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Distribution of bird species richness at a regional scale in tropical dry forest of Central America

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Abstract

Aim The objectives of this study were to identify landscape and habitat characteristics associated with bird species richness at a regional scale. In particular, we examined how these variables affect resident bird, forest bird, fruit-eating bird and restricted-range bird species richness in forest fragments.

Location Study sites were located in seven decreed reserves in Costa Rica and Nicaragua that contain some of the largest and best-protected fragments of tropical dry forests in central America.

Methods Bird censuses were undertaken using point counts at each site and compared with landscape metrics and habitat characteristics of reserves.

Results Forest cover within reserves, zoochoric species richness, tree and shrub species richness, and tree height were associated with resident, forest and fruit-eating bird species richness in tropical dry forests.

Main conclusions The distribution of bird species richness in tropical dry forests of central America can be attributed to a number of interacting factors. Conservation priorities based on bird species richness should focus on Santa Rosa National Park, while the Chacocente and Cosiguina reserves deserve a high priority for conservation within Nicaragua.

Keywords
Tropical dry forest, bird species richness, floristic composition, vegetation structure, landscapes metrics, central America.

Resumen

Objetivo El objetivo de este estudio fue identificar las características del paisaje y medio ambiente asociadas con la abundancia de especies ornitológicas a escala regional. En particular, examinar cómo estas variantes afectan el número de aves residentes, aves forestales, aves frugívoras, y aves de corto alcanze que se observan en la floresta.

Localización Este estudio se realizó en siete reservas naturales de Costa Rica y Nicaragua. Estas reservas contienen algunas de las áreas de bosque seco tropical más grandes y mejor protegidas en la America Central.

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Métodos El censo de aves se realizó mediante el conteo de individuos observados por área de estudio. La cantidad de aves observadas se comparó entonces con la métrica del terreno y las características medio-ambientales de cada reserva.

Resultados La cobertura forestal, la abundancia de especies zoochorica, la variedad de especies de árboles y arbustos, y la altura de árboles en cada reserva, fueron relacionados con la abundancia de especies de áves residentes, forestales y frugívoros en el bosque seco tropical.

Conclusiones La distribución en abundancia de especies ornitolóigcas en el bosque seco tropical de Centro América puede ser atribuída a la interacción de diversos factores. La abundancia de especies en el Parque Nacional Santa Rosa en Costa Rica señalan a ésta reserva como un área a la que se le debe prestar primordial atención para la conservación, mientras que las protección de las reservas Chacocente y Cosiquena merecen prioridad en Nicaragua.

INTRODUCTION

Central America has recently been identified as a biodiversity hotspot or region with an exceptional concentration of endemic species that is experiencing exceptional loss of habitat (Myers *et al.*, 2000). Within central America, tropical dry forest has been identified as one of the most endangered ecosystems because this forest type has been reduced to less than 0.1% of its original expanse (Janzen, 1988a; Long *et al.*, 1996; Laurance *et al.*, 1997). The distribution and diversity of avian communities in the tropical dry forests of central America have certainly been affected by a high degree of deforestation and resulting habitat fragmentation, but little quantitative or comparative data exist (Stiles, 1983; Ceballos, 1995; Corcuera & Butterfield, 1999).

A number of studies have identified landscape and habitat characteristics associated with the distribution of bird species richness in forest fragments that may be used to predict patterns of species richness in remaining tropical dry forests. Landscape metrics such as reserve size and habitat area (Willis, 1979; Newmark, 1991; Bierregaard *et al.*, 1992; Christiansen & Pitter, 1997; Warburton, 1997), degree of isolation (MacArthur & Wilson, 1967; Newmark, 1991; Bierregaard *et al.*, 1992; Estrada *et al.*, 1997), and reserve shape (Diamond, 1975; Bierregaard *et al.*, 1992) have been identified as associated with bird species richness in tropical forest fragments. Measures of habitat quality have also been identified as important predictors of bird species richness in fragmented systems (Wiens, 1989). Habitat characteristics such as plant species richness (James & Wamer, 1982), floristic composition (Snow & Snow, 1971; Rotenberry, 1985; Freifeld, 1999), and vegetation structure (MacArthur, 1964; MacArthur *et al.*, 1966; Lynch & Whigham, 1984) have been identified as good predictors of avian species richness, especially in temperate forests. However, a number of studies have concluded that floristic richness (MacArthur, 1964; Orians, 1969) or simple measures of vegetation structure (Howell, 1971; Karr & Roth, 1971; Stiles, 1983; Terborgh, 1985) are not the only factors affecting avian species richness in continuous evergreen tropical forests.

The importance of these landscape and habitat characteristics for predicting bird species richness undoubtedly vary in influence, depending on spatial scale (Bohning-Gaese, 1997). In particular, there is strong evidence that the influence of some habitat, landscape and environmental predictors of bird species richness vary among local, regional and global spatial scales (Ricklefs, 1987; Currie, 1991; Levin, 1992). Although birds have been the most thoroughly researched taxonomic group in tropical forest fragments, a vast majority of the studies have focused on one fragment or small forest fragments (0.1–100 ha in size) at a small spatial scale (1–100 km^2) (Turner, 1996). There have been few studies undertaken in intermediate sized reserves or habitat fragments (100–1000 ha) at a regional scale (1000–10,000 km), especially in the tropics (Turner, 1996; Zuidema *et al.*, 1996; Bohning-Gaese, 1997). An assessment of bird species richness at a regional scale and species identified as important for regional conservation such as fruit-eating birds (Howe, 1984; Estrada *et al.*, 1993; Silva & Tabarelli, 2000) and restricted-range birds (Long *et al.*, 1996; Poulsen & Krabbe, 1998; Manne *et al.*, 1999), can have significant implications for conservation priorities and management.

