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PATTERNS OF ANIMAL DIVERSITY IN DIFFERENT FORMS OF TREE COVER IN AGRICULTURAL LANDSCAPES

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Abstract. As tropical regions are converted to agriculture, conservation of biodiversity will depend not only on the maintenance of protected forest areas, but also on the scope for conservation within the agricultural matrix in which they are embedded. Tree cover typically retained in agricultural landscapes in the neotropics may provide resources and habitats for animals, but little is known about the extent to which it contributes to conservation of animal species. Here, we explore the animal diversity associated with different forms of tree cover for birds, bats, butterflies, and dung beetles in a pastoral landscape in Nicaragua. We measured species richness and abundance of these four animal taxa in riparian and secondary forest, forest fallows, live fences, and pastures with high and low tree cover. We recorded over 20 000 individuals of 189 species including 14 endangered bird species. Mean abundance and species richness of birds and bats, but not dung beetles or butterflies, were significantly different among forms of tree cover. Species richness of bats and birds was positively correlated with tree species richness. While the greatest numbers of bird species were associated with riparian and secondary forest, forest fallows, and pastures with >15% tree cover, the greatest numbers of bat species were found in live fences and riparian forest. Species assemblages of all animal taxa were different among tree cover types, so that maintaining a diversity of forms of tree cover led to conservation of more animal species in the landscape as a whole. Overall, the findings indicate that retaining tree cover within agricultural landscapes can help conserve animal diversity, but that conservation efforts need to target forms of tree cover that conserve the taxa that are of interest locally. Preventing the degradation of remaining forest fragments is a priority, but encouraging farmers to maintain tree cover in pastures and along boundaries may also make an important contribution to animal conservation.

Key words: agricultural matrix; bat, bird, butterfly, and dung beetle diversity; biodiversity assessment; farming systems; forest fragments; live fences; Nicaragua; riparian forests; species richness; trees in pastures.

Introduction

With agriculture dominating many tropical regions and rapidly encroaching on the last remaining forests (Achard et al. 2002, Lambin et al. 2003), the conservation of biodiversity will depend not only on the establishment of protected areas and reserves, but also on the management of agricultural landscapes (Perfecto and Vandermeer 1997, Daily 2001, Daily et al. 2001, Brooks et al. 2004, Schroth et al. 2004, Green et al. 2005). Active management of the agricultural matrix is important for conserving what biodiversity remains within fragmented landscapes and for buffering the effects of agriculture on nearby forests (Janzen 1983, Glor et al. 2001, Naughton-Treves et al. 2003). Land management options that seek to combine conservation and production goals within agricultural landscapes must be based on a clear understanding of what plant and animal diversity remains in these landscapes, and how the composition and structure of the agricultural matrix influence its conservation potential. The conservation value of agricultural landscapes may vary for different taxa (Burel et al. 2004), so multitaxa comparisons are urgently needed to evaluate the impacts of different land uses on animal diversity. But because they are difficult and costly to conduct (Lawton et al. 1998), few have been published.

The conservation value of the tree cover that is retained within agricultural matrices has generally been overlooked. In the neotropics, tree cover in agricultural landscapes typically occurs in the form of riparian forests, forest fallows, live fences, and dispersed trees in

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fields. These tree resources are often actively managed by farmers to provide products such as firewood, timber, fruits and fodder for cattle, and services such as watershed functions and shade for cattle (Cajas-Giron and Sinclair 2001, Gordon et al. 2003, 2004, Harvey et al. 2004; Harvey et al., *in press*). Although trees are principally retained by farmers for productive purposes, they may also provide habitats, resources, and landscape connectivity for animals (Estrada et al. 2000, Harvey et al. 2004). While there is a growing body of literature comparing animal diversity on agricultural land vs. forest in the neotropics (e.g., Estrada et al. 1993, 1997, 1998, 2000, Daily et al. 2001, 2003), there are no studies that have simultaneously compared the diversity of multiple animal taxa associated with the different types of tree cover found within the agricultural matrix.

The diversity of animal taxa associated with different forms of tree cover may vary as a result of differences in their movement capabilities, dependence on forest cover, and resource requirements, so we measured the animal diversity of four contrasting taxa associated with six different forms of tree cover. The animal taxa that we studied were birds, bats, butterflies, and dung beetles, and these were measured in riparian forests, secondary forests, forest fallows, live fences, and pastures with high and low tree cover. These forms of tree cover not only represent the bulk of trees within the landscape in southwestern Nicaragua that we studied, but are also found more generally within pastoral landscapes throughout Mesoamerica (Guevara et al. 1994, Barrance et al. 2003, Harvey et al. 2004), making the results broadly applicable to agricultural landscapes across the region.

The objectives of this research were (1) to explore the diversity of contrasting animal taxa associated with different forms of tree cover typically retained in agricultural landscapes in Central America, and (2) to consider the implications of the findings for the design of conservation strategies for agricultural land in the region. We started from the general hypothesis that species abundance and richness of animal taxa would vary among different types of tree cover, reflecting differences in their ability to serve as habitats and provide resources for animal species. Specifically, it was expected that the types of tree cover most similar to the original forest cover (secondary and riparian forests) would be associated with higher animal species richness and abundance than tree cover types that had been highly modified. This was expected because forest-like forms of tree cover are likely to provide resources and habitat for the species originally present in the landscape, and so may be expected to have retained more of them. Similarly, we expected that higher densities of tree cover on pastures would be associated with higher animal abundance and species richness because more resources and habitat for forest species would be provided by the tree cover. We also anticipated that different animal taxa, and individual feeding guilds within taxa, might respond differently to different types of tree cover, reflecting differences in their movement patterns, habitat use, resource requirements, forest dependence, and behavior.

By comparing the diversity of a number of animal taxa across different types of tree cover, this study provides the first assessment of animal diversity associated with the common types of tree cover typically present within agricultural landscapes in the neotropics, and highlights the potential importance of tree cover within the agricultural matrix for conservation efforts.

Methods

Study site

The study was conducted in an area roughly 10 × 11 km within the municipality of Belén, in the department of Rivas, in southwestern Nicaragua (11°26′ N, 85°49′ W). The native vegetation is classified as Tropical Dry Forest (Holdridge 1987), which originally extended along the Pacific coast of Central America from Mexico to Costa Rica. It has been reduced to <2% of its original expanse by deforestation and agricultural expansion, and is now considered an endangered ecosystem (Janzen 1988, Murphy and Lugo 1995). The mean annual temperature is 27°C and mean annual precipitation 1173 mm, with most rainfall occurring between May and December (Sabogal and Valerio 1998). The land is fairly flat, with altitudes ranging from 100 to 200 m above sea level. The Rivas area has been populated for several centuries and consists of an agricultural matrix, dominated by cattle-grazed pastures producing both milk and meat (Gómez et al. 2004). Small areas were also planted with crops, mainly plantain, rice, maize, and beans. From analysis of aerial photographs taken in 1996 we estimated that 57% of the land cover was pasture, 18% forest fallows, 13% forest, 5% crop fields, and 7% other land uses (Harvey et al., *in press*).

