

## COUNTRYSIDE BIOGEOGRAPHY: USE OF HUMAN-DOMINATED HABITATS BY THE AVIFAUNA OF SOUTHERN COSTA RICA

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**Abstract.** Understanding the multifaceted relationship between biodiversity and land-use intensity is key to conservation policy. To begin to characterize this relationship in a tropical region, we investigated the bird fauna in an agricultural landscape in southern Costa Rica. Landsat Thematic Mapper (TM) data show that about 27% of the land remains forested in the 15 km radius study region encompassing our sites. The rest was cleared about 40 yr ago for relatively small-scale coffee and cattle production, intermixed with other crops. Our goals were to: (1) compare the composition of the avifauna found in forest-fragment and open habitats of the countryside; (2) assess the faunal change that has occurred since deforestation; and (3) provide a baseline for future comparisons.

We surveyed the avifauna of eight forest fragments (0.3–25 ha) and 13 open-habitat sites (1.0 ha each) in the agricultural landscape. The pre-deforestation avifauna was approximated by the long-term bird list for the largest forest fragment (Las Cruces, LC; 227 ha) in the study region. We assumed conservatively that a species recorded in LC but not detected elsewhere occurred only in LC. Of the 272 locally extant bird species considered in this study, 149 (55%) occurred in forest habitats only. There was a significant positive correlation between forest fragment size and species richness for these forest birds. Of the remaining 123 species, 60 (22% of the total) occurred both in forest and open habitats. Sixty-three species (23%) occurred in open habitats only; the three nonnative species (1%) are in this group. Based on comparisons with larger forest tracts outside of the study region, it appeared that between 4 and 28 species (1–9% of the possible original totals) have gone locally extinct since deforestation began. The avifauna of open habitats was similar throughout the study region and did not vary with proximity to extensive forest.

A substantial proportion of the native bird fauna occurs in a densely (human) populated, agricultural landscape almost a half-century after extensive clearance. There are, however, cautionary messages: (1) the common occurrence of forest birds in human-dominated countryside (including both forest-fragment and open habitats) does not necessarily imply that these species maintain sustainable populations there; (2) about half of the species have little prospect of surviving outside of the forest; and (3) ongoing intensification of land use may greatly reduce avian diversity in countryside habitats. Nonetheless, countryside habitats may buy time for the conservation of some species; at best, they may even sustain a moderate fraction of the native biota.

**Key words:** *avifauna; biodiversity conservation; Costa Rica; extinction; faunal collapse; GIS database; human-dominated landscapes; Landsat Thematic Mapper; land-use intensity; neotropical birds; sustainable agriculture.*

### INTRODUCTION

Tropical landscapes worldwide are being rapidly transformed into a complex array of land covers under different intensities of use. The fates of organisms that once made their homes in large, unbroken tracts of native habitats form a continuum: at one end is population decline to local, and eventually global, extinction; at the other extreme is expansion into human-dominated landscapes. Naturally, and appropriately, a tremendous amount of work has focused on species in the former category, with particular attention directed

toward characterizing patterns of habitat fragmentation and their effects on biodiversity (e.g., Whitmore and Sayer 1992, Saunders et al. 1993, Schelhas and Greenberg 1996, Laurance and Bierregaard 1997). Until recently, relatively little attention was given, outside the context of pest management, to the potential conservation value of countryside habitats, whose extent and intrinsic qualities will largely determine the future of life on the planet (Daily 1997b). Countryside habitats include active agricultural plots, plantation or managed forest, fallow land, gardens, and small remnants of native vegetation embedded in landscapes devoted primarily to human activities.

Understanding the trade-offs between alternative agricultural systems and biodiversity conservation is cen-

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tral to projecting the course of biodiversity change, to developing sustainable agriculture, and to making conservation efforts most effective. First, few large, relatively undisturbed tracts of natural habitat appear likely to remain in the face of projected growth in human impacts (Halffter 1994, Ehrlich et al. 1995, Vitousek et al. 1997, Daily et al. 1998). Second, many ecosystem services (e.g., timber production, pollination, pest control, renewal of soil fertility, flood control) are supplied on local scales, meaning that their delivery depends on the capacity of countryside species to generate them (Daily 1997a). Third, there are growing incentives for augmenting the conservation value of degraded and other lands in many regions of the world (Houghton 1994, Daily 1995, Walker 1999). Finally, from both purely academic and practical perspectives, ecologists should be able to say more than “weedy” about the biota that may survive human impacts. In fact, countryside organisms offer opportunities for studying a variety of fundamental processes in ecology and evolution, such as community assembly and population differentiation.

Biologists have recently begun to document the biotas of countryside habitats, especially avifaunas in the production systems of the temperate zone (e.g., O’Connor and Shrubbs 1986, Pimentel et al. 1992, Bigal and McCracken 1996, Pain and Pienkowski 1997). Some of these systems have great conservation importance: in Europe, for instance, farmland is the land cover with which the largest number of threatened bird species is associated (Tucker and Heath 1994, Tucker 1997). Much less is known about the trade-offs for biodiversity conservation of agricultural practices in the tropics (Estrada et al. 1997). Most work so far has focused on the impacts of cattle and alternative coffee production systems on neotropical migrant land birds, with calls for attention to other systems and taxa (e.g., Martin 1984, Hutto 1989, Robbins et al. 1989, Greenberg 1992, Saab and Petit 1992, Greenberg et al. 1997, Vandermeer and Perfecto 1997).

