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Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats

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Abstract Although an increasing number of studies have shown that diverse, multi-strata agroforestry systems can contribute to the conservation of tropical biodiversity, there is still debate about how the biodiversity within agroforestry systems compares to that of intact forest and alternative land uses. In order to assess the relative importance of agroforestry systems for biodiversity conservation, we characterized bat and bird assemblages occurring in forests, two types of agroforestry systems (cacao and banana) and plantain monocultures in the indigenous reserves of Talamanca, Costa Rica. A total of 2,678 bats of 45 species were captured, and 3,056 birds of 224 species were observed. Agroforestry systems maintained bat assemblages that were as (or more) species-rich, abundant and diverse as forests, had the same basic suite of dominant species, but contained more nectarivorous bats than forests. Agroforestry systems also contained bird assemblages that were as abundant, species-rich and diverse as forests; however the species composition of these assemblages was highly modified, with fewer forest dependent species, more open area species and different dominant species. The plantain monocultures had highly modified and depauperate assemblages of both birds and bats. Across land uses, bird diversity and species richness were more closely correlated with the structural and floristic characteristics than were bats, suggesting potential taxon-specific responses to different land uses. Our results indicate that diverse cacao and banana agroforestry systems contribute to conservation efforts by serving as habitats to high numbers of bird and bat species, including some, but not all, forest-dependent species and species of known conservation concern. However, because the animal assemblages in agroforestry systems differ from those in forests, the maintenance of forests within the agricultural landscape is critical for conserving intact assemblages at the landscape level.

Keywords Banana agroforestry systems - Biodiversity conservation - Cacao agroforestry systems - Costa Rica - Human-modified landscapes - Indigenous agroecosystems - Land use - Talamanca - Tropical forests

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Introduction

One of the greatest challenges facing tropical biologists is how to conserve biodiversity within the agricultural landscapes that increasingly dominate the tropics and continue to encroach upon the remaining forests (Daily 2001; McNeely and Scherr 2003; Harvey et al. 2005). In many tropical regions, especially those where the opportunities for the additional protection of forests or natural habitats have been exhausted or where large-scale conversion of forest to agriculture has already occurred, the long-term conservation of native plant and animal diversity will depend on our ability to design and manage agricultural landscapes in such a way that they conserve as much of the original biodiversity as possible, while still meeting agricultural production goals (Daily et al. 2001; McNeely and Scherr 2003). Achieving conservation within human-dominated landscapes, however, will require a detailed understanding of the ability of different agricultural land uses to conserve both plant and animal taxa and how to appropriately manage these land uses for conservation goals (Perfecto and Vandermeer 1997; Vandermeer and Perfecto 2007).

Recent studies have shown that certain types of agricultural land uses hold the potential to provide habitat and resources for a variety of plant and animal taxa and may contribute significantly to conservation efforts in fragmented landscapes (e.g., Estrada et al. 2000; Daily et al. 2001; Schulze et al. 2004; Harvey et al. 2006b). Of the various land uses studied, agroforestry systems (those that intentionally combine trees within the cultivation of crops and/or animals) stand out as having a particularly high conservation potential, due to their structural complexity, high floristic diversity and close resemblance to forest ecosystems (e.g., Schroth et al. 2004a). For example, numerous studies indicate that shaded cacao plantations, coffee agroforestry systems, traditional rubber agroforests and other multi-strata agroforestry systems can sometimes conserve high numbers of plant and animal species, in some cases even rivaling the species diversity found in the original forests (Perfecto et al. 1996; Moguel and Toledo 1999; Rice and Greenberg 2000; Schroth et al. 2004b; Somarriba et al. 2004). However, despite the high species richness reported, there is still some debate over the conservation potential of agroforestry systems because these systems often host different species assemblages from those of the original forest and may lack the forest-dependent species which are of greatest conservation concern.

In order to evaluate the role of agroforestry systems for biodiversity conservation, it is therefore important to know not only how many species are present within these systems, but also which species are present and whether any of these species are of conservation concern. It is also critical to understand how the species assemblages within agroforestry systems compare not only to the original forest (which they replace), but also to alternate agricultural land uses which could replace agroforestry in the future. This comparison of the biodiversity of agroforestry systems with that of competing land uses allows a more balanced view of the relative conservation potential of agroforestry systems.

In this study we evaluate the potential contribution of agroforestry systems to biodiversity conservation by comparing bird and bat assemblages in forest, agroforestry systems (cacao and banana agroforestry) and plantain monocultures in the indigenous reserves of Talamanca, Costa Rica. Specifically, we compare patterns of bat and bird diversity and species composition across land uses, and relate these patterns to the vegetative characteristics of land uses. We also examine whether birds and bats differ in their response to the types of land uses present within the agricultural landscape, as has been suggested elsewhere (e.g., Faria et al. 2006; Harvey et al. 2006b).

The indigenous reserves of Talamanca are considered a priority region for both national and regional conservation efforts, due to their high levels of plant and animal diversity and their strategic location within the Talamanca-Caribbean biological corridor, which falls within the larger Mesoamerican Biological Corridor (Miller et al. 2001; Olson and Dinerstein 2002). At the same time, the reserves constitute the country's main region of cacao and organic banana production (Municipality of Talamanca 2003). Cacao and banana agroforestry systems are major agricultural land uses within the reserves, but these indigenous agroforestry systems are increasingly being converted to other land uses, such as plantain monocultures, due to disease problems, low prices and changes in market opportunities (Dahlquist et al. 2007, this issue). In light of these ongoing changes, our study of the relative importance of different land uses for bird and bat conservation is critical for gauging the potential effects of these land use changes on wildlife conservation and for informing policy makers who are responsible for ensuring the conservation of biodiversity within the biological corridor over the long-term.

Methods

Study area

The study was conducted in the BriBri and Cabecar indigenous reserves in the Talamanca region, in southeastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). The reserves together cover an area of roughly 60,000 ha and fall within tropical humid forest and premontane wet forest life zones (Tosi 1969), with a mean daily temperature of 25.8°C and a mean annual precipitation of 2,370 mm with a slight dry season during the months of March to April and September to October (Herrera 1985).

In the lowland region of the reserves (<500 masl) where this study was conducted, the agricultural landscape consists of a complex mosaic of agroforestry systems (cacao and banana), agricultural plots (rice, beans, plantains) and pastures, interspersed with forest patches of varying ages and degrees of intervention. Precise data on the landscape structure and composition do not exist, however, it is estimated that less than 25% of the area remains forested (Somarriba et al. 2003).

Land uses studied

Birds and bats were studied in the four main land uses within the reserves: (1) forests, (2) cacao agroforestry systems, (3) banana agroforestry systems, and (4) plantain monocultures. These land uses differ markedly in their structural and floristic composition, as well as in their management practices. The forests are typically small remnants (generally <20 ha) that have been selectively logged in the past but retain an intact, closed canopy and are the most floristically and structurally diverse of all land uses. Cacao and bananas are grown organically in small agroforestry systems (usually <3 ha) that have a variable shade canopy of remnant forest trees, naturally regenerated species, and planted fruit and timber trees. In contrast, plantains are cultivated as monocultures in small areas (usually <3 ha), without a shade canopy, and are produced using insecticides, nematicides, fungicides and herbicides. Additional details on the different land use systems are available in Somarriba and Harvey (2003) and Suatunce et al. (2003).

We selected sites for the bird and bat surveys using lists from Associación de Pequeños Productores de Talamanca (APPTA) of all cacao, banana, and plantain producers in the region. We visited all potential sites that had plots of agroforestry systems, plantain monocultures and/or forest patches >1 ha in size and checked site conditions, accessibility, and owner willingness to participate in the study. Selected forests had to have closed canopies and minimal evidence of logging or other disturbance, while cacao and banana agroforestry systems had to have shade canopies representative of these land uses. Of the 64 potential sites identified, we randomly selected a total of 35, with 7 replicas of forests, banana agroforestry systems and plantain monocultures, and 14 replicas of cacao agroforestry systems. These sites were located in the communities of Amubri, Watsi, Sibuju, Tsuiri, Sepeque, San Miguel, San Vincente, and La Isla. All sites occurred within a complex and heterogeneous land mosaic of forests, agroforestry systems and monocultures, and were less than 1 km from the nearest forests.

Sampling

In each of the 35 sites, we set up a 1 ha plot in which we sampled tree, bat and bird diversity. To characterize the floristic and structural characteristics of the different land uses, we established a temporary 20 × 50 m plot in the center of each site, and identified and measured the heights and diameters of all trees with dbh >10 cm. Vegetative data were summarized as the total tree species richness per plot, tree density, tree diversity (Shannon index) and mean tree height and diameters.

The surveys of bats and birds were conducted during two periods: once during the months of May 2002 to February 2003, and a second time during the months of February 2003 to November 2003. All field work was conducted by the second author, with the help of local assistants. In each sampling period, the order of sites surveyed was randomized (with one randomly chosen plot of each land use type sampled within each sampling excursion) to prevent differences across land uses due to seasonal differences in communities; however the difficult access to the remote study sites and inclement weather sometimes complicated these efforts.

Bats were sampled using ground mist nets, a commonly used technique which samples most of the Phyllostomidae bats but may underestimate the presence or abundance of other species, particularly those that fly high in the canopy (Fenton et al. 1992). Four mist-nets (12 × 2 m) were located in a circle within the 1 ha plot, with mist nets separated distances of approximately 100 m. The mist nets were opened from 18:00 to 23:00, for a total of 20 mist-net hours per site per night. All captured bats were identified using Timm et al. (1999) and Laval and Rodriguez (2002), and were marked (by cutting hair) to avoid counting the same individual twice. Recaptures were excluded from the data base and were not included in analyses. Bats were later classified by their feeding guilds (carnivorous, frugivorous, insectivorous, omnivorous, nectarivorous or sanguivorous) and habitat affinity (forest species, generalists or open area species) using Laval and Rodriguez (2002) and Reid (1997).

