

BIRD COMMUNITY DIFFERENCES IN MATURE AND SECOND GROWTH GARÚA FOREST IN MACHALILLA NATIONAL PARK, ECUADOR

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Resumen. – **Diferencias entre las comunidades de aves de bosque de garúa maduro y secundario en el Parque Nacional Machalilla, Ecuador.** – Las estrategias de conservación a nivel de los ecosistemas son más eficaces si consideran el grado de sensibilidad que presentan los organismos frente a la pérdida o el cambio estructural de su hábitat. Este estudio presenta información sobre las comunidades de aves del bosque húmedo de la región Tumbesina del Ecuador y, compara mediante el uso de redes de neblina y observación directa, la composición de aves presentes en bosque de garúa maduro y secundario dentro del Parque Nacional Machalilla (PNM). En este estudio registramos 159 especies de aves durante las épocas seca y lluviosa de 1999 & 2000. Realizamos un esfuerzo total de muestreo de 1950 h de capturas con redes y capturamos 729 individuos pertenecientes a 85 especies. Alrededor del 60% de las especies capturadas en redes de neblina dentro de uno u otro tipo de bosque no se hallaban compartidas. La riqueza de especies fue mayor en bosque secundario y se sugiere algunas razones autoecológicas: 1) presencia de especies dependientes de bosque maduro ausentes en bosque secundario, 2) especies insectívoras generalistas prefieren bosque secundario, y 3) especies migratorias prefieren habitats marginales secundarios. Tres especies de aves endémicas y amenazadas, *Hylocryptus erythrocephalus*, *Leptotila ochraceiventris* y *Lathrotriccus griseipectus* fueron registradas frecuentemente en bosque secundario y no en bosque maduro. La riqueza de especies pertenecientes a los géneros de hormigueros fue mayor en bosque maduro, y estuvo relacionada con la abundancia de artrópodos. Diecisiete especies se registraron únicamente en bosque de garúa maduro, pero ninguna se halla dentro de alguna categoría de amenaza. Entre las más importantes podemos destacar, *Gymnophithys leucaspis*, *Sclerurus guatemalensis* y *Turdus daguae*. La alta detectabilidad de estas especies dentro del bosque sugiere su uso como especies indicadoras de bosque de garúa, el mismo que se halla en peligro de extinción.

Abstract. – Species monitoring for conservation planning is aided by understanding species' sensitivities to habitat change or loss. We studied bird communities in garúa forest, a type of low elevation tropical cloud forest in western Ecuador and Peru that is threatened by land conversion. We used mist-nets and strip counts to compare bird communities in second growth and mature garúa forest at Machalilla National Park, Ecuador. During the two wet and two dry seasons of 1999 and 2000, we recorded 159 bird species. In 1950 h of mist netting, we captured 729 individuals of 85 species. Over 60% of the species were unique to either second growth or mature forest. Species richness of birds was greater in second growth than in mature garúa forest for reasons apparently unrelated to abundance or diversity of food resources. Generalist insectivore species, dry forest endemic birds, and Neotropical migrants readily used second growth forest, while mature garúa forest species were absent or significantly less abundant. Three endemic and endangered species, Henna-hooded Foliage-gleaner (*Hylocryptus erythrocephalus*), Ochre-bellied Dove

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(*Leptotila ochraceiventris*), and Gray-breasted Flycatcher (*Lathrotriccus griseipectus*) were found in second growth more often than in mature forest. Antbird species richness and abundance was greater in mature garúa forest, than in second growth, possibly due to differential arthropod abundance in forest litter. Seventeen bird species were only encountered in mature garúa forest and none were threatened. Among them, Bicolored Antbird (*Gymnophithys leucaspis*), Scaly-throated Leaf-tosser (*Sclerurus guatemalensis*), and Dagua Thrush (*Turdus daguae*) were easy to detect by sight or song, making them good indicator species for this type of tropical forest. Birds detected by observation and listening were similar in both forest types making trail surveys less useful than mist netting for detecting differences between bird communities in the two forest types. Accepted 4 March 2005.

Key words: Tropical forest conservation, garúa forest, indicator species, endemic birds, western Ecuador, secondary forest, mature forest.

INTRODUCTION

In addition to studying the last primary forest patches in the Neotropics, ornithologists are trying to determine the value of human-modified lands and second growth habitats for bird conservation (Petit & Petit 2002). Since the 1950s, 95% of the primary forest in western Ecuador has been converted to pasture, crops, and second growth forest (Dodson & Gentry 1991). Elsewhere in the Neotropics, such rapid change in land cover caused major declines and extirpations of birds (Kattán *et al.* 1994, Stratford & Stouffer 1999, Estrada *et al.* 2000). With a baseline understanding of what species avoid second growth and prefer mature tropical forest, we can better predict the future composition of bird communities in tropical forests, evaluate the success of restoration efforts, and possibly thwart further extinctions via habitat preservation. In this paper, we compare the composition of bird communities in mature and second growth “garúa” (fog and mist) forests in Machalilla National Park, in the Tumbesian Endemic Bird Area (EBA) of Ecuador, an area of significant importance for 55 restricted-range bird species (Stattersfield *et al.* 1998, Birdlife International 2003).

Along isolated and patchy mountain ridges of the Tumbesian region, a humid forest similar to high elevation Andean cloud forest exists. However, unlike Andean cloud

forests that obtain moisture from clouds, these forests strip moisture from oceanic mists and fog (Becker 1999). Regional botanical experts refer to this type of vegetation as garúa forest (Elao 1996). Garúa forests have physiognomically typical cloud forest vegetation (dense loads of vascular epiphytes and bryophytes on tree branches and trunks) and occur as low as 400 m (Parker & Carr, 1992). Described by Chapman (1926), Best & Kessler (1995), and Stattersfield *et al.* (1998), garúa forest in the Colonche Hills are dominated by tree genera such as *Beilschmiedia*, *Rhedia*, *Ocotea*, *Gleospermum* and *Quararibea* (Elao 1996).