“Countryside biogeography” is the study of the diversity, abundance, conservation, and restoration of species in rural and other human-dominated landscapes (Daily 1997b). This paper reports on the bird community that uses countryside habitats in the vicinity of San Vito, southern Costa Rica. The once virtually continuous forest of our study region has been converted over the past 3–4 decades to a landscape of small-scale coffee and cattle production (on plots typically < 2 ha and 5–50 ha, respectively, the larger of which retain patches of native habitat; Fig. 1–3). Interspersed throughout the countryside are numerous small (typically  $\leq 0.5$ -ha) plots of banana, bean, sugar cane, taro, yucca, and other crops, as well as residential gardens and small bits of native forest. The region is densely populated and is divided into multitudinous small land holdings on fairly rugged terrain, so that the intensity of agricultural practices (as measured by the fraction

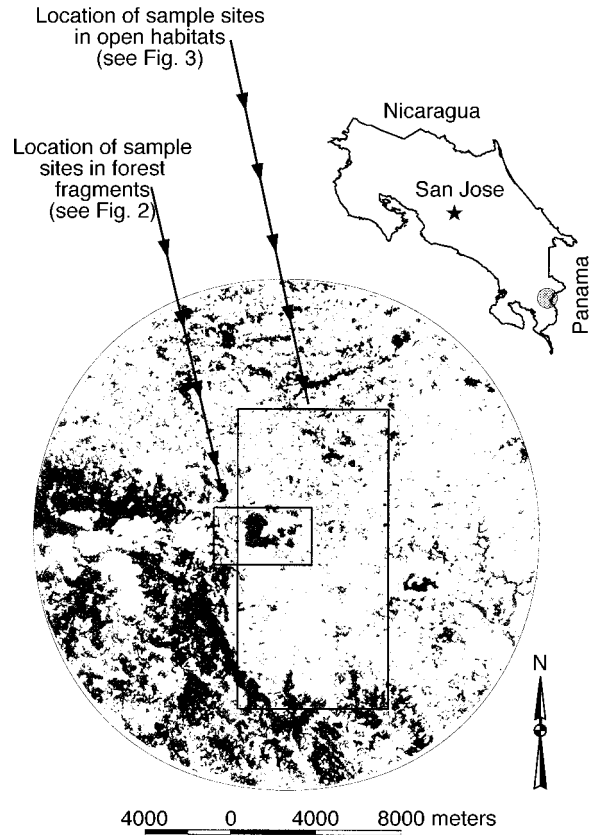


FIG. 1. Location of study sites in the study region, indicated by a 15 km radius circle about the Las Cruces Biological Field Station, in Coto Brus, Costa Rica. Forest is depicted in gray, and nonforest in white;  $\sim 27\%$  of the area in this circle remains under forest cover (averaged over the whole area). The two boxes contain the forest-fragment and open-habitat sample sites (depicted in Figs. 2 and 3).

of land converted to agriculture, plot size, and level of chemical inputs) is much lower than in other Costa Rican regions with larger land holdings dedicated to monocultures of banana, coffee, oil palm, pineapple, rice, or pasture.

Our goals were to: (1) compare the species richness and composition of the avifauna using forest-fragment and open habitats of the countryside; (2) assess the faunal change that has occurred since deforestation; and (3) provide a baseline for future comparisons.

#### METHODS

We based our work out of the Las Cruces Biological Field Station of the Organization for Tropical Studies (OTS/OET), Coto Brus, Costa Rica (elevation 1100 m). The station is situated between the agricultural lands of the Valle de Coto Brus (700–1240 m) and a partially forested and relatively inaccessible ridge (up to 1600 m; Fig. 1). We conducted bird surveys in forest fragments and open habitats of the countryside landscape; these were done in late March–May, which coincides

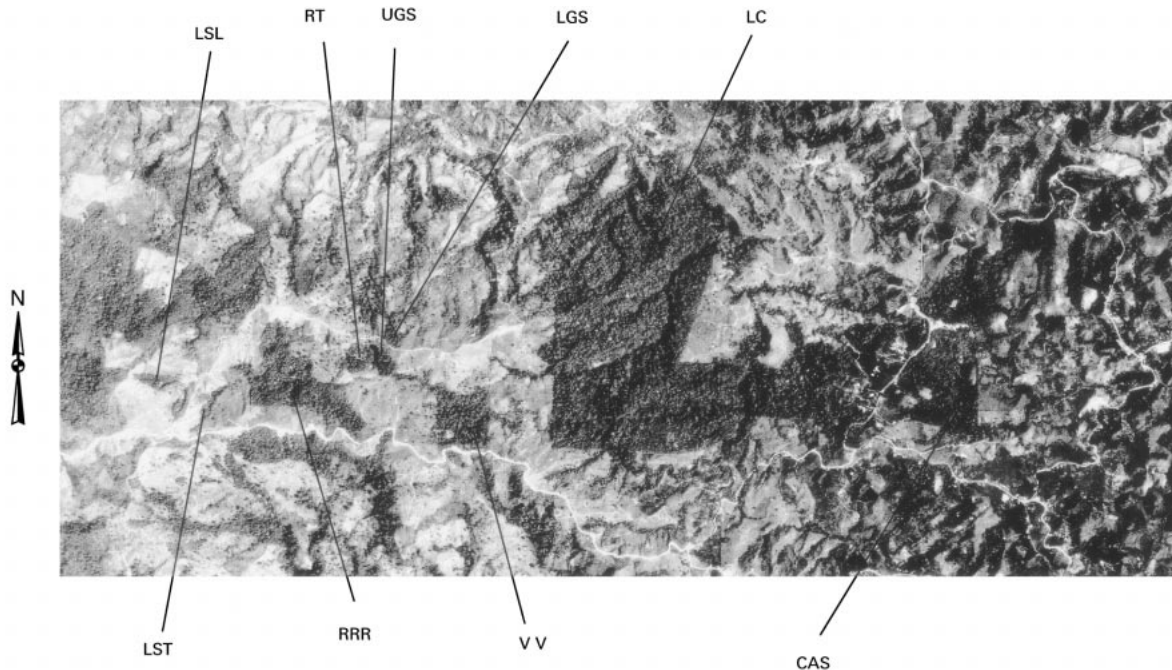


FIG. 2. Locations of surveyed forest fragments near the Las Cruces Forest; ~31% of the land area in this figure remains under forest cover.

with the breeding of many resident species. Survey methods were tailored to the environment and our purpose. Our sites ranged over 760–1420 m elevation; some elevational replacement of species occurs within this range, but the vast majority of species occur throughout it. The taxonomic status of some species is in flux (e.g., Hackett 1996); for ease of interpretation, we use the nomenclature in Stiles and Skutch (1989).

#### *Surveys of forest fragments*

In early May 1995 and again in mid-April 1996, each of eight forest fragments was surveyed using variable circular-plot techniques (Reynolds et al. 1980, DeSante 1981; but see our analysis). The fragments ranged in size from ~0.3 to 25 ha and were located mostly on very steep, rough terrain (Fig. 2). Approximate measures of their area were taken directly (on the ground) to account for the varied topography not apparent from aerial photos or satellite images. For more information on the fragments, see Daily and Ehrlich (1995; the area estimates presented here supercede those reported earlier). We used the bird list of the Las Cruces Biological Field Station Forest (LC; 227 ha), compiled over many years by professional ornithologists (Stiles et al. 1996), as a basis for gauging which species may have originally occurred throughout the now-fragmented study area. We exclude from the list species for which fewer than five reliable records exist. Because the smaller forest fragments (and the open habitats) were surveyed much less intensively, our comparisons with LC are conservative in revealing the numbers and kinds of species that may use countryside habitats.

