted banana among their cacao. ACAPRO farms are certified organic by Ecológica, Oregon Tilth, and Ecocert, and members either sell their organic bananas to a Gerber™ subsidiary for use in baby food or process them into banana vinegar for local sale or export (ACAPRO 2005, Rainforest Relief 2009). Because of their organic certification, we expected these farms to be biologically diverse, providing the opportunity to explore the relationship between agro-forestry system and avian communities across a range of cacao- and banana-based systems.

We studied four agro-forestry cropping systems common to small plantations in Talamanca, Costa Rica, including abandoned cacao, managed cacao, cacao interspersed with banana, and banana-only plantations. We hypothesized that avian communities would differ among agro-forestry systems and that these changes would be correlated with differences in vegetation. The objectives of this study were to: (1) characterize avian community composition across a range of cacao- and banana-based agro-forests, (2) identify vegetation characteristics correlated to avian species diversity, and (3) summarize results into recommendations for growers interested in managing for ecosystem services related to biodiversity and avian conservation.

METHODS

STUDY SITE.—This study took place along a coastal strip of Caribbean lowlands in the canton of Talamanca, Limón province, Costa Rica (9°39' N, 82°48' W) in 2004 and 2005. The average annual temperature of the region is 25.8°C, and the average annual rainfall is 3525 mm with relatively drier seasons in February–March and September–October (Mena 2005). The study area is within the tropical humid forest life zone (Tosi 1969). Currently, there is a mosaic of secondary forest; cacao, banana and plantain plantations; pasture; and other subsistence and export crops. The survey area also included abandoned cacao plantations within the Cahuita

National Park (1068 ha), formed in 1970, and managed cacao plantations within the Kekoldi Indigenous Reserve. Most producers in the study area are small landholders (1–10 ha), including the parcels studied here. Cacao and banana are grown under canopies of planted and remnant shade trees dominated by *Cordia alliodora*, a fast growing timber species. Banana is either planted among the cacao trees or alone where cacao trees have been removed.

We conducted vegetation measurements and fixed radius point-counts for birds on 23 parcels of 0.5–5 ha in size and located on 16 farms. A single point was placed in the center of small parcels (< 0.75 ha), and up to six points were systematically distributed in large parcels (> 0.75 ha) to maximize the total number of points within that parcel (as in Wunderle & Latta 1998). All points were separated by at least 100 m and positioned at least 25 m from an edge. All but one farm was certified organic. Parcels were classified as abandoned cacao (AC), cacao (C), cacao with banana (CB), or banana (B). Abandoned cacao plantations were no longer actively managed, *i.e.*, farmers were not extracting cacao from them. Land-use classifications of adjacent properties in the four cardinal directions from each parcel indicated that 91 percent of parcels bordered properties with tree cover (of which 52% bordered secondary forest and 81% bordered shaded cacao or banana systems), 35 percent bordered roads, 22 percent bordered pasture, 39 percent bordered residential areas, and 22 percent bordered rivers.

VEGETATION SAMPLING.—Vegetation measurements were collected during May 2004 using a method modified from Martin *et al.* (1997). We used large, circular vegetation plots (11.7 m radius) to estimate tree density and species diversity. All trees in the plot were counted, classified as either large canopy trees (> 15 cm dbh [1.3 m]) or small understory trees (< 15 cm dbh and > 1 m tall), and identified to family and morphospecies either in the field or with a branch clipping using Vindas (2001). Four canopy trees were selected randomly and their heights estimated visually. Finally, within a small (5 m radius) vegetation plot centered within the larger plot, we visually estimated percent herbaceous (< 1 m tall) and leaf litter.

BIRD SAMPLING.—We conducted 10-min, fixed radius point-counts to assess avian species composition in each parcel (Petit *et al.* 1995). As parcels were forested, we used a fixed radius of 25 m to minimize detection differences among points. Points were centered on vegetation plots distributed systematically through each parcel (described above). Counts were conducted between 0530 and 0800 h. Within the 25 m radius, we recorded species and the number detected. Individuals flying above the canopy within the point-count circle were not recorded. Each point was sampled six times, split evenly between the dry period from 20 May to 12 July 2004 and the wet period from 28 November 2004 to 13 February 2005. We conducted repeated samples of each point to accurately characterize its avian community and examine correlations with vegetation characteristics (Hutto *et al.* 1986, Petit *et al.* 1995).