Garúa forests are used by a wide variety of birds in western Ecuador, including 22 species of hummingbirds, 79 regionally endemic species, and 15 species listed as threatened and near-threatened (Becker & López-Lanús 1997). Also, microclimate differences between leeward and windward slopes of garúa forest can strongly define bird communities at a local level (Becker 1999). Still, little is known about the community of birds in mature garúa forest, relative to second growth garúa forest and no research on avian sensitivity to forest degradation has been conducted in this type of tropical forest. In this study, we address three questions: 1) Does bird species composition in mature garúa forest differ substantially from that in second growth garúa forest? 2) What factors influ-

ence species richness in mature versus second growth garúa forest? and, 3) What bird species unique to or abundant in mature garúa forest could be good indicators of this habitat type?

Species richness of birds might be expected to be greater in mature than secondary garúa forest, because mature forests are taller and have more vertical heterogeneity than second growth forests (Rice *et al.* 1984). The number of migrant and resident bird species has been found to increase with vertical foliage diversity (Greenberg 1996), and mature forests offer greater potential for niche diversification (Hutchinson 1959, Schoener 1986). On the other hand, species richness has generally been found to be greater in successional habitats than in climax ones because of the variety of generalists species attracted there (Ambuel & Temple 1983, Warkentin *et al.* 1995, Grey *et al.* 1998). We predict that bird communities in both mature and second growth forest patches on Cerro San Sebastián will both be dominated by wide-spread generalist bird species, because the mature forest patches are relatively small. We also predict that second growth will have fewer cavity nesting and terrestrial insectivorous bird species, because they depend on micro-habitats associated with old forest stands (Willis 1974, 1979; Leck 1979, Karr 1982, Canaday 1996, Stratford & Stouffer 1999).

Differences between bird species richness and assemblage composition in mature and second growth forests have previously been explained by habitat selection based on: 1) diversity of substrates, 2) abundance of food resources, 3) competitive species interactions, and 4) physical characteristics of the site (Wiens 1989). Since habitat selection by tropical birds is often correlated with food resources (Loiselle & Blake 1991) and micro-habitat features of nest sites (Borges & Stouffer 1999), we investigated whether bird

species richness is greater where food and cover resources (fruits, flowers, insects, and woody understory) are most abundant and variable.

Finally, for conservation work, the presence of certain bird species can be useful indicators for evaluating forest condition (Karr 1982, Stotz *et al.* 1996). Good indicator species are unique, or common in a particular habitat, are easily detected in that habitat, and show high sensitivity to degradation, fragmentation, or loss of a particular habitat (Stotz *et al.* 1996). Avian indicators have been described for forty-one principal habitats in the Neotropics (Stotz *et al.* 1996), but not for garúa forests of the Tumbesian endemic bird area (EBA).

METHODS

Study area. Machalilla National Park (hereafter, Machalilla) is located in Manabi Prov., Ecuador, and encompasses an area of 55,095 ha including La Plata Island and the ocean surrounding it. Machalilla was established to preserve coastal tropical dry forest, a threatened biome with high bird endemism (Stattersfield *et al.* 1998), and to protect important marine resources (Zambrano & Vargas 1998). Below 300 m, Machalilla is covered by dry forest and arid scrub recovering from excessive grazing and removal of trees for charcoal production (Zambrano & Vargas 1998).

At elevations above 300 m, on west facing slopes, most of Machalilla's primary garúa forest was selectively harvested or completely cleared during the 1950s and 60s (Zambrano & Vargas 1998). Now, with protection from grazing and timbering, about 6000 ha of Machalilla should eventually regenerate to garúa forests (Cuéllar *et al.* 1992). Our study of bird communities took place on Cerro San Sebastián, the highest peak in Machalilla (700 m) where approximately 400 ha of mature garúa forest still remain and are surrounded

by second growth forest.

Average annual temperatures at Machalilla are 18–22°C. Annual rainfall can vary from none to 4000 mm, but averages 375 mm per year (Cañadas-Cruz 1983). December and January are normally the driest months, except during El Niño years when rainfall can be at least an order of magnitude greater than average. Rainfall is highest during February to May, peaking in March. Fog and mist are present from June to November and can contribute as much water to coastal hill forest watersheds as annual rainfall (Becker 1999).

Bird community sampling. We used mist nets and observations along trails to sample birds in mature and secondary garúa forests during the dry and wet seasons of 1999 and 2000. An independent mist netting sample consisted of operating 10 mist nets (12 m x 2.8 m, 36 mm mesh) from 06:00 to 11:00 h for 3 consecutive days in each forest type (mature, secondary). We conducted six independent samples of bird composition in mature forest and seven in second growth forest.

We placed mist nets on or adjacent to the trail every 25–40 m starting with a randomly selected location along a trail. Independent sets of nets were separated by at least 500 m. Elevation, terrain, orientation, and slope were similar for the nets in both forest types. To reduce edge effects (Restrepo & Gomez 1998), nets in mature, closed-canopy forests were at least 1000 m from second growth or edge habitats. Likewise, nets in second growth forest were at least 1000 m from mature forest. Dry forest and scrub associated with lower elevations (below 300 m) was about 5 km from garúa forest sampling areas. During a sampling session we weighed, made standard morphometric measurements, banded, identified to species, sexed, and aged (when possible) each bird captured in the nets (Bibby *et al.* 1992; Ralph *et al.* 1993).

Mist-netting tends to over-sample small,

highly mobile birds in the understory, and under-sample large-bodied birds and canopy species (Remsen & Good 1996). To assess the degree of this bias in garúa forest, we augmented our list of birds in each forest type by sampling along strip transects (Bibby *et al.* 1992) where mist nets were located. Observers (A. Agreda, D. Becker, O. Rodriguez) skilled at identifying birds by song and sight, spent 2–3 h each morning and evening recording bird species in each forest type. Effort per forest type was about 320 person-h. Number of captures and detections were used to rank birds as common, uncommon or rare in the two forest types, and to assess the set of bird species detected by each method. We considered species “common” and “abundant” if they were seen, heard, or netted on most days of the study, “uncommon” if seen, heard, or netted on several sampling days, and “rare” if they were seen, heard, or netted only once or twice during the study.