Our sampling regime was designed to provide as uniform a surveying intensity as possible, given the variety of constraints that pertain in the area. We established the maximum number of 50 m radius circular plots that could be fully contained within each fragment, trying to maintain a 50-m distance between the boundaries of adjacent plots (a few were ~20 m apart). These were arranged not along straight lines, but to best accommodate uneven terrain, odd fragment shapes (e.g., narrow constrictions connecting broader forested areas), and variable levels of disturbance within the fragments (such as those caused by cattle and selective logging). The larger fragments were able to contain 6–10 census plots, and the smaller fragments contained 1–2 census plots each (Table 1). The number of plots per unit area appears somewhat uneven, but actually corresponds fairly well to the available horizontal area with closed canopy. For example, many plots straddled steep ravines, which had a measured surface area much greater than the area projected onto a horizontal plane. Plots in the smallest fragments extended beyond the fragment edge, but only birds detected within the forest are considered in analyses.

Each plot was surveyed three times within a 2-wk period in both years by James Zook, an experienced ornithologist able to recognize the vocalizations of all species encountered. Surveys were conducted between 30 min before sunrise (0530) and 4 h after sunrise; the order in which census plots were visited was varied in an effort to obtain similar levels of bird activity at each. Following Reynolds et al. (1980), DeSante (1981), and

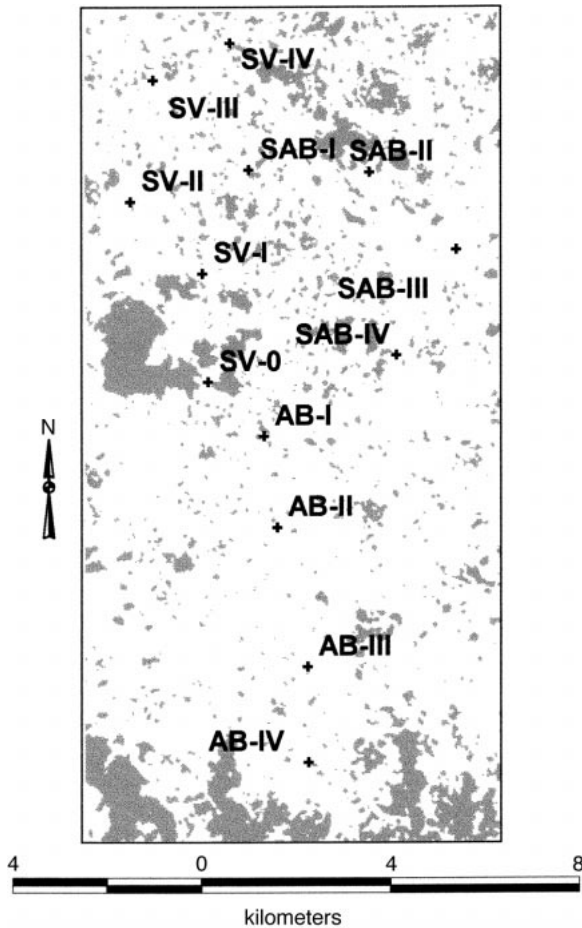


FIG. 3. Location of census sites in open habitats, indicated by crosses; ~16% of the land area in this figure remains under forest cover. The communities of Las Cruces and San Vito are at the same location as sites SV-0 and SV-II, respectively.

scientists working in the Las Cruces area, 8-min stationary counts were conducted at the center of each plot (the census point); all birds detected either visually or aurally were recorded, with an estimate of their distance from the observer. Birds detected beyond a lateral distance of 50 m from the census point were not considered in the analyses.

### Surveys of open habitats

In March–April 1995, we surveyed birds in open habitats representative of the region (760–1090 m). In increasing order of vegetation height and structural complexity, these areas typically contained nonforested agricultural plots, planted hedgerows, and overgrown tangles (of vines, shrubs, and small trees); they also contained forested riparian strips (2–10 m wide) and tiny (0.05–1 ha) forest fragments. We worked along three 12-km road transects (Fig. 3): one transect (SV) ran north from Las Cruces through San Vito and on past Aguas Claras; the second (AB) ran south from Las Cruces through Agua Buena and on toward Ciudad Neily; the third (SAB) stretched from San Vito eastward through Sabalito and on along the border with Panama. Four census sites (200 m × 50 m = 1 ha) were established along each road transect at 3-km intervals from the beginning; an additional site was at the entrance to the Las Cruces Station, for a total of 13 sites.

We recorded a habitat description for the 200 m radius circle about the midpoint of each site to capture land-use patterns typical within and beyond the transects. Within each circle, we estimated plot size, defined as the area covered by a given crop or crop combination (such as coffee interplanted with banana). Abutting plots were considered separate if they had different crops or if they were divided by a distinct hedgerow. We also recorded elevation, agricultural activities within the circle, the approximate number of remaining specimen trees (isolated, mature native trees), the number of buildings, and the relative abundance of powerlines, scored qualitatively (data available from authors).

Each site was censused seven times. Censuses began 30 min before sunrise and ended 3–3.5 h later, depending upon the weather. We varied the order in which census locations were visited. Censuses always involved at least three observers (G. C. Daily, P. R. Ehrlich, and George Burtness), who were competent at identifying birds visually, but were not familiar with the vocalizations of some of the species encountered. We searched out visually any individuals that were detected aurally but not recognized to species; in the open

TABLE 1. Summary of bird species richness and evenness in forest fragments and open habitats.

Parameter	Forest fragments										Σfrag†	Σopen†
	LC	CAS	RRR	VV	UGS	LGS	LSL	LST	RT			
Fragment area (ha)	227	25	25	15	1	1	0.3	0.3	0.3	67.9	—	
No. census plots	—	7	10	6	1	2	2	1	1	30	—	
Total no. individuals	—	648	661	422	84	151	149	86	81	2282	4198	
Total no. species	251	92	71	64	29	49	39	28	33	131	123	
Total no. families	33	24	23	23	14	18	15	13	15	28	25	
Evenness index, $J'$	—	0.88	0.79	0.85	0.91	0.89	0.88	0.90	0.88	0.83	0.76	

Notes: Where cells are blank, data are not applicable.

