FEATURE ARTICLES

NEOTROPICAL FOREST BIRD COMMUNITIES: A COMPARISON OF SPECIES RICHNESS AND COMPOSITION AT LOCAL AND REGIONAL SCALES

JOHN G. BLAKE[1]

*Department of Biology and International Center for Tropical Ecology, University of Missouri–St. Louis,
One University Boulevard, Saint Louis, MO 63121*

Abstract. Species richness and composition of Neotropical forest bird communities vary spatially at both large and small scales, but previous comparisons based on 100 ha plots have not replicated plots within a region. I sampled birds in two 100 ha plots in lowland forest of eastern Ecuador to better understand how species richness and composition vary over smaller spatial scales. Birds were sampled in February and April of 2002–2005 (only in February in 2005). Plots were approximately 1.5 km apart in predominantly terra firme forest. A total of 319 species (285 and 281 per plot) from 43 families were represented in ~16 000 detections per plot; number of species and detections per sample averaged approximately 185 and 2300, respectively. Numbers of species and detections per family were strikingly similar in the two plots, but numbers of detections of individual species often differed, likely in response to differences in habitat between the two plots. Species richness and composition were similar in many respects to comparable data from Ecuador, Peru, and French Guiana, but differed from those of Panama. Differences were most pronounced at the species level, less at the genus level, and least when comparisons were based on families. Differences among sites in South America were correlated with geographic distance at the species and genus levels, but not at the family level. Results illustrate the value of replicated plots within a region for understanding how species richness and composition can vary at small spatial scales, and highlight the importance of beta diversity for determining overall patterns of regional diversity.

Key words: Amazonia, community composition, Ecuador, local scale, regional scale, spatial variation, species richness.

Comunidades de Aves de Bosques Neotropicales: Una Comparación de la Riqueza y Composición de Especies en Escalas Local y Regional

Resumen. La riqueza y composición de especies de las comunidades de aves en bosques neotropicales varían espacialmente a gran y pequeña escala. Sin embargo, las comparaciones que se han realizadas previamente en parcelas de 100 ha no han incluido replicas en una misma región. En este estudio, muestreé aves en dos parcelas de 100 ha localizadas en un bosque de tierras bajas en el este de Ecuador para obtener un mejor entendimiento de la variabilidad en la riqueza y composición de especies a una escala espacial pequeña. Las aves fueron muestreadas en febrero y abril entre los años 2002 y 2005 (en 2005 sólo se muestreó en febrero). Las parcelas estuvieron separadas por 1.5 km en un bosque del tipo terra firme principalmente. Un total de 319 especies (285 y 281 por parcela) pertenecientes a 43 familias estuvieron representadas en aproximadamente 16 000 detecciones en cada parcela; el número de especies y detecciones por muestreo fue en promedio aproximadamente de 185 y 2300, respectivamente. El número de especies y

detecciones por familia fueron increíblemente similares entre las dos parcelas, pero el número de detecciones de cada especie difirió en varios casos, probablemente como respuesta a las diferencias de hábitat entre las dos parcelas. La riqueza y composición de especies fueron similares en varios aspectos a las de otros estudios que han reportado datos comparables en Ecuador, Perú y Guyana Francesa, pero difirieron de los datos reportados para Panamá. Las diferencias fueron más marcadas a nivel de especies, intermedias a nivel de géneros y menores cuando las comparaciones se realizaron a nivel de familias. Las diferencias entre sitios en Sudamérica (excluyendo a Panamá) se correlacionaron con la distancia geográfica a nivel de especie y género pero no a nivel de familia. Estos resultados ilustran el valor de las parcelas replicadas dentro de una misma región para entender cómo la riqueza y composición de especies puede variar a escalas espaciales pequeñas y destacan la importancia de la diversidad beta para determinar los patrones generales de diversidad regional.

INTRODUCTION

Community ecology deals with the distribution and abundance of organisms at different spatial and temporal scales. Patterns apparent at one spatial scale may look quite different when viewed at another (Wiens et al. 1987, Terborgh et al. 1990, Robinson et al. 2000, Pitman et al. 2001). Similarly, habitat heterogeneity can be an important influence on species distribution and abundance, but perception of habitat heterogeneity varies with spatial scale, with consequent implications for understanding diversity (Tuomisto et al. 1995, Pitman et al. 1999, Thiollay 1999, 2002).