Vegetation sampling. In March (wet season), we sampled forest vegetation in 10 x 12 m plots placed at five randomly selected mist net locations in each forest type in 1999. Percentage ground and canopy cover were estimated visually by the same observer in each plot and forest type. The species richness of trees, shrubs, and herbs was determined by counting the number of different species of each plant type. Presence or absence of fruits and flowers on trees and shrubs were noted and estimates of abundance were made. We recorded diameter at breast height (dbh) for trees (single woody stems with a dbh greater than 10 cm), and estimated tree height to the nearest meter using hypsometers. Plants with single or multiple woody stems with a dbh greater than 2.5 cm, but less than 10 cm, were recorded as “shrubs or saplings” and woody stems smaller than 2.5 cm in diameter were counted as “seedlings”. In the center of each plot, soil moisture was measured using a

Kelway soil tester. In March 2000, vegetation data were collected in two 20 x 20 m plots located in randomly selected, but representative areas of each forest type. The sampling method changed when project leadership shifted from Becker to Agreda. The large plots were sub-divided into four quadrats of 10 x 10 m, and one of these was randomly selected to describe the understory layer, canopy cover, number and species of seedlings, height and dbh of trees and percentage cover by shrubs and herbs.

Arthropod sampling. To determine the relative abundance and types of arthropods in the two forest habitats we used sweep sampling (Southwood 1978 *vide* Borror *et al.* 1989) and developed a new leaf litter sampling method. Arthropods in leaf litter were quickly gathered into dip nets from a 50 x 50 cm frame placed on the ground 5 m from the midpoint of each mist net (ordered sampling with a random start). Arthropods found inside the frame were classified to order, counted, and preserved in alcohol. Sixty independent leaf-litter samples were obtained from each forest type: 40 in January 2000 (dry season) and 20 in March 2000 (wet season). Depth of the litter layer (cm) was measured with a ruler, and the air-dried litter (sticks, leaves, and organic material above the soil) was weighed with a spring balance. Prior to collecting litter and arthropods from the framed area, the percentage of bare ground, green vegetation, and decayed organic matter covering the surface of each 2500 cm² leaf-litter plot was estimated.

We sampled arthropods from surfaces of understory vegetation (shrubs, herbs, treelets, tree trunks) using a 30-cm diameter sweep net. An independent sample consisted of 30 sweeps, moving the net across vegetation to the left and right of one's body while advancing slowly through the understory of a randomly selected 10 x 10 m area. Three sweep samples were completed in each forest type at

three randomly selected mist-net sites and on two large vegetation plots (N = 5 per forest type). Arthropod samples were pooled by sampling technique, forest type, and season, and preserved in 70% alcohol. Pooled samples were classified to the lowest taxonomic level possible (usually family or genus) by entomologist, T. McKay (Kansas State University).

Taxonomy, conservation status, and statistical analyses. We followed Ridgely & Greenfield (2001) for taxonomy and general ecology of bird species in Ecuador, and Stattersfield *et al.* (1998) for distribution and ecology of restricted-range species in the Tumbesian EBA. A species was considered a generalist if it was observed or captured in several types of habitats, filled a known broad dietary niche (like some frugivores), and had no obvious morphological adaptation or specialized strategy for obtaining food (Ridgely & Tudor 1989 & 1994, Warkentin *et al.* 1995). Specialist guilds included, cavity nesting, ant-following, bark-probing, nectar-feeding, and leaf tossing. We used recent status categories for endangerment and conservation concern published by Birdlife International (2003).

Univariate and factorial analysis of variance (ANOVA), t-tests, and non-parametric statistical tests of data were performed using Statview 4.5 (Roth *et al.* 1995). Alpha was set at 0.05 for all inferential statistics, and Fisher's protracted least significant difference (PLSD) were applied in *post hoc* tests to reduce Type 1 errors associated with multiple comparisons.

To compare species richness and diversity of bird communities associated with second growth versus mature garúa forest, we used the software program EstimateS 5.0.1 (Colwell 1997). We compared three estimators of species richness: CHAO 1, ICE, and ACE. CHAO 1 is a non-parametric estimator of species richness based on patterns of abundance (Chao & Lee 1992). ICE (Incidence-

TABLE 1. Comparison of forest variables sampled in mature and secondary forests on Cerro San Sebastián, Machalilla National Park, Ecuador (Mean \pm SD) during wet season 1999.

Variables	Mature	Secondary	t-test	P
N (120 m ² plots)	5	5		
% ground cover	63 \pm 18	76 \pm 17	2.21	0.03
% canopy cover	75 \pm 15	46 \pm 23	4.75	0.0001
Tree DBH (cm)	22 \pm 19	12 \pm 5	3.49	0.0008
Tree height (m)	13 \pm 7	7 \pm 3	4.87	0.0001
% shrub cover	30 \pm 13	49 \pm 9	2.78	0.024
% herb cover	70 \pm 13	51 \pm 9	2.70	0.024
Tree density ¹	25 \pm 1.4 (SE)	16 \pm 2.8 (SE)	4.0	0.05

¹Data from 20 x 20 m plots.

based coverage estimator) and ACE (Abundance-based coverage estimator) use probabilities associated with finding rare species in the samples to derive estimates of total species richness in a sampling area (Colwell & Coddington 1994, Colwell 1997).

Using S-Plus 2000 (1999) mathematical programming software, we calculated species rarefaction curves (Magurran 1988) to compare species richness in the two forest types. We did Monte Carlo simulations with 1000 repetitions for equal sample sizes drawn randomly from first capture data using subsets of 50 individuals. We calculated 95% confidence intervals for the most species rich sample as an indication of the maximum variation around the rarefaction curves. Jaccard similarity indices and Morisita-Horn beta-diversity were also compared for the avian communities sampled in the two forest types (Magurran 1988).

RESULTS

Vegetation in garúa forest. Tree genera in mature forest at Cerro San Sebastián included Moraceae (*Ficus*, *Paulesenia*, and *Cecropia*), Lauraceae (*Ocotea* and *Cinnamomum*), Bombacaceae (*Matisia*), and Meliaceae (*Trichillia*). Canopy trees

were 20 to 25 m tall and canopy cover ranged from 60 to 80% (Table 1). Understory cover ranged from 30 to 80% by herbaceous and woody plants in the Araceae, Cyclanthaceae, Gesneriaceae, Melastomataceae, and Rubiaceae families. Mature garúa forest had 5 times more canopy trees (> 15 m tall) than second growth forest, which averaged only two canopy trees per plot (166 per ha). Second growth garúa forest also had a lower canopy height (trees ranging from 5 to 10 m), less canopy cover, and thicker ground cover than mature forest (Table 1). Common tree and shrub genera were different between forest types. *Inga* and *Cordia* were the most common tree genera in second growth and genera of Piperaceae shrubs dominated the understory providing abundant vertical and horizontal surfaces for birds. Both types of forest had similar amounts of genera of bamboo and bird of paradise (*Heliconia* spp.).