† Σfrag and Σopen refer to the collective avifauna of the forest fragments (all but LC) and of the open habitats, respectively.

habitat, and with tapes of local bird vocalizations, this was generally feasible.

We designed a surveying routine with the flexibility to allow detection of birds in the multitude of different farm habitats and microhabitats, while keeping our disruption of farm activities to a minimum. During five of the seven rounds of censusing, one observer remained in a 25-m road segment at the site midpoint while the other two surveyed along a ~100 m length of road in opposite directions. Moving permitted avoidance of disturbances caused by dogs and other farm animals, and by passing pedestrians and motorists (the roads are rough and narrow, but heavily traveled). Each observer recorded all birds detected in a 20-min period from the roadside, while attempting to avoid multiple counting of the same individual. During the fourth and sixth rounds of censusing, the observers covered an area together, more intensively, using side roads and paths adjacent to the original census area as much as possible to minimize the direct influence of road traffic.

On the sixth round of censusing, the three surveyors were accompanied to all sites by Zook, who detected a few species undiscovered by the three regular observers and found a greater abundance than estimated by the others of some of the most secretive species. Overall, the surveys of both forest fragments and open habitats are conservative: more species are likely to be present than were detected.

#### *Remotely sensed information*

We determined land cover (forest vs. nonforest classes) on the basis of remotely sensed information derived from a Landsat Thematic Mapper (TM) image acquired in 1994. The TM data were geocoded to Lambert Conformal Conic (south) projection at the Research Center on Sustainable Development of the University of Costa Rica (CIEDES—UCR). The precise shape of forest fragments and other vegetation types was verified by means of aerial photographs (1:40 000) taken in 1992 by Costa Rica's National Geographic Institute (IGN), and also by ground truthing. All forest units within a minimum mapping unit of 1.2 ha were extracted by means of a supervised classification (Janzen 1986). Discrepancies between the TM data and the actual borders of land cover types (at a scale of ~5 m) resulted from limits of the spatial resolution of the sensor and from mixed pixels of vegetation types with similar spectral signatures (e.g., those with both shade coffee and natural forest).

We constructed a Geographic Information System (GIS) database of the study area, integrating information from the TM image, the aerial photographs, road maps, and other sources, and used it in this study to estimate the proximity of open-habitat census sites to large forest patches ( $\geq 227$  ha).

#### *Analysis*

We do not report information on species that typically pass high overhead, such as raptors, parrots,

swifts, and swallows. At many sites, we did not have clear enough views to detect them or consistently identify them to species. Similarly, we made no attempt to survey owls. We also omit information on birds closely associated with water (e.g., ducks, kingfishers, and some species of rail) because we are concerned here with species capable of using the general countryside; too few sites had major water sources to assess reliably the occurrence of water-affiliated birds in countryside habitats.

The sampling circumstances and methods permit use of relative, but not absolute, measures of abundance. As a measure of relative abundance of species among forest fragments, we use all detections made within each fragment (the census plots within each fragment were visited an equal number of times:six). We also use cumulative totals as a measure of relative abundance in the open habitats (where each site was visited seven times). Sampling was necessarily so different between forest-fragment and open habitats that we do not compare abundances between them.

In an earlier study comparing the diversity of butterflies and moths in the same forest fragments, we found strikingly different patterns of species richness and evenness of species abundance (Daily and Ehrlich 1996; see *Discussion*). For purposes of comparing birds with these taxa, we report estimates of (1) species richness (cumulative total); (2) relative abundance of species among sites; (3) relative evenness of species diversity,  $J'$  ( $J' = (-\sum p_i \ln p_i)/\ln S$ , where  $p_i$  is the proportion of a sample made up of the  $i$ th species and  $S$  is the total number of species in the sample; Pielou 1966); and (4) the percentage overlap in species composition between census locations. We expressed percentage overlap in terms of both percentage of A in B and percentage of B in A to reveal patterns obscured by a single combined statistic. Statistical tests were performed using SYSTAT 7.0 and are described in Sokal and Rohlf (1995) and Zar (1984). To compare diversity indices, we used the  $t$  test developed by Hutchinson (1970) for  $H' = -\sum p_i \ln p_i$ .

We assembled a list of birds that probably occurred in the area prior to deforestation, based on our own personal experience and that of Zook in similar, but more heavily forested, parts of the region. Those species now missing (either reported on the LC list as "accidental" or not found in our surveys), were classified into four categories: (1) accidental; (2) likely overlooked (present in low average density and undetected); (3) likely to have been extirpated; and (4) no basis for judgment. We used this list to make upper- and lower-bound estimates of the degree of faunal change that has occurred in the area, beyond that evident from comparisons of forest-fragment and open habitats with the LC list. The LC forest has almost certainly undergone some faunal change itself. For instance, the White Hawk (*Leucopternis albicollis*), the Great Curassow (*Crax rubra*), the Pale-billed Wood-

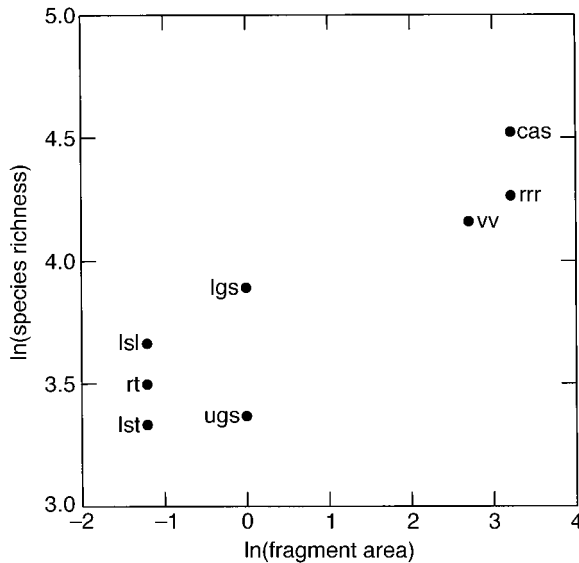


FIG. 4. Relationship between species richness and fragment area for the eight surveyed forest fragments, excluding LC ( $r^2 = 0.83$ ,  $P < 0.01$ ).

pecker (*Campephilus guatemalensis*), and other species appear to have disappeared in recent years.