Birds were sampled using point counts (Ralph et al. 1995). In each site, a total of 5 point counts (each of 25 m radius) were established to census birds based on observations and calls. Points were positioned in a circle within the 1 ha plot, with each point separated by approximately 100 m. Each point count was surveyed for 5 min from 6:30 and 9:00, during two consecutive days (25 min per parcel per day * 2 days = 50 min of observation per plot in each sampling period). Birds were only counted if they were within the given plot; flyovers were not recorded or included in data analyses. In the few plantain plots where an isolated tree was present, only those birds occurring within the plantain were counted. All birds were identified and later classified by residency status (residents or migrants), feeding guild (carnivorous, frugivorous, granivorous, insectivorous, piscivorous, omnivorous or nectarivorous) and habitat preference (forest, generalists or open area species), using Stiles and Skutch (1995) and Blas et al. (2003).

Data analysis

For each plot, we calculated the total abundance and species richness of birds and bats captured (or observed) by combining data from the two sampling periods. We similarly calculated the total number of species and individuals of each feeding guild and of each habitat guild. These per plot data represent a total of 40 mist-net hours for bats (4 mist nets × 5 h × 2 sampling periods) and 50 min of observation of birds (5 point counts × 5 min per point count × 2 sampling periods). We also calculated the Shannon diversity index (Magurran 1988) for each plot, using the program Biodiversity Pro (McAleece 1997).

For bats and birds separately, we compared overall patterns of abundance, species richness and diversity of the overall assemblage (as well as of individual feeding and habitat guilds) across the four land uses, using analysis of variance and/or Kruskal Wallis tests (for non-normally distributed data; Sokal and Rohlf 1995). Since sampling effort was identical across plots, it was not necessary to transform either the bird or bat data before analyses. Analyses of guild data were only conducted for guilds that represented >10% of all captures, to avoid biases due to low sample sizes.

Rarefaction curves were calculated in EcoSim (Gotelli and Entsminger *2000*) and used to compare the expected species richness in each land use type. Curves were plotted against the number of individuals captured (bats) or observed (birds), using the mean expected species richness and 95% confidence intervals, produced on the basis of 500 iterations. Curves were considered significantly different where 95 % confidence intervals did not overlap.

To distinguish between the species composition of tree, bird and bat assemblages present in the four different land uses, cluster analyses (using Jaccard similarity indices and average linkage method) were conducted in Biodiversity Pro (McAleece *1997*) for each taxa separately and dendrograms was produced to facilitate the visualization of patterns of similarity across land use types. Relationships between the structural and floristic characteristics of the different land uses and animal diversity were explored using Pearson correlations between vegetative characteristics (tree density, tree species richness/plot, tree diversity, and mean tree height) and bird and bat abundance, species richness and diversity (Sokal and Rohlf *1995*). All statistical analyses were conducted in InfoStats v 1.4 (Infostat *2004*).

Results

Structural and floristic characteristics of different land uses

A total of 1,071 trees of 251 species were registered in the different land uses. Forests had higher tree densities, species richness and diversity per plot than all other land uses, as well as much greater overall species richness (Table 1). Cacao and banana agroforestry systems had roughly one quarter of the tree density and one fifth of the mean tree species per plot of forests. Plantain monocultures generally lacked shade canopies but had the occasional isolated tree. The mean tree heights and diameters were similar across forests and agroforestry systems, but the floristic composition of forests was markedly distinct from that of the non-forest land uses (Fig. 1a). The most common trees in the forests were *Iriartea deltoidea* (which represented 10.6% of the trees) and *Pentaclethra macrolobra* (3.8%), both of which are native species typical of tropical wet forests. In contrast, the agroforestry systems were dominated by *Cordia alliodora*, a fast-growing pioneer species that is actively managed by farmers for timber and represented 38.6 and 41.3% of the trees in cacao and banana plantations respectively. Other common trees in the agroforestry systems included peach palm (*Bactris gasipaes*) and inga (*Inga edulis*), both of which are planted by farmers for their fruits.

Table 1 Characteristics of the four land uses in which bird and bat diversity were surveyed in Talamanca, Costa Rica

Variable	**Forest (*n* = 7)**	**Cacao agroforestry system (*n* = 14)**	**Banana agroforestry system (*n* = 7)**	**Plantain (*n* = 7)**	**Test statistic**	***p***
Mean area (ha)	12.57 ± 5.52	1.71 ± 0.26	2.00 ± 0.22	2.21 ± 0.49		–

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Mean tree density (trees/ha)	832.9 ± 73.5a	202.3 ± 16.5b	280.0 ± 51.3b	10.0 ± 10.0c	*H* = 26.69	0.0001
Mean tree height (m)	12.45 ± 0.84a	15.61 ± 1.19a	13.34 ± 1.73a	0.82 ± 0.82b	*H* = 18.15	0.0004
Mean tree dbh (cm)	18.72 ± 1.30a	26.43 ± 2.71a	19.84 ± 2.44a	1.90 ± 1.90b	*F* = 16.12	0.0001
Mean number of tree species in 0.1 ha	43.00 ± 1.31a	7.43 ± 0.88b	8.57 ± 2.31b	0.86 ± 0.86c	*H* = 24.41	0.0001
Mean Shannon diversity index	3.44 ± 0.11a	1.58 ± 0.67b	1.52 ± 0.70bc	0.25 ± 0.66c	*H* = 22.34	0.0001
Total number of tree species recorded	195	54	43	6	–	–
The five most abundant species (percent of trees in this land use)	*Iriartea deltoidea* (10.6%); *Pentaclethra macroloba* (3.8%); *Rinorea squamata* (2.9%); *Faramea occidentalis* (2.5%); *Manilkara sapota* (2.1%)	*Cordia alliodora* (38.6%); *Inga edulis* (5.3%); *Bactris gasipaes* (4.5%); *Nephelium lappaceum* (4.2%); *Hamelia patens* (3.2%)	*Cordia alliodora* (41.3%); *Inga edulis* (7.2%); *Bactris gasipaes* (5.6%); *Spondias mombin* (5.6%); *Piper auritum* (4.6%)	–	–	–

Data represent means ± standard errors. Test statistics are from ANOVA's (*F*) or Kruskal Wallis comparisons (*H*)

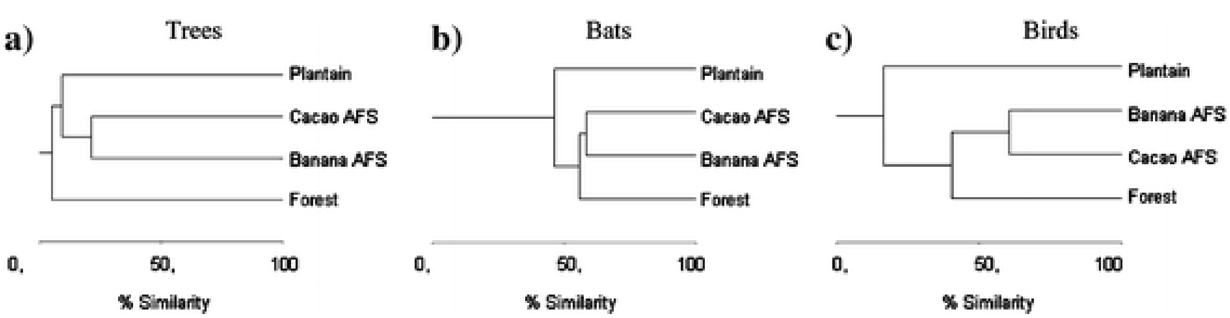

Fig. 1 Dendrograms showing similarity of tree, bat and bird assemblages across four different types of land use in Talamanca, Costa Rica. Analyses are based on Jaccard similarity indices and average-linkage methods. (**a**) Trees, (**b**) Bats, and (**c**) Birds

Bat assemblages

A total of 2,678 bats of 45 species were captured (Appendix 1, Table 2). The most common species was *Carollia perspicillata* (22.6% of all captures), followed by *Artibeus jamaicensis* (15.8%), *Uroderma bilobatum* (13.0%), *Artibeus lituratus* (9.4%), *Glossophaga soricina* (6.6%), and *Artibeus watsoni* (5.6%). The remaining 39 species each represented less than 5% of all captures. Twelve bat species were represented by only a single capture. Frugivores dominated the bat assemblage, accounting for just under half of the species (22 spp.) and 80.8% of all bats. Nectarivorous bats were the second most common feeding guild, accounting for 6 species and 13.0% of all captures. Insectivorous (13 spp, 1.6% of captures) and omnivorous bats (2 spp, 3.7%) were much less abundant. Only one sanguivorous species—*Desmodus rotundus* (0.8% of captures)—and one carnivorous species—*Vampyrum spectrum* (<0.1% of captures)—were captured. Of the 45 species, 36 species are considered forest dependent, but these accounted for less than a third of all captures (29.6%).

Table 2 Summary of sampling effort of bird and bat diversity in different habitats within the Talamanca landscape, Costa Rica

Taxa	Variable	Forest ($n = 7$)	Cacao agroforestry system ($n = 14$)	Banana agroforestry system ($n = 7$)	Plantain monoculture ($n = 7$)	Total
Bats	Total # of mist net hours surveyed	224	448	224	224	1,120
	# Bats captured	327	1244	529	578	2,678
	# Bat spp. captured	26	37	28	19	45
Birds	Total minutes of observations	350	700	350	350	1,750
	# Birds observed	842	1376	672	166	3,056
	# Bird spp. observed	132	160	134	32	224

Bat species richness and diversity varied across the four land uses, while bat abundance did not (Table 3). Bat species richness was greater in cacao agroforestry systems than in forests and plantain monocultures, and bat species richness in forests was greater than that of plantain monocultures. Bat diversity, as measured by the Shannon diversity index, was greater in forest and agroforestry systems than in plantain monocultures. Rarefaction curves also showed that forests and agroforestry systems had similar (and statistically indistinguishable) rates of species accumulation rates, and that both forests and agroforestry systems accumulated species at a significantly greater rate than plantain monocultures (Fig. 2a).