The objectives of this study were to identify landscape and habitat characteristics associated with bird species richness at a regional scale. In particular, we examine how these variables affect resident bird, forest bird, fruit-eating bird and restricted-range bird species richness in remaining fragments of tropical dry forest in central America.

METHODS

Study areas

Study sites were located in seven fragments of tropical dry forests in Costa Rica and Nicaragua: (1) Santa Rosa National Park, Costa Rica, (2) Palo Verde National Park, Costa Rica, (3) La Flor Wildlife Refuge, Nicaragua, (4) Chacocente Wildlife Refuge, Nicaragua, (5) Reserve on the island of Ometepe, Nicaragua, (6) Masaya National Park,

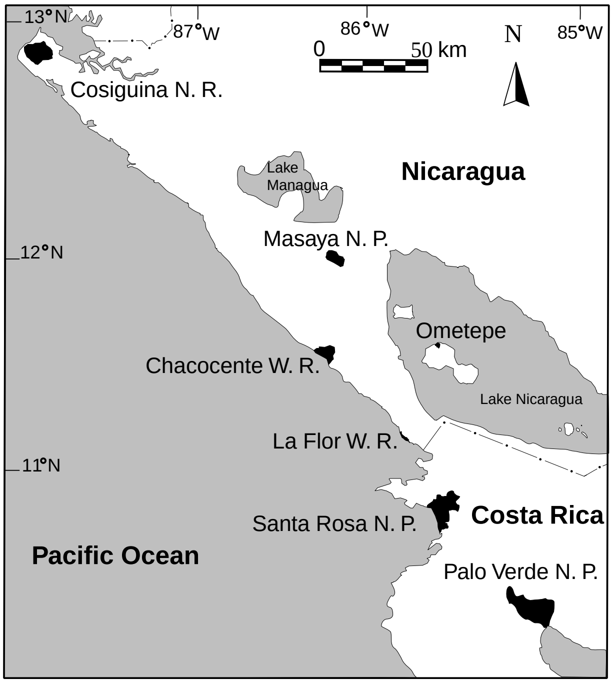

Figure 1 Seven reserves with tropical dry forest in central America.

Nicaragua and (7) Cosiguina Nature Reserve, Nicaragua (Fig. 1). The dominant land use surrounding reserves in Costa Rica is cattle pastures while the dominant land use in Nicaragua is small-scale subsistence agriculture. These forest fragments have all been decreed conservation areas and are some of the best-preserved and largest remaining patches of tropical dry forest in central America.

Bird census methods

All sites were visited a minimum of three times from May to August in 1994, 1995 and 1996 to ensure that all resident birds could be identified by sight and vocalization. Final bird censuses were undertaken from April to July 1997, which corresponds with the breeding season of a majority of tropical dry forest birds (Stiles & Skutch, 1989). Point count surveys following Hutto *et al.* (1986) with minor modifications, were undertaken at each site to determine species richness of resident breeding birds with migratory and nocturnal species excluded. Each site contained 30 points within tropical dry forest, a minimum of 100 m from the edge of the forest and 100 m apart. Point count stations were established in late successional tropical dry forest within an area *c.* 2 km^2 at each site. Each point was surveyed for 10 minutes and all species detected within the fixed radius of 25 m were tallied. All surveys were carried out between 5:30 a.m. and 8:00 a.m. and were not undertaken in windy conditions or during increment weather. The point count method was chosen to insure that sampling effort, habitat type and area surveyed were the same at all sites (Remsen, 1994). All family and species level taxonomy follow Stiles & Skutch (1989) which is based on the American Ornithologist's Union checklist.

Landscape characteristics

Although there are over 64 landscape metrics that have been developed to characterize habitat fragments (McGarigal & Marks, 1994), we selected five metrics from the literature that have been the most successful at predicting species richness: reserves area, forest cover within reserve, distance to nearest reserve, isolation of reserve and reserve shape (Forman, 1995; Kupfer, 1995; Estrada *et al.*, 1997; Warburton, 1997). Data on decreed reserve area and forest cover within reserves came from government publications, aerial photographs and satellite imagery. The methods are described elsewhere (Gillespie *et al.*, 2000). Maps of reserves (1 : 525,000) were imported and georeferenced in Imagine 8.3.1. (ERDAS, Incorporated, Atlanta, GA, USA) in order to calculate distance, isolation and shape metrics for all reserves. Reserve distance metrics were calculated as the linear distance (km) from the perimeter of a reserve to the perimeter of the nearest reserve with tropical dry forest (Newmark, 1991; Estrada *et al.*, 1997). Reserve isolation metrics were calculated as the mean total distance from the perimeter of a reserve to the perimeter of all reserves with tropical dry forest in the study area (Siegfried *et al.*, 1998). Reserve shape indices were calculated for each reserve as $\log_e$ [edge (m)]/area (Krummel *et al.*, 1987).