STATISTICAL ANALYSES.—All statistical analyses were conducted using the *R* statistical program (R Development Core Team

2008) and associated packages. For each vegetation survey point, we characterized the composition of canopy and understory trees using species richness (R) and the Shannon–Weiner diversity index (H') as well as Pielou's J' (J') as an index of the relative evenness of tree species' abundances within cropping systems (Magurran 1988). Bird species were categorized by habitat affinities (Canterbury *et al.* 2000, Reitsma *et al.* 2001) that included: agricultural generalists (AGs), species found in open habitats and scattered tree patches; woodland generalists (WGs), species found in forest and large patches of trees; and forest specialists (FSs), species found exclusively in forests.

Because of the unequal number of points surveyed per agro-forestry parcel and number of parcels surveyed per agro-forestry system, we compared vegetation measures and avian species richness among agro-forestry systems using mixed-effects linear models (lme function, nlme package, Pinheiro *et al.* 2008), also known as hierarchical models. The mixed-effects model specifies a fixed effect, in this case agro-forestry system, as well as random effects for nested factors, in this case the parcel in which a point is located. The mixed-effect model is analogous to an analysis of variance with nested factors, but it is robust to unbalanced data structures (Pinheiro & Bates 2000).

To visualize differences in avian community composition, we conducted nonmetric multidimensional scaling ordination based on Bray–Curtis distances (Bray & Curtis 1957). Distances were calculated from a community matrix assembled from the maximum number of individuals per species observed at each point. Ordinations were constructed with all survey points in each season using all species as well as species grouped by habitat affinity. When species groups were used, a dummy species present at all points was added to allow comparisons among sites with no species in common. When the range of individuals was sufficiently great, we standardized the maximum abundance per species per point by the maximum number of observations per point for each species, the so-called 'Wisconsin transformation' suggested by Faith *et al.* (1987). Because ordination was used to visualize patterns in the data and not to test hypotheses, we applied the transformation as needed. The multidimensional scaling algorithm (metaMDS function, VEGAN package, Oksanen 2008) generated the ordination of survey points with axes rescaled around zero. Stress is the accuracy of the ordination in representing Bray–Curtis distances. The metaMDS function includes multiple random start configurations and comparisons of results to maximize the probability of finding the true minimum stress solution (Oksanen 2008). We also plotted the degree and direction of correlation between the ordination axes and measured vegetation variables (envfit function, VEGAN package, Oksanen 2008) to examine relationships between vegetation and avian community composition.

Finally, we calculated Pearson's product-moment correlations between avian species richness per point and vegetation measures. Correlations were calculated for all species as well as groups based on habitat affinity group and foraging-height guild. Examined foraging-height guild designations included: canopy, sub-canopy, trunk, understory, and ground foragers.

RESULTS

VEGETATION.—In total, 48 points were classified into the four agro-forests studied: AC (14 plots), C (11 plots), CB (12 plots), and B (11 plots). We counted 1484 canopy trees representing *ca* 31 families and 59 morphospecies, and 1307 small understory trees and shrubs representing *ca* 36 families and 62 morphospecies. Mixed-effects models revealed differences among agro-forestry systems in all vegetation measures and indices except canopy height (Table 1). Based on model estimates, AC agro-forests had higher species diversity (H') and a more even distribution of species abundances (J'), whereas AC and B agro-forests had similarly high densities of canopy trees and canopy species richness. In the understory, AC had notably higher tree density as well as greater species richness and diversity per point. The distribution of tree species abundances in the understory was similar for AC and CB agro-forests. On the ground, herbaceous cover was greatest in CB and B systems and lowest in C systems, whereas leaf litter was greater in AC, C, and CB systems.