Mean percentages of shrub and ground cover were greater in second growth than in mature forest (Table 1). Species richness of trees (9 to 18 species per plot) and shrubs (13 to 16 species per plot) were not significantly different in the two forest types. Herbs were more diverse in mature forest than in the second growth forest. Mature forest had a mean

TABLE 2. Mean counts \pm SD of arthropods in mature and secondary forest quadrants (area = 0.25 m²) at Cerro San Sebastián, Machalilla National Park, Ecuador, and statistical outcomes of Fisher's PLSD *post-hoc* comparisons of means based on analysis of variance for each taxon by season (PS) and forest type (PF).

Arthropod taxa	Mature forest		Second growth		PS	PF
	Dry	Wet	Dry	Wet		
Araneida (spiders)	6.0 \pm 0.6	11.0 \pm 1.3	4.7 \pm 4.0	7.6 \pm 4.0	0.000	0.008
Formicidae (ants)	6.0 \pm 10.0	12.0 \pm 18.0	1.6 \pm 6.0	8.7 \pm 11.0	0.003	0.05
Coleoptera (beetles)	0.6 \pm 0.8	5.5 \pm 6.0	0.2 \pm 0.5	5.1 \pm 4.0	0.000	ns
Orthoptera (hoppers)	0.5 \pm 0.7	0.5 \pm 0.8	0.3 \pm 0.6	0.05 \pm 0.2	ns	0.06
Centi/millipedes	0.5 \pm 1.0	3.0 \pm 3.0	0	0.6 \pm 0.9	0.000	0.000
Total count	18.1 \pm 18.0	37.0 \pm 31.0	7.5 \pm 8.8	25.2 \pm 16.0	0.0001	0.0024

of 7 \pm 1.6 species of herbs in small quadrat plots, whereas second growth only averaged 3.3 \pm 3 species per plot ($t_7 = 2.7$, $P < 0.05$).

Resource abundance and richness in mature vs second growth forests. Abundance of food was either the same in both forest types or more abundant in mature forest. Fruit counts were similar in both forest types (Kruskal-Wallis; $P = 0.61$) across seasons. Flowers (mean \pm SE) were in greater abundance in the understory of mature forest (11 \pm 1) flowers per 120 m², $n = 5$) than in second-growth (1.4 \pm 2 flowers per 120 m², $n = 5$, $P < 0.03$) during the dry season of 1999, but no significant difference in flower abundance was detected during other sampling periods.

Arthropod abundance in litter varied by season ($P < 0.001$) and forest type ($P < 0.002$). Mean counts of arthropods differed according to moisture levels and litter depth associated with season and forest habitat type (Table 2). In mature forest, the mean number of arthropods \pm SE was 25 \pm 3 per litter sample, nearly doubling the mean of 13 \pm 2 in second growth forest sites (ANOVA, Fisher's PLSD_{1,118}; $P < 0.003$). During the dry season of 2000, soil moisture averaged 46 \pm 12% in the mature forest, but was only 12 \pm 2% in second-growth forest ($U_{16} = 13$; $P < 0.05$). Biomass of litter in the two habitats was simi-

lar, averaging 212 g per 50 x 50 cm quadrat sample, but litter was significantly deeper (Mean \pm SD) in the mature forest, 41 \pm 3 cm deep ($n = 59$) versus 29 \pm 2 cm ($n = 60$) in the secondary forest ($t_{117} = 3.4$, $P < 0.05$). The proportion of roaches and spiders was greater in dry conditions, while ants and isopods were more abundant in relatively moist conditions. During the dry season of 2000, ants made up 22% of the mature forest sample, but represented only 3% of the arthropod in second growth. During the wet season of 2000, ants represented 54% and 45% of the arthropods in mature and secondary forest, respectively.

A similar number of arthropods per sweep sample were recorded in both habitats with spiders, chrysomelid beetles, and lauxaniid flies most common. Litter samples from the two forest types were dominated by arachnids (spiders), isopods (pillbugs), ants, and *Blattaria* (roaches). Both forest types were similar in richness of arthropod taxa, averaging 20 families per sample for pooled sweeps and litter samples. The richness of non-insect taxa (Chilopoda, Diplopoda, Isopoda, Araneida, *Acarina*, Scorpionida, Chelonethida, Phalangida) averaged one taxon in sweep samples and five in litter samples (Fisher's PLSD_{1,7}; $P < 0.02$), but richness of arthropod taxa was not significantly different by forest type.

TABLE 3. Results of multivariate analysis of variance on daily captures of birds by forest type (mature and second growth), season (dry and wet), year (1999 or 2000), and day (1, 2, 3). Data are from mist-net samples on Cerro San Sebastián in Machalilla National Park, Ecuador. Insignificant interactions are not shown.

Sources	Number of birds captures per day		
	df	F	P
Forest type	1,12	9.9	0.008
Season	1,12	5.9	0.03
Year	1,12	15.2	0.002
Day	2,12	7.0	0.009
Forest type * Year	1,12	8.3	0.01

Avian community: metrics and estimates of species richness. We detected 159 bird species in Cerro San Sebastián study area (Appendix 1). During 1950 h of mist netting, we captured 729 individuals (866 captures in total) belonging to 85 species (53.4% of the total species recorded). The percentage of recaptures across seasons was 15.8%.

An equal effort comparison using six samples from each forest type resulted in 771 captures with more captures in second growth: 56% vs 44% in the mature forest. Forty-nine species were netted in mature garúa forest, whereas 66 species were netted in second growth. The two forest types were estimated to share 42 species, a Morisita-Horn value of 0.58. When all mist-netting results were included (uneven effort), a Jaccard similarity score (Magurran 1988) of 0.60 resulted from 32 species netted in both forest types (76% of the Morisita-Horn estimate). Still, 53 species detected with mist nets were unique to either mature or second growth garúa forest. Birds detected by observation were typically larger and were found in both forest types making strip counts less useful than mist netting for detecting differences

between the two forest types.