Recent studies on Neotropical tree communities have addressed the question of whether or not geographically distant regions tend to be dominated by similar sets of species, genera, or families, the "oligarchy hypothesis" of Pitman et al. (2001). Comparisons among Ecuador, Peru, and Bolivia, for example, indicate strong similarities in the composition of tree communities, particularly at higher taxonomic levels (Pitman et al. 2001, 2002, Valencia et al. 2004, Macía and Svenning 2005; but see Ruokolainen and Tuomisto 2002, Tuomisto et al. 2003). Dominance of individual species was suggested to reflect ecological superiority of those species. Similar studies on other organisms are needed to further evaluate the relative roles of regional and local processes on species distribution patterns.

Until recently, comparative analyses of tropical bird communities have been hampered by a lack of studies conducted at spatial scales appropriate to the distribution and abundance patterns of many tropical birds. Terborgh et al. (1990) were the first to point out that study plots of at least 100 ha are required for studies of tropical bird communities, because many tropical species are rare, patchy in distribution, have large territories, or all of the above. Several later studies have sampled tropical bird communities in plots of approximately 100 ha (French Guiana: Thiollay 1994; Ecuador: English 1998; Panama: Robinson et al. 2000). These studies have allowed comparisons of composition and species richness at relatively large spatial scales (e.g., >1000 km between sites), but not evaluation of smaller-scale (i.e., local, between-plot) variation in community composition, because plots were not replicated. Although not based on plots, Thiollay's (2002) studies of bird communities across French Guiana provide a valuable comparison of mesoscale variation, with sites separated by 15–100 km and a maximum (north–south) separation of 320 km. Without replication to evaluate local-scale variation, we do not know how representative patterns obtained from a single plot are. That is, we do not know what proportion of differences (or similarities) in community composition reflects broad, historical processes and what proportion reflects local responses to environmental variation (Pitman et al. 2001, Tuomisto et al. 2003).

The major goal of this study was to address this basic question on the relative importance of local versus regional differences in bird communities. Thus, I compared the composition of bird communities in two 100 ha plots in eastern Ecuador that were sampled from 2002 to 2005. To my knowledge, this is the first study to use replicated plots of this size, sampled over several years, in a relatively undisturbed (by humans) Neotropical forest. More specifically, I compared patterns of species richness and abundance, as well as family and species composition, of bird communities found in two tracts of similar (terra firme) forest that were separated by only 1.5 km. Given that the

two plots almost certainly experienced broadly similar long-term histories, I expected their bird communities to be broadly similar as well. Yet, given small-scale variation in habitat, topography, resources, and other factors that affect species distributions (Terborgh et al. 1990, Cohn-Haft et al. 1997, Robinson et al. 2000), I also expected some species to show pronounced differences in abundance between plots. In other words, I expected community composition to reflect both regional (biogeographical) and local (ecological) processes. Following this local-scale analysis, I used data from this study to make comparisons with previously published data from large plots located elsewhere in the Neotropics. Comparisons with other tropical regions would obviously also be of great interest but, with the exception of one study that used replicated plots to compare numbers of Timaliidae in Malaysia (bin Hussin and Francis 1999), I am not aware of comparable plot-based data from regions outside the Neotropics, so detailed comparisons among tropical regions are not yet possible.

METHODS

STUDY SITE

Research was conducted at Tiputini Biodiversity Station, Orellana Province, Ecuador (~0°37′S, 76°10′W, 190–270 m elevation). Tiputini was founded in 1994 by the Universidad San Francisco de Quito on a tract of undisturbed lowland rainforest within the 1.5 million ha Yasuní Biosphere Reserve, a region noted for its biodiversity (Valencia et al. 2004). The station and nearby areas contained a variety of habitats including terra firme and varzea forest, palm swamps and other wetlands, and numerous areas of natural regrowth. Average annual rainfall was approximately 2740 mm (Karubian et al. 2005). Average monthly rainfall during the drier period (October–February) was ~140 mm, with January often particularly dry (JGB, pers. obs.); monthly rainfall during the wetter period (April–August) was ~385 mm. September and March were transition months. Two ~100 ha plots (Harpia and Puma; ~1 km × 1 km each) were established in terra firme forest during 2001. Both plots were gridded (100 × 200 m grid lines) and marked with tagged, 1.5 m tall PVC tubes every 50 m along each grid line. The Harpia plot ranged from 201 to 233 m in elevation and was characterized by dissected upland forest. The Puma plot had less topographic relief overall, although the range in elevation was similar, from 209 to 235 m. Both areas experienced partial, temporary inundation (approximately 5 to 10 ha, depending on the height of the flood) when small streams filled and overflowed their banks as the Tiputini River rose; Puma had more areas that filled with persistent standing water during the rainy season (Loiselle et al. 2007).