Using the aerial photograph, six types of tree cover were identified within the landscape: (1) riparian forests (RF); (2) secondary forests (SF); (3) forest fallows (FF); (4) live fences (LF); and pastures with dispersed trees at either (5) high (16–25%; PH) or (6) low (0–5%; PL) tree cover. No primary forest patches were included, as all of the remaining forest patches in the landscape had been heavily disturbed by timber extraction, fires, and grazing. The secondary forests were small patches of regenerated forest, usually on sloping land or areas with difficult access, with a minimum height of 15 m and a developed understory. The riparian forests were usually located on flat land (with slopes of <15%), along the banks of small streams or rivers, and were open to cattle grazing. The forest fallows were pasture or previously cultivated areas left fallow, on which vegetation had reached a height of between 3 and 10 m. These three forest tree cover types (RF, SF, and FF) were subject to degradation by cattle grazing, fires, and extraction of firewood and timber, but riparian forests were generally less degraded because of their importance as water sources. The live fences were anthropogenic features consisting of single lines of trees that had been planted to divide paddocks, prevent cattle movement, or to delimit farm boundaries (Harvey et al. 2005). Pastures were dominated by Jaragua grass (*Hyperrhenia rufa*) and were extensively grazed by cattle (1.4 ± 0.8 livestock units/ha; mean ± SE [Gomez et al. 2004]). Most of the dispersed trees in pastures had regenerated after initial clearance, but there were a few relicts of the original forest.

Data collection

For each type of tree cover, eight replicate sample areas were randomly chosen from the aerial photograph. Each of these 48 sample areas was visited to ensure that it was of sufficient size for the monitoring protocol to be established. This required establishment of a square 1-ha plot for secondary forests, forest fallows, and pastures, a rectangular 1-ha plot of 500 × 20 m for riparian forests, and a linear plot of 350 m × 2 m for live fences. Live fences were not selected if they were next to a busy road. Sample areas that did not fulfill these criteria were replaced with another randomly chosen area.

Each plot was sampled for two days between April and December 2002 for trees, birds, bats, dung beetles, and butterflies. The mean distance between all combinations of plots was 4.84 ± 0.077 km, and because of the fine-grained fragmentation of the landscape, there was no observable spatial pattern in the distribution of sample areas for any tree cover type. In each sampling excursion, one plot of each type of tree cover was sampled in random order. The methods for sampling each taxon are explained below.

Trees

To characterize tree cover, a subplot was established within each plot. In the secondary forests, forest fallows, and pastures, trees were surveyed in a 20 × 50 m subplot (0.1 ha), located randomly in one of the four corners of the main plot. In the riparian forests, a subplot of 100 × 10 m (0.1 ha) was established, because the linear nature of the riparian forest did not permit wider plots. Live fences were characterized by doing a complete inventory of trees present within a 350 m length of live fence.

In the subplots, all trees with dbh >10 cm (stem diameter at 1.3 m height) were identified and their dbh measured. When trees could not be identified in the field, a botanical sample was collected for later identification in the National Herbarium of the Universidad Centroamericana (UCA), Nicaragua using the *Flora of Nicaragua* (Stephens et al. 2001).

Birds

Four point count stations were located in each plot, 100 m apart. In the square plots, the point counts were located in the four corners of the 1-ha plot, whereas in the linear plots, the point counts were located in a line. Birds were observed at each point count during 10 minutes, with observations being conducted between 06:00 and 07:40 hours during two consecutive days per plot. This gave a total of eight point counts (80 minutes of observation) per plot and 64 point counts (four point counts × 2 days × 8 replicates; or 640 minutes of observation) per type of tree cover. All observed birds were recorded and identified and classified by their feeding guild using Stiles and Skutch (1989). A settling period of five minutes was used before observations commenced, and days with heavy rain or high winds were avoided.

Bats

Bats were sampled using eight mist nets (each 12 × 2.5 m wide, with mesh size of 1.5 cm) positioned at a distance of 50 m apart. In the secondary forests, forest fallows, and two types of pastures, the nets were positioned in a circle with a 55-m radius, whereas in the linear tree cover types (riparian forests and live fences) mist nets were in a line. Each mist net was located at a distance of 50 m from the nearest net. Mist nets were open from 18:30 to 01:00 hours during two nights in each plot, for a total of 104 mist net hours per plot and 832 hours per type of tree cover. All captured bats were removed from the mist nets and identified to species level using keys by Laval and Rodriguez (2002) and Reid (1997). The hair on the bats' heads was cut to enable recognition in subsequent captures and avoid counting the same bat twice. Each bat species was also classified by feeding guild using Laval and Rodriguez (2002) and Reid (1997). Nights with heavy rain, high winds, or a full moon were avoided.

Dung beetles

Dung beetle populations were surveyed using 32 pitfall traps per plot baited with pig dung. In the secondary forests, forest fallows, and two types of pastures, the 32 traps were located in two square grids of 16 traps, with traps 7 m apart. In the linear tree cover types (riparian forests and live fences), the 32 traps were placed in a line, with traps 7 m apart. Each pitfall trap consisted of a 355-mL plastic cup, 17 cm in diameter at the top, filled with soapy water and buried in the soil, with a wire mesh on top supporting the dung. In each plot, the pitfall traps were left outside for two consecutive nights. All beetles were collected and taken to the Museo Entomológico de León for identification by B. Hernández and J. M. Maes.

Butterflies

In each plot, three transects were established for trapping butterflies. Each transect was 100 m long and separated from the other transects by 50 m, except in live fences where they were contiguous. Each transect was walked for 30 minutes each day for two days, during which time all butterflies seen were collected with a collecting net. This resulted in a sampling effort of 3 hours in each plot and 24 hours in each type of tree cover. To avoid possible misidentification of species, only butterflies that were captured were recorded. Butterflies were identified using DeVries (1987, 1997) and by J. M. Maes at the Museo Entomológico de Leon, Nicaragua. Each species was characterized as either a frugivore or nectarivore according to DeVries (1987, 1997), Maes and Brabant (2000), and local experience. Days with heavy rain and high winds were avoided.

