

Effects of farm and landscape management on bird and butterfly conservation in western Honduras

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Abstract. Previous research has indicated that a substantial portion of native flora and fauna may persist in agricultural mosaics in the Neotropics. However, understanding the relative importance of different habitat factors and management practices at different scales for sustaining this biodiversity has proven somewhat elusive. In addition, most such research has taken place in only a few fairly well-studied landscapes, thus limiting our ability to infer broader patterns that might be transferred to unstudied locales. This study expands the geographic breadth of prior research by evaluating bird and butterfly assemblages in an agricultural landscape in the Río Copán watershed of western Honduras. The study also provides a systematic assessment of the relative influence of categorical and continuous habitat variables across a range of scales likely to be significant for birds and butterflies. Overall, we recorded 145 tree species, 139 bird species, and 119 butterfly species. Birds and butterflies displayed contrasting responses to land cover: birds were most strongly associated with dense vegetation in broadleaf forests, forest fallows, shade-grown coffee farms, and live fences, while butterflies were most abundant in live fences, pastures, and riparian forests. Bird assemblages were heavily skewed toward common and non-forest-dependent species, likely due to the young age and high disturbance level of forest plots. In contrast, butterfly assemblages contained a substantial proportion of forest-dependent species, which were observed in forests as well as pastures and live fences. Contrary to expectations, categorical land cover descriptors were more effective at explaining faunal assemblage patterns than continuous habitat descriptors related to vegetation and landscape context. In addition, plot scale (25–100 m) habitat features had a greater influence on faunal assemblages than did neighborhood scale (200–3000 m) landscape composition or structure, although differences in management intensity at the scale of the entire watershed (5–20 km) also exerted a strong influence on conservation outcomes.

Key words: agriculture; agroforestry; biodiversity conservation; birds; butterflies; ecoagriculture; Honduras; land cover; landscape ecology; silvopasture.

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INTRODUCTION

In recent years, conservationists have placed increasing emphasis on the importance of con-

serving biodiversity and ecosystem services outside of protected areas, including in agricultural landscapes (Harvey et al. 2008a, Gardner et al. 2009). Such efforts are recognized as critical

for buffering and connecting nature reserves, maintaining populations of native species, and increasing the resilience of rural regions to climate change and other disturbances (Bennett 2003, Fischer and Lindenmayer 2007, WRI 2008). Considerable evidence also suggests that conservation in agricultural regions can help sustain economically important ecosystem services, including crop pollination, pest control, and water purification (Perfecto et al. 2004, Ricketts et al. 2004, 2008, Zhang et al. 2007).

Advocates of wildlife-friendly farming and ecoagriculture suggest that agriculture conducted at moderate intensity, with deliberate efforts to manage wild biodiversity and agrobiodiversity for multiple benefits, can play a substantial role in global conservation efforts (Vandermeer and Perfecto 2007, Scherr and McNeely 2008). Such strategies may be particularly appropriate on hilly or marginal lands not suitable for large-scale monoculture agriculture, and in areas where rural populations depend on small-scale farming for their livelihoods (McNeely and Scherr 2003).

The potential for wildlife-friendly farming may be especially great in Central America (Harvey et al. 2008a). This region experienced heavy deforestation from 1950–1990, driven in part by policies and market forces that encouraged conversion of forest to pasture for beef production (Kaimowitz 1996). Although deforestation has now slowed in most parts of Central America, its legacy remains: pastures occupy 27% of the region's land base, more than three times the area occupied by all other agricultural production systems combined (FAOSTAT 2004). Decades later, these pasture-dominated landscapes are in various states of degradation or regeneration, with many of them consisting of fine-grained mosaics of pasture, annual and perennial crops, fallows, and patches of second-growth forest. These landscapes also support rural indigenous and Mestizo populations, many of them living in poverty on small plots of land. In this context, wildlife-friendly approaches to livestock production, such as silvopastoralism, have been advocated as win-win strategies that can simultaneously increase farmer incomes and improve the conservation value of the agricultural matrix (Dagang and Nair 2003, Pagiola et al. 2004). Production of coffee and other peren-

nial crops in structurally diverse agroforestry systems has also been promoted as a way to conserve biodiversity while enabling small farmers to produce cash crops for global markets (Mas and Dietsch 2004).

A substantial body of research has examined the potential for wildlife-friendly farming in Central America by quantifying plant and animal occurrences within various farming systems and relating these distributions to variables such as agricultural management, land cover, and landscape context. Most of these studies, however, have taken place in only a few fairly well-studied landscapes. For example, more than a decade of research in a rural landscape in Coto Brus, Costa Rica has documented the area's substantial—albeit modified—assemblage of native biodiversity (Daily and Ehrlich 1995, Daily et al. 2001, 2003, Hughes et al. 2002, Horner-Devine et al. 2003, Luck and Daily 2003, Mayfield and Daily 2005, Lindell et al. 2006, Ranganathan et al. 2007, Sekercioglu et al. 2007). Other research hotspots have included coffee agroecosystems in Chiapas, Mexico (Perfecto et al. 2003), mosaics of lowland rainforest and various cropping systems in Los Tuxtlas, Veracruz, Mexico (Estrada et al. 1993, 1994, 1997, 1998, 2000, Estrada and Coates-Estrada 2001, 2002), cacao agroforests and competing land uses in Talamanca, Costa Rica (Reitsma et al. 2001, Suatunce et al. 2003, Harvey et al. 2006a), and several pasture-dominated landscapes in Costa Rica and Nicaragua (Harvey et al. 2005, Harvey et al. 2006b, Pérez et al. 2006, Medina et al. 2007). This collective body of research has provided important evidence on the contributions and limitations of wildlife-friendly farming as a conservation strategy in Central America. However, the limited geographic range of the research to date—particularly the strong focus on Costa Rica—hinders the ability of scientists and policy makers to derive valid understandings of broader patterns or to transfer knowledge to unstudied locales (Gardner et al. 2009).

This study expands the geographic breadth of research on the conservation potential of Central American agricultural mosaics by evaluating the effects of agroecosystem management and landscape context on bird and butterfly assemblages in an agricultural landscape in western Honduras. In many ways, Honduras epitomizes the

challenge of reconciling conservation and rural livelihoods in Central America. With a deforestation rate of 3.1% per year, Honduras has, by far, the highest proportional and absolute rates of forest loss of any Central American nation (FAO 2006). Honduras also has the region's highest proportion of rural people living in poverty (75%) and extreme poverty (63%)—three times the rates in Costa Rica (IFAD 2009). These statistics underscore the importance of advancing both conservation and development objectives in the nation's rural areas. In addition, recent catastrophic destruction caused by Hurricane Mitch and other storms has highlighted the vulnerability of many current land management approaches and the importance of ecosystem-based management to improve the resistance and resilience of rural landscapes and livelihoods to such events.

In addition to expanding the geographic scope of research on conservation in agricultural mosaics, this study seeks to provide a deeper understanding of the environmental controls on conservation outcomes by evaluating the influence of a wide range of potentially relevant site- and landscape-scale habitat factors. The general hypothesis underlying this approach is that bird and butterfly distributions are a function of habitat conditions created by human management decisions, which in turn influence the fitness of individuals and the viability of populations. However, understanding the relative importance of different habitat factors at different scales is a significant challenge, and has proved somewhat elusive in prior research. Many studies have compared conservation outcomes in different land covers or agricultural management regimes, but such categories often contain significant internal variability with respect to ecologically relevant habitat characteristics, thus confounding interpretation (Ferrier 2002). Other studies have evaluated the effect of continuous habitat gradients—such as tree density or distance from source habitats—which offer the theoretical advantage of better representing the range of habitat variability (McGarigal and Cushman 2005, McGarigal et al. 2009). However, most prior studies have considered only a small number of habitat co-variables without evaluating other habitat characteristics that might allow for cross-study comparisons or the testing of alter-

native hypotheses. To address these limitations, this study takes a systematic approach to evaluating the relative influence of both categorical and continuous habitat factors across a range of scales likely to be significant for birds and butterflies.