Habitat characteristics

Data on floristic composition and vegetation structure of tropical dry forests were collected at each site following Gentry (1982, 1988). Ten sample plots totalling 1000 m^2 were established near the centre of the bird survey areas at each site. The first sample plots were established at a randomly selected starting point and adjacent transects were established approximately 20 m apart (Gentry, 1982). All trees, shrubs and lianas rooted in plots with a stem diameter > 2.5 cm were included. All species encountered were classified by dispersal mechanisms: Autochory, Anemochory, Zoochory and Diplochory (Gentry, 1982; Gillespie, 1999). Zoochoric species (defined as plants with a fleshy exocarp) were further divided into a bird-dispersed category (defined as fleshy diasphores, < 2 cm that are usually blue-black or red at maturity) following Gentry (1982). The height of all arborescent plants, excluding lianas, were determined using a clinometer for all individuals recorded in plots at all sites to measure forest structure.

Environmental characteristics

Environmental variables of elevation, annual precipitation and the qualitative rank of anthropogenic disturbance (based on the intensity and frequency of fire, cattle grazing and wood collection within each reserve) were collected for all seven study sites (Veblen *et al.*, 1992; Gillespie *et al.*, 2000).

Data analysis

Spearman's rank correlations were used to identify relationships between landscape metrics, habitat characteristics, and four categories of bird species richness in seven fragments of tropical dry forest and to detect intercorrelation between landscape and habitat characteristics significantly associated with categories of bird species richness. Four categories of bird species richness were examined: resident bird species richness, forest bird species richness, fruit-eating bird species richness and restricted-range bird species richness. Resident bird species richness includes all resident breeding birds recorded during point counts at each site. Forest bird species richness is based on Stiles (1985) classification of bird dependence on forest and includes species requiring solid or patchy forest. Birds that can persist in non-forest habitats were excluded. The diets of fruit-eating birds are complex with the intensity and frequency of fruit consumption varying significantly between species and seasons (Stiles, 1983). For this reason, fruit-eating birds were identified as species that include some fleshy fruits in their diet according to Stiles & Skutch (1989). Restricted-range species were identified following Manne *et al.* (1999), which found that birds with a geographical range of 1000–100,000 km^2 were exceptionally vulnerable to extinction in the Neotropics. Geographical ranges were calculated based on a species breeding range and determined using a number of range maps and breeding records (Gillespie, 2001).

RESULTS

Bird species richness

A total of 1591 individual birds were encountered during 210 point counts in seven fragments of tropical dry forest. Seventy-one resident bird species were recorded in seven tropical dry forest reserves (Appendix 1). Fifty of the species encountered (70%) required solid or patchy forest and were considered forest birds while 37 birds (52%) were known to include some fruit in their diet and were classified as fruit-eating (Table 1). There were 22 (31%) restricted-range birds encountered with a geographical range less than 100,000 km^2.

The distribution of bird species richness varied between sites. Santa Rosa National Park contained the highest resident bird, forest bird, and fruit-eating bird species richness. The smallest reserves at Ometepe and La Flor maintained the lowest resident bird, forest bird, fruit-eating bird and restricted-range bird species richness. Chacocente and Cosiguina contained the most restricted-range species.

Landscape, environmental, and habitat characteristics of reserves

Landscape, environmental, and habitat data were collected for all seven tropical dry forest sites (Table 2). Cosiguina and Santa Rosa have the most tropical dry forest cover within decreed reserves. All reserves were relatively isolated with the closest distance between two reserves 36 km. Cosiguina and Palo Verde were the most isolated reserves based on distance to the nearest reserve and isolation between reserves in the tropical dry forest region of Costa Rica and Nicaragua. Cosiguina was the most disturbed reserve and had the highest annual precipitation while Santa Rosa was the least disturbed site and Masaya was the driest site. Floristically, Santa Rosa contained the highest total plant species richness along with the highest zoochoric and bird-dispersed species richness. Ometepe and Masaya had the lowest plant species richness and trees and shrub species richness, while La Flor had the lowest zoochoric and bird-dispersed species richness. The density of trees and shrubs, lianas, zoochoric and bird-dispersed varied among sites. Santa Rosa and Palo Verde contained the most trees over 20 m tall, but Santa Rosa contained a high number of stems greater than 10 cm diameter at breast height (d.b.h.) and contained the highest basal area of all sites.

Correlates of bird species richness

For landscape metrics, there was a significant correlation among forest cover in reserves and resident bird, forest bird and fruit-eating bird species richness (Table 3). For habitat characteristics, measures of floristic richness, composition, and vegetation structure were significantly correlated with bird species richness. Tree and shrub species richness was significantly correlated with resident bird and forest bird species richness, while zoochoric species richness (number of trees, shrubs and lianas) was correlated with resident bird, forest bird, fruit-eating bird and restricted-range bird species richness. There was a significant correlation between the number of trees greater than 10 and 20 m in height and resident birds, forest birds and fruit-eating birds. There was

Table 1 Summary of bird species richness in seven fragments of tropical dry forest in central America

Study sites	Resident species per point	Resident bird species richness	Forest bird species richness	Fruit-eating bird species richness	Restricted-range bird species richness
Santa Rosa N.R.	6.5 ± 1.6	46	35	27	14
Palo Verde N.R.	4.3 ± 0.9	37	29	18	13
Chacocente W.R.	4.7 ± 1.6	37	25	17	18
Cosiguina N.R.	5.6 ± 1.4	35	23	18	16
Masaya N.P.	3.7 ± 1.4	24	16	11	11
La Flor W.R.	4.9 ± 0.8	23	14	7	9
Ometepe N.R.	5.7 ± 1.0	21	12	12	10

Table 2 Summary of landscape, environmental, floristics, and structural characteristics of seven tropical dry forest reserves in central America