Data analysis

For each taxon we compared the total species richness and abundance per plot across the six types of tree cover using ANOVA for normally distributed data (followed by Duncan comparisons) or Kruskal-Wallis for non-normally distributed data (followed by pairwise comparisons). For the taxa where feeding guild data were available (birds, bats, and butterflies), we similarly compared differences in species richness and abundance of different guilds, among the forms of tree cover. Differences across tree cover forms were only compared for guilds that represented $>10\%$ of the total abundance of a particular taxon (for birds, frugivores, insectivores, and omnivores; for bats, frugivores and insectivores; for butterflies, frugivores and nectarivores), to ensure sufficient data for comparisons across tree cover types. The sampling effort for birds, bats, butterflies, and beetles was identical across the six types of tree cover, so all comparisons were made using the total abundance and species richness (of all species or of a particular feeding guild) recorded in each plot. Because the total area of vegetation sampled for live fences differed from the other types of tree cover, live fences were not included in the analyses comparing tree species richness or abundance.

The degree of similarity in species composition among pairs of tree cover types was calculated using the Jaccard similarity index (Magurran 2004). In addition, cluster analyses of species were conducted in Biodiversity Pro v7 (Biodiversity Pro 1997) using Bray-Curtis similarity and average linkage method to explore similarity in species assemblages across tree cover types. To explore relationships among the species richness of trees, birds, bats, butterflies, and dung beetles we used pairwise Pearson's correlations (Sokal and Rohlf 1995). For each taxon, the total number of species expected to be present in the landscape was estimated by creating species–area accumulation curves for the entire landscape in EcoSim v5 (EcoSim 2000), and then applying the Clench equation (Clench 1979) to estimate expected species richness. Species–area curves were constructed on the basis of individuals sampled, rather than the number of plots, as recommended by Gotelli and Colewell (2001). All statistical analyses were conducted in InfoStat v1.4 (2004).

Results

Floristic and structural comparison of different forms of tree cover

The different forms of tree cover found in the Rivas landscape varied in their tree species richness and abundance (Table 1). The mean number of individual trees and tree species per plot was higher for all forest forms of tree cover than for pastures. Among forest forms, riparian forest had more trees than forest fallows and more species than both secondary forest and forest fallows. While not statistically comparable because of different sampling effort, live fences were closer to forest fallows than pasture in terms of tree abundance and species richness. Riparian forests, secondary forests, and forest fallows were characterized by tree species typical of tropical dry forest (Gillespie et al. 2000), whereas pastures with high and low tree cover tended to be dominated by species deliberately planted or retained by farmers for timber or fodder. Live fences were dominated by planted species (*Gliricidia sepium* and *Pachira quinata*), but also included a few individuals of 32 other tree species that had naturally regenerated. The different forms of tree cover also varied in their structure, with taller trees in riparian forests and secondary forests than in all other forms of tree cover. Trees in the riparian forests and live fences had larger diameters than those in pastures with high tree cover.

Animal abundance and species richness associated with different forms of tree cover

More than 20 000 individual animals were sampled, comprising a particularly large number of dung beetles, many birds and bats, but fewer butterflies. There were generally more individuals and species of birds and dung beetles sampled in forest forms of tree cover than in pastures or live fences (Table 2). Bats were sampled in greatest numbers in riparian forests and live fences, while butterflies were most abundant, but least species rich, in pastures with low tree cover (Table 2). Modeled estimates of total landscape species richness were higher than the numbers of species that we recorded for birds (89), bats (26), and butterflies (61).

Mean abundance and species richness per plot were significantly different among forms of tree cover for birds and bats but not for dung beetles and butterflies (Fig. 1). While abundance was correlated with species richness for birds, dung beetles, and butterflies, use of abundance as a covariate did not change the results. Riparian forest had significantly higher abundance of both birds and bats than all other forms of tree cover, whereas pastures with low tree cover hosted the smallest number of individuals of both taxa. For birds, both abundance and species richness were higher in the forest forms of tree cover than in live fences and pastures with low tree cover, but pastures with high tree cover were not different from any forest forms in species richness, or from forest fallows in abundance. For bats, live fences were important, hosting the second highest number of individuals and species, and bat species richness was significantly higher in riparian forests and live fences than secondary forest and pastures with low tree cover.

TABLE 1. Structural and floristic characteristics of six forms of tree cover in Rivas, Nicaragua.

Tree characteristics	RF	SF
Total no. individuals	298	251
Total no. species	69	51
Mean no. species/0.1 ha†	$18.9^{a} \pm 0.33$	$12.4^{b} \pm 0.35$
Mean no. individuals/0.1 ha†	$37.3^{a} \pm 0.34$	$31.4^{ab} \pm 0.85$
Mean dbh (cm)	$31.25^{a} \pm 2.33$	$26.52^{ab} \pm 2.90$
Mean tree height (m)	$15.41^{a} \pm 0.89$	$14.87^{a} \pm 1.29$
Five most abundant tree species (in order of decreasing abundance)	*Thouinidium decandrum*, *Guazuma ulmifolia*, *Simarouba amara*, *Calycophyllum candidissimum*, *Spondias mombin*	*Cochlospermum vitifolium*, *Guazuma ulmifolia*, *Calycophyllum candidissimum*, *Spondias mombin*, *Gliricidia sepium*

Notes: Forest cover types: RF, riparian forests; SF, secondary forests; FF, forest fallows; LF live fences; PH, pastures with high tree cover; PL, pastures with low tree cover. Trees with dbh > 10 cm were measured in eight subplots in each tree cover type. Values with error terms are means ± SE. Different superscript letters in the same row indicate significant differences ($P < 0.05$), by ANOVA or Kruskal-Wallis analyses.

† Subplots were 0.1 ha except for live fences (LF), where they were 350 × 2 m (700 m^2). Live fences were not included in the statistical comparisons of species richness or abundance because of the difference in sampling effort.

When taxa were classified into feeding guilds, some guilds followed the same pattern of abundance and species richness as their parent taxon, while others did not, and for the same guilds, different taxa were favored by different forms of tree cover (Fig. 1; Table 3).

Abundance and species richness of frugivorous bats (83.2% of all bats) and birds (12% of all birds) showed the same pattern in relation to tree cover as their parent taxa. In contrast, frugivorous butterflies (24.3% of all butterflies) were more abundant and species rich in forest fallows and secondary forests than in the more open pastures, whereas the undivided butterfly taxon was not significantly different among tree cover types. So, the various frugivorous taxa responded differently from one another to the different forms of tree cover. Riparian forest had the highest abundance and species richness of frugivorous birds and bats but not butterflies, and live fences were particularly important for frugivorous bat species richness but not for frugivorous birds or butterflies.