Drawing on findings from previous studies in nearby countries (cited above), we hypothesized that higher levels of tree cover and tree diversity at the plot scale as well as greater forest and tree cover in the surrounding landscape would correspond to higher bird and butterfly abundance and species density. In addition, for reasons stated above, we hypothesized that continuous habitat descriptors related to tree cover, landscape composition, and landscape structure would be more effective than categorical land cover descriptors at explaining bird and butterfly distributions.

METHODS

Study site

We conducted this study in the Río Copán watershed in the Copán Department of western Honduras (14°47' to 14°54' N, 89°2' to 89°10' W) (Fig. 1). The watershed comprises an area of 598 km² with elevations ranging from 600 to 1,700 m above sea level. To avoid the confounding effects of elevation, however, we confined this study to the lower, central part of the watershed between 600 and 1,200 m elevation. This zone includes many of the more heavily impacted agricultural portions of the watershed. Local rainfall averages 1,600 mm per year, with a distinct dry season from December to April and a rainy season from May through November. Average daily temperature in the study area is approximately 24°C.

Biogeographically, the Río Copán watershed is noteworthy in that it occupies a zone of convergence between the Atlantic and Pacific slopes, and contains diverse native ecosystems including humid broadleaf forest, pine/oak forest, and pre-montane moist forest (Sanfiorenzo 2008). The resulting vegetational diversity supports diverse animal assemblages, including at least 382 bird species recorded in the watershed (R. Gallardo, *unpublished data*). In addition, Río Copán is a tributary of the Motagua River, which is considered a global conservation priority in its own right and because the quality of its water

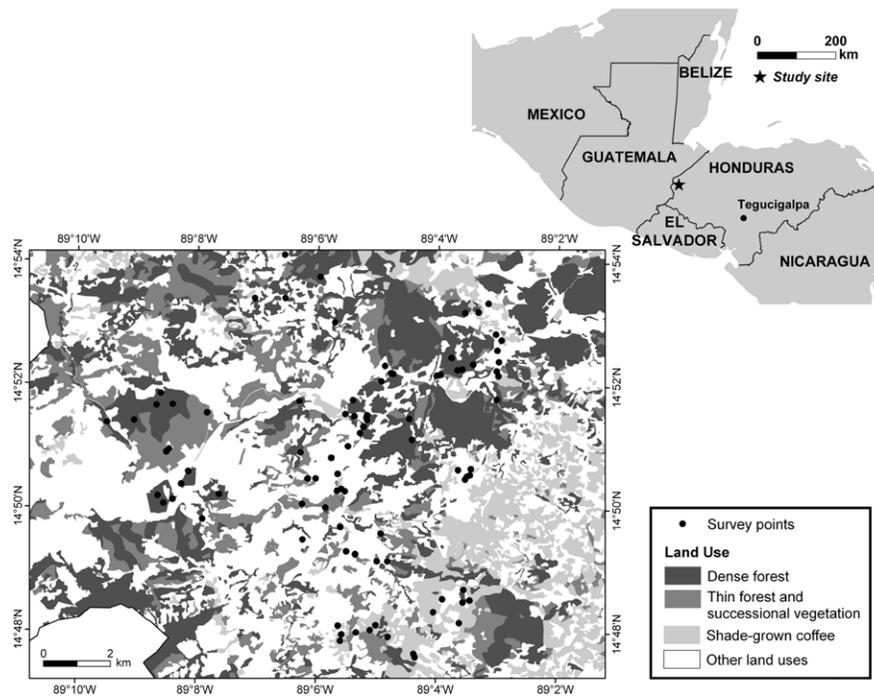


Fig. 1. Map of the study landscape and its geographic context.

strongly affects the health of the Mesoamerican Reef where it empties into the Caribbean Sea in eastern Guatemala (TNC 2007).

The Río Copán watershed consists of a fine-grained mosaic of pasture, small agricultural plots, forest, and other habitats. The majority of the land is occupied by agriculture, including pasture (40%), shade-grown coffee (24%), and annual crops (1%). About one-fourth of the watershed is forest, including pine/oak forest (7%), broadleaf riparian forest (6%), broadleaf upland forest (8%), and mixed forest (3%). Eight percent of the watershed is in forest fallow (successional vegetation), while 3% consists of urban and other land covers (Sanfiorenzo 2008). The watershed contains no nationally or internationally recognized protected areas. The largest patches of broadleaf forest (several patches of approximately 500 ha each) are in the upper reaches of the watershed, outside of the study area. In the central portion of the watershed evaluated in this study, the largest patch of broadleaf forest is 110 ha, while the largest patches of pine forest are 200, 290, and 360 ha. The study area contains essentially no primary forest, and its second-growth forest is young

(typically 15–25 years old) and often heavily impacted by cattle grazing and firewood and timber extraction. Patches of regenerating vegetation are often managed as rotational fallows and converted back into pasture or cropland before they reach the stature of forests.

The Copán Department, which encompasses the Río Copán watershed, has a population density of 100 persons per km², one of the densest in rural Honduras. Land ownership in the watershed is moderately fragmented, with many small (<1–20 ha) and medium (20–60 ha) farms and a few large farms and cattle and coffee estates. Consistent with other regions of Honduras (Barrance et al. 2003) and Central America (Harvey and Haber 1999, Harvey et al. 2008b), farmers in the Río Copán watershed maintain a significant quantity and diversity of trees on their farms and report that these trees provide a variety of important goods including firewood, fence posts, and lumber (Sánchez 2006).

Biodiversity sampling

We conducted field sampling at 79 points stratified across eight land cover types (Table 1). We sampled ten points per land cover, except live

Table 1. Descriptions of the eight sampled land cover types.

Land Cover	Description
Broadleaf forest	Second-growth broadleaf forest with a closed canopy
Pine forest	Pine or pine/oak forest
Riparian forest	Forest bordering perennial rivers or streams
Successional vegetation	Abandoned or fallowed agricultural land containing shrubby or woody vegetation approximately 3–8 years old
Shade-grown coffee	Coffee plantation with a tree overstory, typically containing multiple species
Pasture with high tree density	Pasture with 15–30% tree canopy cover
Pasture with low tree density	Pasture with 5–15% tree canopy cover
Live fence	Continuous row of trees separating pastures or farms, and composed of multiple tree species and strata

fences, for which only nine suitable sample points could be identified. Within each land cover, five of the sample points were located in zones of low tree cover in the surrounding area (as defined by total tree cover within 400 m of the sample point) while the remaining points were located in zones of high surrounding tree cover. Except in a few instances where logistical constraints dictated otherwise, we separated points of any given land cover by at least 400 m, and all sample points by at least 200 m. In addition, to minimize the confounding influence of edge effect, all sample points were located at least 40 m from boundaries between land cover types. We sampled all 79 points for birds and vegetation, and a subset of these points for butterflies. All field sampling protocols—as well as the landscape context analyses described in the next subsection—were spatially oriented around these 79 points (Fig. 2).

At each point, we established a 0.1 ha vegetation quadrat within which we recorded the species name and diameter at breast height (dbh; 1.4 m above ground) of all trees ≥ 5 cm dbh. Quadrats for most of the land cover types consisted of a 20×50 m plot situated around the central sampling point. These standard dimensions were modified for riparian forests and live fences because of their linear form. Riparian forest plots consisted of a 10×100 m quadrat of riparian vegetation along one side of the stream. Live fence plots consisted of a 5×200 m fence segment. D.M.S. conducted the vegetation sampling in July 2008.