BIRDS.—We recorded 950 detections of birds representing 88 species in May–July, and 1655 detections representing 97 species in November–February (see Table S1 for a complete species list). A mixed-effects model constructed for the entire dataset revealed a significant seasonal effect on the species richness per point ($F = 44.3$, $P < 0.0001$). Estimated species richness was approximately 10 species per point in May–July and 15 in November–February. Because richness differed between seasons, subsequent analyses were conducted separately on data from each season.

Nonmetric multidimensional scaling ordinations spatially arrange each survey point such that its distance from adjacent points is proportional to dissimilarities in their community composition. Ordination plots (Fig. 1) differentiated between avian communities at survey points with only cacao (AC or C, closed shapes) and those with banana (CB or B, open shapes). This pattern was detected when only AG or WG species were included in the analysis, but not FSs (Fig. 1).

Ordination axes partition the variation in the Bray–Curtis distance measures among survey points, but may be difficult to interpret biologically (McCune & Grace 2002). Arrows in Figure 1 display the direction and magnitude of correlation between ordination axes and vegetation measurements. All plotted correlations were significant at $\alpha = 0.05$. Understory and groundcover characteristics correlated most often with avian community composition in both seasons and when all species were pooled (ALL) or grouped by habitat affinity (AG, WG, or FS). The relationship between avian species richness and vegetation is defined in greater detail in the correlation analyses (below). Histograms of species richness plotted along the horizontal axis of ordinations reveal two contrasting qualitative trends captured in the first axis of ordinations for AG and WG species: AG species richness appears greater in agro-forests with banana (open shapes) whereas WG species richness appears greater in agro-forests lacking banana (closed shapes).

Analyses based on mixed-effects models confirmed several patterns in avian species richness identified in the ordinations

TABLE 1. Estimated mean values per sampling point of vegetation measurements and calculated diversity indices in four agro-forestry systems in Talamanca, Costa Rica. AC, abandoned cacao; C, cacao; CB, cacao with banana; and B, banana. Values with the same letter (^{a,b,c}) are not significantly different.

Forest strata	Vegetation measure (abbreviation)	Estimated mean \pm SE				Mixed-effects model	
		AC	C	CB	B	F	P-value
Canopy	Individuals per plot (cindiv)	8.1 \pm 0.9 ^a	4.9 \pm 1.4 ^b	4.2 \pm 1.4 ^b	6.8 \pm 1.4 ^{ab}	3.05	0.049
	Species richness (crich)	5.4 \pm 0.4 ^a	2.7 \pm 0.7 ^b	3.5 \pm 0.6 ^b	4.3 \pm 0.7 ^{ab}	6.18	0.003
	H' (ch)	1.5 \pm 0.2 ^a	0.8 \pm 0.2 ^b	0.8 \pm 0.2 ^b	1.1 \pm 0.2 ^b	4.06	0.019
	J' (ceven)	0.9 \pm 0.1 ^a	0.6 \pm 0.1 ^b	0.5 \pm 0.1 ^b	0.7 \pm 0.1 ^b	3.42	0.034
	Height in meters	14 \pm 1.7	16.2 \pm 2.6	13.8 \pm 2.6	15.7 \pm 2.6	0.396	0.757
Understory	Individuals per plot (uindiv)	84.2 \pm 16.5 ^a	-2.6 \pm 23.3 ^b	16.9 \pm 23.5 ^b	10.3 \pm 26.5 ^b	5.42	0.006
	Species richness (urich)	7.2 \pm 0.9 ^a	1.0 \pm 1.4 ^b	2.7 \pm 1.4 ^b	1.4 \pm 1.5 ^b	8.68	< 0.001
	H' (uh)	1.2 \pm 0.1 ^a	0.3 \pm 0.2 ^c	0.7 \pm 0.2 ^b	0.2 \pm 0.2 ^c	16.0	< 0.001
	J' (ueven)	0.6 \pm 0.1 ^a	0.3 \pm 0.1 ^b	0.7 \pm 0.1 ^{ab}	0.2 \pm 0.1 ^b	6.50	0.002
Ground	% Herbaceous cover (herb)	55 \pm 8 ^b	26.8 \pm 13 ^c	64 \pm 13 ^a	76.7 \pm 13 ^a	5.12	0.007
	% Litter (litter)	80 \pm 9 ^a	86.8 \pm 13 ^a	59.9 \pm 13 ^a	31.3 \pm 13 ^b	6.41	0.003