Sites	Decreed reserve area (ha)	Forest cover in reserve (ha)	Reserve distance (km)	Reserve isolation	Reserve shape	Anthro-pogenic disturbance	Elevation (m)	Annual precipitation (mm)
Landscape and environmental characteristics								
Palo Verde	16,804	1646	68	152	0.076	4	100	1717
Santa Rosa	10,800	3556	40	107	0.080	3	250	1552
La Flor	800	449	36	92	0.123	5	18	1805
Chacocente	4800	1500	49	94	0.086	5	30	1362
Ometepe	420	420	53	96	0.180	6	42	1695
Masaya	5100	1300	48	109	0.081	8	231	1251
Cosiguina	12,420	5132	193	241	0.079	9	295	1827
	Plant species richness	Tree and shrub species richness		Liana species richness	Zoochoric species richness	Bird-dispersed species richness	Anemochoric species richness	
Floristic characteristics from 1000-m^2 plots								
Palo Verde	65	48		17	24	14	15	
Santa Rosa	75	54		21	34	17	13	
La Flor	59	45		14	17	7	20	
Chacocente	54	43		11	24	15	11	
Ometepe	45	27		18	17	14	6	
Masaya	44	33		11	19	13	9	
Cosiguina	48	38		10	23	11	7	
	Tree and shrub density	Liana density	Zoochoric density	Bird-dispersed density	Trees > 20 m height	Trees > 10 m height	Trees > 10 cm d.b.h.	Basal area (m^2 ha^{-1})
Structural characteristics from 1000-m^2 plots								
Palo Verde	185	42	107	63	16	47	45	22.84
Santa Rosa	169	77	77	41	8	53	61	25.08
La Flor	202	62	33	10	3	35	42	22.84
Chacocente	177	38	91	59	5	51	62	21.23
Ometepe	107	47	76	63	1	27	48	17.77
Masaya	223	20	121	94	1	15	52	21.18
Cosiguina	118	17	55	24	4	37	52	23.31

also a significant correlation between range-restricted species and the number of trees with a d.b.h. greater than 10 cm. There were no correlations among environmental characteristics and any measures of bird species richness.

Landscape and habitat characteristics associated with measures of bird species richness are presented in Table 4. There was a correlation between zoochoric richness of all plants recorded in plots and forest cover in reserves, as well as a correlation between the number of trees greater than 20 m in height and tree and shrub species richness. There was no correlation between forest cover in reserves and tree and shrub species richness or vegetation height ($P = 0.253$, $P = 0.119$, respectively).

DISCUSSION

Landscape characteristics and species richness

The relationship between bird species richness and habitat area has been well documented in studies of avian communities and forest fragmentation at a local spatial scale (Turner, 1996; Zuidema *et al.*, 1996). It is not surprising that this study yielded similar results at a regional scale. It should be noted that reserve area is not always the best predictor of forest bird species richness, because a number of reserves in Nicaragua and Costa Rica contain other habitats such as wetlands, successional shrub vegetation and agricultural areas. This suggests that caution should be used when assessing the adequacy of a country's nature reserve system based solely on decreed reserve area and not forest extent within reserves, at least as it relates to forest birds (Siegfried *et al.*, 1998; Gillespie, 2001).

Some landscape characteristics not associated with bird species richness at a regional scale are of equal interest. Distance and isolation metrics have been cited as important predictors of species richness when the distance between habitat fragments is between 100 m and 10 km (Newmark, 1991; Bierregaard *et al.*, 1992; Warburton, 1997). However, the predictive power of these metrics may be attenuated at a

Table 3 Spearman's rank correlations ($n = 7$) among landscape and habitat characteristics and measure of bird species richness from seven tropical dry forest sites

Variables	Resident bird species richness	Forest bird species richness	Fruit-eating bird species richness	Restricted-range species richness
Landscape characteristics				
Decreed reserve area	0.685	0.750	0.703	0.500
Forest cover in reserve	0.775*	0.786*	0.829*	0.750
Reserve distance	0.036	0.071	0.414	0.429
Reserve isolation	0.288	0.357	0.559	0.357
Reserve shape	−0.685	−0.750	−0.703	−0.500
Environmental characteristics				
Elevation	0.396	0.429	0.667	0.429
Annual precipitation	−0.198	−0.143	0.108	−0.143
Anthropogenic disturbance	−0.609	−0.063	−0.400	−0.360
Floristic characteristics				
Plant species richness	0.685	0.714	0.559	0.179
Tree and shrub species richness	0.757*	0.786*	0.523	0.214
Liana species richness	0.136	0.182	0.255	−0.360
Zoochoric species richness	0.782*	0.775*	0.973**	0.775*
Bird-dispersed species richness	0.222	0.184	0.574	0.385
Anemochoric species richness	0.180	0.214	−0.090	−0.357
Structural characteristics				
Tree and shrub density	0.018	0.357	−0.487	−0.286
Liana density	0.090	0.107	0.541	−0.429
Zoochoric density	0.273	0.288	0.073	0.198
Bird-dispersed density	−0.162	−0.143	−0.073	0.198
Number of trees > 10 m height	0.883**	0.857**	0.775*	0.679
Number of trees > 20 m height	0.873**	0.901**	0.764*	0.559
Trees > 10 cm d.b.h.	0.582	0.487	0.464	0.810*
Basal area	0.624	0.655	0.633	0.309

*$P < 0.05$, **$P < 0.01$.