Bird sampling was conducted using a standard point count method in which all birds heard or seen within 25 m of the central sampling point during a 10-min sampling period were recorded (Ralph et al. 1995). Point counts were conducted

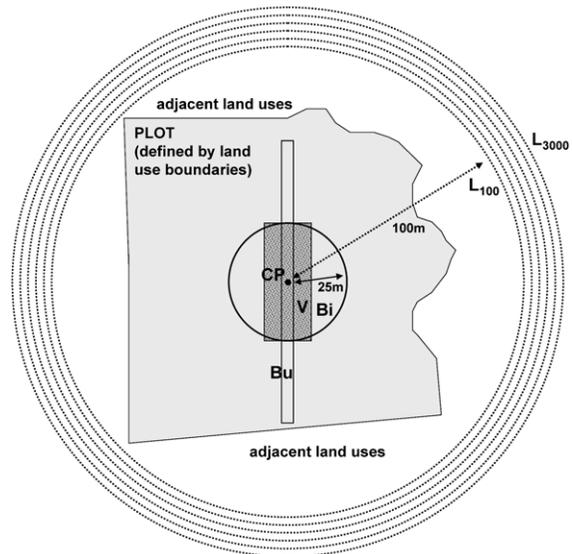


Fig. 2. Schematic diagram of the sampling protocol. The central point (CP) is the point of orientation for all sampling, including a 20×50 m vegetation quadrat (V; shaded dark grey), a 25 m radius bird point count (Bi), and a 120×5 m butterfly transect (Bu). For each point, all these samples are contained within a single land cover plot. Surrounding the central point, we evaluated metrics of landscape composition and structure for six concentric radii ranging from 100 to 3000 m (L_{100} through L_{3000} ; depicted by dotted lines and not drawn to scale).

from 06:00 to 10:00 only in good weather conditions without heavy rain or strong winds. Upon arriving at each sampling location, the field technician waited five min prior to the start of the counting period to minimize the effect of any initial flushing of birds. Point counts were repeated six times per point from November 2008 through February 2009 for a total sampling

effort of one hr per location, 10 hr per land cover, and 79 hr for the entire study. Unfamiliar birds were identified by using a field guide (Howell and Webb 1995) or by comparing reference bird songs (R. Gallardo, *personal communication*) to the audio recordings that the field technician created during each sampling period. Birds observed flying high above the plot were excluded from the analysis when they were judged to be unassociated with the habitat from which they were observed.

We sampled butterflies at 36 of the 79 bird and vegetation points. These points included six sampling locations within each of the following six land cover types: broadleaf forest, riparian forest, successional vegetation, pasture with high tree density, pasture with low tree density, and live fences. D.E.T. and two field assistants sampled butterflies by establishing a 120 m-long transect through the central sampling point at each location (Fig. 2). Each transect was surveyed by walking its length at a slow, constant pace for 45 min and recording all adult butterflies observed within 2.5 m to either side of the transect. Transects were visited between 08:00 and 16:00 on days with good weather. Each transect was surveyed six times between September 2008 and March 2009 for a total sampling effort of 4.5 hr per location, 27 hr per land cover, and 162 hr for the entire study. To avoid time-of-day biases, we alternated morning and afternoon visits at each sampling location. Individuals that could not be identified by sight were captured by net for later identification. Field guides, keys, and

illustrations were used to identify unfamiliar species (DeVries 1987, 1997).

Landscape analysis

To assess the influence of landscape context on faunal assemblages, we quantified continuous variables related to landscape composition and structure at multiple scales defined by concentric radii surrounding each sample point (Fig. 2). We selected a set of six landscape metrics according to following criteria: (1) the metrics follow directly from the hypotheses posed earlier, in the Introduction, (2) they have a strong ecological relation to the habitat and life history requirements of Neotropical birds and butterflies, and (3) they have performed well in prior studies of this type (Table 2). By circumscribing the set of landscape metrics and tying them to specific hypotheses, we were able to reduce the degree of multicollinearity often found among sets of landscape metrics and minimize the risk of drawing spurious conclusions from metrics with a weak theoretical or empirical basis (Hargis et al. 1998, Tischendorf 2001, Li and Wu 2004).

Three of the six landscape metrics were derived from a land cover map that classified the watershed into 14 discrete cover types based on visual interpretation of a 1 m resolution IKONOS satellite image acquired during February 2007 (Sanfiorenzo 2008). The initial image classification was field verified and corrected as necessary by spending 350 hr in the field visiting at least 50 plots of each land cover, with additional plots for difficult-to-distinguish cover

Table 2. Metrics of landscape composition and structure calculated for each concentric radius of analysis surrounding each sample point.

Metric	Type	Data source	Description
Percent forest	Composition	Land cover map	Percentage of land consisting of closed-canopy broadleaf, pine/oak, or riparian forest
Percent tree cover	Composition	Land cover map	Percentage of land with at least 15% tree cover (including all forest types, shade-grown coffee, successional vegetation, and pasture with high tree density)
Contrast-weighted edge density	Structure	Land cover map	FRAGSTATS metric that measures the length of edge between adjacent patches, per unit area, weighted by the degree of dissimilarity between adjacent patches (McGarigal et al. 2002)
NDVI	Composition	Multi-spectral imagery	Mean NDVI value within the radius of analysis
Tasseled-cap brightness	Composition	Multi-spectral imagery	Mean tasseled-cap brightness value within the radius of analysis
Tasseled-cap wetness	Composition	Multi-spectral imagery	Mean tasseled-cap wetness value within the radius of analysis

types. The minimum mapping unit was 0.5 ha. Based on this map, we used the software program FRAGSTATS (version 3.3; McGarigal et al. 2002) to calculate the percentages of the land within each radius surrounding each sample point that were forested and tree-covered (see Table 2 for further explanation of these categories). In addition, we calculated contrast-weighted edge density to quantify graininess and habitat heterogeneity around each sample point.

The remaining three landscape metrics were composition measures derived from a 15 m resolution multi-spectral ASTER image acquired during February 2007. These metrics included the Normalized Difference Vegetation Index (NDVI), tasseled-cap wetness, and tasseled-cap brightness. NDVI uses the red and near-infrared spectral bands to evaluate the level of green vegetation in an area, and has been used as a proxy for vegetation characteristics such as leaf area index (Liang 2004, Pettorelli et al. 2005). The Kauth-Thomas transformation, known more commonly as the tasseled-cap transformation, scales down the visible, near-infrared, and short-wave infrared bands of multi-spectral imagery (a total of nine bands in the case of ASTER imagery) to three axes of variation corresponding to the ground properties of brightness, wetness, and greenness (Kauth and Thomas 1976, Crist and Kauth 1986, Yarbrough et al. 2005). The tasseled-cap transformation has been used successfully to monitor vegetation properties and, in at least one instance, as a proxy for Neotropical bird assemblages (Ranganathan et al. 2007). Since the tasseled-cap greenness metric is closely related to NDVI, only brightness and wetness were used in this study. A detailed description of the method for processing and interpreting the ASTER imagery to calculate these indices is provided elsewhere (Milder 2010).

We calculated landscape metrics for six concentric radii (100, 200, 400, 800, 1500 and 3000 m) surrounding each sample point. To test for spatial autocorrelation in the data, we generated spatial correlograms (Moran's I; Cliff and Ord 1973) for model residuals across a range of distances from 250 m to 10 km. This analysis revealed no systematic patterns of spatial autocorrelation that would lead to a violation of the assumption of independent errors in our statistical tests (Wagner and Fortin 2005).

Data analysis

We analyzed the raw field data to characterize plant and animal assemblages at each sampling point. For vegetation, we calculated tree abundance, tree species density (i.e., species per quadrat, sensu Whittaker et al. 2001), and total basal area (as derived from dbh measurements). For birds and butterflies, we calculated abundance and species density. To attain normally distributed data and avoid skewed results due to large groups of flocking birds observed at some points, we natural log (ln)-transformed all faunal abundance data. Given the timing of our bird surveys during the boreal winter, migratory species were an important part of the observed bird fauna. We analyzed migratory and resident birds both separately and together to evaluate whether there were important differences between these two groups of species. We also partitioned the bird and butterfly species observed in each land cover type according to their degree of forest dependence, as classified by previous studies (for birds: Stiles [1985] supplemented by natural history information from Stiles and Skutch [1989] and Howell and Webb [1995]; for butterflies: DeVries [1987, 1997]).