(Table 2). Estimates of total species richness per point did not differ with agro-forestry system in either May–June or November–February. More AG species occurred in banana agro-forests in November–February, but not May–June. More WG species occurred in abandoned cacao and banana in May–June with a similar pattern, although not significant at $\alpha = 0.05$, in November–February. There was no significant difference in FS species richness among systems, but a trend toward higher FS species richness in abandoned cacao in November–February. Among foraging-height guilds, trunk- and sub-canopy-foraging species richness was unaffected by agro-forestry type. More canopy-foraging species occurred in banana agro-forests in November–February, particularly AG canopy foragers. WG canopy foragers showed a similar pattern, although not significant at $\alpha = 0.05$. Ground-foraging species richness was highest in abandoned cacao plantations. All of these ground-foraging species were either WG or FS species (Table S1). Finally, understory-foraging WG species were more diverse in abandoned cacao or managed cacao agro-forests than systems with banana. Guilds with three or fewer species were excluded from grouped analyses of species richness and correlations with vegetation measures (see ‘Birds and vegetation’). Therefore, the sum of species counts in species sub-groups does not always equal the number of species in the next highest group (Tables 2 and S2). Guild-level analyses were not conducted for FS species because of the group’s low richness.

BIRDS AND VEGETATION.—Product-moment correlations identified which characteristics of vegetation composition and structure may be driving patterns in avian species community composition. Generally speaking, correlations between vegetation measures and pooled species richness per point were weaker ($P < 0.3$) than those between vegetation and species richness within habitat affinity groups or foraging-height guilds ($0.3 < P < 0.55$; Table S2). Therefore, we focused on the latter which revealed several patterns. First, the number of AG species per point in both seasons correlated

positively with herbaceous cover and negatively with leaf litter, whereas the number of all understory-foraging species as well as understory-foraging WG species correlated negatively with herbaceous cover and positively with leaf litter. Second, WG species richness correlated positively with understory tree species richness and diversity as well as understory tree density. Richness of understory-foraging WG species correlated positively with a number of understory measures, particularly understory species richness ($P = 0.532$ and 0.546 in May–July and November–February, respectively), but also understory tree diversity and density. Finally, the number of FS species per point correlated with understory tree species richness and diversity in both seasons.

Canopy measures were less frequent correlates to species diversity than understory measures. However, overall species richness correlated with measures of canopy diversity in November–February as did richness of FS species, particularly in November–February. Canopy height was not correlated with richness of any species groups.

DISCUSSION

CROPPING SYSTEM ALTERS VEGETATION STRUCTURE.—Vegetation in the canopy, understory, and on the ground differed among the four agro-forestry systems studied (Table 1). Generally, managed systems had fewer trees and tree species in the canopy and understory than abandoned cacao, and systems with banana had more herbaceous vegetation and less leaf litter than systems with cacao. We did not observe any differences in canopy height among systems, a result also found in secondary forest, cacao, and banana agro-forests elsewhere in Talamanca (Harvey & González Villalobos 2007). Canopy height has repeatedly correlated positively with avian diversity (Znajda 2000, Harvey & González Villalobos 2007, Philpott *et al.* 2008); however, all canopies in our plots were tall enough to have correlated with high avian diversity elsewhere (Mas & Dietsch 2004).