The mean number of birds netted per day varied by forest type, year, season, and day of a netting session (ANOVA, Table 3, Fig. 1). Because “day” did not interact significantly with other variables, daily means were treated as independent in parametric statistical comparisons. In 1999, mean daily captures were significantly higher in second growth than in mature garúa forest, and higher during dry than wet season (ANOVA with *post hoc* Fisher’s PLSD; $P < 0.05$, Table 3, Fig. 1). In 2000, no significant differences in mean daily captures were noted by sample, season, or forest type (Fig. 1). Overall, the mean number of species captured per day in second growth (15 ± 4.7) was greater than in mature garúa forest (11.6 ± 3.4 , $t_{34} = -2.5$, $P = 0.02$) and daily species richness was correlated with the number of individuals captured in both habitats ($r^2 = 0.8$, $P < 0.001$).

Rarefaction (Smith *et al.* 1985) and Monte Carlo simulation show that species accumulation in second growth consistently exceeds that for mature forest (Fig. 2). Bird species richness estimates generated by EstimateS were also higher for second growth than mature forest. ACE, ICE, and CHAO 1 estimates of species richness were $82 \text{ species} \pm 2.5$, 84 ± 1.7 , and 91 ± 15 , respectively, for second growth, but only $65 \text{ species} \pm 4$, 63 ± 4.5 , and 62 ± 8.5 , respectively, for mature forest.

Composition of Avian Communities. Generalists bird species dominated second growth areas, but were less abundant in the small patch of mature forest. Species richness of nectar feeders and frugivorous cavity nesting birds were similar in the two forest types. Sallying insectivores and canopy insectivores (generalist insectivores) were more numerous in second growth (Fig. 3). Nearctic migrants, flexible generalists in foraging and habitat use, represented 2.3% of the individuals captured in

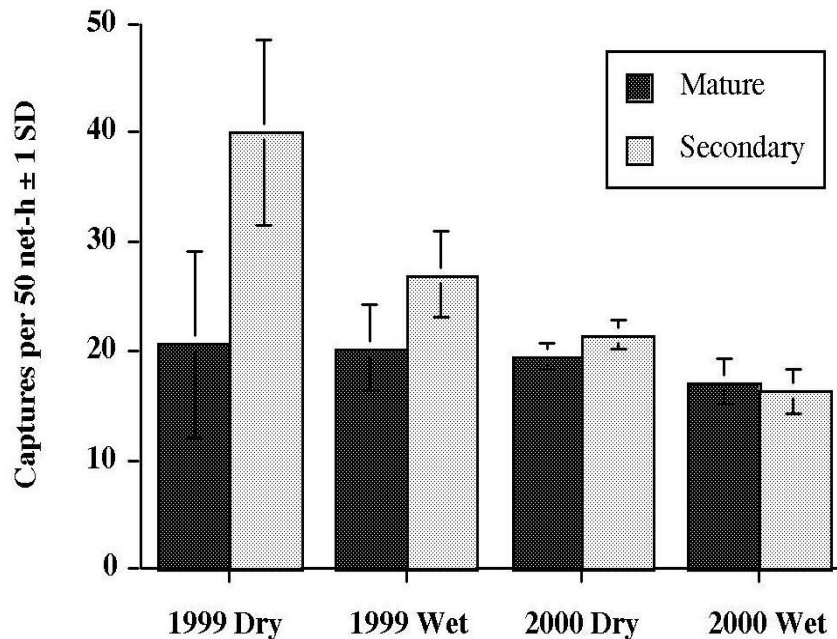


FIG. 1. Variation in mean capture rate of birds in mature and secondary garúa forest by season (dry, wet) and year on Cerro San Sebastián in Machalilla National Park, Ecuador. Error bars are standard deviations.

second growth, showing a clear preference for marginal habitats (Fig. 3). Specialist insectivores such as ant-following and leaf-tossing terrestrial foragers, and bark-probers were more prevalent in mature forest than second growth (Fig. 3; $\chi^2_8 = 67.6$, $P < 0.0001$).

Of the 15 most common species sampled in mist-nets, less than half were frequently mist-netted in both forest types (Table 3). Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) and Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) were abundant in mature forest samples, but were rare or absent in second growth samples (Appendix 1, Table 3). Slaty Antwren (*Myrmotherula schisticolor*) and Black-headed Anthrush (*Formicarius nigricapillus*) were among the 15 most commonly mist-netted birds in mature forest, but were not recorded in second growth. Captures of spotted Nightingale-thrush (*Catharus dryas*) were ten-fold higher in mature forest than second

growth. Ecuadorian Thrush (*Turdus maculirostris*) and Swainson's Thrush (*Catharus ustulatus*) were fairly common in second growth, but absent in mature forest samples (Appendix 1, Table 3). Olivaceous Woodcreeper (*Sittasomus griseicapillus*) was common in second-growth, but was half as likely to be caught in mature forest (Appendix 1, Table 3).

Moderately common species, representing at least 1% of the captures in both habitats, accounted for 445 captures, or 51% of the total (Appendix 1). Nine of these 38 moderately common species had significantly higher captures in mature forest than in the second growth ($P < 0.05$, PLSD adjusted). For example, Spotted Woodcreeper (*Xiphorhynchus erythropygius*), Plain-brown Woodcreeper (*Dendrocincla fuliginosa*), Chestnut-capped Brush-finch (*Buarremon brunneinucha*), and Gray-breasted Wood-Wren (*Henicorhina leucophrys*) were twice as likely to be captured in mature forest as in

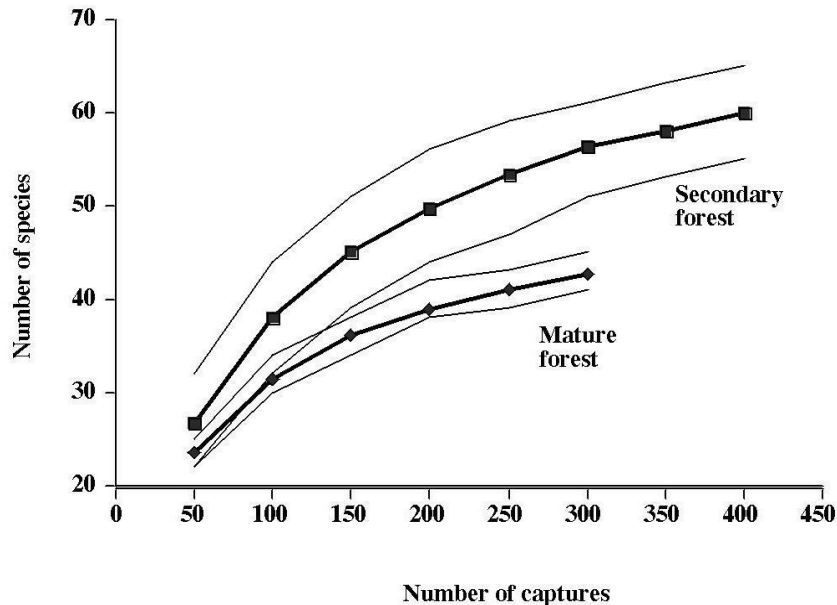


FIG 2. Rarefaction curves for equal-effort samples of bird species netted in mature and secondary garúa forest at Cerro San Sebastián, Machalilla National Park, Ecuador. The dotted lines are 95% confidence intervals.

second growth.