We used one-way ANOVA to evaluate differences in bird and butterfly species density and ln-adjusted abundance among different land cover types (all of these variables met the assumptions for ANOVA). Tukey's Honestly Significant Difference (HSD) test was used to evaluate the statistical significance of these differences. To evaluate differences in tree, bird, and butterfly species composition among land cover types, we used the software program InfoStat (Grupo InfoStat, Córdoba, Argentina) to conduct non-metric multidimensional scaling and the program PAST (version 2.01; Hammer et al. 2001) to conduct ANOSIM on Bray-Curtis similarity matrices.

We conducted simple linear regression to evaluate the relationships between faunal assemblage characteristics and each of the continuous vegetation and landscape context variables. Because many of the landscape context variables were significantly correlated with plot-scale land cover, we used ANCOVA to evaluate the significance of each landscape context variable at each scale of analysis once the effect of land cover was considered.

Finally, we used multiple regression to identify the most important combinations of habitat descriptors for explaining each faunal assemblage response variable. We began this process by using stepwise regression to identify the model that most fully yet parsimoniously explained the variability in the response variable at each scale and for each combination of categorical, plot-scale continuous, and landscape-scale continuous predictor variables. We used four criteria to select the best model in each category: (1) the model had the lowest, or nearly the lowest, Akaike information criterion (AIC) value (Burnham and Anderson 2002), (2) the model explained the most, or nearly the most, variability in the response variable, (3) individual variables in the model were significant at $\alpha = 0.10$ or better, and (4) variables in the model had little multicollinearity ($R < 0.40$). In cases where all four criteria could not be met, we selected the model that provided the best overall compromise for satisfying these considerations. We then used these same criteria to compare the best models for each bird and butterfly assemblage characteristic. Except as noted otherwise, all statistical analyses were conducted in JMP (version 8.0; SAS Institute, Cary, North Carolina, USA).

RESULTS

Tree, bird, and butterfly abundance and species richness

We observed a total of 2211 trees of 145 species, 3939 birds of 139 species, and 5287 butterflies of 119 species (Table 3). Estimated total species richness across all sample plots, based on species accumulation curves using the Chao1 estimator (Colwell 2005), was 159 for trees, 155 for birds, and 143 for butterflies. Because species accumulation curves did not level off for some land cover types, estimated species richness by land cover is not reported here and observed species richness by land cover should be interpreted cautiously.

The five most common tree species were *Pinus oocarpa*, *Gliricidia sepium*, *Quercus sapotifolia*, *Guazuma ulmifolia*, and *Bursera simaruba*. Patterns of tree abundance, species density, and basal area were significantly different among the eight land cover types evaluated (ANOVA, $P < 0.0001$ for all three variables) but these three factors did not

co-vary consistently (Table 3). Across all land cover types, mean tree species density per plot was only a small fraction of total observed species richness in the study area, indicating a high level of beta diversity across the landscape (Table 3).

The five most common bird species were *Dives dives*, *Dendroica virens*, *Psarocolius wagleri*, *Dendroica magnolia*, and *Saltator atriceps*. The five most common butterfly species were *Hermeuptychia hermes*, *Anartia fatima*, *Eurema daira*, *Eurema nise*, and *Mechanitis polymnia*. Bird species density was strongly correlated with bird abundance at the plot level ($R = 0.86$). Butterfly species density and abundance were also well correlated ($R = 0.67$), although this relationship did not hold true in pasture with low tree density, which had among the highest butterfly abundances but the lowest species density. Measures of bird species density and abundance were uncorrelated with measures of butterfly species density and abundance ($R = 0.07$ and 0.01 , $P = 0.70$ and 0.94 for species density and abundance, respectively).

Patterns of diversity associated with different land covers

Land cover was a significant predictor of abundance and species density for both birds and butterflies (ANOVA results for bird species density: $F_{(7,71)} = 6.57$, $P < 0.0001$; bird abundance: $F_{(7,71)} = 5.78$, $P < 0.0001$; butterfly species density: $F_{(5,30)} = 3.24$, $P = 0.02$; butterfly abundance: $F_{(5,30)} = 5.90$, $P = 0.0007$). Mean bird abundance and species density were highest in successional vegetation and somewhat lower in broadleaf forest, riparian forest, shade coffee, and live fences (Fig. 3a). Pine forest and pasture supported more depauperate bird assemblages. Surprisingly, pasture with low tree density had more bird individuals and species per plot, on average, than pasture with high tree density, although these differences were not statistically significant.

The observed bird species were consistently partitioned between residents (about 65–70%) and migrants (about 30–35%) across all land cover types (Table 3). Bird abundance was partitioned between residents and migrants in a similar way (about 70%/30%) for most habitat types, although pine forest and shade-grown coffee had a proportionally higher abundance of

Table 3. Total observed abundance and species richness of trees, resident birds, migratory birds, all birds, and all butterflies in each of the surveyed land cover types.

Species assemblage characteristic	Land cover								Total
	BF	PF	RF	SV	SC	PH	PL	LF	
Trees									
Individuals	362	219	412	348	251	160	70	389	2211
Species	72	5	75	53	29	17	17	57	145
Mean species per plot	13.6	1.6	17.1	11.1	5.3	3.6	2.6	13.3	8.5
Mean basal area per plot (m ²)	1.72	2.52	2.75	0.58	0.85	0.74	0.23	2.08	1.42
Resident birds									
Individuals	340	170	261	490	253	264	274	644	2696
Percent of total	70%	49%	62%	73%	50%	70%	74%	86%	68%
Species	41	28	46	49	44	32	44	51	96
Percent of total	65%	70%	68%	68%	72%	65%	68%	71%	69%
Migratory birds									
Individuals	144	180	161	184	257	111	98	108	1243
Percent of total	30%	51%	38%	27%	50%	30%	26%	14%	32%
Species	22	12	22	23	17	17	21	21	43
Percent of total	35%	30%	32%	32%	28%	35%	32%	29%	31%
All birds									
Individuals	484	350	422	674	510	375	372	752	3939
Species	63	40	68	72	61	49	65	72	139
All butterflies									
Individuals	527	§	1079	572	§	944	1064	1101	5287
Species	58	§	77	56	§	59	43	70	119

Note: Abbreviations are as follows: BF = broadleaf forest; PF = pine forest; RF = riparian forest; SV = successional vegetation; SC = shade-grown coffee; PH = pasture with high tree density; PL = pasture with low tree density; LF = live fence.
§ Not sampled.

migrant birds (about 50% of all observed birds in these habitats) while live fences had a proportionally lower abundance of migrants (only 14% of the total). Patterns of bird species density and abundance by land cover were quite similar for migratory species, resident species, and all species together. In addition, ANOSIM revealed similar patterns of species composition (i.e., degree of similarity in the bird fauna among pairs of habitat types) for migratory species, resident species, and all species together (Table 4).

Mean butterfly abundance and species density were highest in the two linear land cover types: riparian forest and live fences (Fig. 3b). Slightly lower mean abundances were found in pasture, while successional vegetation and broadleaf forest had substantially lower mean abundances. Mean species density was intermediate in broadleaf forest, successional vegetation, and pasture with high tree density, and slightly lower in pasture with low tree density. None of the pairwise comparisons of butterfly species density among land cover types were statistically significant (Tukey's HSD test, $\alpha = 0.05$), although the model as a whole was significant.

Very few forest-dependent bird species were

observed at the sample plots, even though many such species have been recorded in the Río Copán watershed. Not surprisingly, broadleaf forest had the highest proportion of forest-affiliated bird species, followed by pine forest, shade-grown coffee, and successional vegetation (Fig. 4a). Live fences had the lowest proportion of forest-affiliated bird species, although they were among the most species rich land cover. In contrast to the low proportion of forest-affiliated bird species, 42% of the 119 observed butterfly species are considered to be forest-dependent (Fig. 4b). The proportion of forest-dependent butterfly species was highest in the most densely forested and tree covered plots. Contrary to the pattern observed for birds, live fences supported an intermediate number and percentage of forest-dependent butterfly species. Distinctions in butterfly assemblage characteristics among land cover types were much stronger for forest-dependent species (ANOVA, $F_{(5,30)} = 12.08$, $R^2 = 0.67$ for species density; $F_{(5,30)} = 13.41$, $R^2 = 0.69$ for abundance) than for all species (ANOVA, $F_{(5,30)} = 3.24$, $R^2 = 0.35$ for species density; $F_{(5,30)} = 5.90$, $R^2 = 0.50$ for abundance).