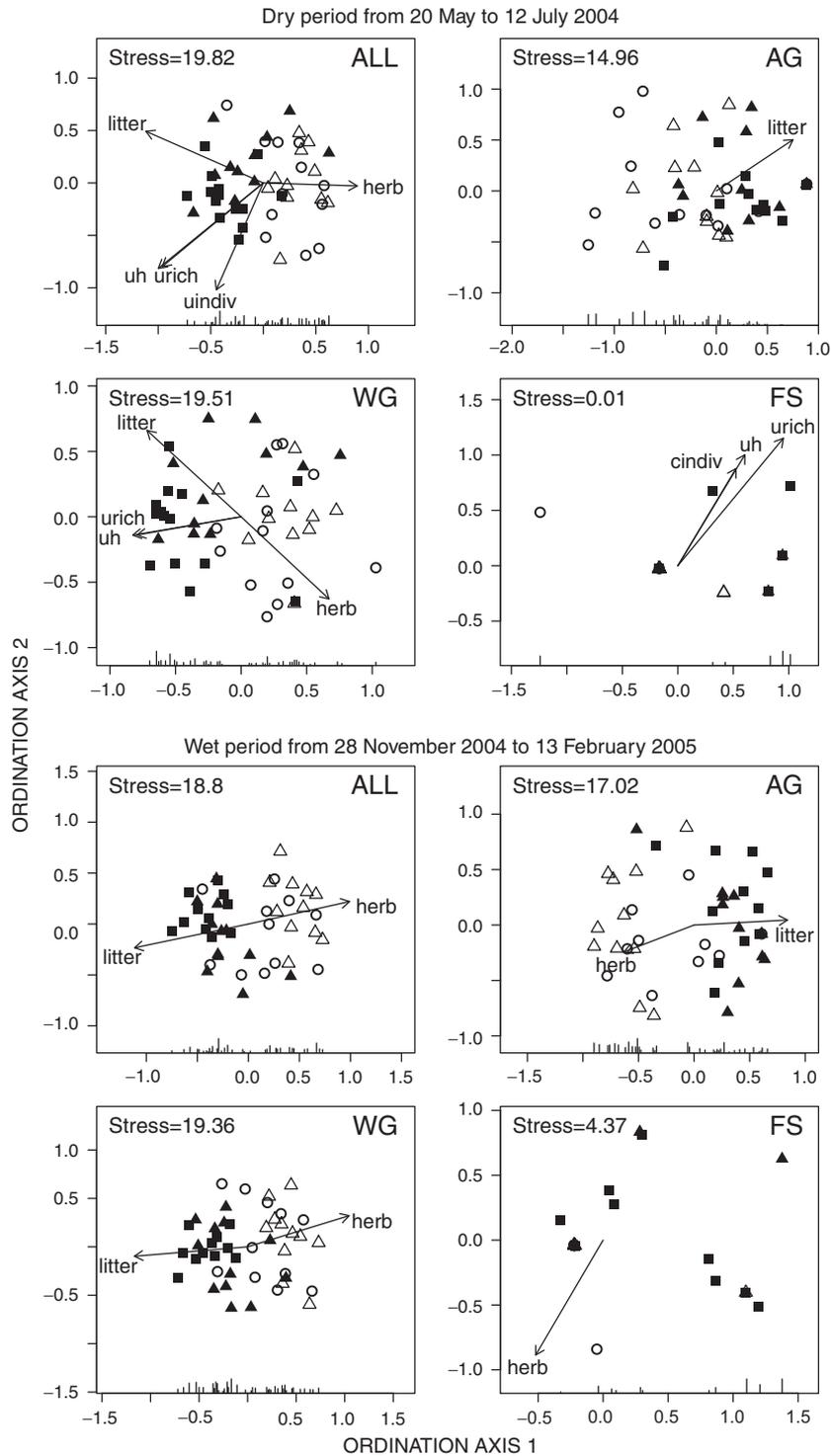


FIGURE 1. Ordination plots of survey points in abandoned cacao (solid squares), cacao (solid triangles), cacao with banana (open circles), and banana (open triangles) using a nonmetric multidimensional scaling of Bray–Curtis distance coefficients based on maximum observed avian species abundances. Community data used to generate plots are grouped by season (top four and bottom four panels) and habitat affinity groups. The horizontal axis includes a histogram of species richness per point. Abbreviations for vegetation measures are included in Table 1. Shown are the first and second dimensions of a three-dimensional ordinations.

TABLE 2. Estimated mean species richness per sampling point for two seasons in four agro-forestry systems in Talamanca, Costa Rica. Species were grouped by habitat affinity and foraging-height guild. AC, abandoned cacao; C, cacao; CB, cacao with banana; and B, banana. Values with the same letter (^{a,b,c}) are not significantly different.