## RESULTS

### Forest fragments

There is a significant species–area relationship for species that occur in the forest fragments:  $\ln(\text{species richness})$  and  $\ln(\text{fragment size})$  are correlated ( $r^2 = 0.83$ ,  $P < 0.01$  excluding the Las Cruces Forest, LC [Fig. 4];  $r^2 = 0.81$ ,  $P < 0.01$  including LC), as are  $\ln(\text{family richness})$  and  $\ln(\text{fragment size})$  ( $r^2 = 0.86$ ,  $P < 0.01$  without LC;  $r^2 = 0.93$ ,  $P < 0.01$  including LC) (Appendix A and Table 1). There were few migrant birds present at the time of our surveys; hence, excluding migratory species ( $n = 36$ ) from these analyses yielded similar results: the correlation between  $\ln(\text{resident species richness})$  and  $\ln(\text{fragment size})$  is  $r^2 = 0.87$ ,  $P < 0.01$  without LC, and  $r^2 = 0.82$ ,  $P < 0.01$  with LC.

The forest fragments are similar in terms of relative evenness of species diversity,  $J'$ , which ranges between 0.79 and 0.91 (Table 1); none is dominated by a disproportionately abundant species or set of species. We found no significant difference in species diversity,  $H'$ , among sites, contrasting the sites with the biggest difference (CAS and LST;  $t = 1.33$ ,  $df = 360$ ,  $P > 0.10$ ). Using the same test, we also contrasted  $H'$  for the sites with the biggest difference in  $J'$ , and again found no significant difference ( $t = 0.212$ ,  $df = 744$ ,  $P > 0.50$ ).

A progressively smaller fraction of the pre-deforestation fauna, as inferred from the LC list, was detected in the smaller and more isolated fragments (Table 2, LC column). Of the LC species, 53% were found in the eight fragments combined ( $\Sigma\text{frag}$ ). Examining

the upper right boxed part of Table 2, one sees that a majority (52–86%) of the species found in the smallest fragments (0.3–1.0 ha) are also present in the largest fragments (15–25 ha). In contrast, comparatively few of the species contained in the largest were detected in the smallest fragments (16–55%), as shown in the lower left box. The upper left box shows that the larger fragments share 47–78% of their species; the smaller fragments share a similar fraction (47–83%; lower right box). The highest fraction (39%) of LC species was found in CAS, a large fragment nearly contiguous with LC (it is separated by a 16-ha manicured botanical garden with abundant trees).

How many families are missing from the forest fragments? Among those considered, five of the 33 families reported on the LC list were not found in the fragments: the Nyctibiidae (potoos), Caprimulgidae (nightjars), Galbulidae (jacamars), Bucconidae (puffbirds), and Fringillidae (finches, siskins). The latter family should not be considered missing: its species are open-habitat specialists. Each of these families has only one local representative.

### Open habitats

We characterized the similarity of the avifauna among open census sites in several ways. First, we tested for independence of site and species composition, considering species for which at least 30 detections were made ( $n = 34$ , or 28% of the 122 species observed in the open habitats; Appendix A, where the right-most column reports the sum of all 13 open sites). We imposed this cutoff to obtain sufficiently large frequencies for statistical analysis (Zar 1984). Thus, we are characterizing the avifauna in terms of the commoner species that were detected, on average, at least 2.3 (or 30/13) times per site.

Three open-habitat specialists had clumped distributions across census locations and times (chi-square tests:  $df = 11$  and  $P < 0.001$  in each case): the Cattle Egret (*Bubulcus ibis*), the Smooth-billed Ani (*Crotophaga ani*), and the Rufous-collared Sparrow (*Zonotrichia capensis*). For example, of the 60 Cattle Egrets seen during the entire study, 45 were found in a single flock on a single day at site AB-III. Excluding these three species from the analysis, species richness and composition were similar across census locations ( $G$  test: Pearson  $\chi^2 = 23.345$ ,  $df = 372$ ,  $P > 0.999$ ).

A second measure of similarity among open-habitat sites was the overlap in species composition among sites (Fig. 5). Considering all species in the study, 87% of the 156 possible pairwise comparisons yielded a level of overlap  $\geq 60\%$ . This site-to-site similarity is clearly a function of both the wide distribution of one set of species (14 ubiquitous and 30 widespread, found in  $\geq 10$  sites) and the sporadic occurrence of many more (29 detected only once in all surveys, and 53 detected  $\leq 5$  times). The 30 widespread species made up 81% of the 4198 individuals recorded.

TABLE 2. Percentage overlap in species composition between forest fragments and open habitat.

Habitat	Bird species overlap in forest fragments (%)									$\Sigma$ frag	$\Sigma$ open
	LC	CAS	RRR	VV	UGS	LGS	LSL	LST	RT		
LC		98	93	94	90	92	95	86	88	93	73
CAS	39		66	67	66	65	70	54	52	70	38
RRR	29	51		78	79	80	79	86	82	54	25
VV	26	47	70		76	71	69	71	67	49	22
UGS	11	20	32	34		49	54	60	64	22	14
LGS	19	35	55	55	83		62	82	79	37	19
LSL	16	29	44	42	72	49		75	64	30	16
LST	10	16	34	31	59	47	54		58	21	12
RT	13	18	38	34	72	53	54	68		25	14
$\Sigma$ frag	53	100	100	100	100	100	100	100	100		50
$\Sigma$ open	38	50	42	42	59	47	49	50	52	46	

Notes: Each entry is the percentage of species in the site in that column also found in the site in that row;  $\Sigma$ frag refers to the collective avifauna of all forest fragments except LC; and  $\Sigma$ open refers to the collective avifauna of the 13 open-habitat sites. Fragments are listed in descending order of size (left to right, top to bottom). Open-habitat specialists are excluded from LC for this analysis. Upper-right box: 52–86% of species found in smaller fragments were also present in the largest fragments. Lower-left box: 16–55% of species found in the largest fragments were detected in the smallest fragments. Upper-left box: large fragments shared 47–78% of their species. Lower-right box: small fragments shared 47–83% of their species. See *Results, Forest fragments* for further details.