Table 3 Bat abundance, species richness and diversity in four land use types in Talamanca, Costa Rica

	Variable	Forest ($n = 7$)	Cacao agroforestry system ($n = 14$)	Banana agroforestry system ($n = 7$)	Plantain monoculture ($n = 7$)	Test statistic	*p* value

All bats	Number of bats	46.71 ± 6.01	88.86 ± 12.48	75.57 ± 8.79	82.57 ± 23.19	*H* = 5.56	0.1347
	Number of bat spp.	12.57 ± 0.87b	15.21 ± 0.52a	14.43 ± 1.07ab	10.00 ± 1.11c	*F* = 7.99	0.0004
	Shannon diversity index	2.03 ± 0.09a	2.22 ± 0.05a	2.19 ± 0.10a	1.72 ± 0.11b	*F* = 8.34	0.0003
Individual feeding guilds	Number of frugivorous spp.	9.00 ± 0.72a	9.79 ± 0.37a	8.86 ± 1.10a	6.14 ± 0.70b	*F* = 5.52	0.0037
	Number of frugivorous bats	39.43 ± 5.72	71.57 ± 11.42	53.14 ± 8.89	73.29 ± 22.04	*H* = 4.01	0.2604
	Number of nectarivorous spp.	1.57 ± 0.48b	2.64 ± 0.20ab	3.57 ± 0.30a	2.00 ± 0.31b	*H* = 11.88	0.0038
	Number of nectarivorous bats	4.71 ± 2.01c	11.93 ± 2.58ab	15.29 ± 1.02a	5.86 ± 1.06bc	*H* = 13.20	0.0040
Habitat guilds	Number of forest spp.	7.57 ± 0.84a	9.14 ± 0.43a	8.00 ± 0.79a	4.29 ± 0.68b	*F* = 10.57	0.0001
	Number of forest bats	19.29 ± 3.51bc	29.43 ± 2.94a	23.57 ± 1.65ab	11.57 ± 3.11c	*F* = 6.28	0.0019

Values represent means and standard errors per plot. Test statistics are for ANOVA (*F*) or Kruskal Wallis (*H*). Different letters within the same row indicate differences across land use types

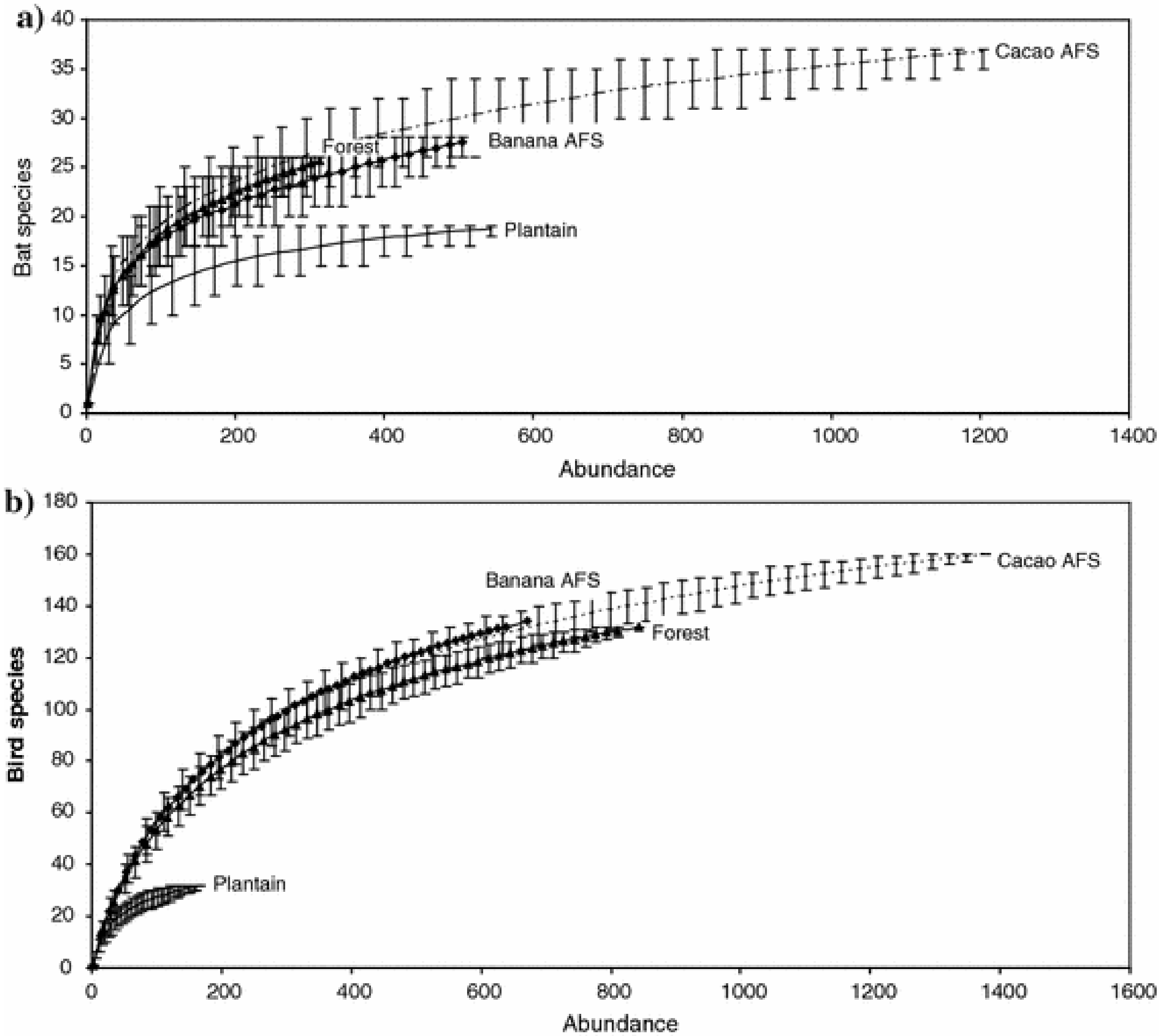

Fig. 2 Rarefaction curves for bird and bats species in forests, cacao agroforestry systems, banana agroforestry systems and plantains in Talamanca, Costa Rica. Bars represent 95% confidence intervals, based on 500 iterations

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With the exception of the single carnivorous bat species (captured in a cacao agroforestry system), all land uses harbored bats in each of the feeding guilds. However, there were some differences in the abundance and species richness of feeding guilds across land uses. For example, plantain monocultures had significantly fewer frugivorous species per plot than the other land uses, and banana agroforestry systems had a greater number of nectarivorous bat species and nectarivorous bats than forests or plantain monocultures. Cacao agroforestry systems also had a greater number of nectarivorous bats per plot than forests. The mean number of forest bat species per plot was greater in forests and both agroforestry systems than in plantain monocultures, but the mean abundance of forest bats per plot was greater in cacao agroforestry systems than in forests or plantain monocultures. In contrast, there were no differences in either mean species richness or abundance of open-area species across the four land uses (p's > 0.05).

The bat assemblages within the different land use were dominated by the same basic set of species, but differed in the abundance of many of the less-frequently captured species. All four land uses had a similar suite of dominant species, with *Artibeus jamaicensis* and *Carollia perspicillata* being among the top three most abundant species in each land use (Table 4). However despite being dominated by many of the same species, bat assemblages did show some subtle differences across land uses. One notable difference in the bat species assemblage among land uses was the dominance of *Uroderma bilobatum* in plantains, where it accounted for 32.3% of all captures. This species was also present in cacao (8.2% of captures in this land use) and banana (13.8%) agroforestry systems, but was rarely caught in forest habitats (1.5% of forest captures). Conversely, other species—such as *Artibeus intermedius*, *Chiroderma trinitatum*, *Choeroniscos godmani*, *Ectophlylla alba* and *Sturnira ludovici*—were present in agroforestry systems and forests, but missing from plantain monocultures (Appendix 1). A cluster analysis, based on Jaccard similarity indices, highlights these differences in bat assemblage composition across land uses, with forests and agroforestry systems having a distinct composition from that of plantains and forests being further separated from the agroforestry systems (Fig. 1b).

Table 4 Ten most common bat species captured in each of the four land uses in Talamanca, Costa Rica, in decreasing order

Rank	Forest	Cacao agroforestry system	Banana agroforestry system	Plantain monoculture
1	***Artibeus jamaicensis*** (20.2%)	***Carollia perspicillata*** (23.8%)	***Artibeus lituratus*** (15.1%)	***Uroderma bilobatum*** (32.2%)
2	***Carollia perspicillata*** (19.0%)	***Artibeus jamaicensis*** (18.0%)	***Artibeus jamaicensis*** (14.4%)	***Carollia perspicillata*** (31.3%)
3	***Artibeus watsoni*** (13.8%)	*Uroderma bilobatum* (8.2%)	***Carollia perspicillata*** (14.4%)	***Artibeus jamaicensis*** (9.2%)
4	***Artibeus lituratus*** (8.6%)	***Artibeus lituratus*** (7.3%)	*Uroderma bilobatum* (13.8%)	***Artibeus lituratus*** (8.7%)
5	***Carollia castanea*** (8.0%)	***Glossophaga soricina*** (6.2%)	***Glossophaga soricina*** (8.5%)	***Glossophaga soricina*** (5.2%)
6	***Glossophaga soricina*** (7.0%)	***Artibeus watsoni*** (5.6%)	*Phyllostomus hastatus* (6.4%)	*Platyrrhinus helleri* (2.1%)
7	*Carollia brevicauda* (3.7%)	***Carollia castanea*** (5.4%)	***Glossophaga commissarici*** (4.9%)	***Artibeus watsoni*** (1.9%)
8	*Chiroderma trinitatum* (3.4%)	***Glossophaga commissarici*** (4.4%)	*Lonchophylla robusta* (4.5%)	*Carollia brevicauda* (1.7%)
9	***Glossophaga commissarici*** (2.4%)	Artibeus phaeotis (2.7%)	***Artibeus watsoni*** (3.2%)	***Carollia castanea*** (1.6%)
10	*Artibeus intermedius* (1.8%)	*Lonchophylla robusta* (2.7%)	***Carollia castanea*** (2.1%)	***Glossophaga commissarici*** (1.6%)

Numbers in parenthesis indicate the percent of all captures within this habitat that the species represents (based on 327 captures in forests, 1244 captures in cacao agroforestry systems, 529 captures in banana agroforestry systems, and 578 captures in plantain monocultures). Bold letters indicate species present in the top ten species of all four land uses

Bird assemblages

A total of 3,056 birds of 224 species were observed in the 35 plots during the point counts (Appendix 2, Table 2). The most commonly observed bird species were (in descending order) *Psarocolius montezuma*, *Pionus senilis*, *Ramphocelus passerinii*, *Ramphastos sulfuratus*, *Psarocolius wagleri*, *Pitangus sulphuratus*, *Amazona autumnalis* and *Patagioenas nigrirostris*, but each represented only 2–6% of the total observations.