Species pool	Species count	May–June						November–February						
		Estimated species richness				Mixed-effects model		Estimated species richness				Mixed-effects model		
		AC	C	CB	B	F	P-value	AC	C	CB	B	F	P-value	
All Species	88	10.7	8.5	8.7	10.8	0.7	0.562	97	15.8	13.8	11.6	17.6	2.38	0.097
Canopy foragers	40	3.9	3.4	5.1	6.3	2.74	0.067	41	6.2 ^b	5.9 ^b	6.5 ^b	12.4 ^a	7.87	0.001
Understory foragers	25	5.1	3.9	3.3	3.2	1.69	0.196	34	7.9 ^a	6.2 ^a	4.3 ^b	3.3 ^b	8.27	0.001
Trunk foragers	8	0.8	0.6	0.5	0.6	0.219	0.882	6	0.7	1	0.7	0.9	0.247	0.863
Ground foragers	5	0.6 ^a	0.3 ^{ab}	0.2 ^b	0 ^b	3.06	0.049	5	1.0 ^a	0.4 ^b	0.3 ^b	0.1 ^b	3.36	0.037
Sub-canopy foragers	7	0.3	0.1	0.3	0.5	0.652	0.59	10	0.2	0.2	0.2	0.8	1.87	0.165
Agricultural Generalists	34	2.5	2.7	4.2	4.5	1.4	0.268	34	3.3 ^b	3.0 ^b	4.6 ^b	7.7 ^a	5.95	0.004
Canopy foragers	17	1.1	1.1	2.2	2.6	2.88	0.058	15	1.0 ^c	0.8 ^c	2.6 ^b	5.1 ^a	14.0	< 0.001
Sub-canopy foragers	6	0.2	0.1	0.4	0.4	0.682	0.572	8	0.2	0.1	0.2	0.7	2.76	0.066
Understory foragers	9	1.1	1.4	1.9	1.4	0.869	0.471	10	1.9	2	2.1	1.7	0.253	0.859
Woodland Generalists	48	7.7 ^a	5.7 ^b	4.4 ^b	6.1 ^{ab}	3.15	0.044	56	12	10.5	7.1	10	2.99	0.053
Canopy foragers	21	2.4	2.3	2.6	3.6	1.43	0.261	24	4.8	4.9	4	7.2	2.90	0.058
Trunk foragers	8	0.8	0.6	0.5	0.6	0.219	0.882	6	0.7	1	0.7	0.9	0.247	0.863
Understory foragers	15	4.1 ^a	2.5 ^b	1.2 ^b	1.8 ^b	5.55	0.005	21	6.0 ^a	4.1 ^a	2.2 ^b	1.7 ^b	13.6	< 0.001
Forest Specialists	5	0.5	0.1	0.2	0.1	0.661	0.584	7	0.7	0.2	0.1	0.1	2.61	0.077

P-values significant at $\alpha = 0.05$ in bold.

The range of structural complexity among agro-forestry types in this study does not include a planted monoculture or a system with sparsely planted leguminous shade trees, as is common in coffee (Moguel & Toledo 1999) and cacao (Rice & Greenberg 2000) production. Inclusion of these systems in a descriptive study such as this provides a broad spectrum for comparison, but may create statistically significant system effects while masking important management-level effects. Because of their prevalence, we chose to compare bird community composition in only the more densely shaded systems of cacao and/or banana. The correlations that we observed between vegetation and avian communities are notable because they occurred among relatively similar shaded systems.

AVIAN COMMUNITY COMPOSITION IN AGRO-FORESTRY SYSTEMS.—Ordination plots depicted differences in avian community composition among agro-forestry systems and highlighted a trend toward greater WG species richness in systems with only cacao (AC and C) and greater AG species richness in those with banana (CB and B; Fig. 1). Estimates of species richness based on mixed-effects models revealed no difference in overall avian species richness and less pronounced patterns within habitat affinity groups. Banana plantations did have higher AG species richness. Both abandoned cacao and banana systems, however, had higher WG species richness and there were no differences in the number of AG, WG, and FS species detected per point in managed cacao and cacao with banana systems.