Nectarivorous bats (11.7% of all bats) showed similar patterns of abundance to the overall bat community, but did not significantly differ in species richness (Fig. 1; Table 3) whereas nectarivorous butterflies (75.7% of all butterflies) showed no significant differences across different forms of tree cover in either abundance or species richness from that of their parent taxon.

Insectivorous birds (40.8% of all birds) showed similar responses to all birds in both abundance and species richness (Table 3), whereas omnivorous birds (16.7% of all birds) showed no differences in either abundance or species richness across different forms of tree cover.

Species composition of animal taxa associated with different forms of tree cover

There are no definitive species lists for any of the taxa that we studied for tropical dry forest in Nicaragua, but

TABLE 2. Total number of individuals and species sampled across the different tree cover types for four animal taxa in Rivas, Nicaragua.

Taxon	No. samples RF	SF	FF	LF	PH	PL	Total (48 plots)
Birds							
Individuals	486	369	340	199	253	193	1840
Species	42	49	42	32	41	35	83
Bats							
Individuals	770	290	283	440	296	220	2299
Species	19	14	14	18	15	14	24
Dung beetles							
Individuals	2565	3626	2867	2522	2288	1759	15 627
Species	23	29	28	24	24	20	32
Butterflies							
Individuals	97	74	96	68	79	145	559
Species	27	22	26	25	22	18	50

Notes: Forest cover types: RF, riparian forests; SF, secondary forests; FF, forest fallows; LF, live fences; PH, pastures with high tree cover; PL, pastures with low tree cover ($n = 8$ plots per tree cover type). Sampling effort was identical across all six types of tree cover for each animal taxon.

TABLE 1. Extended.

FF	LF†	PH	PL
196	305	62	25
45	34	20	17
$9.9^{b} \pm 0.40$	9.1 ± 0.12	$4.5^{c} \pm 0.30$	$2.9^{c} \pm 0.69$
$24.5^{b} \pm 1.09$	38.1 ± 0.54	$7.8^{c} \pm 0.42$	$3.13^{c} \pm 0.79$
$23.31^{ab} \pm 2.40$	$29.32^{a} \pm 4.20$	$18.99^{b} \pm 1.92$	$26.66^{ab} \pm 5.40$
$10.20^{bc} \pm 1.12$	$11.94^{b} \pm 0.82$	$10.61^{bc} \pm 0.62$	$8.87^{c} \pm 0.84$
Guazuma ulmifolia, Cochlospermum vitifolium, Dalbergia retusa, Myrospermum frutescens, Calycophyllum candidissimum	*Gliricidia sepium, Cordia dentata, Pachira quinata, Myrospermum frutescens, Tabebuia rosea*	*Cordia alliodora, Gliricidia sepium, Karwinskia calderonii, Byrsonima crassifolia, Guazuma ulmifolia*	*Guazuma ulmifolia, Tabebuia rosea, Cordia alliodora, Gliricidia sepium, Diphysa americana*

all the species that we recorded have been also been observed in tropical dry forest elsewhere in Central America. We recorded 14 endangered bird species, 13 on CITES Appendix 2 and one on Appendix 3 (IUCN 1999). Most of these were recorded in very low numbers (<20 individuals), four of which (*Asturina nitida*, *Ciccaba virgata*, *Otus cooperi*, and *Phaethornis longuemareus*) were only observed in forest forms of tree cover. Three of the four species more frequently encountered (*Amazilia rutila*, *Amazona albifrons,* and *Brotogeris jugularis*) were found in all forms of tree cover, while *Aritinga nana* was found in all cover types except secondary forest. There is not enough information about the conservation status of butterfly, bat, and dung beetle species in Nicaragua to identify whether the species recorded are of conservation concern (Martínez Sánchez et al. 2001).

The majority of the 10 most common species in all taxa were generalist species that were observed in all types of tree cover: all 10 of the most common dung beetle and bat species, 8 of the most common birds, and 7 of the most common butterflies (Table 4). In contrast, the species of all taxa that were found only in forest forms of tree cover (RF, SF, and FF) were present only at low abundances. We observed 27 bird species (437 individuals) in Rivas that have been classified as forest dependent (Stiles 1983), of which we saw only 16 in forest forms of tree cover, 10 in both forest and nonforest forms of tree cover, and one, *Lophornis helenae*, only once in a pasture with low tree cover.