Four species had a statistically higher capture rate in second growth than in mature forest: endemic Gray-and-gold Warbler (*Basileuterus fraseri*), endemic and vulnerable Gray-breasted Flycatcher (*Lathrotriccus griseipectus*), Speckled Hummingbird (*Adelomyia melanogenys*), and Plain Antvireo (*Dysithamnus mentalis*) ($P < 0.05$, PLSD adjusted). Of the 85 species detected by mist nets, 17 species were unique to mature garúa forest (Appendix 1). Of these 17 species, 13 are dependent on mature or old-growth forest morphology for their survival and reproduction. For example, Red-headed Barbet (*Eubucco bourcierii*), Red-rumped Woodpecker (*Veniliornis kirkii*), Crimson-rumped Toucanet (*Aulacorhynchus haematopygus*), Collared Trogon (*Trogon collaris*), Red-billed Scythebill (*Campylorhynchus trochilirostris*), Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*), and Northern Barred-

Woodcreeper (*Dendrocolaptes certhia*) are all cavity nesters that require large and old trees for nesting (Ridgely & Greenfield 2001). Scaly-throated Foliage-gleaner (*Anabacerthia variegaticeps*) forage on epiphytes, and these plants are more abundant on larger, older trees (C. D. Becker pers. observ.). Scaly-throated Leaf-tosser (*Sclerurus guatemalensis*), Dagua Thrush (*Turdus daguae*), and Orange-billed Sparrow (*Arremon aurantirostris*) forage in moist litter on the mature forest floor, where litter is thicker, softer, and contains more arthropod food resources in mature forest than in second growth forest. Finally, Immaculate Antbird (*Myrmeciza immaculata*) and Bicolored Antbird (*Gymnopithys leucaspis*) are obligate army ant followers, and army ants were more available year round in mature than in secondary forest sites.

In total, 35 bird species were unique to second growth (Appendix 1). Nineteen are

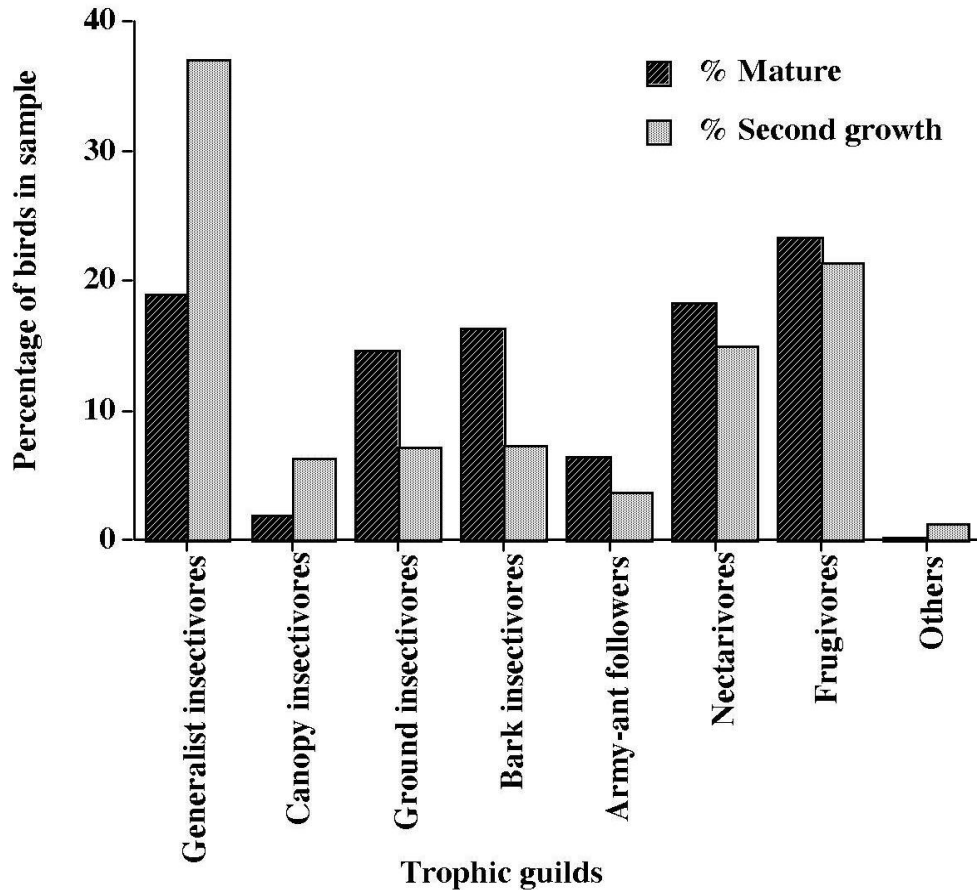


FIG 3. Percentage of netted individuals in different trophic guilds in mature and secondary garúa forest on Cerro San Sebastián, Machallia National Park, Ecuador. Asterisk indicates a significant difference in proportional representation of the guild by forest type (χ^2 ; $P < 0.05$).

widespread species commonly found in secondary and scrub forest of northern South America and parts of Central America (details in Ridgely & Greenfield 2001). Six species recorded only in second growth included Tumbesian endemics that mainly inhabit lowland dry forests and scrub: Henna-hooded Foliage-gleaner (*Hylodyptes erythrocephalus*), Watkin's Antpitta (*Grallaria watkinsi*), Ecuadorian Thrush, Plumbeous-backed Thrush (*Turdus reevei*), Speckle-breasted Wren (*Thryothorus sclateri*), and Black-capped Spar-

row (*Arremon abeillei*). Nearctic migrants were netted in second growth mainly during the wet season. Swainson's Thrush were most abundant followed by Acadian Flycatcher (*Empidonax virescens*), and Summer Tanager (*Piranga rubra*), and all were noted during both years. One Olive-sided Flycatcher (*Contopus cooperi*) netted in second growth in 1999 was a new record for the area. Other new records at Machalilla were: Yellow-margined Flatbill (*Tolmomyias flavotectus*), Pacific Flatbill (*Rhynchocyclus pacificus*), Song Wren (*Cyborhinus*

phaeocephalus), and Smoke-colored Pewee (*Contopus nigrescens*).