Table 4 Spearman's rank correlations between landscape and habitat characteristics associated with bird species richness

Variables	Forest cover in reserve	Tree and shrub species richness	Zoochoric species richness	Tree > 20 m height
Trees and shrub species richness	0.500			
Zoochoric species richness	0.847*	0.432		
Trees > 20 m height	0.685	0.847*	0.673	
Trees > 10 cm d.b.h.	0.433	0.018	0.600	0.191

*$P < 0.05$.

larger scale when reserves are used instead of habitat fragments. The average distance between nearest reserves in this study was 70 km apart, which may result in lower levels of dispersal and colonization of birds among sites. Although a number of studies have identified the importance of reserve or habitat shape at a small spatial scale, the importance of reserve shape declines at a regional scale. Saunders *et al.* (1991) noted that shape of habitat fragments is only important for relatively small areas because of edge effects. The fact that reserve shape was not associated with bird species richness is not surprising because decreed boundaries of reserves contain little ecological information about the habitat and in some cases can be arbitrary lines drawn on maps (Lovejoy, 1982).

Environmental characteristics and species richness

Although a number of studies use energy measured by temperature and precipitation as an indicator of ecosystem productivity (Rosenzweig & Abramsky, 1993), within tropical dry forest, there does not appear to be a significant relationship between precipitation and bird species richness. This may be because of the fact that all sites were classified as tropical dry forest according to the Holdridge life zone classification system (Holdridge *et al.*, 1971) and there may not be enough variance among sites to test the importance of energy in the study area.

It is interesting to note that levels of anthropogenic disturbance were not associated with any measure of bird species richness. This was because one of the largest sites, Cosiguina, experiences annual fires, intensive wood collection and cattle grazing, but still maintained relatively high bird species richness. Whereas, the smallest sites, like Ometepe and La Flor, had a relatively low level of anthropogenic disturbance and contained low species richness. It appears that forest area, floristics composition and structure can negate some impacts of anthropogenic disturbance, however, it is probably not the case if disturbance continues.

Habitat characteristics and species richness

MacNally (1990) and James & Wamer (1982) reported that bird species richness was influenced by both floristics and physiognomy at a regional scale in south-eastern Australia woodlands and temperate deciduous forests in North America. The same appears true in tropical dry forests of central America where three habitat characteristics of floristic diversity (tree and shrub species richness), composition (zoochoric species richness), and vegetation structure (tree height) were associated with bird species richness. It should be noted that the vegetation sampling methods in our study were not taken at all individual point count stations but a sample of a tropical dry forest at each site. However, Gentry's transect method appears appropriate for estimating species richness at a site because of the amount of species packing that occurs in tropical forests in which a diversity of trees can coexist in a relatively small area and this can provide a first-order approximation of species richness at reserves (Gentry, 1982).

Floristic species richness and composition are rarely measured to explain patterns of bird species richness in the tropical forest fragments (Wiens, 1989; Turner, 1996). Snow & Snow (1971) found that bird species diversity and floristic diversity were directly correlated in the tropical forest of Trinidad and the same appears true in the tropical dry forest of central America. In particular, the number of tree and shrub species in stands of tropical dry forest may be a good predictor of bird species richness at a regional scale.

Zoochoric richness in tropical dry forest was the only variable associated with all measures of bird species richness: resident bird, forest bird, fruit-eating bird, and restricted-range bird species richness. Silva & Tabarelli (2000) recently estimated that 34% of tree species in the Atlantic forest of Brazil will become extinct on a regional scale because of the loss of fruit-eating birds in forest remnants. Results from tropical dry forest fragments of central America suggest that there are fewer zoochoric species in small reserves, but this was not necessarily associated with less bird-dispersed species. First, there was no correlation with any measure of bird species richness and the richness or abundance of bird-dispersed plants. Only when plants with large diaspores > 2 cm were included was there a significant correlation. Secondly, a number of studies in tropical forests have noted that large fruits and seeds are generally late-successional plants that are more diverse in mature forests (Janzen, 1988b; Hammond & Brown, 1995). Although all vegetation plots were established in mature stands of forest following Gentry (1982), it may be the case that bird species richness is higher in late-successional tropical dry forests. In particular, zoochoric species richness may be a good indicator of successional status of tropical dry forests. Finally, there is little evidence of obligate seed dispersal between any fruit-eating birds and plants in the tropical dry region of central America (Howe, 1984). Most seeds are dispersed by a diversity of species including mammals such as bats, which may be more important to long-distance seed dispersal than birds (Medellin & Osiris, 1999). It is difficult to determine from this study if the lack of zoochoric species in small reserves is the result of the lack of bird dispersal between sites or other ecological processes.

A number of researchers have concluded that vegetation structure (generally measured by foliage height diversity) cannot be used as the sole predictor of avian diversity in tropical lowland forests (Howell, 1971; Stiles, 1983; Terborgh, 1985). However, a simple measure of vegetation structure based on tree height was significantly correlated with bird species richness in tropical dry forest fragments. The relationship between vegetation structure and bird diversity is well documented in the north-eastern forests of the USA, and it may be the case that a similar relationship occurs in tropical dry forests (MacArthur *et al.*, 1966). First, tropical dry forest structure in central America is similar to temperate deciduous forests. Although tropical dry forests and temperate deciduous forests differ in species diversity and temperature regimes, both forests have relatively similar annual precipitation, tree heights, and above ground biomass (Whittaker, 1975; Gentry, 1988). Secondly, with the exception of large frugivores, there may be a greater similarity in species guilds between the tropical dry forest and the eastern deciduous forest than between the tropical dry forest and the lowland tropical rainforest. There are a number of wet forest guilds (i.e. ant-followers, small obligate frugivores, and dead leaf-gleaners) that are rare or absent from tropical dry forests (Stiles, 1983). Finally, most species in the temperate deciduous forest of the USA and tropical dry forests of central America require only patchy forest to persist, not solid forest (Stiles, 1985; Bull & Farrand, 1987). This generalist nature of tropical dry forest birds appears more similar to eastern deciduous forest than lowland evergreen forests, which contain a proportion of species restricted to solid forest (Stiles, 1983; Gillespie, 2001).