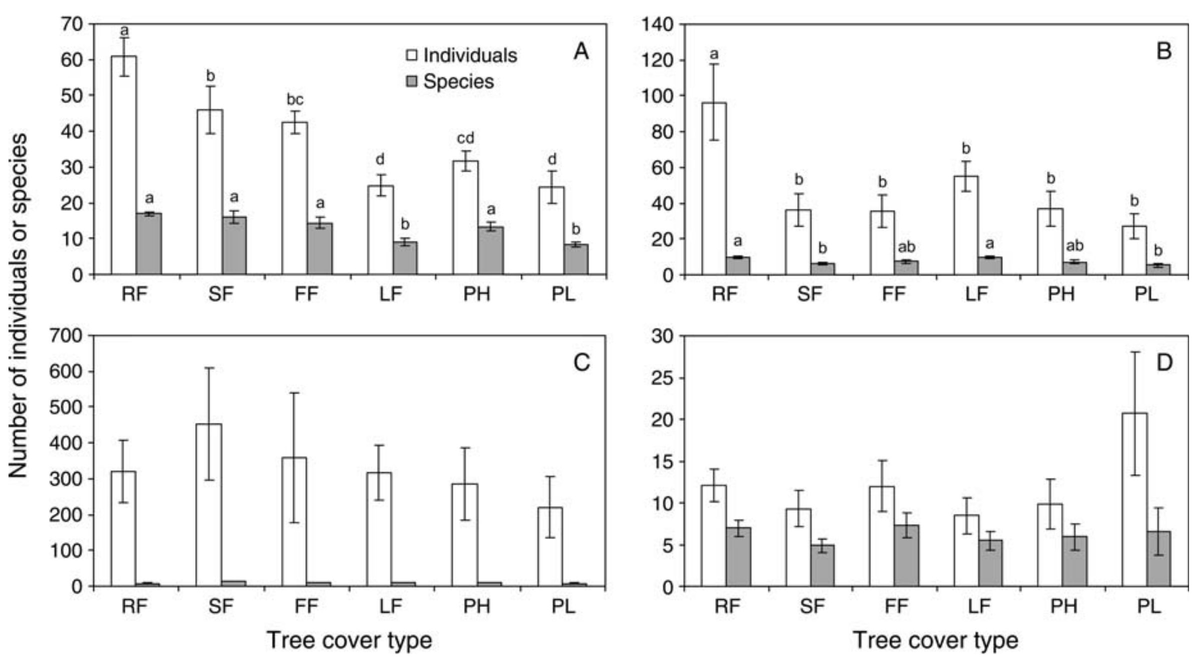

FIG. 1. Abundance of individuals and species richness of (A) birds, (B) bats, (C) dung beetles, and (D) butterflies in six types of tree cover: riparian (RF) and secondary (SF) forests, forest fallows (FF), live fences (LF), and pastures with high (PH), and low (PL) tree cover in the agricultural matrix of Rivas, Nicaragua. Bars show the mean (±SE) abundance (open bars) and species richness (gray bars) per plot (1 ha for all forms except the live fences [LF], which were 350 m long) for $n = 8$ plots in each type of tree cover. Different letters in the same column series indicate significant differences among tree cover types ($P < 0.05$), from ANOVA (F) or Kruskal-Wallis (H) analyses. Details on sampling effort per group can be found in the *Methods* section.

TABLE 3. Abundance and species richness of animal feeding guilds in six tree cover types in the agricultural matrix of Rivas, Nicaragua.

Guild	RF	SF	FF	LF	PH
Abundance (no. individuals)					
Frugivorous birds	$11.75^{a} \pm 2.93$	$4.38^{ab} \pm 1.28$	$3.38^{b} \pm 1.00$	$1.38^{b} \pm 0.56$	$3.13^{b} \pm 0.79$
Insectivorous birds	$28.25^{a} \pm 1.94$	$23.12^{a} \pm 2.80$	$18.50^{ab} \pm 2.57$	$8.13^{c} \pm 1.08$	$10.38^{bc} \pm 2.31$
Frugivorous bats	$77.63^{a} \pm 19.01$	$29.75^{b} \pm 7.49$	$29.38^{b} \pm 8.17$	$46.13^{b} \pm 7.88$	$32.28^{b} \pm 9.43$
Nectarivorous bats	$13.00^{a} \pm 3.21$	$5.13^{b} \pm 1.72$	$4.38^{b} \pm 1.21$	$5.50^{b} \pm 1.24$	$2.88^{b} \pm 1.04$
Frugivorous butterflies	$2.73^{ab} \pm 0.94$	$5.13^{a} \pm 1.46$	$4.38^{a} \pm 1.00$	$2.50^{ab} \pm 0.87$	$0.63^{b} \pm 0.32$
Species richness (no. species)					
Frugivorous birds	$2.25^{a} \pm 0.37$	$1.25^{ab} \pm 0.31$	$1.38^{ab} \pm 0.18$	$0.50^{b} \pm 0.19$	$1.25^{ab} \pm 0.31$
Insectivorous birds	$6.13^{ab} \pm 0.44$	$6.38^{a} \pm 0.42$	$5.25^{ab} \pm 0.59$	$3.38^{cd} \pm 0.32$	$4.63^{bc} \pm 0.94$
Frugivorous bats	$7.13^{a} \pm 0.58$	$4.50^{b} \pm 0.57$	$5.63^{ab} \pm 0.86$	$6.75^{a} \pm 0.65$	$5.50^{ab} \pm 1.00$
Frugivorous butterflies	$2.25^{ab} \pm 0.62$	$2.88^{a} \pm 0.64$	$3.50^{a} \pm 0.89$	$2.13^{ab} \pm 0.64$	$0.50^{c} \pm 0.27$

Notes: Forest cover types: RF, riparian forests; SF, secondary forests; FF, forest fallows; LF, live fences; PH, pastures with high tree cover; PL, pastures with low tree cover ($n = 8$ plots per tree cover type). Only guilds with significant differences among tree cover types, based on ANOVA (F) or Kruskal-Wallis (H) analyses, are shown ($P < 0.05$), with different superscript letters in the same row indicating these differences. Details on sampling effort per group can be found in *Methods*. Values with error terms are means ± SE.

Four of the bat species, observed only once each in Rivas, are considered highly forest dependent. These were *Chrotopterus auritus* and *Micronycteris hirsuta* observed in riparian forest, *Natalus stramineus* in a secondary forest, and *Saccopteryx leptura* in a live fence. Forest dependency of most of the dung beetle and butterfly species is not known (Martínez Sánchez et al. 2001), but at least one dung beetle species that we captured in all habitats, *Magioniella astyanax*, has been previously reported as a forest species (Escobar 1997).

The species composition of all taxa (birds, bats, dung beetles, and butterflies) varied among different forms of tree cover, with pairs of different types of tree cover sharing 32.7–54.5% of all bird species, 52–81% of all bat species, 63–88% of the dung beetle species, and 27–65% of all butterfly species. In all taxa, less than half of the species were found in all six forms of tree cover (12 of 83 bird species, 11 of 24 bat species, 15 of 32 dung beetle species, and 5 of 50 butterfly species).

When the forms of tree cover were grouped using dendrograms of Bray-Curtis similarity indices, that take both species richness and abundance into account, distinct patterns for different animal taxa emerged (Fig. 2). For birds, riparian forests, forest fallows, and live fences were the most similar tree cover types and were distinct from other forms of tree cover. Bats, in contrast, showed three main groups of tree cover: (1) live fences and riparian forests; (2) pastures with high tree cover, pastures with low tree cover, and forest fallows; and (3) secondary forests. Dung beetle composition differed between the pastures and other types of tree cover, while butterflies had a distinct composition in secondary forests compared to all other forms of tree cover.

Correlations in species richness and diversity among taxa

The total number of tree species was positively correlated with the species richness of all birds, frugivorous birds, insectivorous birds, all bats, frugivorous bats, and frugivorous butterflies, but not with omnivorous birds, insectivorous bats, nectarivorous bats, dung beetles, all butterflies, or nectarivorous butterflies (Table 5). There were no clear general associations between species richness of birds, bats,

TABLE 4. Lists of the 10 most common bird, bat, butterfly, and dung beetle species recorded at Rivas, Nicaragua, and the percentage of total observations in each taxon that they represented.