A third measure of similarity among census sites is the relative evenness of species diversity ( $J'$ ), which ranged between 0.80 and 0.89 (0.76 overall; Table 1). This indicates that sites had comparable distributions of individuals among species. A relatively few species were superabundant in each site: the Blue-grey Tanager (*Thraupis episcopus*) was at least the third most common species at each site (and was the most abundant in 10 of 13 sites); the Clay-colored Robin (*Turdus grayi*) was at least the fourth most common species at 12 of 13 sites (and was at least the third most common at 10 of 13 sites); and the Scarlet-rumped Tanager (*Ramphocelus passerinii*) was at least the fifth most common at 10 of 13 sites.

Fourth, using the GIS data, we tested for variation in species richness and abundance of individuals as a function of distance from relatively extensive forest (defined as  $\geq 227$  ha, about the size of the LC fragment). To the south of our open-habitat sites lies extensive forest on a very steep slope that drops down

to sea level in a few horizontal kilometers; sites AB-III and AB-IV were closer to the upper part of this forest than to LC (Figs. 1 and 3). LC was the closest large patch to the other sites, however, as verified by ground truthing; the next largest patch to these other sites was 63 ha in area (Fig. 1; some fragments appear larger than they actually are because of poor resolution on the satellite image).

Considering all species found in open habitats, there was no correlation between the direct distance from the nearest edge of the largest forest patch and either species richness ( $r^2 = 0.014$ ,  $df = 11$ ,  $P > 0.90$ ) or the number of individuals detected at a site ( $r^2 = 0.006$ ,  $df = 11$ ,  $P > 0.90$ ; Fig. 6). Neither of these correlations was significant when considering only the forest-affiliated birds found in open habitats ( $r^2 = 0.002$ ,  $df = 11$ ,  $P > 0.50$  for species richness; and  $r^2 = 0.015$ ,  $df = 11$ ,  $P > 0.50$  for abundance). Generally, open habitats are influenced little by proximity to native forest at the geographic scale of this study.

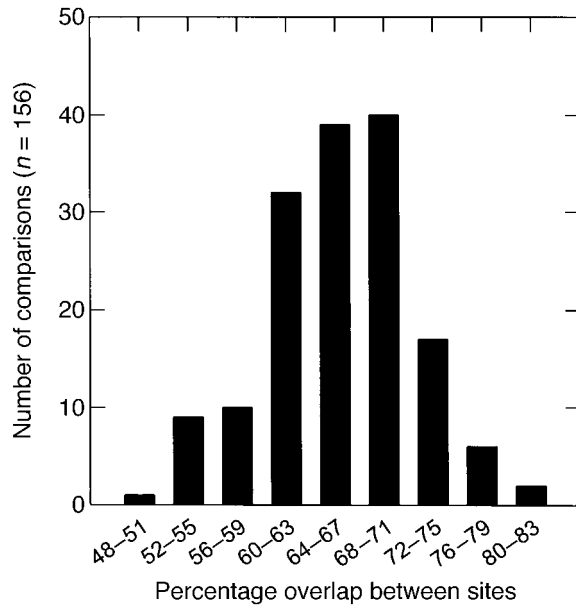


FIG. 5. Distribution of the percentage overlap in species composition between open-habitat sites, including all species ( $n = 13^2 - 13 = 156$ ).

Nonetheless, there was sufficient variation in the abundance of species and individuals among sites to test for correlations with other site attributes. There was a weak rank correlation between the relative abundance of specimen trees and bird species richness (Kendall's tau- $b = 0.390$ ,  $P \leq 0.10$ ,  $n = 13$ ). There was also a weak correlation between the relative abundance of powerlines and the abundance of individuals found at a site (Kendall's tau- $b = 0.390$ ,  $P \leq 0.10$ ,  $n = 13$ ). There were, however, no statistically significant correlations between species richness or bird abundance and relative agricultural plot size or the number of buildings at a site.

#### Comparison of forest and open habitats

Of the 272 species considered in the analysis, 149 (55%) were listed or detected in forested habitats only; 60 species (22% of the total) were found to occur in open habitats as well as in forest; and 63 (23% of the total) were recorded in open habitats only (one of the latter species, the Indigo Bunting, *Passerina cyanea*, was not observed during survey periods, but occurs only in open habitats). Although 73% of the birds surveyed in the open habitats are on the LC list, relatively few of these were found in the individual forest patches (12–38%, Table 2, right-most column); a similar fraction (10–39%) of LC birds was detected in the forest patches.

Typically, ~50% of the avifaunas of the forest fragments was found in open habitats (Table 2,  $\Sigma_{\text{open}}$  row). The smaller fragments were not composed disproportionately of birds found in open habitats; in fact, they shared more species in common with each other than

with open habitats ( $\Sigma_{\text{open}}$ ). Of the collective open-habitat fauna, a greater fraction was found in forest fragments as fragment size increased (12–38%; Table 2, right-most column). The fraction of birds on the LC list found in the open habitats was 38%; the fraction found in the forest fragments ( $\Sigma_{\text{frag}}$ ) was 53%. The percentage shared between the forest fragments and open habitats was 46–50%.

Of the 28 families that we surveyed in the forest fragments, five are not represented by any species in the surveys of open habitats (Appendix A). These five families (11 spp.) included: four species in the Trogonidae (trogons), three species in the Pipridae (manakins), two species in the Cracidae (guans, etc.), and one each in the Phasianidae (quails, etc.) and the Cap-