Species composition analysis revealed significant clustering by habitat type for trees (Fig. 5a;

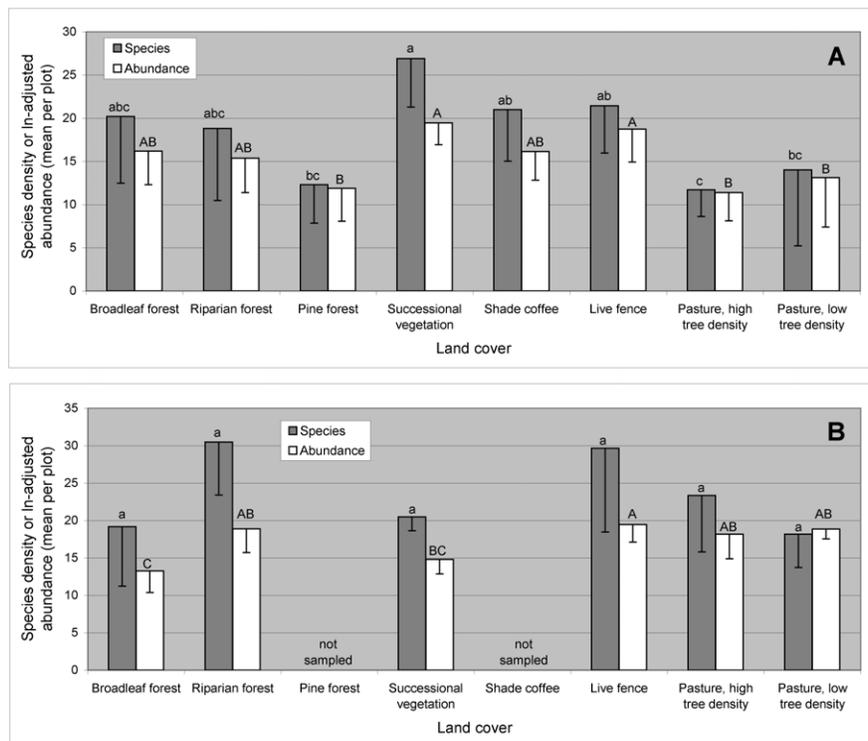


Fig. 3. ANOVA of bird (a) and butterfly (b) mean species density and mean In-adjusted abundance per plot. Error bars indicate one standard deviation. Different letters above each data series (lowercase for species density, uppercase for abundance) denote significant differences between pairs of land covers (Tukey's HSD test, $P < 0.05$).

ANOSIM global $R = 0.58$, $P < 0.0001$), birds (Fig. 5b; ANOSIM global $R = 0.37$, $P < 0.0001$), and butterflies (Fig. 5c; ANOSIM global $R = 0.41$, $P < 0.0001$). For trees, the pine forests exhibited substantially different vegetation composition than all other land covers with the exception of pastures with low tree density, which contained relicts from pre-conversion pine forest (Table 4). Broadleaf forest and successional vegetation were compositionally quite similar, while shade-grown coffee differed significantly from both of these. For birds, pine forest had the most distinct species assemblage, while broadleaf forest, riparian forest, successional vegetation, and shade-grown coffee were all similar to one another in species composition (ANOSIM, $R < 0.43$ for all such pairwise combinations; Table 4). For butterflies, species composition in broadleaf forests was distinct from all other habitats except riparian forest. There were few strong distinctions among the other habitat types (ANOSIM, R

< 0.51 for all such pairwise combinations; Table 4).

Effects of vegetation and landscape context on bird and butterfly assemblages

Bird abundance and species density were significantly positively correlated with plot-scale tree abundance and tree species density, but uncorrelated with total basal area (Table 5). None of the vegetation variables were significant predictors of species density or abundance of forest-affiliated birds. This null result likely reflects the minor presence of forest-affiliated birds at the study plots, which yielded an undetectably weak signal in this analysis. Butterfly species density was significantly positively correlated with tree species density and total basal area, while butterfly abundance was not significantly related to any of the vegetation parameters. Stronger relationships ($R > 0.50$) were observed between forest-affiliated butter-

Table 4. ANOSIM results for species composition by land cover type for trees, resident birds, migratory birds, all birds, and all butterflies.

Land cover	PF	RF	BF	SC	LF	PH	PL	SV
Trees								
PF	...	0	0	0	0	0	0	0.0002
RF	0.99	...	0.057	0	0	0	0	0.0001
BF	0.96	0.10	...	0	0	0	0	0.029
SC	0.76	0.58	0.69	...	0.0002	0	0.0027	0
LF	0.99	0.47	0.38	0.48	...	0	0.0007	0.0002
PH	0.74	0.87	0.82	0.66	0.59	...	0.0005	0
PL	0.52	0.61	0.50	0.35	0.49	0.34	...	0.0001
SV	0.96	0.33	0.13	0.67	0.39	0.64	0.56	...
Resident birds								
PF	...	0	0	0	0	0.018	0.090	0.0001
RF	0.54	...	0.62	0.073	0.0007	0.042	0.0059	0.19
BF	0.61	-0.03	...	0.27	0.0001	0	0	0.85
SC	0.38	0.10	0.04	...	0.0002	0.069	0.037	0.014
LF	0.49	0.32	0.50	0.37	...	0.0011	0.11	0
PH	0.15	0.13	0.39	0.10	0.24	...	0.61	0
PL	0.088	0.18	0.32	0.11	0.08	-0.02	...	0.0003
SV	0.64	0.05	-0.07	0.17	0.49	0.41	0.28	...
Migratory birds								
PF	...	0	0	0	0.0006	0.0008	0.0037	0
RF	0.70	...	0.0083	0	0.0014	0.0005	0.0001	0.0029
BF	0.70	0.19	...	0.0006	0.0009	0.0003	0.0001	0.30
SC	0.63	0.46	0.26	...	0.0001	0.0024	0.0001	0.027
LF	0.43	0.35	0.38	0.56	...	0.0013	0.004	0.0003
PH	0.23	0.37	0.25	0.18	0.30	...	0.39	0.0009
PL	0.23	0.44	0.43	0.37	0.26	0.01	...	0.0017
SV	0.68	0.26	0.02	0.15	0.42	0.24	0.33	...
All birds								
PF	...	0	0	0	0	0.0001	0.0087	0.0001
RF	0.79	...	0.080	0	0.0001	0.0005	0.0002	0.014
BF	0.82	0.10	...	0.004	0	0.0002	0	0.75
SC	0.69	0.43	0.24	...	0	0.0009	0	0.0005
LF	0.64	0.45	0.52	0.66	...	0.0007	0.010	0.0001
PH	0.29	0.35	0.35	0.20	0.38	...	0.75	0.0001
PL	0.21	0.40	0.45	0.31	0.21	-0.04	...	0.0005
SV	0.81	0.20	-0.05	0.32	0.53	0.44	0.38	...
All butterflies								
RF	...	0.082	0.0045	0.0053	0.002	0.050		
BF	0.23	...	0.0026	0.002	0.0024	0.0052		
LF	0.28	0.82	...	0.065	0.012	0.013		
PH	0.37	0.83	0.21	...	0.16	0.030		
PL	0.51	0.90	0.43	0.13	...	0.0046		
SV	0.23	0.65	0.38	0.24	0.46	...		

Notes: Numbers above the diagonal are *P* values (sequential Bonferroni significance); values <0.0001 are indicated as "0". Numbers below the diagonal are *R* values. Pairs of habitats that are highly distinct ($R > 0.65$) are indicated with boldface. Land cover type abbreviations are as in Table 3.

flies and vegetation characteristics (Table 5).