The majority of birds were insectivorous, accounting for 125 species and 50.9% of all observations. Frugivorous birds were the second most common guild (47 spp., 35.9% of observations). Each of the remaining feeding guilds represented less than 5% of the total observations. Most birds were generalist species (86 spp, 49% of individuals), followed by forest species (100 spp, representing 36% of individuals) and open area specialists (38 spp, 15% of individuals).

There were no differences in the mean abundance, species richness or diversity of birds observed in forests, cacao agroforestry systems and banana agroforestry systems. However, both forests and agroforestry systems had much greater abundance, species richness and bird diversity than plantain monocultures (Table 5). Rarefaction curves showed a similar pattern: at any given sample size, forests and agroforestry systems had significantly higher species richness than plantain monocultures (Fig. 2b). These differences were mainly due to the greater number of frugivorous and insectivorous birds in the forest and agroforestry habitats, compared to plantains. Forests also had a greater number of frugivorous birds than both agroforestry systems and plantains.

Table 5 Abundance, species richness and diversity of birds in four land use types in Talamanca, Costa Rica, based on point count data

	Variable	Forest (*n* = 7)	Cacao agroforestry system (*n* = 14)	Banana agroforestry system (*n* = 7)	Plantain monoculture (*n* = 7)	Test statistic	*p* value
All birds	Number of bird species	50.00 ± 2.90a	43.21 ± 1.90a	45.57 ± 3.88a	11.57 ± 0.97b	*F* = 40.78	<0.0001
	Number of birds	120.29 ± 8.41a	98.29 ± 6.82a	96.00 ± 10.68a	23.71 ± 3.71b	*F* = 22.9	0.0002
	Shannon diversity	3.57 ± 0.07a	3.45 ± 0.08a	3.54 ± 0.08a	2.28 ± 0.07b	*F* = 49.07	<0.0001
Feeding guilds	Number of frugivorous bird species	16.57 ± 1.23a	13.14 ± 0.93a	13.14 ± 1.79a	1.43 ± 0.20b	*F* = 27.32	<0.0001
	Number of frugivorous birds	51.57 ± 3.65a	36.07 ± 4.89b	30.57 ± 5.90b	2.43 ± 0.72c	*H* = 21.59	0.0001
	Number of insectivorous species	23.86 ± 1.32a	22.21 ± 1.40a	24.14 ± 2.11a	6.71 ± 0.87b	*F* = 24.28	<0.0001
	Number of insectivorous birds	53.43 ± 4.44a	50.29 ± 3.85a	53.43 ± 5.35a	15.14 ± 2.66b	*F* = 15.62	0.0001
	Number of forest species	30.29 ± 2.49a	14.43 ± 1.82b	11.86 ± 2.34b	0.14 ± 0.14c	*F* = 30.53	<0.0001

Habitat guilds	Number of forest individuals	74.43 ± 8.91a	29.93 ± 5.12b	23.14 ± 4.57b	0.14 ± 0.14c	*H* = 25.01	0.0001
	Number of generalist species	17.86 ± 1.14b	22.00 ± 1.69ab	24.29 ± 1.92a	6.14 ± 0.74c	*F* = 20.27	0.0001
	Number of generalist birds	40.86 ± 2.63a	55.14 ± 4.87a	50.71 ± 6.97a	11.86 ± 2.23b	*F* = 14.04	<0.0001
	Number of open area bird species	1.71 ± 0.52c	6.29 ± 0.67ab	8.43 ± 0.95a	5.29 ± 0.71b	*F* = 11.38	0.0001
	Number of open area birds	4.00 ± 1.66c	12.50 ± 1.70b	21.14 ± 3.43a	11.71 ± 2.60b	*F* = 12.21	<0.0001

Values represent means and standard errors per plot. Test statistics are for ANOVA (*F*) or Kruskal Wallis (*H*). Different letters within the same row indicate differences across land use types

Not surprisingly, the mean number of forest bird and forest species per plot was greatest in the forest habitats, followed by the agroforestry systems (cacao and banana) and lowest in the plantain habitats. Generalist species were more abundant in banana agroforestry systems than in either forests or plantains, while both forests and agroforestry systems had greater numbers of generalist birds than plantains. Conversely, the species richness and abundance of open area species was greater in banana agroforestry systems than either forests or plantains, with forests having the lowest numbers of open area species.

There were also striking differences in bird species composition across land uses. Only 15 of the 224 bird species were reported in all 4 land uses, illustrating the highly distinct assemblages of the different land uses. In contrast, 87 bird species were reported in only a single habitat type: of these, 39 species were sighted only in forests, 28 only in cacao agroforests, 18 only in banana agroforests and two only in plantain. A cluster analyses separated the land uses into two main groups—one containing the forests and agroforestry systems, and the other containing the plantain monocultures. In addition, it further separated the forests from the cacao and banana agroforestry systems (Fig. 1c). The dramatic shifts in species composition among land uses are also evident in a comparison of the most abundant species in each land use (Table 6): of the ten most abundant bird species in forest, five were also ranked within the top ten in cacao agroforestry systems and four were ranked within the top ten in banana agroforestry, but none were among the most common species in plantain monocultures. In general, the differences in bird species composition reflect both the low numbers of shared species across land uses as well as the replacement of forest-dependent species by generalists and open-area species in the non-forest habitats.

Table 6 Ten most common bird species observed using point counts each of the four land uses in Talamanca, Costa Rica, in decreasing order

Rank	Forest	Cacao agroforestry system	Banana agroforestry system	Plantain monoculture
1	*Psarocolius montezuma* (6.4%)	*Psarocolius montezuma* (7.8%)	*Pionus senilis* (6.3%)	*Pitangus sulphuratus* (13.3%)

2	*Psarocolius wagleri* (5.9%)	*Pionus senilis* (4.7%)	*Psarocolius montezuma* (4.8%)	*Ramphocelus passerinii* (9.7%)
3	*Ramphastos sulfuratus* (5.1%)	*Ramphocelus passerinii* (3.2%)	*Ramphocelus passerinii* (3.9%)	*Cathartes aura* (6.6%)
4	*Pionus senilis* (4.3%)	*Pionus menstruus* (2.8%)	*Pitangus sulphuratus* (3.3%)	*Crotophaga sulcirostris* (6.6%)
5	*Amazona autumnalis* (3.8%)	*Ramphastos sulfuratus* (2.8%)	*Myiozetetes similis* (3.0%)	*Myiozetetes similis* (6.0%)
6	*Patagioenas nigrirostris* (3.1%)	*Melanerpes pucherani* (2.5%)	*Psarocolius wagleri* (2.8%)	*Turdus grayi* (5.4%)
7	*Pionopsitta haematotis* (2.7%)	*Amazona autumnalis* (2.4%)	*Euphonia luteicapilla* (2.5%)	*Arremonops conirostris* (4.8%)
8	*Pteroglossus torquatus* (2.6%)	*Icterus galbula* (2.2%)	*Polioptila plumbea* (2.5%)	*Coragyps atratus* (4.8%)
9	*Querula purpurata* (2.6%)	*Patagioenas nigrirostris* (2.1%)	*Pteroglossus torquatus* (2.2%)	*Cyanocorax morio* (4.2%)
10	*Ramphastos swainsonii* (2.6%)	*Polioptila plumbea* (2.0%)	*Coragyps atratus* (2.2%)	*Chaetura cinereiventris* (3.6%)

Numbers in parenthesis indicate the percent of all observations within this habitat that the species represents (based on 842 observations in forests, 1376 captures in cacao AFS, 672 captures in banana, and 166 captures in plantain). Sampling effort per habitat is shown in Table 1.

Species of conservation concern

We registered a total of 23 bird species and three bat species that are of known conservation concern (Table 7). Of these, forests contained 19 bird species and one bat species, while cacao agroforestry systems contained 16 bird species and three bat species, and banana agroforestry systems registered 11 bird species and one bat species. No bat or bird species of conservation concern were registered within the plantain monocultures.

Table 7 Bat and bird species of conservation concern (listed on IUCN red lists; WWF et al. *1999*) found in different land uses within Talamanca, Costa Rica

Species name	Common name	Family	Forest	Cacao agroforestry system	Banana agroforestry system	Plantain monoculture
Bats						
Choeroniscos godmani	Godman's Bat	Phyllostomidae	1	1	11	
Sturnira mordax	Yellow-shouldered Bat	Phyllostomidae		5		

Vampirum spectrum	False Vampire Bat	Phyllostomidae		1		
# Bat species			**1**	**3**	**1**	**0**
# Bats registered			**1**	**7**	**11**	**0**
Birds						
Amazona farinosa	Mealy Parrot	Psittacidae	10		1	
Amazona autumnalis	Red-lored Parrot	Psittacidae	32	33	5	
Ara macao	Scarlet Macaw	Psittacidae	4			
Aratinga finschi	Crimson-fronted Parakeet	Psittacidae	16	10	13	
Brotogeris jugularis	Orange-chinned Parakeet	Psittacidae		11		
Buteogallus urubitinga	Great Black-Hawk	Accipitridae	3	2	4	
Cyanocorax affinis	Black-chested Jay	Corvidae		1	2	
Falco peregrinus	Peregrine Falcon	Falconidae	1	1		
Icterus mesomelas	Yellow-tailed Oriole	Icteridae		1	1	
Lophostrix cristata	Crested Owl	Strigidae	8	11	4	
Micrastur mirandollei	Slaty-backed Forest Falcon	Falconidae		3		
Micrastur semitorquatus	Collared Forest-Falcon	Falconidae	3	1		
Odontophorus erythrops	Rufous-fronted Wood-Quail	Phasianidae	11			
Megascops guatemalae	Vermiculated Screech-Owl	Strigidae	2	2		
Penelope purpurascens	Crested Guan	Cracidae	3			
Pionopsitta haematotis	Brown-hooded Parrot	Psittacidae	23	13	2	
Pionus menstruus	Blue-headed Parrot	Psittacidae	6	39	9	
Pionus senilis	White-crowned Parrot	Psittacidae	36	65	42	
Sarcoramphus papa	King Vulture	Cathartidae	4	1	2	
Tinamus major	Great Tinamou	Tinamidae	4			

Touit costaricensis	Red-fronted Parrotlet	Psittacidae	3	2		
Trogon clathratus	Lattice-tailed Trogon	Trogonidae	3			
# Bird species			**18**	**16**	**11**	**0**
# Birds registered			**172**	**196**	**85**	**0**

Numbers represent the number of individuals found in each land use. Species are organized alphabetically within taxa

Correlations between vegetation characteristics and bat and bird diversity

Bird abundance, species richness and diversity were all strongly correlated with the structural and floristic characteristics of land uses (Table 8), with all correlations being highly significant. In contrast, bat species richness and diversity showed no relationships with vegetative characteristics, while bat abundance was only weakly (and negatively) related to these characteristics.