Unlike other measures of bird species richness, the number of restricted-range species was only associated with the number of trees greater than 10 cm d.b.h. The distribution of restricted-range species is probably a result of the historical biogeography of species in central America than any particular landscape or habitat characteristics of the fragments. Long *et al.* (1996) reported that the endemic bird areas within tropical dry forest in central America were restricted to the Pacific slope of Mexico, Guatemala, El Salvador, Honduras, and Nicaragua, and did not extend south to Costa Rica. Results from our study concur with Long *et al.* (1996) in that restricted-range birds are concentrated in this area. An examination of bird species richness in remaining forest fragments in this endemic bird region of central America appears warranted.

CONCLUSIONS AND IMPLICATIONS

This research concurs with a number of studies that measures of bird species richness are determined by a diversity of factors, such as forest area, floristic diversity, vegetation composition, and structure at a regional scale and that there is no single factor that can completely examine the distribution of bird species richness (Terborgh, 1985; Cueto & Lopez de Casenave, 1999; Freifeld, 1999). Some commonly used landscape metrics were not significant in predicting bird species richness at a regional scale. Further research that tests the utility and accuracy of landscape characteristics with empirical observations in regions with fragmented forest over different spatial scales is needed.

Based on resident and forest bird species richness, Santa Rosa National Park should receive a high priority for regional conservation. Currently, this reserve is one of the best managed and protect reserves in central America (Janzen, 1988b). The Cosiguina and Chacocente reserves in Nicaragua also contain relatively high species richness and contain a number of restricted-range species that are of importance to regional conservation. These reserves should receive the highest conservation priority in the tropical dry forest region of Nicaragua.

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REFERENCES

Bierregaard, R.O. Jr, Lovejoy, T.E., Kapos, V., Augusto dos Santos, A. & Hutchings, R.W. (1992) The biological dynamics of tropical rainforest fragments. *Bioscience*, **42**, 859–866.

Bohning-Gaese, K. (1997) Determinants of avian species richness at different spatial scales. *Journal of Biogeography*, **24**, 49–60.

Bull, J. & Farrand, J. (1987) *The Audubon society field guide to North American birds*. Alfred A. Knopf, New York.

Ceballos, G. (1995) Vertebrate diversity, ecology and conservation in neotropical dry forests. *Seasonally dry tropical forests* (eds S.H. Bullock, H.A. Mooney and E. Medina), pp. 195–220. Cambridge University Press, Cambridge.

Christiansen, M.B. & Pitter, E. (1997) Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. *Biology Conservation*, **80**, 23–32.

Corcuera, P.M. & Butterfield, J.E. (1999) Bird communities of dry forest and oak woodland of western Mexico. *Ibis*, **141**, 240–255.

Cueto, V.R. & Lopez de Casenave, J. (1999) Determinants of bird species richness: role of climate and vegetation structure at a regional scale. *Journal of Biogeography*, **26**, 487–492.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *American Naturalists*, **137**, 27–49.

Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biology Conservation*, **7**, 129–145.

Estrada, A., Coates-Estrada, R., Meritt, D., Montiel, S. & Curiel, D. (1993) Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio*, **107/108**, 245–257.

Estrada, A., Coates-Estrada, R. & Meritt, D.A. Jr (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, **6**, 19–44.

Forman, R.T. (1995) *Landscape mosaics*. Cambridge University Press, Cambridge.

Freifeld, H.B. (1999) Habitat relationships of forest birds on Tutuila island, America Samoa. *Journal of Biogeography*, **26**, 1191–1213.

Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1–84.

Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.

Gillespie, T.W. (1999) Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America. *Journal of Tropical Ecology*, **15**, 637–649.

Gillespie, T.W. (2001) Application of conservation and extinction theories for forest birds of Nicaragua. *Conservation Biology*, **15**, 699–709.

Gillespie, T.W., Grijalva, A. & Farris, C.N. (2000) Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, **147**, 37–47.

Hammond, D.S. & Brown, V.K. (1995) Seed size of woody plants in relation to disturbance, soil type in wet Neotropical forests. *Ecology*, **76**, 2544–2561.

Holdridge, L.R., Grenske, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. (1971) *Forest environments in tropical life zones*. Pergamon Press, New York.

Howe, H.E. (1984) Implications of seed dispersal by animals for tropical reserve management. *Biology Conservation*, **30**, 261–281.

Howell, T.R. (1971) A comparative ecological study of birds of the lowland pine savanna and adjacent rainforest in North-eastern Nicaragua. *Living Bird*, **10**, 185–242.

Hutto, R.L., Pletschet, S.M. & Hendricks, P. (1986) A fixed-radius point count method for nonbreeding and breeding season use. *Auk*, **103**, 593–602.

James, F.C. & Wamer, N.O. (1982) Relationships between temperate forest bird communities and vegetation structure. *Ecology*, **63**, 159–171.

Janzen, D.H. (1988a) Tropical dry forests: the most endangered major tropical ecosystem. *Biodiversity* (ed. E.O. Wilson), pp. 130–137. Natural Academy Press, Washington.