Birds ($n = 1840$)		Bats ($n = 2299$)		Butterflies ($n = 559$)		Dung beetles ($n = 15\,627$)	
Species	%	Species	%	Species	%	Species	%
Thryothorus pleurostictus	10.6	*Artibeus jamaicensis*	40.4	*Phoebis sennae*	23.1	*Onthophagus championi*	23.3
Calocitta formosa	9.2	*Artibeus lituratus*	12.9	*Heliconius charithonius*	6.4	*Canthon cyanellus sallei*	19.7
Amazona albifrons	7.3	*Carollia perspicillata*	11.1	*Euptoieta hegesia*	5.2	*Canthon deyrollei*	14.8
Campylorhynchus rufinucha	7.1	*Glossophaga soricina*	10.9	*Eurema daira*	5.2	*Copris lugubris*	8.1
Crotophaga sulcirostris	5.8	*Sturnira lilium*	6.2	*Dryas iulia*	4.5	*Ateuchus rodriguezi*	7.8
Dendroica petechia	5.0	*Desmodus rotundus*	4.2	*Heliconius hecale zuleika*	4.5	*Onthophagus marginicollis*	6.5
Brotogeris jugularis	4.0	*Artibeus intermedius*	4.0	*Myscelia pattenia*	3.9	*Onthophagus batesi*	6.1
Myiarchus tuberculifer	3.8	*Carollia subrufa*	2.6	*Siproeta stelenes*	3.9	*Deltochilum lobipes*	2.5
Melanerpes hoffmannii	3.5	*Phyllostomus discolor*	2.4	*Vareuptychia similis*	3.8	*Onthophagus landolti*	1.9
Aimophila ruficauda	3.1	*Artibeus phaeotis*	1.7	*Junonia evarete*	3.6	*Dichotomius yucatanus*	1.9

TABLE 3. Extended.

PL	Test statistic (F or H) df = 5, 42	P
2.38[b] ± 1.58	18.10 (H)	0.0023
5.50[c] ± 1.69	33.32 (H)	<0.001
23.75[b] ± 6.77	3.51 (F)	0.0097
2.88[b] ± 1.25	4.52 (F)	0.0022
1.25[b] ± 0.49	16.87 (H)	0.0036
0.50 ± 0.33	15.30 (H)	0.0048
2.25[d] ± 0.37	8.73 (F)	<0.0001
3.88[b] ± 0.64	3.01 (F)	0.0208
0.75[bc] ± 0.25	16.89 (H)	0.0034

dung beetles, and butterflies, although there were a few weak relationships between bats and omnivorous birds, omnivorous birds and frugivorous bats, and between nectarivorous butterflies and bats.

DISCUSSION

Species richness and abundance of animal taxa associated with different forms of tree cover

The form of tree cover retained on farms in the Rivas landscape, quite apart from the amount, clearly affected the overall abundance and species richness of birds and bats, but not butterflies and dung beetles. This is consistent with the more direct dependence on tree cover displayed by birds and bats for foraging, nesting, roosting, or perching when compared with dung beetles and butterflies, coupled with the fact that different forms of tree cover supply these resources differently. Both bird and bat species richness were positively correlated with that of trees, reinforcing the strong associations between the floristic and structural diversity of tree cover with bird and bat communities that are well established in the literature (e.g., MacArthur and MacArthur 1961, James and Wamer 1982, Fenton et al. 1992, Medellin et al. 2000, Schulze et al. 2000, Hughes et al. 2002). In contrast, dung beetle diversity and abundance has generally been found to correlate principally with favorable microclimatic conditions such as shade and moisture, the availability of sustainable substrates for oviposition and feeding, and microhabitat diversity (Howden and Nealis 1975, Klein 1989, Horgan 2002). These conditions are likely to be supplied to a reasonable extent by all the forms of tree cover in Rivas, supplemented with dung that is widely distributed by roaming livestock. The lack of clear associations of butterflies with different types of tree cover may be because their patterns of diversity and abundance were most sensitive to microclimate and the abundance of flowers, including those in the understory, rather than being primarily influenced by trees (Gilbert 1984, Ouin et al. 2004). The relatively small sample size of butterflies, however, indicates a need for caution in this

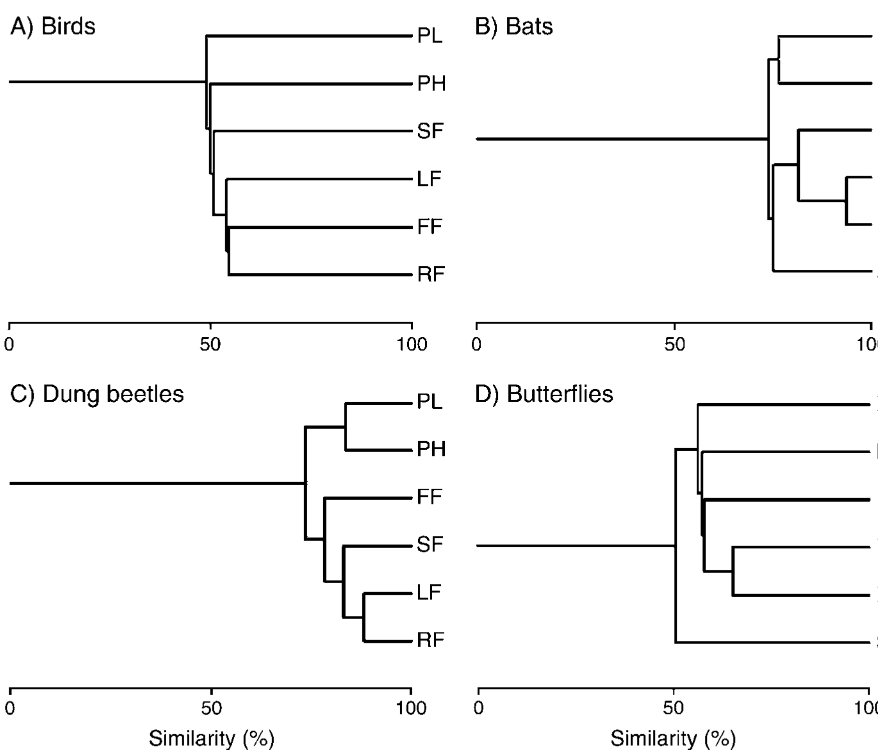

FIG. 2. Cluster analysis of tree cover types based on Jaccard index of similarity of (A) birds, (B) bats, (C) dung beetles, and (D) butterflies in Rivas, Nicaragua.

TABLE 5. Relationships between species richness of trees, birds, bats, dung beetles, butterflies, and their feeding guilds.