Table 8 Relationships between the structural and floristic characteristics of land uses (all four land uses combined), with the abundance, species richness and diversity of birds and bats

Vegetative characteristics	Bat abundance	Bat species richness	Bat diversity	Bird abundance	Bird species richness	Bird diversity
Number of tree species/0.1 ha	–0.37*	–0.03	0.06	0.54***	0.50**	0.43**
Tree density/ha	–0.41**	–0.04	0.19	0.57***	0.55***	0.49**
Tree diversity (Shannon)	–0.35*	0.13	0.13	0.66***	0.63***	0.58***
Mean tree height	–0.33*	0.25	0.40	0.69***	0.66***	0.62***

Numbers represent the Pearson correlations (r), while asterisks indicate the significance of the correlations (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Discussion

Contribution of agroforestry systems to biodiversity conservation

In Talamanca, the cacao and banana agroforestry systems appear to contribute significantly to biodiversity conservation, as they host high numbers of bird and bat species, including many forest-dependent species and at least three bat and 18 bird species of known conservation concern. But although they are still species-rich, the assemblages in agroforestry systems differ from those in the original forests, with minor differences in the composition of bat assemblages and more striking differences in the bird assemblages.

The bat assemblages in agroforestry systems were as abundant and diverse as forests, included forest-dependent species and species of conservation concern, and had similar (and, in the case of cacao agroforests, higher) species richness to forests. Interestingly, cacao agroforestry systems had the greatest mean species richness per plot of any land use and even had a greater number of forest-dependent bat species than forest habitats. In addition, a greater number of bat species of conservation concern were registered in the cacao agroforests than in the forests (3 spp. vs 1 sp.), though this may partially reflect greater sampling in the cacao agroforestry systems. The composition of agroforestry bat assemblages was quite similar to that of forests, with similar numbers of forest dependent and frugivorous bat species, the same basic suite of dominant bat species, and high overlap of species. There were, however some subtle differences in bat assemblages across forests and agroforestry systems, such as the greater number of nectarivorous bats in banana agroforestry systems relative to forests and the greater number of nectarivorous bat species in both agroforestry systems compared to forests. These patterns are likely due to the greater availability of nectar from banana plants within both the banana and cacao agroforestry systems (most cacao plantations also contain some banana plants).

Studies of bats in cacao agroforestry systems elsewhere in the tropics have similarly pointed to the existence of a rich and diverse bat fauna within these systems. Faria et al. (*2006*) found that bat assemblages in diversified cacao agroforests in the Atlantic forest region of Brazil ('cabrucas') were richer and more diversified than those in nearby forests, while Estrada and Coates-Estrada (*2001a*) reported that cacao and coffee agroforestry systems in Veracruz, Mexico supported 71% of the bat species present in the intact forest. Taken together, these studies suggest that bats can readily take advantage of the resources and habitats within cacao agroforestry systems and that these habitats provide ample opportunities for bat conservation. At the same time, our study provides the first evidence that banana agroforestry systems with a diverse and complex shade tree canopy can confer similar conservation benefits.

Like bats, the abundance, species richness and diversity of birds in the agroforestry systems were as high as those in forests. However, in contrast to bats, birds showed very clear differences in species composition across land uses, with more frugivorous species and more forest-dependent birds and species in forests than in agroforestry systems (and conversely more open area and generalist species in the agroforestry systems), and low overlap in species composition across land uses (e.g., Fig. 1c). Birds species that are of immediate conservation concern were abundant in cacao agroforestry systems and forests, but less so in banana agroforestry systems. Studies elsewhere have also noted high numbers of bird species in shaded cacao agroforests (e.g., Ibarra et al. *2001*). For example, a total of 125 bird species (or 54% of all species recorded in the study area) were recorded in cacao agroforestry systems in Veracruz, Mexico (Estrada et al. *1997*), 144 species were observed cacao agroforests in a previous study within the Talamancan region (Reitsma et al. *2001*), and in Bahía, Brazil the number of bird species recorded visiting cabruca agroforestry systems (173 spp.) was even higher than that of adjacent forests (150 spp.; Faria et al. *2006*). In addition, these studies documented important shifts in the composition of bird species within cacao agroforestry systems, relative to intact forests, with a general reduction or loss of forest specialists. We similarly observed a reduction of forest-dependent species and frugivorous species within both the agroforestry systems and plantain monocultures and important shifts in overall species composition. Our findings therefore reinforce the growing consensus that while agroforestry systems are able to maintain high numbers of bird species, their assemblages are highly modified and unable to support all of the original forest species.

Factors contributing to the high bat and bird diversity in agroforestry

systems

The overall high levels of bat and bird diversity within the agroforestry systems can be attributed to a combination of factors. First, although the agroforestry systems are much less floristically diverse and have lower tree densities than their forest counterparts, they retain a structurally complex canopy of similar height to that of forest fragments, thereby providing a range of perching, nesting and roosting sites, and creating microclimatic conditions that are appropriate for many forest species (Estrada et al. *1997*, *2000*; Estrada and Coates-Estrada *2001a*, *b*). The more open and simplified nature of the tree canopy within cacao agroforestry systems (relative to intact forest) may even facilitate bat flight (Faria et al. *2006*), potentially contributing to the high numbers of bats captured in these habitats.

Second, the agroforestry systems appear to offer abundant food resources for wildlife. Although the agroforestry systems are much less floristically diverse than forests, many of the planted tree species within the agroforestry systems (such as *Inga edulis*, *Persea americana* and *Citrus* spp.) provide fleshy fruits or nectar that attract birds and bats into the cultivated areas (González *1999*; Carlo et al. *2004*). In addition, some of the native tree species that have regenerated naturally within the agroforestry systems—such as *Hamelia patens*, *Cecropia obtusifolia*, and species of *Ficus* and *Piper*—are known to provide key resources to frugivorous species (Fleming *1991*; Carlo et al. *2004*; Thies and Kalko *2004*). Insects are also likely to be plentiful within the agroforestry systems, due to the structural and floristic diversity of these habitats and the fact that these systems do not use pesticides or other inorganic chemicals (Wunderle and Latta *1998*; Johnson *2000*; Hole et al. *2005*).

Finally, the close proximity of the agroforestry systems to forest patches (most are <1 km from the closest forest) and the highly heterogeneous nature of the agricultural matrix in which the agroforestry systems are embedded are also likely to contribute to high animal diversity by maintaining landscape connectivity and creating a permeable matrix that permits animal movement. Studies of animal diversity in agricultural landscapes elsewhere have shown the importance of forest proximity, landscape connectivity and landscape heterogeneity for not only birds (e.g., Estrada et al. *1997*, *2000*; Reitsma et al. *2001*; Luck and Daily *2003*; Waltert et al. *2004*) and bats (e.g., Estrada and Coates-Estrada *2001a*, *b*; Faria et al. *2006*), but also other animal taxa (Medellín and Equihua *1998*). In fact, the maintenance of a diverse mosaic of connected forest patches, agroforestry systems and other types of tree cover is emerging as a key guiding principle for conservation efforts in agricultural landscapes (Hughes et al. *2002*; Benton et al. *2003*; Harvey et al. *2006b*; Vandermeer and Perfecto *2006*).

Low diversity of plantain monocultures

In stark contrast to the agroforestry systems, the other agricultural land use studied (plantain monocultures) showed little potential for biodiversity conservation. Not only did plantains have significantly lower abundances, species richness and diversity of both birds and bats, relative to the other land uses, but they also had highly modified species assemblages that were dominated by generalist and open area species and contained no species of conservation concern. The low animal diversity observed within plantain monocultures likely reflects the general lack of food resources and habitats. There are few trees within the areas planted with plantains and farmers usually remove most of the understory vegetation and any weeds that could provide resources or habitat to wildlife. In addition, the flowers and fruits of the plantains are usually covered with plastic bags to prevent insects from damaging the fruits, further limiting food availability (pers. obs.). The use of toxic chemicals (insecticides, fungicides, nematicides and herbicides) within these plantations (Henriques et al. *1997*) is also likely detrimental to wildlife, as has been documented in other conventional agricultural systems where chemicals are used (e.g. Hole et al. *2005*). Previous studies of other animal taxa within the plantain monocultures (Harvey et al. *2006a*) have similarly reported very low species richness and highly modified assemblages of terrestrial mammals and dung beetles, reinforcing the notion that plantain monocultures have little, if any, value for conservation. The current trend of conversion of existing agroforestry systems to plantains and other monocultures (Dalhquist et al. *2007*, this issue) should therefore be of great conservation concern.

Differences in bird and bat responses to the agricultural landscape

In addition to demonstrating differences in the ability of different land uses to support diverse bird and bat assemblages, our study also highlights that fact that different taxa may use and perceive agricultural landscapes in distinct ways. In our study area, bird assemblages appeared to show greater sensitively to the different land uses than did bat assemblages, with more evident changes in species composition across forests, agroforests and monocultures. The apparent greater sensitivity of bird assemblages to the different land uses within the agricultural landscape may be explained by a stronger relationship of birds with floristic and structural characteristics, as suggested by the greater number of strong correlations between vegetative characteristics and bird diversity (e.g., Table 8). These strong relationships indicate that even small changes in the structure and composition of the tree cover may potentially significantly impact bird assemblages, while having less of an impact on bat assemblages. It is also possible that birds may move less freely within the agricultural landscape and limit their movements to those areas of greater tree cover (where they are less exposed to predators) as opposed to bats who appear to move readily across agricultural landscapes and routinely cross large areas of open habitat (Estrada et al. *1997*; Fenton et al. *1992*; Medina et al. *2007*). However, more detailed studies of animal movement and demographics within agricultural landscapes are needed in order to determine the underlying factors driving these patterns. With increasing numbers of studies reporting taxon-specific responses to land uses within agricultural landscapes (e.g., Lawton et al. *1998*; Perfecto et al. *2003*; Pineda et al. *2005*; Faria et al. *2006*; Harvey et al. *2006a*, *b*), it is now clear that understanding the nature of these taxon-specific responses is a key issue for achieving conservation within human-dominated landscapes.