Endangered and endemic birds. Several endangered and restricted-range species were found in higher numbers in second growth than in mature garúa forest. Endemic and vulnerable Gray-breasted Flycatcher was four times more likely to be captured in second growth than in mature forest (Appendix 1). Four vulnerable species, Rufous-headed Chachalaca (*Ortalis erythroptera*), Little Woodstar (*Chaetocercus bombus*), Henna-hooded Foliage-gleaner, and Ochre-bellied Dove (*Leptotila ochraceiventris*) were netted, heard, or observed in second-growth, but were not detected by any method in mature forest (Appendix 1). Ochraceous Atilla (*Attila torridus*), vulnerable, was commonly heard in the canopy of forest borders as well as inside mature forest at San Sebastián. Gray-backed Hawk (*Leucopternis occidentalis*), globally endangered, was heard several times at Cerro San Sebastián in both years, but showed no obvious associations by forest type. Capture rates of other endemic species are listed in Appendix 1.

Strip counts. There were no significant differences in species abundance in mature vs second growth forest based on strip count results. Strip counts were more effective than mist nets for detection of large and/or vocal birds like tinamous, toucans, ant-thrushes, parrots, and raptors. Appendix 1 provides a list of species detected during strip counts and their categories of abundance (common, uncommon, rare).

DISCUSSION

Tropical bird assemblages change along natural gradients of elevation (Terborgh & Weske 1975, Young *et al.* 1998, Blake & Loiselle 2000) and at ecotones (Smith 1977). Substantial divergence in bird assemblages occur in

response to forest degradation (Rappole & Morton 1985, Greenberg 1996, Borges & Stouffer 1999) and fragmentation (Bierregaard 1986, Parker & Carr 1992, Stouffer & Bierregaard 1995, Gascon-Claude *et al.* 1999). Community structure often changes in response to disturbance (Connell 1978, Karr 1981, Tilman & Pacala 1993) and when monitored over time, species richness, evenness, and abundance are useful measures of community resilience and stability (Magurran 1988). At San Sebastián, avian species composition in mature and second growth garúa forest differed more than expected given the small patch size of the mature forest. However, the two types of garúa forest differed substantially accentuating the importance of habitat variables for the presence and absence of bird species. Tree and shrub species were entirely different in the two forest types. Mature forest had old, large trees with abundant epiphytes, and had more invertebrate food resources in a deep litter layer. Second growth forest had more horizontal and vertical woody structure in the understory,

Given the loss of primary forest and the rate of fragmentation of mature garúa forest patches in western Ecuador, the sustainability of such isolated and distinctive bird communities is probably in peril. We suggest that staff at Machalilla monitor the bird community in mature garúa forest, using the most sensitive indicator species described in this study, and that they promote the regeneration of mature forest through reforestation and removal of grazing animals in the highlands.

Indicator species for mature Garúa forest. Because they are relatively common, easily detected throughout the year with minimal netting, and appear to show high sensitivity to habitat degradation, at least 23 bird species serve as good indicator species for mature garúa forest (see Appendix 1). Thirteen of these species are especially useful as they exhibit behavioral adaptations for mature for-

est such as nesting in older trees with cavities, foraging on epiphytes, or requiring deep, moist leaf litter to obtain terrestrial arthropods. The presence and proportions of particular antbird species might also be used for habitat evaluation in garúa forest. At Machalilla, Bicolored and Immaculate antbirds avoided second growth, whereas White-backed Fire-eye (*Pyriglena leuconota*) used both forest types. In general, ant-following bird species are extinction prone (Willis 1978, 1979) and they respond negatively to roads (Canaday 1996) and fragmentation (Stouffer & Bierregaard 1995) making their decline a potential indicator of negative anthropogenic activities and their increase a potential sign of forest habitat improvement.

Avian indicators in Ecuadorian garúa forest show little overlap with other major Neotropical habitats (Stotz *et al.* 1996). Our list of indicator species for garúa forest shares only three species with the list for the Chocó lowland forest of northwestern Ecuador (Stotz *et al.* 1996): Immaculate Antbird, Barred Woodcreeper, and Red-billed Scythebill. Chocó lowland forest is the closest endemic bird area (EBA) to Machalilla National Park, and is located immediately north of the Tumbesian EBA.

Given the unique assemblage of birds in mature garúa forest and the rapid decline in this forest type, it is surprising that none of the birds we mist-netted are species of conservation concern. Many bird species in mature garúa forest may belong to historically widespread populations now isolated due to fragmentation. Plant communities on Cerro San Sebastián have greater similarity to those observed in Río Palenque, 200 km northeast in the Andean foothills than with forest communities of the Chocó (northwestern Ecuador) or Jauneche region (headwaters of río Guayas) (Parker & Carr 1992). Gentry (*vide* Parker & Carr 1992) speculated that forest cover had previously been contiguous

between the western Andes and the coastal hills. Furthermore, some garúa forest species have recently been recognized as new species [e.g., White-necked Thrush (*Turdus albicollis*) recently split as Dagua Thrush (*Turdus daguae*) in Ridgely & Greenfield (2001)]. As we learn more about the genetics and ecology of garúa forest birds of the Tumbesian region, we may realize that some species are more of a conservation concern than previously thought.

Species richness in second growth forest. Relative to mature forest, the high avian species richness in second growth appears to be caused by the absence of mature forest specialists, and the presence of widespread generalist insectivores and canopy foragers. Lack of territorial specialists would permit an influx of species (Tilman 1999) from different sources (low elevation dry forest, long-distance migratory pathways, dispersal from other moist forest areas) filling the vacant niches (Holt 1993). Second growth forest on Cerro San Sebastián was well-represented by generalist species from the lowlands, as 41.7% of birds captured and observed in this forest type are common inhabitants of lower elevation transitional and dry forest.