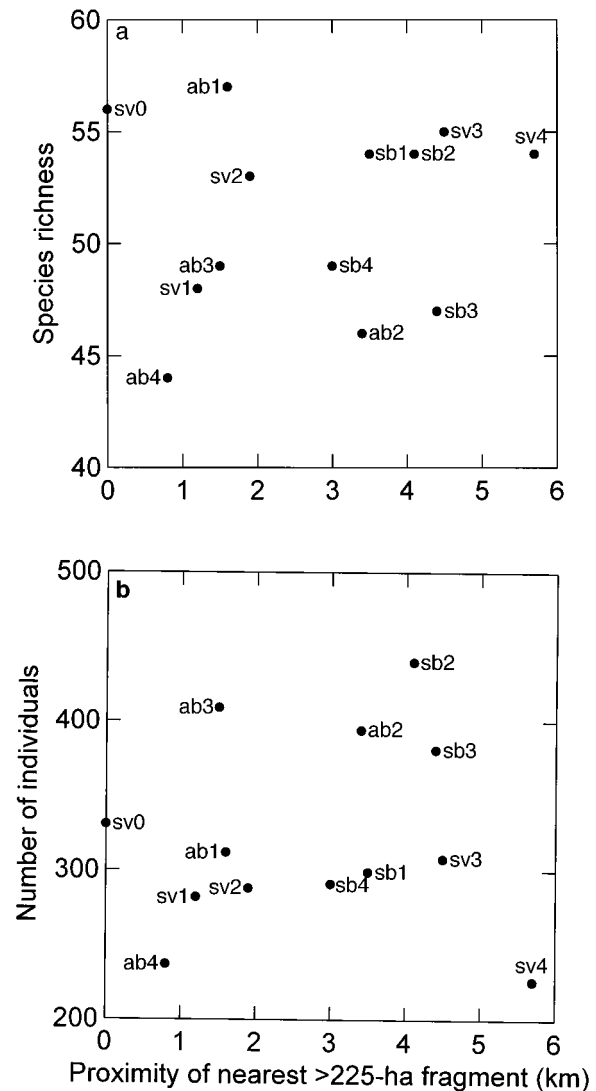


FIG. 6. (a) Species richness and (b) number of individuals detected in the open-habitat surveys, in relation to proximity to a large tract of forest (at least as large as the LC fragment, 227 ha).

itonidae (barbets). We have since found representatives of each of these families except the Phasianidae in open areas, although none are common (J. B. Hughes, G. C. Daily, and P. R. Ehrlich, *unpublished manuscript*). Conversely, two families surveyed in open habitats were not found in our surveys of forest fragments; their only two representatives were the Cattle Egret (Ardeidae: *Bubulcus ibis*) and the Lesser Goldfinch (Fringillidae: *Carduelis psaltria*), both open-country birds.

There is no significant difference between the diversity indices ( $H'$ ) for the combined forest fragment ( $\Sigma_{\text{frag}}$ ) and open habitat ( $\Sigma_{\text{open}}$ ) data (Table 1;  $t_c = 0.244$ ,  $df = 6470$ ,  $P > 0.50$ ).

#### Faunal change

For a lower bound estimate, considering only those species judged as likely to have been extirpated, the study area appears to have lost four species in four families (from both forest fragments and open sites) in the four decades since extensive clearing began (Appendix B). Considering, at the other extreme, all species in Appendix B (including those that may still occur, but are accidental or overlooked), the study area may have lost 28 species in 14 families. (The "overlooked" category includes a mix of species, such as those whose preferred habitats were not surveyed, but that still occur locally in the study region, as well as *Empidonax* flycatchers, which are difficult to identify in the nonbreeding season). No family-level extinctions occurred in either estimate. Of those groups under consideration, it thus appears that the study region lost between four and 28 bird species (1.4–9.3% of the possible original totals of 276 and 300).

#### DISCUSSION

A substantial fraction of the forest-affiliated bird fauna occurs in the intermediate-intensity agricultural landscape of southern Costa Rica, a pattern of land use found commonly in the tropics. Relatively large (>200 ha) forest tracts doubtless contribute greatly to the high species richness in the study region; species richness falls off steeply from the large to small forest fragments, a result also found in a mist-netting study in the same area (Borgella 1995). Nonetheless, ~45% of all species (272 total) considered in this study were found in open habitats; of the 209 forest-affiliated species, 29% occurred in open habitats as well as in forest. In a similar study at Los Tuxtlas, Mexico, 70% of the 226 species surveyed were found in agricultural habitats; some habitats, such as cacao and citrus plantations, were more arboreal than those in our region (Es-trada et al. 1997).

Our assessment of the occurrence of birds in open habitats is conservative for several reasons. First, we conducted our surveys over a < 2-mo period; we doubtless missed some species that move regionally (Hilty 1994), as well as intertropical migrants that sometimes occur in great abundance in open habitats around Las

Cruces. Second, the surveys were done during the breeding season for many species, when habitat requirements typically become more restricted (Stiles and Skutch 1989). Third, we did not survey some countryside habitats known to be relatively rich in bird species, such as certain types of shade coffee plantations (Perfecto et al. 1996, Greenberg et al. 1997). Fourth, most of the surveying was done by observers unfamiliar with the vocalizations of rarer species. Finally, the Las Cruces (LC) list, which we use to estimate the species pool that could potentially inhabit open habitats, represents an upper bound. Thus, for instance, the Giant Cowbird (*Scaphidura oryzivora*), an open-habitat specialist, is recorded on the LC list and is counted among the 272 species considered, but was not encountered in any of our surveys. For these reasons, it is possible that > 45% of the avifauna uses open countryside. Indeed, in our later, intensive study of the use of particular features of open habitats and microhabitats by the avifauna, an additional 23 forest-affiliated species were found in open areas, raising the total in open countryside to 49% (J. B. Hughes, G. C. Daily, and P. R. Ehrlich, *unpublished manuscript*).

On the other hand, our surveys may convey a misleadingly favorable impression of the capacity of countryside (both forest-fragment and open) habitats to support bird species over the long run. First, even relatively abundant species may be undergoing slow declines to extinction, a process that can take hundreds to thousands of years (e.g., Diamond 1972, Soulé et al. 1979, Tilman et al. 1994). Other studies suggest, however, that the loss of sensitive forest specialists occurs early (within a few years or decades) in the land conversion process (Warkentin et al. 1995, Terborgh et al. 1997, Brooks et al. 1999, Renjifo 1999). The scale of remnant habitat and earlier extinction filters may account for the difference among these studies (Balmford 1996, Brooks et al. 1999); more work is needed to understand the process of faunal change.

Second, although our open sites were kilometers from large forest fragments, making it unlikely that the small-bodied species (many of whom were observed nesting in the open) commute regularly from them to forest, some species may use the open habitats only during certain seasons and depend on disappearing large tracts of forest at other times of year (Stiles and Skutch 1989). For instance, many migrants and resident canopy species move out into edge and open habitats to exploit seasonal fruit resources, but use forest habitats most of the year.