Conservation implications

Our study adds to the growing consensus that agroforestry systems that are structurally and floristically diverse can contribute significantly to the conservation of biodiversity within fragmented landscapes by providing habitat for a large number of animal species, including some forest-dependent and threatened species (e.g., Johns *1999*; Rice and Greenberg *2000*; Schroth et al. *2004a*). It also highlights the fact that agroforestry systems have much greater conservation value than the monoculture crops that often replace them. However, our results also illustrate that the animal assemblages within agroforestry systems may be somewhat distinct from those in forest habitats and do not necessarily contain the same suite of species as the original forests. The protection of the remaining forest fragments will therefore be critical for the conservation of intact animal assemblages in agricultural landscapes and should continue to form the backbone of conservation strategies.

Based on our work and other studies, we suggest three key approaches to ensure the conservation of biodiversity within agricultural landscapes where agroforestry systems are present: (1) diversifying existing agroforestry systems with native trees and other plants that ensure structural complexity and provide fruits and other resources to wildlife; (2) preventing the simplification of agroforestry systems and especially their conversion to monocultures, and (3) conserving abundant and well-connected forest within the agricultural matrix.

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Appendix 1 Total number of bats captured in mist nets in four land uses in Talamanca, Costa Rica, with species organized alphabetically

Species	Feeding guild	Habitat guild	Forest (n = 7)	Cacao agroforestry system (n = 14)	Banana agroforestry system (n = 7)	Plantain monoculture (n = 7)	Total
Artibeus intermedius	F	F	6	14	2		22
Artibeus jamaicensis	F	G	66	224	76	53	419
Artibeus lituratus	F	G	28	91	80	50	249
Artibeus phaeotis	F	F	5	34	8	1	48
Artibeus watsoni	F	F	45	70	17	11	143
Carollia brevicauda	F	F	12	33	3	10	58
Carollia castanea	F	G	26	67	11	9	113
Carollia perspicillata	F	G	62	296	76	181	615
Chiroderma salvini	F	F			1		1
Chiroderma trinitatum	F	F	11	6	1		18
Chiroderma villosum	F	F		2			2
Choeroniscos godmani	N	F	1	1	11		13
Cormura brevirostris	I	F	1				1
Desmodus rotundus	S	G	2	11	3	6	22
Ectophlylla alba	F	F	2	9	1		12
Glossophaga commissarici	N	F	8	55	26	8	97
Glossophaga soricina	N	F	23	77	45	30	175

Hylonycteris underwoodi	N	F	1				1
Lonchophylla mordax	N	F			1		1
Lonchophylla robusta	N	F		34	24	3	61
Mesophylla macconnelli	F	F		1			1
Micronycteris hirsuta	I	F	4	1			5
Micronycteris microtis	I	F		3			3
Mimon crenulatum	I	F	1	7		2	10
Mycronycteris minuta	I	F	1				1
Myotis albences	I	F		2		2	4
Myotis nigricans	I	G		1		1	2
Myotis riparios	I	F			1		1
Noctilio albiventris	I	F				1	1
Phyllostomus discolor	O	G		18	11	3	32
Phyllostomus hastatus	O	G	3	22	34	9	68
Platyrrhinus helleri	F	F	5	32	10	12	59
Pteronotus parnellii	I	F		2	1		3
Sturnira lilium	F	F			1		1
Sturnira ludovici	F	F	1	5	6		12
Sturnira luisi	F	F		4	4		8
Sturnira mordax	F	F		5			5
Tonatia brasiliense	I	F		1			1
Tonatia saurophila	I	F	6	5			11
Trachops cirrhosus	I	F		1			1
Uroderma bilobatum	F	G	5	102	73	186	366

Vampyrum spectrum	C	F		1			1
Vampyressa pusilla	F	F		3	1		4
Vampyressa nymphaea	F	F	1	3			4
Vampyrodes caraccioli	F	F	1	1	1		3
Total number of individuals			327	1244	529	578	2,678
Total number of species			26	37	28	19	45

Feeding guilds include frugivorous (F), insectivorous (I), nectarivorous (N), omnivorous (O) and sanguivorous (S). Habitat guilds include forest species (F) and generalists (G)

Appendix 2 Total number of bird observed in four land uses in Talamanca, Costa Rica, with species organized alphabetically

Species	**Family**	**Feeding guild**	**Habitat guild**	**Forest (*n* = 7)**	**Cacao agroforestry system (*n* = 14)**	**Banana agroforestry system (*n* = 7)**	**Plantain monoculture (*n* = 7)**	**Total**
Actitis macularius	Scolopacidae	P	A	5				5
Amazilia tzacatl	Trochilidae	N	G	2	3	2	2	9
Amazona autumnalis	Psittacidae	F	F	32	33	5		70
Amazona farinosa	Psittacidae	F	F	10		1		11
Amblycercus holosericeus	Icteridae	I	F	5	3	4		12
Anthracothorax prevostii	Trochilidae	N	G			1		1
Ara macao	Psittacidae	F	F	4				4
Aramides cajanea	Rallidae	I	G	1	4	2		7
Aratinga finschi	Psittacidae	F	OA	16	10	13		39

Arremon aurantiirostris	Emberizidae	I	F	1				1
Arremonops conirostris	Emberizidae	G	G	1	7	4	8	20
Attila spadiceus	Tyrannidae	I	G	5	6	1		12
Automolus ochrolaemus	Furnariidae	I	F	1				1
Baryphthengus martii	Momotidae	F	F	2	12	2		16
Brotogeris jugularis	Psittacidae	F	OA		11			11
Buteo jamaicensis	Accipitridae	CAV	G		2			2
Buteo magnirostris	Accipitridae	CAV	G	3	9	1		13
Buteogallus anthracinus	Accipitridae	CAV	OA	1	3			4
Buteogallus urubitinga	Accipitridae	CAV	F	3	2	4		9
Butorides virenscens	Ardeidae	P	A		5			5
Cacicus uropygialis	Icteridae	I	G	12	5	1		18
Calidris minutilla	Scolopacidae	I	A		1	1		2
Campephylus guatemalensis	Picidae	I	F	1				1
Campylorhynchus zonatus	Troglodytidae	I	G			1		1
Camptostoma obsoletum	Tyrannidae	I	G		3			3
Carpodectes nitidus	Cotingidae	F	F		6	3		9
Caryothraustes poliogaster	Cardinalidae	I	F		3	3		6
Cathartes aura	Cathartidae	CAR	G	12	15	4	11	42
Catharus fuscescens	Turdidae	F	F		1			1
Cercomacra tyrannina	Tamnophilidae	I	F	2				2
Ceryle alcyon	Alcedinidae	P	A		1			1
Ceryle torquatus	Alcedinidae	P	A			1		1

Chaetura cinereiventris	Apodidae	I	OA		10	7	6	23
Chaetura pelagica	Apodidae	I	OA				5	5
Chalybura urochrysia	Trochilidae	N	G	6		1		7
Chloroceryle aenea	Alcedinidae	P	A			1		1
Chloroceryle amazona	Alcedinidae	P	A			2		2
Chloroceryle americana	Alcedinidae	P	A	3		1		4
Chlorophanes spiza	Thraupidae	F	G	2				2
Ciccaba nigrolineata	Strigidae	CAV	F	2				2
Ciccaba virgata	Strigidae	CAV	G	16	18	5		39
Circus cyaneus	Accipitridae	CAV	OA		1			1
Claravis pretiosa	Columbidae	G	OA		7	4		11
Coereba flaveola	INCERTAE SEDIS	N	G		2			2
Colonia colonus	Tyrannidae	I	G	1	7	7	1	16
Columbina passerina	Columbidae	G	OA			1		1
Columbina talpacoti	Columbidae	G	OA	2	6	5		13
Conopias albovittatus	Tyrannidae	I	G			2		2
Contopus cinereus	Tyrannidae	I	G		6	2		8
Contopus sordidulus	Tyrannidae	I	G		1	1		2
Contopus virens	Tyrannidae	I	G	1	1	4	1	7
Coragyps atratus	Cathartidae	CAR	G	9	20	15	8	52
Crotophaga sulcirostris	Cuculidae	I	OA		2	7	11	20
Crypturellus soui	Tinamidae	G	F	6	13	6		25
Cyanerpes cyaneus	Thraupidae	F	G		8	1		9
Cyanerpes lucidus	Thraupidae	F	G		1	2		3

Cyanocampsa cyanoides	Cardinalidae	F	F	7	6	2	1	16
Cyanocorax affinis	Corvidae	I	G		1	2		3
Cyanocorax morio	Corvidae	I	G		10	15	7	32
Cymbilaimus lineatus	Tamnophilidae	I	F	14	8	2		24
Cyphorhinus phaeocephalus	Troglodytidae	I	F	1				1
Dacnis cayana	Thraupidae	I	F			1		1
Dendrocolaptes sanctithomae	Furnariidae	I	G	1	1			2
Dendroica caerulescens	Parulidae	I	F		1			1
Dendroica fusca	Parulidae	I	G		2	2		4
Dendroica palmarum	Parulidae	I	G			4		4
Dendroica pensylvanica	Parulidae	I	G	1	17	6		24
Dendroica petechia	Parulidae	I	G		4	1		5
Dendroica virens	Parulidae	I	F		2			2
Dryocopus lineatus	Picidae	I	F	2	8	2		12
Dysithamnus mentalis	Tamnophilidae	I	F	2				2
Dysithamnus striaticeps	Tamnophilidae	I	F	1	1			2
Elaenia flavogaster	Tyrannidae	I	G		2	3		5
Elanoides forficatus	Accipitridae	CAV	F	4				4
Electron platyrhynchus	Momotidae	F	F	6	1	1		8
Empidonax alnorum	Tyrannidae	I	G		1	2		3
Empidonax virescens	Tyrannidae	I	G		1	1		2
Euphonia gouldi	Fringillidae	F	G	11	15	8	1	35
Euphonia luteicapilla	Fringillidae	I	OA	4	23	17	1	45