Within each land cover, sample points situated in a landscape context of low tree cover did not have significantly different bird or butterfly assemblage characteristics than those situated in a context of high tree cover (two-way ANOVA, $P > 0.10$ for landscape context, across all faunal response variables). Similarly, once the effect of plot-scale land cover was considered, almost none of the six continuous landscape metrics strongly or consistently explained patterns in

faunal response variables at any scale (ANCOVA, $\alpha = 0.05$). The only exception to this pattern was for tasseled-cap wetness, which was positively correlated with butterfly abundance for radii of 100, 200, and 400 m ($P < 0.05$).

Combinations of factors explaining patterns of bird and butterfly diversity

While few of the individual landscape metrics were significant predictors of faunal characteristics, taken together these metrics were signifi-

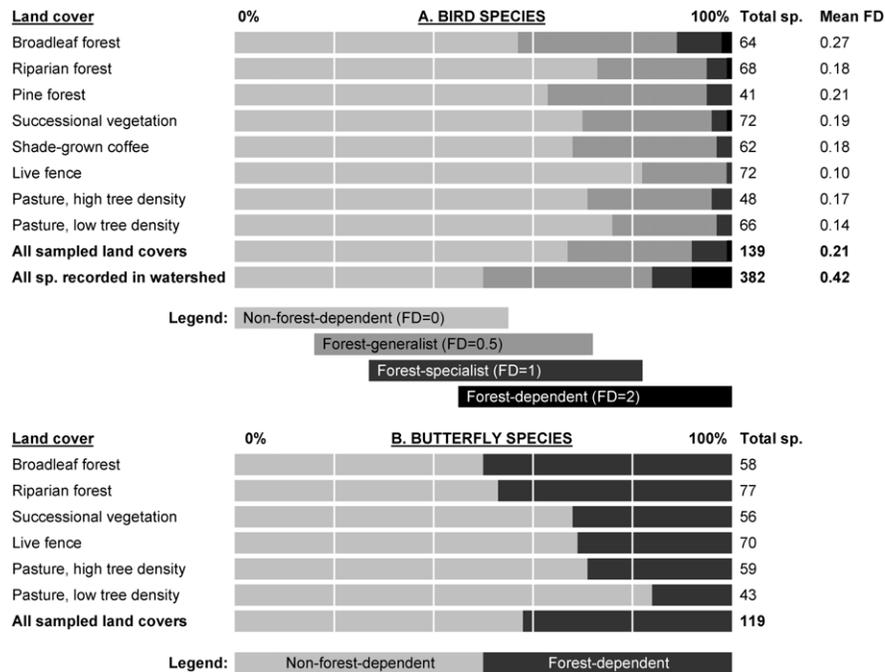


Fig. 4. Analysis of the bird (a) and butterfly (b) species observed in each land cover according to their degree of forest dependence. Bird forest dependent classifications are based on Stiles (1985): “non-forest-dependent” includes forest dependency classifications 2–3 and 3; “forest-generalist” corresponds to category 2; “forest-specialist” corresponds to classification 1–2; and “forest-dependent” corresponds to category 1. The “Mean FD” for each land cover is the mean of the forest dependence scores (indicated in the legend) for all bird species observed in that land cover.

cantly related to bird and butterfly community attributes (Table 6, part 4). However, for the most part, bird and butterfly responses were better explained by land cover than by landscape context, vegetation characteristics, or a combination of these (Table 6, comparison of part 1 to parts 2, 4, and 5). The best explanatory multivariate models for bird abundance, bird species density, and butterfly abundance included combinations of continuous and categorical habitat descriptors. The best model for butterfly species density included only continuous variables. For all response variables, the best explanatory models were those that included landscape context variables for the 100 m context zone, although in each instance one or more models containing landscape context variables from other radii were nearly as good. Overall, the best models explained between 36% and 64% of the variability in the bird and butterfly response variables (Table 6, parts 5 and 6).

The best model for each response variable included a different set of predictor variables (Table 7). Four of the candidate predictor variables (tree abundance, total basal area, contrast-weighted edge density, and NDVI) did not appear in any of the models.

DISCUSSION

Species assemblages in the agricultural mosaic, and their conservation value

Similar to other studies of farming landscapes in Central America, this study found that the agricultural mosaic of the Río Copán watershed contains a high diversity of trees, birds, and butterflies (145, 139, and 119 species, respectively). Yet, as discussed further below, the picture that emerges from an assessment of species composition and land management practices is of a degraded landscape that falls short of its potential to conserve native biodiversity. The biggest limitation is not necessarily the manage-

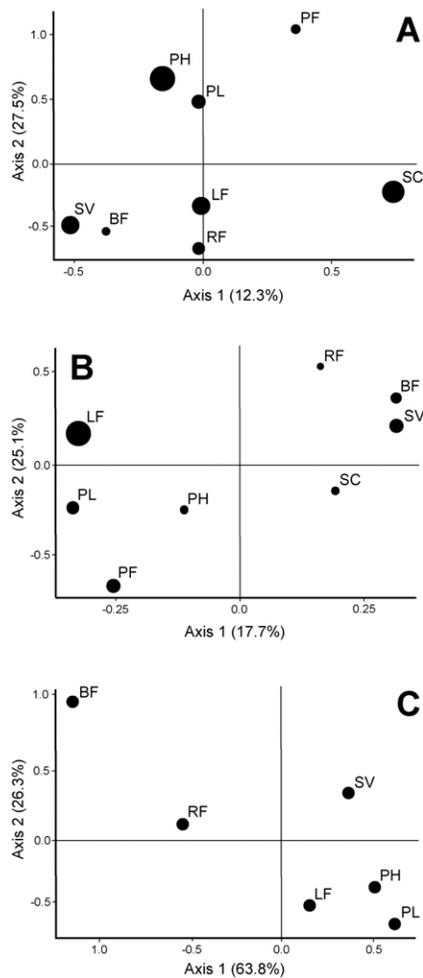


Fig. 5. Non-metric multidimensional scaling results based on Bray-Curtis similarity matrices for: (a) trees, (b) birds, and (c) butterflies. Points indicate the centroid for each land cover type. Panels (a) and (b) show distances in three dimensions, with the third dimension represented by the size of the point. For butterflies, most of the variation is explained by two dimensions, so only these are shown (stress of the two-dimensional configuration = 0.11). Land cover type abbreviations are as in Table 3.

ment of the pastures, coffee farms, and fallow plots in the study area, each of which contains significant species diversity and added several unique species to our overall tallies. Rather, it may be the condition of the forests, which are generally young and heavily affected by activities such as grazing and wood extraction that diminish floristic and structural diversity. These

land management practices, however, appear to affect birds and butterflies to differing degrees.

The observed bird assemblage represents well less than half of the 382 documented bird species in the Río Copán watershed. Increased sampling effort in the study area would likely have revealed some additional species, especially cryptic and uncommon species that have low detection rates. In addition, some of the species that are present in the watershed but absent in our study area have an affinity for montane forests, which are located at the periphery of the watershed and were not sampled in this study. Other species, however, apparently require larger or higher quality forest patches than those found in the more intensively managed central portion of the watershed. Indeed, the vast majority of the bird species we observed were of low conservation concern: none are on the IUCN Red List (Baillie et al. 2004) and less than 10% are considered to be forest-dependent.

The observed butterfly assemblages were much more evenly balanced between forest-dependent and non-forest-dependent species than were the bird assemblages. (These results must be treated with some caution, however, since forest dependence classifications for butterflies may be less reliable than those for birds, which have been more widely studied.) Since we are not aware of any butterfly species list for the watershed as a whole, it was not possible to evaluate the degree to which the study area represents the butterfly fauna of the entire watershed. Nevertheless, based on species composition, this zone does appear to provide a more complete set of suitable habitat niches and resources for butterflies than for birds.