Janzen, D.H. (1988b) Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden*, **75**, 105–116.

Karr, J.R. & Roth, R.R. (1971) Vegetation structure and avian diversity in several new world areas. *American Naturalist*, **105**, 423–435.

Krummel, J., Gardner, R.H., Sugihara, G., O'Neill, R.V. & Coleman, P.R. (1987) Landscape patterns in a disturbed environment. *Oikos*, **48**, 321–324.

Kupfer, J.A. (1995) Landscape ecology and biogeography. *Progress in Physical Geography*, **19**, 18–34.

Laurance, W.F., Bierregaard, R.O. Jr, Gascon, C., Didham, R.K., Smith, A.P., Lynam, A.J., Viana, V.M., Lovejoy, T.E., Sieving, K.E., Sites, J.W. Jr, Andersen, M., Tocher, M.D., Kramer, E.A., Restrepo, C. & Moritz, C. (1997) Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. *Tropical forest remnants* (eds W.F. Laurance and R.O. Bierregaard), pp. 502–514. University of Chicago Press, Chicago.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Long, A.J., Crosby, M.J., Stattersfield, A.J. & Wege, D.C. (1996) Towards a global map of biodiversity: patterns in the distribution of restricted-range birds. *Global Ecology and Biogeography Letters*, **5**, 281–304.

Lovejoy, T.E. (1982) Designing refugia for tomorrow. *Biology diversification in the tropics* (ed. G.T. Prance), pp. 673–680. Columbia Press, New York.

Lynch, J.F. & Whigham, D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biology Conservation*, **28**, 287–324.

MacArthur, R.H. (1964) Environmental factors affecting species diversity. *American Naturalist*, **98**, 387–397.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

MacArthur, R.H., Recher, H.F. & Cody, M.L. (1966) On the relation between habitat selection and species diversity. *American Naturalist*, **100**, 319–332.

MacNally, R.C. (1990) The roles of floristics and physiognomy in avian community composition. *Australian Journal of Ecology*, **15**, 321–327.

Manne, L.L., Brooks, T.M. & Pimm, S.L. (1999) Relative risk of extinction of passerine birds on continents and islands. *Nature*, **399**, 258–261.

McGarigal, K. & Marks, B. (1994) Fragstats: spatial pattern analysis program for quantifying landscape structure. Oregon State University, Corvallis.

Medellin, R.A. & Osiris, G. (1999) Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, **31**, 478–485.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Newmark, W.D. (1991) Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara mountains, Tanzania. *Conservation Biology*, **5**, 67–78.

Orians, G.H. (1969) The number of bird species in some tropical forests. *Ecology*, **50**, 783–801.

Poulsen, B.O. & Krabbe, N. (1998) Avifaunal diversity of five high-altitude cloud forests on the Andean western slope of Ecuador: testing a rapid assessment method. *Journal of Biogeography*, **25**, 83–93.

Remsen, J.V. Jr (1994) Use and misuse of bird lists in community ecology and conservation. *Auk*, **111**, 225–227.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.

Rosenzweig, M.L. & Abramsky, Z. (1993) How are diversity and productivity related? *Species diversity in ecological communities: historical and geographical perspectives* (eds R.E. Ricklefs and D. Schluter), pp. 52–65. University of Chicago Press, Chicago.

Rotenberry, J.T. (1985) The role of habitat in avian community composition: physiognomy or floristics? *Oecologia*, **67**, 213–217.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Siegfried, W.R., Benn, G.A. & Gelderblom, C.M. (1998) Regional assessment and conservation implications of landscape characteristics of Africa national parks. *Biology Conservation*, **84**, 131–140.

Silva, J.M.C. & Tabarelli, M. (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, **404**, 72–74.

Snow, B.K. & Snow, D.W. (1971) The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk*, **88**, 291–322.

Stiles, F.G. (1983) Birds: introduction and checklist. *Costa Rican natural history* (ed. D.H. Janzen), pp. 502–544. University of Chicago Press, Chicago.

Stiles, F.G. (1985) Conservation of forest birds in Costa Rica: problems and perspectives. *Conservation of tropical forest birds* (eds A.W. Diamond and T.E. Lovejoy), pp. 141–168. ICBP Technical Publication no. 4, Cambridge.

Stiles, F.G. & Skutch, A. (1989) *A guide to the birds of Costa Rica*. Cornell University Press, New York.

Terborgh, J.W. (1985) Habitat selection in Amazonian birds. *Habitat selection in birds* (ed. M.L. Cody), pp. 311–338. Academic Press, Orlando.

Turner, I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.

Veblen, T.T., Kitzberger, T. & Lara, A. (1992) Distrubance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *Journal of Vegetation Science*, **3**, 507–520.

Warburton, N.H. (1997) Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. *Tropical forest remnants* (eds W.F. Laurance and R.O. Bierregaard), pp. 190–206. University of Chicago Press, Chicago.
Whittaker, R.H. (1975) *Communities and ecosystems*. Macmillan, New York.
Wiens, J.A. (1989) *The ecology of bird communities, Vol. 1: foundations and patterns*. Cambridge University Press, Cambridge.
Willis, E.O. (1979) The composition of avian communities in remanescent woodlots in southern Brazil. *Papeis Avulsos Zoologia*, **33**, 1–25.
Zuidema, P.A., Sayer, J.A. & Dijkman, W. (1996) Forest fragmentation and biodiversity: the case for intermediate-sized conservation areas. *Environmental Conservation*, **23**, 290–297.