Third, the supply of important resources, such as food and nesting locations secure from predation, may not be sustainable over the long run, even in the absence of further land use change. For instance, a substantial drop in the species richness of open areas may occur when long-lived trees and other plant species with poor recruitment in the countryside habitats die off (Terborgh 1986, Nason et al. 1997, Mawdsley et

al. 1998). Generalizations are difficult in the absence of detailed knowledge of the natural history of the species in question (Stiles 1990, Simberloff 1994, Sieving and Karr 1997). For example, little is known about the interdependence of particular tree and bird species (Bawa 1990).

Fourth, social interactions may change in open habitats to the detriment of some species. Spatial concentration of resources in open habitats may increase their defensibility, favoring socially dominant over subordinate species (Daily and Ehrlich 1994, Greenberg et al. 1996). Flocking species may also be at risk: flocks in tropical forest may involve great cohesion and intricacy of structure, existing year-round and consisting of species with complementary foraging styles and social behavior (Munn and Terborgh 1979, Munn 1985, 1986; but see Hutto 1994). We found associations among some species, but not the species richness and diversity or individual abundance characteristic of flocks in forest habitats (Hutto 1987; J. B. Hughes, G. C. Daily, and P. R. Ehrlich, *unpublished data*).

Finally, ongoing trends of deforestation and agricultural intensification almost certainly will reduce the capacity of countryside habitats (both forest fragments and open areas) to support the avifauna. For example, whereas the mixed agricultural landscape around Las Cruces appears to support ~100 resident species of the groups censused, the more intensified agricultural (and urban) landscape around the University of Costa Rica (in San Jose) maintains about half that number (Stiles 1990).

Open habitats are clearly not suitable for all of the major groups of birds in question. In our study, 55% of the species considered were listed or detected in our surveys in forest fragments only. During our open habitat surveys, for instance, no trogons (Trogonidae) or manakins (Pipridae) were found; some species in these families, however, were found by us outside of our survey periods and are known to occur in mostly open habitats (e.g., the Orange-collared Manakin, *Manacus aurantiacus* is found in gardens; Stiles and Skutch 1989). Few woodcreepers (Dendrocolaptidae) and antbirds (Formicariidae) were recorded in open habitats; in addition to the notable dependence of some species on intact forest (Canaday 1997, Sieving and Karr 1997), this could trace, in part, to their secretiveness. With regard to faunal change, the high estimate (9% of species lost of the possible original total number of species) is probably more accurate than the low one (1% thereof). Some of the species classified as accidental or as likely to have been overlooked probably owe their present rarity to habitat alteration (as opposed to secretiveness, being at the edge of their elevation range, or other factors). The decline of others, however, such as the Black Guan (*Chamaepetes unicolor*) and parrots and other species not considered here, is attributable more to ongoing persecution (for food or for pets) than to direct effects of habitat alteration.

The more common open-habitat species appear to be uniformly distributed across the landscape: they show a high degree of similarity in species composition and relative evenness of diversity among open-habitat sites. Neither species richness nor abundance, even for only the forest-affiliated species of open habitats, was correlated with proximity of large forest tracts. Agricultural plots and seminatural habitats are sufficiently small, diverse, and evenly distributed in the study region that most sites contain most countryside habitats. As reported in studies of bird and arthropod diversity in other parts of the world (e.g., Duelli et al. 1990, Loman and von Schantz 1991), small (<0.5-ha) fragments of seminatural habitat appear to be very important, being utilized by a wider array of species than other agricultural habitats (J. B. Hughes, G. C. Daily, and P. R. Ehrlich, *unpublished manuscript*). Such fragments remain ubiquitous in our study region, and were present at all sites.

Few nonnative species occur in the Costa Rican countryside, relative to many temperate zone and island areas (Mooney et al. 1995, Blair 1996). Only three species among the groups considered are invasive: the Rock Dove (*Columba livia*), an early invader, and the Smooth-billed Ani (*Crotophaga ani*) and Cattle Egret (*Bubulcus ibis*), first recorded in Costa Rica in 1931 and 1954, respectively. There were few superabundant species in our surveys, unlike some temperate and tropical landscapes where certain passerines (e.g., blackbirds, queleas, and others) often occur in very large numbers (Briggs and Elliot 1989). Our measures of relative evenness of species diversity ( $J'$ ) are similar and high in both forest-fragment and open habitats. This contrasts with the butterfly faunas of the same fragments, where  $J'$  was high in larger fragments (0.73 for LC, 0.80 for CAS), but ranged between 0.10 and 0.42 for the smaller, more isolated fragments where a single species was superabundant (Daily and Ehrlich 1995). Light-trapped moths, however, show a pattern of evenness of abundance similar to that of the birds, with  $J'$  values ranging between 0.74 and 0.92 in the forest fragments (Daily and Ehrlich 1996). The variable response of different taxa to habitat fragmentation dims the prospects for finding reliable single groups as indicators of biodiversity (Daily and Ehrlich 1996, Lawton et al. 1998), and supports the need for use of multiple taxa (Kremen et al. 1993).

#### CONCLUSIONS

Forest clearance does not necessarily spell doom for all forest species. Indeed, many can probably persist in countryside landscapes that maintain forest fragments and a diversity of small agricultural plots. Much more information is needed about the specific features of countryside habitat that are important for the maintenance of bird species richness and abundance (e.g., Petersen 1998; Hughes et al., *in preparation*). Ideally, those features or surrogate measures thereof would be

discernable on remotely sensed images, allowing regional prediction of patterns of bird species richness and abundance as a function of patterns of land use and land-use change. More information is also needed on the mechanisms by which land-use changes influence the distribution and abundance of species to serve as a basis for a theoretical framework relating agricultural practices, ecological processes, and biodiversity (e.g., Wiens et al. 1993, Wiens 1995).

Although the occurrence of nearly half of the forest species in open habitats is cause for optimism, there are also cautionary messages. First, at least half of the forest bird species seem to have no prospects for survival outside of forest. Second, little is known about the sustainability of the countryside biota that exists today. Third, more intensively managed agricultural countryside is likely to support much less biodiversity, and intensification of agriculture is a 10 000-yr-old trend that is accelerating. Overall, agricultural habitats and policy merit much more consideration in strategies to conserve biodiversity.

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#### APPENDIX A

A table presenting bird species richness and relative abundance in forest patches vs. open habitats studied in southern Costa Rica is available in ESA's Electronic Data Archive: *Ecological Archives* A011-001-A1.

#### APPENDIX B

A table of bird species, expected to have once occurred in the Costa Rican study area, but not found in 1995–1996 surveys, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-001-A2.