Eutoxeres aquila	Trochilidae	N	G	1				1
Falco columbarius	Falconidae	CAV	OA	1				1
Falco peregrinus	Falconidae	CAV	OA	1	1			2
Florisuga mellivora	Trochilidae	N	F		2			2
Formicarius analis	Formicariidae	I	F	5				5
Formicarius nigricapillus	Formicariidae	I	F	1				1
Geothlypis poliocephala	Parulidae	I	G			1		1
Glaucidium griseiceps	Strigidae	CAV	G	1				1
Glyphorhynchus spirurus	Furnariidae	I	G	1	2	3		6
Gymnocichla nudiceps	Tamnophilidae	I	F	3				3
Gymnopithys leucapsis	Tamnophilidae	I	F	8	4	1		13
Habia fuscicauda	Thraupidae	I	G	3	15	2		20
Harpagus bidentatus	Accipitridae	I	F	1	2			3
Heliotryx barroti	Trochilidae	N	F	1				1
Henicorhina leucophrys	Troglodytidae	I	F	1				1
Henicorhina leucosticta	Troglodytidae	I	F	1				1
Herpethotheres cachinnans	Falconidae	CAV	G		5	1		6
Hyloctistes subulatus	Furnariidae	I	F	1				1
Hylopezus dives	Formicariidae	I	F	6	8	4		18
Hylophilus decurtatus	Vireonidae	I	F		1			1
Hylophylax naevioides	Tamnophilidae	I	F	6				6
Icterus dominicensis	Icteridae	I	G		21	8	4	33
Icterus galbula	Icteridae	F	G	2	30	12		44
Icterus mesomelas	Icteridae	I	G		1	1		2

Laterallus albigularis	Rallidae	I	A		3	1		4
Lepidocolaptes affinis	Furnariidae	I	F	1				1
Lepidocolaptes souleyetti	Furnariidae	I	G	7	25	13		45
Leptotila cassinii	Columbidae	G	G	5	5	2		12
Leucopternis princeps	Accipitridae	CAV	F	2				2
Lipaugus unirufus	*INCERTAE SEDIS*	F	F	1				1
Lophostrix cristata	Strigidae	I	F	8	11	4		23
Malacoptila panamensis	Bucconidae	I	F	1				1
Manacus candei	Pipridae	F	F	7	9	2		18
Megarhynchus pitangua	Tyrannidae	I	G	11	25	14	5	55
Megascops guatemalae	Strigidae	I	F	2	3			5
Melanerpes pucherani	Picidae	I	G	6	35	14	4	59
Micrastur mirandollei	Falconidae	CAV	F		3			3
Micrastur ruficollis	Falconidae	CAV	F	1				1
Micrastur semitorquatus	Falconidae	CAV	F	3	1			4
Microchera albocoronata	Trochilidae	N	F			2		2
Microrhopias quixensis	Tamnophilidae	I	F	9	2			11
Milvago chimachima	Falconidae	CAV	OA		1			1
Mionectes oleagineos	Tyrannidae	I	G	9	8	3		20
Mniotilta varia	Parulidae	I	G		8	4		12
Molothrus aeneus	Icteridae	I	OA			1		1
Monasa morphoeus	Bucconidae	I	F	2	4			6
Myiarchus crinitus	Tyrannidae	I	F		1			1

Myiarchus tuberculifer	Tyrannidae	I	G		5	2	1	8
Myiodynastes hemichrysus	Tyrannidae	I	F		1			1
Myiodynastes luteiventris	Tyrannidae	I	F		1			1
Myiodynastes maculatus	Tyrannidae	I	G	1				1
Myiozetetes granatensis	Tyrannidae	I	OA		7	6		13
Myiozetetes similis	Tyrannidae	I	OA		20	20	10	50
Myrmeciza exsul	Tamnophilidae	I	F	14	9	1		24
Myrmeciza immaculata	Tamnophilidae	I	F	2	1			3
Myrmotherula axillaris	Tamnophilidae	I	F	1	2	1		4
Myrmotherula fulviventris	Tamnophilidae	I	F	1	2			3
Nyctibius grandis	Nyctibidae	I	F	2	5			7
Nyctibius griseus	Nyctibidae	I	G	5	1	1		7
Nyctidromus albicollis	Caprimulgidae	I	OA		13	12	1	26
Odontophorus erythrops	Phasianidae	I	F	11				11
Oncostoma cinereigulare	Tyrannidae	I	G		5			5
Oporornis philadelphia	Parulidae	I	G		1			1
Ortalis cinereiceps	Cracidae	F	F	7	8	6		21
Oryzoborus funereus	Emberizidae	G	OA		2	1	2	5
Pachyramphus cinnamomeus	INCERTAE SEDIS	I	F	2	2			4
Pachyramphus polychopterus	INCERTAE SEDIS	I	G	4	2	3		9
Parula pitiayumi	Parulidae	I	F			1		1
Passerina cyanea	Cardinalidae	G	G		1			1
Patagioenas cayennensis	Columbidae	F	G		2	2		4

Patagioenas flavirostris	Columbidae	F	G		1			1
Patagioenas nigrirostris	Columbidae	F	F	26	29	9		64
Patagioenas subvinacea	Columbidae	F	F		1			1
Penelope purpurascens	Cracidae	F	F	3				3
Phaenostictus mcleannani	Tamnophilidae	I	F	1	1			2
Phaeothlylpis fulvicauda	Parulidae	I	F	3		3		6
Phaethornis guy	Trochilidae	N	F			3		3
Phaethornis longirostris	Trochilidae	N	G	9	14	2	2	27
Phaethornis striigularis	Trochilidae	N	G	3	6	5		14
Piaya cayana	Cuculidae	I	G	10	18	6	2	36
Piculus simplex	Picidae	I	F		1			1
Pionopsitta haematotis	Psittacidae	F	F	23	13	2		38
Pionus menstruus	Psittacidae	F	G	6	39	9		54
Pionus senilis	Psittacidae	F	G	36	65	42		143
Pipra mentalis	Pipridae	F	F	9	2			11
Piranga rubra	Thraupidae	F	G	1	5	4		10
Pitangus sulphuratus	Tyrannidae	I	OA	2	26	22	22	72
Poecilotriccus sylvia	Tyrannidae	I	F	1	1	1		3
Polioptila plumbea	Sylviidae	I	F	2	27	17		46
Psarocolius montezuma	Icteridae	I	G	54	107	32		193
Psarocolius wagleri	Icteridae	I	F	50	12	19		81
Pseudoscops clamator	Strigidae	CAV	G		1			1
Pteroglossus torquatus	Ramphastidae	F	F	22	22	15		59
Pulsatrix perspecillata	Strigidae	CAV	F	1		1		2

Querula purpurata	Cotingidae	F	F	22	16	8		46
Quiscalus mexicanus	Icteridae	O	OA			1		1
Ramphastos sulfuratus	Ramphastidae	F	F	43	38	8		89
Ramphastos swainsonii	Ramphastidae	F	F	22	7	5		34
Ramphocelus passerinii	Thraupidae	I	G	7	44	26	16	93
Saltator atriceps	Cardinalidae	F	G		3	3		6
Saltator coerulensces	Cardinalidae	F	G		8	1		9
Saltator grossus	Cardinalidae	F	G	4				4
Saltator maximus	Cardinalidae	F	G		17	2		19
Sarcoramphus papa	Cathartidae	CAR	F	4	1	2		7
Schiffornis turdina	INCERTAE SEDIS	I	F	2	1			3
Sclerurus guatemalensis	Furnariidae	I	F	2				2
Sporophila americana	Emberizidae	G	OA		10	5	6	21
Stelgidopteryx serripennis	Hirundinidae	I	OA			2		2
Synallaxis brachyura	Furnariidae	I	G		3	1		4
Tachyphonus delatrii	Thraupidae	I	F	5				5
Tachyphonus rufus	Thraupidae	I	G		4		1	5
Tangara larvata	Thraupidae	F	G		3	2		5
Tapera naevia	Cuculidae	I	G			1		1
Terenotriccus erythrurus	Tyrannidae	I	F	3				3
Thamnistes anabatinus	Tamnophilidae	I	F	6				6
Thamnophilus atrinucha	Tamnophilidae	I	F	19	16	1		36
Thamnophilus doliatus	Tamnophilidae	I	F	1	2			3

Thraupis episcopus	Thraupidae	F	OA		14	8	5	27
Thraupis palmarum	Thraupidae	F	OA		2	8	1	11
Thryothorus atrogularis	Troglodytidae	I	F		3			3
Thryothorus modestus	Troglodytidae	I	G	1	3			4
Thryothorus nigricapillus	Troglodytidae	I	G	4	7	2		13
Thryothorus thoracicus	Troglodytidae	I	F	1				1
Tiaris olivaceus	Emberizidae	G	OA				4	4
Tinamus major	Tinamidae	F	F	4				4
Tityra semifasciata	INCERTAE SEDIS	F	G	9	20	10		39
Todirostrum cinereum	Tyrannidae	I	G		11	3		14
Todirostrum nigriceps	Tyrannidae	I	G	2	1	4		7
Tolmomyias assimilis	Tyrannidae	I	F		4	1		5
Touit costaricensis	Psittacidae	F	F	3	2			5
Troglodytes aedon	Troglodytidae	I	OA		3	5	6	14
Trogon clathratus	Trogonidae	F	F	3				3
Trogon massena	Trogonidae	F	F	8	10			18
Trogon rufus	Trogonidae	F	F	6	3	2		11
Trogon violaceus	Trogonidae	F	F	4	21	6		31
Turdus grayi	Turdidae	F	G		11	10	9	30
Tyrannus melancholicus	Tyrannidae	I	OA		3	2	2	7
Tyto alba	Tytonidae	CAR	OA			1		1
Vermivora peregrina	Parulidae	I	G		8	2		10
Vireo flavifrons	Vireonidae	I	G		1	1		2
Vireo flavovirides	Vireonidae	I	G		1			1
Vireo olivaceus	Vireonidae	I	G		1			1
Xiphorhynchus lachrymosus	Furnariidae	I	F	4	4	1		9

Xyphorhynchus susurrans	Furnariidae	I	F	1				1
Zimmerius vilissimus	Tyrannidae	I	G		1			1
Total number of species				132	160	134	32	224
Total number of individuals				842	1,376	672	166	3,056

Feeding guilds include frugivorous (F), insectivorous (I), nectarivorous (N), omnivorous (O), carnivorous (CAV), carrion-feeding (CAR), and piscivorous (P). Habitat guilds include forest species (F), generalists (G),open area species (OA) and aquatic species (A)

References

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182–188
crossref

Blas D, Blas L, Solana T (2003) Guía de campo ilustrada de las aves de Costa Rica. Incafo Costa Rica, S. A. Madrid.