Canopy-foraging species were major contributors to observed differences in richness of AG and WG species. Canopy and sub-canopy foragers comprised 53 percent of all species recorded during

both seasons and were the most diverse foraging-height guild within the AG and WG habitat affinity groups (Table 2). Canopy foragers, whether pooled or grouped by habitat affinity, were most diverse in banana agro-forests (Table 2). This increased AG and WG richness in banana relative to the two other managed systems. Multiple studies have emphasized the importance of shade trees for avian diversity in coffee agro-forests (Wunderle & Latta 1998, Johnson 2000, Philpott *et al.* 2008), and they are equally important in cacao and banana systems.

Observed patterns in understory- and ground-foraging species were consistent with ordination results. Understory and ground foragers, especially understory-foraging WG species, were most diverse in cacao-based systems (AC and C). Because all of the ground-foraging species were either WG or FS species, this is strong evidence that cacao-based systems are important to understory- and ground-foraging woodland and forest species. Previous studies have found few understory-foraging forest species in cacao (Alves 1990, Greenberg *et al.* 2000a, Znajda 2000, Reitsma *et al.* 2001, Harvey & González Villalobos 2007). Our results suggest that remaining understory species are threatened by banana introductions.

Migrant species were either rare or did not differ in their occurrence in the four agro-forestry systems. Three migrant species, *Dendroica pensylvanica*, *Vermivora peregrina*, and *Icterus galbula*, were abundant (Table S1) in all four agro-forests. This is consistent with studies completed in Mexico observing large seasonal increases in the number of migrant birds in shaded coffee plantations (Greenberg *et al.* 1997). Migrant densities may respond positively to arthropod densities in canopy foliage (Johnson 2000), or increased flowering during the relatively wet season in

November–February. Two understory-foraging migrant species, *Hylcoichla mustelina* and *Oporornis formosus*, were found only in plantations of abandoned or managed cacao (Table S1), suggesting that they may also distinguish between the cacao and banana understory. Other studies conducted in Talamanca (Reitsma *et al.* 2001) and nearby Panama (Van Bael *et al.* 2007b) found more migrants than this study, but surveyed ten times the number of points per system.

We detected on average five more species per point in November–February than May–July. Detections of the ubiquitous migrants, *D. pensylvanica*, *V. peregrina*, and *I. galbula*, in November–February probably account for a portion of this seasonal difference. Some residents were only observed in one season. The net turnover of resident species was +2 (Table S1). Some of these turnover species may have been regional migrants, but others may have been yearlong residents that were hard to detect. Most turnover species had fewer than six detections. Of the 25 species that increased by more than ten detections in November–February, 16 (64%) were canopy-foraging species that were difficult to detect unless calling. Thus, the remaining seasonal increase in detections was likely due to increased bird activity between rain events in November–February. On whole, higher species richness in November–February reinforced observed patterns (Table 2).

RELATIONSHIPS BETWEEN AVIAN SPECIES RICHNESS AND HABITAT MEASUREMENTS.—All habitat affinity groups and foraging-height guilds showed significant correlations to vegetation measurements (Table S2). Understory tree species diversity and groundcover were most commonly associated with species richness measures. Coefficients of determination for all correlations did not exceed 30 percent, suggesting that other factors influence avian community composition aside from the vegetation measurements collected. These may include other measures of vegetation previously associated with avian diversity, such as clearing and pruning practices, canopy cover, phenological characteristics of shade trees (*i.e.*, flowering and fruiting), or landscape features such as land-use configuration and proximity to forest.

Understory and groundcover measures revealed the largest contrasts between agro-forestry systems (Table 1) and were most frequently correlated to species richness. Groundcover was associated with AG and understory-foraging species richness, understory vegetation was associated with WG and FS species richness, and canopy diversity was associated with FS species richness and overall species richness (Table S2). Canopy-foraging species richness correlated with groundcover but not canopy vegetation measures. Groundcover measures may approximate the effects of forest cover, but a measure of percent forest cover would likely have provided a stronger correlate to canopy-foraging species richness.