Prior studies have shown that second-growth forests of varying ages can sustain a high proportion of plant or animal species normally associated with tropical primary forests (Chazdon et al. 2009). However, the persistence of relatively intact species assemblages in second-growth forests may depend on several conditions, including nearby patches of primary forest to provide source populations, a high proportion of older second-growth forest, substantial connectivity among forest patches, and low levels of anthropogenic disturbance following abandonment of agriculture or logging. In fact, the study area has none of these conditions that might help

Table 5. Pairwise correlations (R) between plot-level vegetation variables and plot-level bird and butterfly assemblage characteristics.

Vegetation characteristic	Faunal assemblage characteristic			
	Bird		Butterfly	
	Abundance	Species density	Abundance	Species density
All observed species				
Tree abundance	0.33*	0.28*	-0.10	0.20
Total basal area	0.02	0.01	0.00	0.35*
Tree species density	0.40***	0.38***	0.06	0.47**
Forest-affiliated species only				
Tree abundance	0.12	0.14	0.34	0.40*
Total basal area	-0.05	0.08	0.54***	0.56***
Tree species density	0.04	0.09	0.53***	0.62***

Notes: Statistical significance of the relationships is indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Forest-affiliated bird species include those classified by Stiles (1985) into forest dependence categories 1, 1-2, and 2. Forest-affiliated butterfly species are as classified by DeVries (1987, 1997).

mitigate biodiversity loss. Thus, while further study would be needed to isolate the specific factor(s) that are most detrimental, overall it is clear that the study area has surpassed a threshold of management intensity beyond which much biodiversity cannot persist.

Relationships between land cover and faunal assemblages

Contrary to our hypothesis, faunal assemblages responded more strongly to land cover than to the continuous habitat descriptors that we evaluated. While continuous variables have the theoretical advantage of being able to describe landscape heterogeneity more precisely and less subjectively than categorical ones, in the case of our study area, land cover classifications appear to describe habitat in a manner that is ecologically relevant for birds and butterflies. The significance of land cover as a biodiversity correlate is consistent with many prior studies and suggests that this proxy may offer an expedient and reasonably accurate basis for managing and monitoring the conservation value of agricultural landscapes over time. However, it is important to recognize that land cover classifications often exclude important aspects of land management that significantly affect conservation outcomes—for example, the young age and high disturbance level of forests in the study area.

Birds and butterflies responded somewhat differently to land cover patterns: in general, birds were more affiliated with dense vegetative cover from trees, shrubs, and vines while

butterflies reached their greatest abundance and species density in semi-open habitats and linear land covers. Interestingly, there was no significant difference between pasture with low tree density and pasture with high tree density with respect to bird or butterfly species density, abundance, or composition. This finding is generally consistent with other studies of Neotropical pasture-dominated landscapes, which have shown few significant differences between these two pasture land cover types (Harvey et al. 2006b, Milder 2010, but see Cardenas et al. 2003). However, live fences emerged as one of the most significant landscape elements contributing to both bird and butterfly diversity. This result supports previous observations that live fences can function both as ecotones and as corridors through agricultural landscapes, attracting a diversity of species that use these habitats for a portion of their life (Lang et al. 2003, Harvey et al. 2005). These functions may be especially important in the agricultural zones of the Río Copán watershed, where forest quality and connectivity are relatively low.

Several factors may explain the observed patterns of butterfly distribution by land cover. First, butterflies tend to be especially diverse at the forest-air interface (DeVries 1987, Wood and Gillman 1998). This interface is a dominant feature in live fences and strips of riparian forest, the two land covers with the highest observed butterfly abundance and species density. Second, butterfly distribution is strongly influenced by temperature and humidity levels; in the dry season, many species retreat to river bottoms or

Table 6. Comparison of different combinations of categorical and continuous habitat descriptors for explaining bird and butterfly assemblage characteristics.

Model results	Faunal assemblage characteristic			
	Bird		Butterfly	
	Abundance	Species density	Abundance	Species density
1. Land cover only				
AIC	451	531	182	257
R ²	0.36	0.39	0.50	0.35
P	<0.0001	<0.0001	0.001	0.02
2. Vegetation only				
AIC	458	544	195	251
R ²	0.18	0.17	0	0.23
P	0.0004	0.0009	N/A	0.004
3. Plot-scale factors only (land cover + vegetation)				
AIC	same as model 1	same as model 1	180	256
R ²			0.56	0.42
P			0.0003	0.01
4. Landscape context only				
L.C. scale of analysis	100	100, 800	100	100, 200, 400
AIC	457	544	182	256
R ²	0.20	0.19	0.40	0.13
P	0.0002	0.001	0.0008	0.03
5. Continuous habitat descriptors only (vegetation + landscape context)				
L.C. scale of analysis	100, 400, 800	800	100	100, 200
AIC	450	534	181	250
R ²	0.29	0.27	0.43	0.36
P	<0.0001	<0.0001	0.0004	0.002
6. All variables				
L.C. scale of analysis	100, 200	100, all others	100, 200, 400	same as model 3
AIC	448	529	177	
R ²	0.43	0.44	0.64	
P	<0.0001	<0.0001	<0.0001	

Notes: For each category of model, the best individual model was selected according to the criteria described in the Methods section. For each response variable, the model with the lowest Akaike information criterion (AIC) value is denoted by boldface. "L.C. scale of analysis" indicates the scale(s) (m radius) over which the landscape context variables yielded the best model. In these rows, the scale of the single best model is underlined, while the scales of comparable models ($\Delta AIC \leq 2$ and $\Delta R^2 \leq 0.05$) are also listed. Vegetation variables include tree abundance, tree basal area, and tree species density. Landscape context variables include the six metrics described in Table 2.

other moist locations (DeVries 1987). This behavior could help explain the rich butterfly fauna observed in riparian forests during the mainly dry-season field outings. Third, the relative paucity of species observed in the broadleaf forest plots may be attributable to the high disturbance level that characterizes most of these forests. Neotropical forest butterflies tend to exhibit vertical stratification according to their preference for understory, canopy, or light gap niches (Horner-Devine et al. 2003). However, since many of the sampled forest plots contained neither a well-developed understory nor light gaps associated with tree senescence, it is not surprising that the ground-based transects yielded comparatively few butterfly species. Sampling in the canopy of these forests might be expected to reveal many additional species.

Other habitat co-variates and proxies of faunal assemblages

Although there were many significant relationships among vegetation predictor variables and bird and butterfly response variables, overall the vegetation variables offered little explanatory power beyond that already provided by land cover (Table 6). Tree species density was the vegetation variable most strongly associated with bird and butterfly assemblages characteristics at the plot scale. This finding is consistent with theories of niche differentiation that predict that a greater diversity of habitat resources—characterized by horizontal heterogeneity, vertical heterogeneity, and diverse food resources—will support more diverse animal assemblages (Schoener 1974).

Surprisingly, there were few significant rela-

Table 7. Attributes of the best multivariate models of habitat effects on bird abundance, bird species density, butterfly abundance, and butterfly species density, respectively.