Generalists tend to replace specialists when habitats are degraded (Ambuel & Temple 1983, Warkentin *et al.* 1995, Grey *et al.* 1998). Second growth lacks the habitat features of mature forest (tall canopy covered with epiphytes, moist soil with a higher abundance of arthropods) so specialists like antbirds and leaf tossers avoid such areas, creating vacancies for generalist species. Antbirds are known to rely on moist mature forest settings where large arthropods (Willis 1978) and bivouacs for ants (Roberts *et al.* 1998) are sustained. Since more species can coexist in marginal habitat if they are temporary visitors in space and time (Nee & May 1992), high turnover rates of species in second growth forest also help explain the more

species-rich assemblage there. Migrants from North America, common during the dry season, contributed to turnover of species in second growth.

Avian species richness in garúa forest was not correlated with food resource diversity or abundance. For example, although litter arthropods were more abundant in mature forest, avian species richness was lower there than in second growth forest. According to sweep net samples, and flower and fruit counts, there were no striking differences in food resources available to birds in the understory vegetation of the two forest types, yet avian diversity was greater in second growth forest.

One clear difference between the two forest types was shrub cover. Shrubby undergrowth in secondary forest provides foraging sites and perches, possibly accommodating more birds in the forest strata best sampled by mist-nets. Canopy birds typically follow the foliage-air interface as they forage (Schemske & Brokaw 1981). Canopy species [Bay-headed Tanager (*Tangara gyrola*), Lesser Greenlet (*Hylophilus decurtatus*), Bananaquit (*Coereba flaveola*), Tropical Parula (*Parula pitaiayumi*), and non-migratory Red-eyed Vireo, (*Vireo olivaceus chivi*)] were observed in old-growth forest, but were more frequently netted in second growth.

We cannot eliminate landscape level processes as an explanation for the different species counts in mature and second growth garúa forest. Since mature forest is relatively isolated and small in area, forest dependent species may have already been lost due to area effects (Stratford & Stouffer 1999). Comparing species composition in larger fragments of garúa forest along the Chongón-Colonche Cordillera, where Cerro San Sebastián is located, may help determine the effects of fragmentation.

Biases in mist netting. Although Remsen &

Good (1996) outline many pitfalls of interpreting data based on mist netting only, it remains a reliable method for sampling terrestrial insectivores and small understory species. We failed to detect major differences in community composition between mature and second growth garúa forest using strip counts, but mist netting revealed major differences in bird composition. Our mist-netting effort sampled slightly more than half the bird species recorded in garúa forest habitats. Most were small, highly mobile insectivorous birds that use the ground and understory layer of the forest. Mist netting is an appropriate sampling method for detecting avian responses to degradation because so many sensitive species are terrestrial insectivores (Stouffer & Bierregaard 1995, Canaday 1996). More studies combining mist netting and censuses along transects would increase our understanding of probabilities of consistent detection of birds in different strata of the forest and biases of mist netting in the tropics.

Implications for conservation in the Tumbesian endemic bird area. Some endemic bird species of the Tumbesian region in southwestern Ecuador are associated with specific habitat types (Stattersfield *et al.* 1998). Five species, Blackish-headed Spinetail (*Synallaxis tithys*), Pacific Parrotlet (*Forpus coelestis*), Short-tailed Hummingbird (*Myrmia micrura*), Collared Antshrike (*Sakesphorus bernardi*), and Watkinsí Antpitta are mainly found in scrub forest at low elevations (below 200 m). Scrub dry forest in western Ecuador, a special vegetation type found on the Pacific coast, is heavily disturbed by human activities. This disturbance has a long history, with evidence of human settlements dating 6000 B.C. (e.g., Valdivia). This may be why some lowland species appear to be adapted to secondary habitats and disturbed forest. This highlights the importance of understanding variation in species' sensitivity

ties to habitat change or loss in this region and for gathering information on habitat requirements of endemic bird species in order to determine the degree of habitat specialization of some of these species.

An important trait in the life history of many Tumbesian endemics might be their ability to move across habitats and to disperse or perform seasonal and altitudinal movements in different habitats. Evidence for local migration exists given the variety of species associated with specific habitats and elevations in different months of the year (Best 1992). We have also noted seasonal movements along altitudinal gradients and between dry and humid cloud forest at Loma Alta Ecological Reserve (Becker, field data) for Henna-hooded Foliage-gleaner, Ochre-bellied Dove, Little Woodstar, Plumbeous Thrush, Gray-breasted Flycatcher, Gray-and-gold Warbler, and Black-capped Sparrow. All these species have been recorded in secondary forest at different elevations and may depend on natural corridors of humid forests, strips of forest along rivers or patches of transitional forest at intermediate elevations, to move between habitats. For this reason conservation efforts should focus on the protection of elevational gradients in the Chongón-Colonche Cordillera.

Machalilla National Park is an important reserve because it encompasses an ecological gradient that includes plant communities of deciduous and humid cloud forests. This study provides information on the differences in bird communities in mature and second growth humid forest and the use of second growth forest habitat by many Tumbesian endemics. We identified specific bird species assemblage in mature and second growth garúa forest and provide a list of species useful as indicators of mature forest conditions. Such information is valuable for management of garúa forest in Machalilla, and for monitoring the expansion of mature garúa forest in

the region. Garúa forest in the Tumbesian region are unique and dynamic due to pronounced annual fluctuations in rainfall and fog capture. Bird populations seem exhibit some adaptations to climate fluctuation including vertical migration and use of multiple habitat types.

Social interactions, resource availability, and autecological factors interact over short time scales, while vicariance, dispersal, and speciation operate over longer time scales to determine assemblages of species in a particular place, season, and time (Wiens 1989, Robinson *et al.* 1992). Given that many Tumbesian endemic and threatened species use second growth garúa forest, preservation of garúa forest in various successional stages is an important conservation goal for western Ecuador (Becker & Agreda 2001).

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APPENDIX 1. Bird species mist-netted and observed in mature and second growth garúa forest on Cerro San Sebastián, Machalilla National Park, Ecuador.

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