Carlo TA, Collazo JA, Groom MJ (2004) Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. Biotropica 36(4):602–614

Dahlquist, R. M., Whelan MP, Winowiecki L, Polidoro B, Candela S, Harvey CA, Wulfhorst JD, McDaniel PA, Stoian D, Bosque-Perez NA (2007) Incorporating livelihoods in biodiversity conservation: a case study of cacao agroforestry systems in Talamanca, Costa Rica. Biodivers Conserv (this issue)

Daily GC (2001) Ecological forecasts. Nature 411:245
PubMed crossref ChemPort

Daily GC, Ehrlich PR, Sanchez-Azofeifa GA (2001) Countryside biogeography: use of human dominated habitats by the avifauna of southern Costa Rica. Ecol Appl 11:1–13

Estrada A, Coates-Estrada R, Merritt DA (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodivers Conserv 6:19–42
SpringerLink

Estrada A, Cammarano PL, Coates-Estrada R (2000) Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. Biodivers Conserv 9:1399–1416
SpringerLink

Estrada A, Coates-Estrada R (2001a) Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. J Trop Ecol 17:627–646
crossref

Estrada A, Coates-Estrada R (2001b) Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24:94–102

Faria DR, Laps R, Baumgarten J, Cetra M (2006) Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodivers Conserv 15: 587–612

Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MKD, Syme M (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica 24(3):440–446

Fleming TH (1991) The relationship between body size, diet, and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). J Mammal 72:493–501

González J (1999) Diversidad y abundancia de aves en cafetales con y sin sombra. Ciencias Ambientales 17:70–80

Gotelli NJ, Entsminger GL (2000) Ecosim: null models software for Ecology. Acquired Intelligence Inc and Kesey-Bear

Harvey CA, Alpizar F, Chacón M, Madrigal R (2005) Assessing linkages between agriculture and biodiversity in Central America: historical overview and future perspectives. Mesoamerican & Caribbean Region, Conservation Science Program. The Nature Conservancy (TNC), San José, Costa Rica

Harvey CA, González J, Somarriba E (2006a) Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodivers Conserv 15:555–585

Harvey CA, Medina A, Merlo Sánchez D, Vílchez S, Hernández B, Sáenz JC, Maes JM, Casanoves F, Sinclair FL (2006b) Patterns of animal diversity associated with different forms of tree cover retained in agricultural landscapes. Ecol Appl 16 (5):1986–1999
<Occurrence Type="DOI"><Handle>10.1890/1051-0761(2006)016[1986:POADID]2.0.CO;2</Handle></Occurrence>

Henriques W, Jeffers RD, Lacher T, Kendall RJ (1997) Agrochemical use on banana plantations in Latin America: perspectives on ecological risk. Environ Toxicol Chem 16:91–99

Herrera W (1985) Vegetación y clima de Costa Rica. San Jose, EUNED

Hole DG, Perkins AJ, Wilson JD, Alexander IH, Grice PV, Evans AD (2005) Does organic farming benefit biodiversity? Biol Conserv 112:113–130

Hughes JB, Daily GC, Ehrlich PR (2002) Conservation of tropical forest birds in countryside habitats. Ecol Lett 5:121–129

Ibarra I, Arriaga S, Estrada A (2001) Avifauna asociada a dos cacaotales tradicionales en la región de la Contalpa, Tabasco, México. Universidad y Ciencia 17(34):101–112

InfoStat (2004) InfoStat versión1.4. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina

Johns ND (1999) Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environ Manage 23(1):31–47

Johnson MC (2000) Effects of shade tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade crop plantation. Biotropica 32(1):133–145

Laval R, Rodriguez B (2002) Murciélagos de Costa Rica, 1st edn. INBio, Santa Domingo de Heredia, Costa Rica

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammon PM, Hodd M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Luck GW, Daily GC (2003) Tropical countryside bird assemblages: richness, composition and foraging differ by landscape context. Ecol Appl 13:225–247
<Occurrence Type="DOI"><Handle>10.1890/1051-0761(2003)013[0235:TCBARC]2.0.CO;2</Handle></Occurrence>

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey

McAleece N (1997) BioDiversity Professional. The National History Museum and The Scottish Association For Marine Science. Version Beta. http://www.nhm.ac.uk/zoology/bdpro

McNeely JA, Scherr SJ (2003) Ecoagriculture: strategies to feed the world and save biodiversity. Island Press, Washington, DC

Medellín RA, Equihua M (1998) Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. J Appl Ecol 35:13–23

Medina A, Harvey CA, Sánchez D, Vílchez S, Hernández B (2007) Bat diversity and movement in a neotropical agricultural landscape. Biotropica 39(1):120–128

Miller K, Chang E, Johnson N (2001) Defining the common ground for the Mesoamerican biological corridor. World Resources Institute, Washington, DC

Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conserv Biol 13(1):11–21

Municipality of Talamanca (2003) Plan local de desarollo: 2003 a 2013. Municipality of Salamanca, BriBri, Costa Rica

Olson DM, Dinerstein E (2002) The global 200: priority ecoregions for global conservation. Ann Missouri Bot Gard 89:199–224

Perfecto I, Rice R, Greenberg R, Van der Voorst ME (1996) Shade coffee: a disappearing refuge for biodiversity. BioScience 46(8):598–608

Perfecto I, Vandermeer J (1997) The agroecosystem: a need for the conservation biologist's lens. Conserv Biol 11:591–592

Perfecto I, Mas A, Dietsch T, Vandermeer J (2003) Conservation of biodiversity in coffe agroecosystems: a tri-taxa comparison in southern Mexico. Biodivers Conserv 12:1239–1252

Pineda E, Moreno C, Escobar F, Halffter G (2005) Frog, bat and dung beetle diversity in the cloud forest and coffee agroecosystem of Veracruz, Mexico. Conserv Biol 19(2):1–11

Ralph CJ, Sauer JR, Droege S (1995) Monitoring bird populations by point counts. USDA Forest Service, Albany, USA

Reid F (1997) A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press, Oxford, New York

Reitsma R, Parrish JD, McLarney W (2001) The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. Agroforest Syst 53:185–193

Rice A, Greenberg R (2000) Cacao cultivation and the conservation of biological diversity. AMBIO 29(3):167–173 <Occurrence Type="DOI"><Handle>10.1639/0044-7447(2000)029[0167:CCATCO]2.0.CO;2</Handle></Occurrence>

Schroth G, Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac AMN (2004a) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, DC

Schroth G, Harvey C, Vincent G (2004b) Complex agroforests: their structure, diversity, and potential role in landscape conservation. In: Schroth G, da Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac AMN (eds) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, DC, pp 227–260

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shadbuddin D, Veddeler M, Mühlenberg S, Gradstein R, Leuschner C, Steffen-Dewenter I, Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. Ecol Appl 14:321–1333

Sokal RR, Rohlf F (1995) Biometry, 3rd edn. W. H. Freman, New York, NY, USA

Somarriba E, Harvey C (2003) Cómo integrar producción sostenible y conservación de biodiversidad en cacaotales orgánicos indígenas? Agroforestería en las Américas 10:12–17

Somarriba E, Trivelato M, Villalobos M, Suárez A, Benavides P, Moran K, Orozco L, López A (2003) Diagnostico agroforestal de pequeñas fincas cacaoteras orgánicas de indígenas Bribri y Cabécar de Talamanca, Costa Rica. Agroforestería en las Américas 10:24–30

Somarriba E, Harvey CA, Samper M, Anthony F, González J, Staver C, Rice R (2004) Biodiversity in coffee plantations. In: Schroth G, da Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac AMN (eds) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington, DC, pp 198–226

Stiles G, Skutch A (1995) Guía de aves de Costa Rica. Instituto Nacional de Biodiversidad, San Jose, Costa Rica

Suatunce P, Somarriba E, Harvey C, Finegan B (2003) Composición florística y estructura de bosques y cacaotales en los territorios indígenas de Talamanca, Costa Rica. Agroforestería en las Americas 10(37–38):31–35

Thies DW, Kalko EKW (2004) Phenology of Neotropical pepper plants and their association with their main dispersers, two short-tailed fruit-bats, *Carollia perspicillata* and *C. castanea*. Phyllostomidae. Oikos 104:362–376

Timm RM, Laval RK, Rodríguez B. (1999) Clave de campo para los murciélagos de Costa Rica. Brenesia 52:1–32

Tosi JA (1969) Republica de Costa Rica: mapa ecológico según la clasificación de zonas de vida de L.R. Holdridge. Centro Científico Tropical, San José, Costa Rica

Vandermeer J, Perfecto I (2007) The agricultural matrix and a future paradigm for conservation. Conserv Biol 21:274–277

Waltert M, Mardiastuti A, M•hlenberg M (2004) Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv Biol 18(5):1339–1346

Wunderle JM Jr, Latta S (1998) Avian resource use in Dominican shade coffee plantations. Wilson Bull 110:271–281

WWF, UICN and SICA (1999) Lista de fauna de importancia para la conservación en Centroamérica y México: listas rojas, listas oficiales y especies en apéndices CITES. Sistemas de Integración Centroamericana. Dirección ambiental. UICN-HORMA y WWF Centroamérica, San José