ECOSYSTEM SERVICES IN CACAO AND BANANA AGRO-FORESTS.—Results support the hypothesis that avian communities respond to differences among the four shaded agro-forestry systems studied. Richness of understory and ground-foraging WG and FS species was highest in abandoned cacao and managed cacao systems. Conversion of existing abandoned cacao forests and cacao agro-forest hab-

itats to banana production or other land uses lacking understory vegetation would threaten these populations. Therefore, cacao-based agro-forestry should be promoted for providing habitat to understory and ground-foraging woodland and forest species. Similar conclusions have been reached regarding rustic vs. planted-shade and full-sun coffee agro-forests (Philpott *et al.* 2008). Conversion may also result in a loss of ecosystem services provided by a diverse avian community that includes understory-foraging insectivores. Avian predation has been shown to reduce insect damage in cacao trees (Van Bael *et al.* 2007a) and coffee (Greenberg *et al.* 2000b). Maintenance of a diverse understory bird community should be a priority for organic and ‘biodiversity friendly’ certified producers.

Canopy-foraging AG and WG species were as diverse in banana systems as in abandoned cacao. Therefore, banana agro-forests can have high canopy-foraging WG species richness even though understory-foraging WG and FS species richness is low. Shaded banana system should not be promoted over cacao, but they can have high canopy tree density and species richness, and high WG species richness. Restoring canopy trees to existing banana monocultures or replacing other nonforest land uses with shaded banana agro-forests would benefit canopy-foraging species.

Based on these observations, we recommend that managers separate stands of cacao and banana. Excluding banana from cacao agro-forests will maintain the leaf litter and understory vegetation correlated with higher understory bird species richness. Other management recommendations applicable to both cacao and banana agro-forestry systems include: (1) maintaining high canopy tree density and species diversity and (2) increasing understory diversity by planting saplings, reducing the frequency of understory clearing, and promoting berry-producing vegetation attractive to wildlife. These suggestions are implied by our observed correlations, but should also be tested experimentally or in a study that incorporates more detailed vegetation measures as well as landscape-scale metrics.

Results suggest along with others (Greenberg *et al.* 2000a, Harvey & González Villalobos 2007) that agro-forests based on cacao and banana do not conserve many currently endangered or threatened species. None of the species observed in this study were of conservation concern in 2008 (IUCN 2009); however, avian communities associated with agro-forests are important for maintaining the overall diversity of human dominated-landscapes (see Daily *et al.* 2001). Conversion of either shaded cacao or banana systems to monocultures would result in widespread impacts on understory and canopy species diversity (as documented by Gallina *et al.* 1996, Roberts *et al.* 2000, Goehring *et al.* 2002, Siebert 2002, Harvey & González Villalobos 2007). In addition, introduction of banana to cacao agro-forestry systems could cause local extirpation of understory forest species. Dispersal studies on three understory species showing strong preference for cacao-only systems, *Thamnophilus atrinucha*, *Myrmeciza exsul*, and *Habia fuscicauda*, revealed that individuals of these species could rarely disperse across open areas > 100 m (Moore *et al.* 2008). Therefore, widespread conversion to banana-based systems could have implications for the distribution of these or similar species.

In tropical regions dominated by agricultural land uses and fragmented secondary forests, shaded cacao agro-forestry should be promoted and conversion of cacao to banana minimized. Shaded banana agro-forestry should be promoted as an alternative to non-shaded agriculture or other nonforest land uses. Ongoing conversion of cacao to banana reflects economic incentives that undervalue cacao agro-forests. Both the cacao- and banana-based agro-forests featured in this study would likely meet most criteria for the certification of shade-grown coffee plantations (Mas & Dietsch 2004), but there are no shade-grown certifications for cacao or banana production. Certifications as well as affiliations with conservation advocacy groups would help to support cacao and banana agro-forestry by providing technical outreach to producers and increasing access to consumers willing to pay a premium for ecosystem services. Such certifications and affiliations are needed to align economic incentives with the ecosystem services associated with cacao and banana agro-forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Observed avian abundances with habitat affinity and guild designations.*

TABLE S2. *Pearson's correlation coefficients for avian species richness and vegetation measures.*

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