Group	Birds (all)	F birds	I birds	O birds	Bats (all)	F bats	I bats	N bats	Dung beetles (all)	Butterflies (all)	F butterflies	N butterflies
Trees	0.44**	0.41**	0.39**	0.35	0.43**	0.36**	0.22	0.22	0.12	0.13	0.37**	0.07
Birds (all)		0.23	0.40**	0.22	0.23	0.21	0.14	0.12	0.11	0.13	0.32*	0.11
F birds			0.40**	0.44**	0.19	0.22	0.14	0.04	0.05	−0.12	0.12	−0.15
I birds				0.16	0.07	0.05	0.14	0.04	0.11	0.03	0.24	0.04
O birds					0.33*	0.39**	−0.04	0.26	−0.06	0.06	0.14	−0.004
Bats (all)						0.96***	0.18	0.59***	0.11	0.17	0.14	0.32*
F bats							−0.01	0.52***	0.06	0.15	0.08	0.31*
I bats								−0.07	0.24	−0.01	0.10	−0.07
N bats									0.04	0.22	0.24	0.18
Dung beetles (all)										0.17	0.04	0.25
Butterflies (all)											0.34*	0.79***
F butterflies												−0.08

Notes: Feeding guilds are: F, frugivorous; I, insectivorous; O, omnivorous; N, nectarivorous. The numbers represent the correlations of species richness (Pearson's r), and asterisks indicate the levels of significance of the correlations: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Values without asterisks were not statistically significant. See *Correlations in species richness and diversity among taxa*.

interpretation and suggests that further research using complementary techniques to those in the present study, such as baited traps, would be merited to evaluate more thoroughly the possible associations between butterfly populations and tree cover (Sparrow et al. 1994).

For the birds and bats, where significant associations were found with different tree cover types, there were differences in which forms of tree cover hosted most species and individuals. Whereas the greatest bird species richness and abundance was associated with high tree cover forms (secondary forests and riparian forests, forest fallows and pastures with high tree cover), bat species richness and abundance was greatest in linear tree features (riparian forests and live fences). There were also some common patterns across the two taxa: riparian forests were important for both birds and bats, and pastures with low tree cover had the lowest abundance of both these taxa. Our sampling spanned several months, so differences in mean species richness among tree cover types may reflect not only how many species are present at any point in time, but also the species turnover through time. Animal species turnover through time has been found to vary markedly in different vegetation types within fragmented landscapes (Moreno and Halffter 2001, Arellano and Halffter 2003).

The high abundance and species richness of birds associated with high tree cover was largely explained by the presence of many frugivorous and insectivorous species, reflecting the availability of foraging, nesting, and perching sites provided by these structurally and floristically diverse types of tree cover. In contrast, pastures with low tree cover and live fences hosted less diverse bird communities than areas with higher tree cover, as has been reported elsewhere (Saab and Petit 1992, Estrada et al. 1993, 1997). This low bird abundance and species richness in more open forms of tree cover may not only reflect less resources provided by trees, but also a greater exposure to raptors (Estrada et al. 1997) and to weather extremes (Wilson et al. 2005). The number of bird species in live fences depends on their composition and structure, with taller, denser live fences supporting higher species richness (Harvey et al. 2005). Live fences at Rivas might support more forest-dependent bird species if they were denser and more structurally and floristically complex (Hinsley and Bellamy 2000). In particular, the abundance and species richness of frugivorous birds within live fences might be increased by inclusion of more tree species that produce edible fruits for birds.

For bats, the two most important types of tree cover were linear features, the riparian forests and live fences. Riparian forests have been reported to be key habitats for bats and other animal species in tropical dry forest ecosystems, particularly during dry months when many animals retreat to these areas to find refuge, seasonal food, and water (Ceballos 1995, Stoner 2001). In the Rivas landscape, the riparian forests were the most floristically diverse forms of tree cover, and presumably offered a wide range of food resources for bats. From observations during the research, the hollow trees and cavernous rooting systems along the river banks also appeared to be important roosting sites for some bat species. The high species richness and abundance of bats found in live fences could be explained by a number of factors, such as enhanced insect availability on the leeward side of live fences (Epila 1986, Dix and Leatherman 1988, Estrada and Coates-Estrada 2001), the availability of fruits attractive to frugivorous bats (e.g., *Cordia dentata, Mangifera indica, Spondias mombin*, and *Spondias purpurea*), the presence of tree species pollinated by bats (e.g., *Pachira quinata*), the preference for bats to travel along live fences to reduce energy costs and avoid predation by nocturnal birds (Estrada and Coates-Estrada 2001), and the use of linear elements as sonar guidelines that facilitate movement across the landscape (Limpens and Kapteyn 1989, Verboom and Huitema 1997).

In most cases, the feeding guilds within taxa followed the same patterns of abundance and species richness as their parent taxon, but frugivorous butterflies had higher abundance and species richness in the forest forms of tree cover than in pastures, while butterflies as a whole showed no significant differences among forms of tree cover. This probably reflects the greater dependence on fruiting plants and trees present in the more forest-like forms of tree cover, for frugivorous as compared with nectarivorous butterflies.

The same feeding guilds in different taxa showed different patterns of species richness and abundance across tree cover types, indicating that they either feed on different tree species, or that provision of food resources by trees was not the dominant influence on the use of the tree cover by these species. So, while frugivorous birds and bats were most abundant and species rich in riparian forest, frugivorous bats but not birds were also abundant and species rich in live fences. In even more marked contrast, frugivorous butterflies were most abundant in forest fallows and secondary forests. These differences reflect the fact that dietary overlap between frugivorous birds and bats is low, as each taxon selects different types of fruits with varying sizes, shapes, colors, and location (Palmeirin et al. 1989, Gorchov et al. 1995). Because the availability of the fruit resources within a given tree cover type is distinct for different animal groups, similar feeding guilds of one taxon are unlikely to be good indicators for those of another. Tree dependence of species is clearly complex, involving interactions among several factors, including the provision of food sources, shelter, and appropriate resting and breeding sites. Grouping organisms in terms of their reliance or preference for particular tree configurations would, therefore, cut across conventional animal taxonomy and commonly used feeding guilds.

Species composition of animal communities associated with different forms of tree cover

Most of the common species of all taxa that we recorded in Rivas were generalists capable of using all forms of tree cover, but some-forest dependent species of birds and bats were observed, albeit in low numbers. Even though the landscape was largely deforested and the remaining tree cover highly fragmented, 14 endangered bird species were observed, indicating a potential contribution to conservation from the agricultural matrix. Other studies have reported that highly modified landscapes of low habitat quality for many forest species of birds, bats, dung beetles, and butterflies, are nevertheless used by some of these species, and can be strategically important in facilitating movement and gene flow between remaining areas of high habitat quality (Estrada et al. 1993, 1998, Daily et al. 2001, Haddad and Tewksbury 2005).