Candidate predictor variables and model attributes	Faunal assemblage characteristic			
	Bird		Butterfly	
	Abundance	Species density	Abundance	Species density
Land cover (categorical)	✓	✓	✓	
Tree abundance				
Tree total basal area				
Tree species density			✓[+]	✓[+]
Percent forest				✓[-]
Percent tree cover	✓[-]	✓[-]		
Contrast-weighted edge density				
NDVI				
Tasseled-cap brightness	✓[+]			
Tasseled-cap wetness		✓[-]	✓[+]	✓[+]
Model R^2	0.43	0.44	0.64	0.36
F	5.70	6.14	7.18	6.05
P	<0.0001	<0.0001	<0.0001	0.002

Notes: For each response variable, the best model was selected according to the criteria described in the Methods section. Check marks indicate predictor variables that are included in each model while the bracketed sign to the right of the check mark indicates whether the partial slope for each continuous variable is positive or negative. All landscape context variables listed in the table are those calculated for the 100 m context radius. The bottom three rows report the overall model fit and analysis of variance.

tionships between the faunal response variables and the six measures of landscape composition and structure that we evaluated. The reasons for this result are not obvious, but we can offer some plausible explanations. With regard to the role of forest and tree cover in the surrounding landscape, the disturbed condition of the study area's forests suggests that they may not be fulfilling key ecological roles—such as supporting source populations or providing complementary habitat resources—that in other mosaic landscapes foster strong relationships between the proximity of forest patches and the observed fauna in agricultural plots. Additionally, since the total pool of bird species in the study area is both significantly diminished and overall well-adapted to agricultural habitats (apparently as a result of the limited aggregate quantity and quality of forest habitat at the landscape level), even to the extent that individual patches provide suitable forest habitat, many of the bird species that might benefit from the proximity of such resources are absent from the landscape. For butterflies, the ability of many species to migrate through pasture-dominated mosaics and across pasture plots (Marín et al. 2009), suggests that a heavily forested landscape context may be unnecessary to support a high species diversity.

An alternative explanation is related to the fact that habitat heterogeneity is a key driver of

species diversity in the study area, with each land cover type contributing unique bird and butterfly species. Because five of the eight land covers surveyed for birds (and three of the six land covers surveyed for butterflies) are either forested or heavily tree-covered, nearby open areas would tend to increase local habitat heterogeneity and thus the diversity of resources available to generalist species. Similar patterns have been observed in suburban landscapes, where complementary habitats can support relatively high overall species richness but few species that depend on large forest patches (e.g., Marzluff 2005).

The landscape composition metrics calculated from mid-resolution ASTER imagery (NDVI and tasseled-cap wetness and brightness) also contributed little to explaining patterns of bird and butterfly distribution, either for forest-affiliated species or for all species collectively. This result contrasts with a recent study in Coto Brus, Costa Rica, which found significant relationships between tasseled-cap wetness, brightness, and bird species richness by group (Ranganathan et al. 2007). Two factors could help explain the weaker predictive power of these remote sensing metrics in Copán. First, the metrics did not strongly track tree cover or forest cover in simplistic ways, a result that may reflect a greater biophysical heterogeneity in Copán than in Coto Brus. In

general, relationships between land cover and the remote sensing metrics were as expected, with forests having relatively high values for NDVI and wetness and low values for brightness, while pastures, annual crops, and bare soil fell toward the opposite end of the spectrum. However, the variation within each land cover was high relative to the differences in the mean values among land covers. This variation is consistent with earlier research on the tasseled-cap metrics, which identified intra-annual vegetation cycles, canopy architecture, soil properties, and moisture gradients as important determinants of tasseled-cap values (Crist et al. 1986). In Copán, these properties vary somewhat independently across different land cover types, especially during the dry season, when the ASTER image was acquired.

Second, bird and butterfly abundance and species density were not consistently associated with landscape contexts containing high levels of forest or tree cover. Thus, even to the extent that the remote sensing metrics tracked vegetation density, it does not follow that these metrics would consistently predict bird and butterfly distribution patterns. Overall, our results affirm a conclusion of the meta-analysis conducted by Nagendra (2001), who cautioned against over-optimism that remote sensing metrics will be able to predict species distributions consistently, especially in heterogeneous landscapes.

Overall, the best fit models combining continuous and categorical predictor variables explained 36–64% of the variability in the different animal assemblage response variables. This result underscores the potential to parameterize species-habitat relationships to aid in the management of human-dominated tropical landscapes. However, it also indicates that there are other important co-variates—many of them likely context-specific attributes that would be difficult to identify, let alone measure—that play an important role in influencing patterns of bird and butterfly diversity. Thus, habitat proxies may offer a suitable coarse filter for biodiversity conservation in agricultural landscapes, upon which conservationists can layer more detailed management and monitoring initiatives focused on particular taxa of concern.

Effects of scale

Discerning the effects of scale on species assemblages is a perennial challenge in landscape ecology. Species and populations may respond in varying and interacting ways to habitat attributes and ecological processes at multiple scales, including the local, neighborhood, landscape, and regional scales (Desrochers et al., *in press*). Our results suggest that bird and butterfly assemblages in the study area are most strongly affected by local (plot-scale) habitat factors, represented by the land cover, vegetation, and 100 m radius (3.1 ha context zone) landscape variables. To the extent that the landscape context of different biodiversity sample points varied at intermediate scales of several hundred to a few thousand meters, this context appeared to exert little influence on species assemblages. This finding is consistent with several previous studies of butterflies and other taxa, which found that the scale of influence of habitat features in agricultural landscapes was limited to a few hundred meters at the most (Horner-Devine et al. 2003, Weibull et al. 2003, Kohler et al. 2008). On the other hand, research in Costa Rica demonstrated that the influence of a relatively large forest patch on faunal assemblages can extend at least two km for moths (Ricketts et al. 2001) and birds (Luck and Daily 2003). Although our study area contained several sizable forest patches (>100 ha), we found no evidence that these were exerting a “halo effect” (Ricketts et al. 2001) of increased faunal diversity in the surrounding area.

It is important, however, to clarify that these results do not necessarily indicate that landscape context at intermediate scales is unimportant within the Río Copán watershed. It could mean simply that we were unable to detect landscape context effects because many of the sample points had very similar landscape contexts at intermediate scales, where forested, tree-covered, and open lands tended to be interspersed in a somewhat regular mosaic. In fact, the difference in bird species richness and composition between the study area and the Río Copán watershed as a whole suggests that ecological context at the scale of roughly 5–20 km is exerting a strong influence on species assemblages. This regional context, in turn, affects the ways in which context at smaller scales influences the species assem-

blages—for example by filtering the pool of species that is available to move through neighborhood-scale habitat mosaics and colonize particular habitat plots. While our dataset is not geographically broad enough to characterize the effect of context at scales above a few km, it does suggest that paying greater attention to these larger scales could yield valuable insights in future studies of biodiversity in mosaic landscapes.

Conservation and management implications

As discussed in the Introduction, conservationists have rightly begun to focus more attention on agricultural landscapes in their effort to conserve biodiversity at local, regional, and global scales. Within this realm, there is considerable scientific evidence, not to mention compelling narratives, on the ability of Neotropical smallholder farming systems to sustain a wide diversity of native plants and animals, as well as ecosystem services (Perfecto and Vandermeer 2008). Yet, these narratives require some qualification. First, much of the research on biodiversity in Neotropical agricultural mosaics, including this study, has found such landscapes to be of limited value for conserving rare or specialized species. Second, conservation outcomes depend significantly on agricultural management practices and intensity.

Our study area within the Río Copán watershed is a case in point. Although agricultural management within the landscape is not intensive in the sense of large monocultures or heavy use of external inputs, it has followed a path of intensification typical of smallholder systems under increasing population pressure. Farmers in the landscape have eliminated primary forests, shortened the length of fallow cycles, increased grazing and resource extraction in secondary forests, and reduced tree cover in productive areas. These practices are quite likely a major reason why bird assemblages in the study area are depauperate relative to those at the edge of the watershed, where management intensity is lower.

Recent household surveys in the study area (Sánchez 2006) suggest that a combination of economic and cultural barriers limit the use of potentially wildlife-friendly land management practices, especially on small and medium-sized

farms. Given high rates of poverty in the study area, it is not surprising that biodiversity conservation is a low priority for most farmers. This tension between conservation and livelihood needs may make it difficult to increase substantially the quantity of forests in the landscape. Fortunately, however, there are many other management practices that can provide both conservation and livelihood benefits. For instance, excluding cattle from riparian forests can improve water quality for human and livestock consumption; re-foresting steep slopes can reduce sedimentation and the risk of landslides; and increasing the use of multi-strata live fences can help increase forest connectivity while providing farmers with timber, firewood, and fodder, thereby reducing pressure on forests. These practices offer win-win opportunities for the Río Copán watershed and other Neotropical agricultural landscapes and are worthwhile irrespective of any benefit to rare or endangered species.

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