BIOSKETCHES

Tom Gillespie received his PhD in Geography from the University of California Los Angeles in 1998. His research interests focus on predicting patterns of bird and plant species richness in fragments of tropical dry forest in the Caribbean, central America, and south-east Asia.

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Appendix 1 Life history characteristics and distribution of birds encountered in seven reserves with tropical dry forest in central America

Family and scientific name	Fruit-eating	Forest preference	Restricted range	Santa Rosa	Palo Verde	Chacocente	Cosiguina	Masaya	La Flor	Ometepe
Tinamidae										
Crypturellus cinnamomeus	F	P	R	x	x	x	x	x		
Cathartidae										
Cathartes aura		O		x	x	x		x	x	x
Coragyps atratus		O		x	x	x	x	x	x	x
Accipitridae										
Buteo magnirostris		O		x	x	x		x	x	x
Buteogallus urubitinga		F							x	
Leptodon cayannensis		F					x			
Falconidae										
Herpetotheres cachinnas		P			x					
Polyborus plancus		O				x			x	
Columbidae										
Columba flavirostris	F	P		x			x			x
Columbina inca		O				x	x		x	
Leptotila plumbeiceps	F	P				x	x			
L. verreauxi		P		x	x	x	x	x	x	x
Zenaida asiatica		O		x						
Psittacideae										
Amazona albifrons	F	P		x		x			x	
A. auropalliata	F	P	R	x	x	x	x			x
Aratinga canicularis	F	P	R	x	x	x	x	x	x	x
A. strenua	F	P	R					x		
Brotogeris jugularis	F	O	R	x		x	x			x
Cuculidae										
Piaya cayana		P		x	x	x	x	x		
Trochilidae										
Amazilia cyanura		P	R			x	x			
A. rutila		P	R	x	x	x		x	x	x
A. saucerottei		P	R	x	x	x		x	x	x
A. tzacatl		O				x	x	x	x	
Chlorostilbon canivetti		O	R			x	x		x	x
Heliomaster constantii		P				x			x	

Appendix 1 *Continued*

Family and scientific name	Fruit-eating	Forest preference	Restricted range	Santa Rosa	Palo Verde	Chacocente	Cosiguina	Masaya	La Flor	Ometepe
Trogonidae										
Trogon elegans	F	P	R	x	x	x	x			
T. melanocephalus	F	P	R	x	x	x	x	x	x	x
T. violaceus	F	P		x						
Momotidae										
Eumomota superciliosa		O	R		x		x			
Momotus momota	F	P		x	x					
Picidae										
Campephilus guatemalensis	F	P		x	x					
Dryocopus lineatus	F	P					x			
Melanerpes hoffmannii	F	P	R	x	x	x	x	x	x	x
Dendrocolaptidae										
Dendrocolaptes certhia		P		x	x					
Lepidocolaptes souleyetii		P		x	x					
Sittasomus griseicapillus		P		x	x					
Xiphorhynchus flavigaster		P		x			x			
Formicariidae										
Thamnophilus doliatus		P		x						
Pipridae										
Chiroxiphia linearis	F	P	R	x	x	x				
Tyrannidae										
Camptostoma imberbe	F	P		x	x					x
Elaenia flavogaster	F	O		x						
Megarhynchus pitangua	F	P		x	x	x	x	x		
Myiarchus nuttingi	F	P		x		x			x	
M. tuberculifer	F	P		x	x	x	x	x	x	x
M. tyrannulus	F	P		x	x	x	x	x	x	x
Myiodynastes maculatus	F	P		x	x		x			
Myiozetetes similis	F	O		x	x					
Pachyramphus aglaiae	F	P			x					
Pitangus sulphuratus	F	O		x	x	x	x	x		x
Tityra semifasciata	F	P		x			x			
Todirostrum sylvia		P		x		x				
Tolmomyias sulphurescens	F	O		x	x	x	x	x		
Corvidae										
Calocitta formosa	F	O	R	x		x	x	x	x	x
Vireonidae										
Vireo flavoviridis	F	O	R				x			
Troglodytidae										
Campylorhynchus rufinucha		P	R	x	x	x	x	x		
Thryothorus pleurostictus		P	R	x	x	x	x	x	x	x
T. rufalbus		P	R			x				
Sylviidae										
Polioptila albiloris		P	R	x	x	x	x	x	x	
Hirundinidae										
Progne chalybea		O				x			x	
Parulidae										
Basileuterus rufifrons	F	P		x	x			x		
Parula pitiayumi	F	P								x
Emberizidae										
Aimophila ruficauda		P	R				x			
Arremon aurantiirostris		P		x	x					

Appendix 1 *Continued*

Family and scientific name	Fruit-eating	Forest preference	Restricted range	Santa Rosa	Palo Verde	Chacocente	Cosiguina	Masaya	La Flor	Ometepe
Thraupidae										
Cyanerpes cyaneus	F	P		x						
Eucometis penicillata	F	P		x						
Euphonia affinis	F	P					x			
Icteridae										
Icterus pustulatus		O			x		x	x		
Psarocolius montezuma	F	P	R			x				
Quiscalus mexicanus	F	O								x
Total	37	71	22	46	36	37	35	24	23	21

Family and scientific name follow Stiles & Skutch (1989). Fruit-eating: F – birds that include fleshy fruit in their diet following Stiles & Skutch (1989). Forest preference following Stiles (1985): F – requires almost solid forest, P – requires at least patchy forest, O – does not require forest. Restricted range birds: R – birds with a geographic range of less than 100,000 km^2.