All species that we recorded in Rivas are also found in tropical dry forest of the region. This makes a comparison of the species richness at Rivas with that of a nearby national park of some relevance to conservation planning. The Rivas agricultural landscape contained almost 40% of the bird species found in the nearest area of protected Tropical Dry Forest for which data were available (the Santa Rosa National Park, 65 km to the south in Costa Rica) and more than half of the tree, bat, and dung beetle species found there. Care is required in interpreting this static comparison of species numbers, because there may be a time lag between landscape modification and changes in diversity, and because the composition of species may change over time (e.g., Brooks et al. 1999, Sekercioglu et al. 2002, Ferraz et al. 2003). It is likely, however, that the species that we found there now are able to persist in the modified agricultural landscape because most are native to the region, and land cover in Rivas has been predominantly agricultural for more than a century. Similar conclusions about the potential importance of tree cover within agricultural landscapes for conservation efforts are emerging from other studies in landscapes in the neotropics, such as in Coto Brus, Costa Rica (e.g., Daily et al. 2001, 2003, Ricketts et al. 2001, Hughes et al. 2002, Horner-Devine et al. 2003), Veracruz, Mexico (Estrada et al. 1993, 1997, 1998, 2000, Estrada and Coates-Estrada 2001, 2002), and elsewhere (Petit and Petit 2003).

All four animal taxa showed clear distinctions in species composition among the different tree cover types, but the nature of these relationships varied among taxa. Dung beetle assemblages were distinct in pastures compared to other tree cover types, whereas the butterfly assemblages were most distinct in secondary forests. Bats showed three distinct types of assemblages (live fences and riparian forests, pastures, and forest fallows), whereas bird assemblages were only weakly associated with tree cover types.

Species composition was generally distinct across the different types of tree cover, with no form of cover containing all species of any animal taxon. This indicates that the different types of tree cover are likely to contribute to the conservation of different species, even within those taxa for which overall species richness and abundance were similar among forms of tree cover. It also suggests that the relatively high species richness at a landscape scale is achieved by retaining a diversity of forms of tree cover, as each contains a somewhat distinct species assemblage.

The importance of the density of dispersed tree cover on pastures for conservation

Among the general patterns of diversity across tree cover types, there was some evidence that pastures with high tree cover (16–25% tree cover) had greater conservation potential than pastures with low tree cover (<5% tree cover). Pastures with high tree cover had significantly more bird species and more insectivorous bird species per plot than pastures with low tree cover.

Similarly, the total number of species found in pastures with high tree cover was consistently higher than the total found in pastures with low tree cover (41 vs. 35 bird species, 15 vs. 14 bat species, 24 vs. 20 dung beetle species, and 22 vs. 18 butterfly species). These patterns probably reflect the higher availability of sites for foraging, perching, calling, roosting, and shelter within pastures with higher tree densities, and add to the growing recognition that tree density within pastures may be critical for bird and bat conservation (Estrada et al. 1997, Law and Lean 1999, Fischer and Lindenmayer 2002 *a*, *b*, Luck and Daily 2003, Lumsden and Bennett 2005).

Conservation implications

These results provide several key insights into the role of tree cover within an agricultural matrix for animal conservation. First, conservation strategies that involve retaining trees need to be sensitive about which animal taxa are favored by which forms of tree cover; one animal group cannot be used as a surrogate indicator for another, as they may have very different responses to changes within a landscape. This implies that forms of tree cover will be valued differently as conservation tools in different contexts depending on the taxa of concern. While some studies have shown significant correlations in species richness of different taxa across different land-use systems (birds and butterflies [Blair 1999]; birds, trees, butterflies, and dung beetles [Schulze et al. 2004]), most studies agree with our findings that different animal taxa are not closely correlated (Flather et al. 1997, Lawton et al. 1998, Burel et al. 2004), consistent with differences in the way that individual taxa and species perceive and use different vegetation types and landscapes. Consequently, unless there is evidence to the contrary for a particular landscape, it is best to assume that no animal taxa serve as adequate indicators of others.

Second, because different animal taxa are favored by different forms of tree cover, conservation efforts focused on specific taxa may need to target the conservation of specific types of tree cover within the agricultural landscape. In Rivas, for example, the retention of linear tree cover in the form of riparian forests and live fences appears particularly important for bat conservation, while areas of high tree cover are important for bird conservation. Further research would be required to determine how general the patterns observed in Rivas are for tropical agricultural landscapes, but some site specificity is anticipated, associated with the particular characteristics of the tree cover types found at different sites, as well as the composition and structure of different landscapes (Steffan-Dewenter 2002, Bergman et al. 2004, Burel et al. 2004).

Third, it is clear from the present study that maintaining a diversity of forms of tree cover in the agricultural matrix is important for maintaining diversity among and within animal taxa. Heterogeneity of vegetation on farms is emerging as a key factor for animal conservation within agricultural landscapes both in the tropics (e.g., Estrada et al. 1997, Harvey et al. 2004) and in temperature regions (e.g., Weibull et al. 2000, Benton et al. 2003, Wilson et al. 2005). Farmers, however, make frequent alterations to tree cover on their farms (e.g., Arnold and Dewees 1998, Villanueva et al. 2003) in ways that may have profound impacts on the conservation value of the agricultural landscape as a whole (Tscharntke et al. 2005). For example, gradual shifts from the more forest-like tree cover types, such as riparian and secondary forests, to more open forms of tree cover, such as dispersed trees in pastures, would be likely to reduce the animal diversity within a landscape. Even small changes, such as the reduction or increase of tree densities within pastures, or a change in the diversity of tree species within them, may lead to profound changes in bird species richness and composition. Consequently, any efforts to actively manage the tree cover within agricultural landscapes need to be closely coordinated with farmers to ensure that a diversity of tree cover is maintained over sufficiently large spatial and temporal scales.

There is a clear need for conservation organizations working in the neotropics to recognize the importance of maintaining and, where necessary, restoring or recreating, a diversity of tree cover within agricultural landscapes. Given the generally high levels of animal diversity in forest-like forms of tree cover, particular emphasis should be placed on conserving the remaining riparian and secondary forests, and protecting them from degradation by cattle incursion, fire, and extraction of firewood and timber. As found in other studies (e.g., Fischer and Lindenmayer 2002*c*), even small patches of forest and narrow riparian strips hold considerable value for conservation efforts and merit inclusion in conservation plans. There are also clear conservation gains possible through adopting strategies and incentives that encourage farmers to make marginal enhancements to tree cover in their fields, such as increases in the density of dispersed trees in pastures, the number of live fences along field boundaries, and the tree diversity within them. These are all incremental changes that are compatible with agricultural production (Gordon et al. 2003, Harvey et al. 2005), and hence readily adoptable by farmers.

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