SAMPLING METHODS

I sampled birds during February and April, 2002–2005 (only in February in 2005). Locations of all birds seen or heard were noted on scale maps of the plots as I walked slowly, with many stops, along transects. Unknown songs were tape-recorded for later identification. I covered approximately 1–1.4 km during a morning; starting positions were distributed throughout the plots and rotated between monthly samples to ensure, as much as possible, that all parts of the plots were covered early in the morning when vocal activity was greatest. Each plot took approximately 12–13 days to cover; transects were not covered more than once during a given sample. Total effort expended (i.e., numbers of hours and numbers of kilometers) was equivalent between plots and among samples. Following Terborgh et al. (1990), and my own experience, I started counts well before light, when the first diurnal birds were beginning to sing (e.g., forest-falcons, some puffbirds, woodcreepers, tinamous, cracids, thrushes, and others) and when many nocturnal species (e.g., owls, currasows, potoos, and nightjars) were still vocalizing (Parker 1991). Vocal activity typically was high until approximately 2 hr after sunrise, when it often declined rapidly (Blake 1992). Thus, I confined my counts to the first few hours of the morning. Periods of rain occasionally interrupted or ended counts early.

Not all species or groups of species were equally well sampled. For example, some canopy tanagers (*Tangara* spp.) were difficult to identify by their often relatively indistinguishable songs; small flycatchers and hummingbirds in the canopy likely were often overlooked, as were other canopy birds that

do not vocalize much (e.g., some puffbirds). In contrast, highly vocal species with distinctive songs likely were not missed and may be overrepresented. Yet, because I conducted counts in both plots in the same way, between-plot comparisons should not be affected. Comparisons with other studies, in contrast, are made with the realization that differences in counting methods may influence results. However, because I do not make direct comparisons of density, comparisons likely are valid (e.g., comparisons based on numbers of species per family). Hawks, psittacids, and other species flying above the canopy were noted, but not included in most analyses if they were not observed using the plot. Swifts (Apodidae) and swallows (Hirundinidae) were observed flying over the forest but numbers were not estimated and these two families are not included in results or comparisons. Taxonomy follows Remsen et al. (2007) except as otherwise noted (e.g., Dendrocolaptidae separated from Furnariidae).

STATISTICAL ANALYSES

I do not attempt to present estimates of density for the species found in these two plots. Rather, I present a snapshot (repeated across years) of the numbers of individuals detected (by sight or sound) in two 100 ha plots. I took this approach because I did not have sufficient time to repeatedly sample all parts of each plot as was done, for example, by Terborgh et al. (1990) and Robinson et al. (2000).

I used rarefaction analyses to compare rates of species accumulation in the two plots; analyses were based on a Monte Carlo simulation procedure (1000 runs) implemented with EcoSim version 7 (Gotelli and Entsminger 2006). I also calculated an interpolated jackknife estimate of number of species present during a given sample using program SPEC-RICH (Hines 1986).

I followed the methods of Pitman et al. (2001) to compare the relative importance of different families (based on number of species or detections per family) and different species (number of detections per species) in the two plots, with data combined across all samples. I arbitrarily selected the Harpia plot as the x-axis and calculated the slope of the line between Puma and Harpia to test the null hypothesis that the two samples were equivalent in terms of species or family composition. If the numbers of detections or species per family, or detections per species, were the same in the two plots, the slopes of the lines should be equal to one (Pitman et al. 2001:2107). I used a similar approach to compare number of species per family between Tiputini (based on comparisons with one of the Tiputini plots, arbitrarily selected) and a second site in Ecuador (Yasuní Research Station, hereafter simply referred to as Yasuní; English 1998), a site in Peru (Terborgh et al. 1990), one in French Guiana (Thiollay 1994), and one in Panama (Robinson et al. 2000); all sites were represented by ~100 ha plots. Species identified as migrants or vagrants were eliminated prior to the analyses.

I used several approaches to analyze differences and similarities in community composition. First, nonmetric multidimensional scaling was used to graphically represent similarities (and differences) in species composition between plots and among samples (Clarke and Warwick 2001, McCune and Grace 2002). Next, I used analysis-of-similarity (ANOSIM; described in Clarke and Warwick 2001) to compare the level of similarity in species composition among a set of related samples (e.g., Puma plot vs. Harpia plot) to the level of similarity across all samples, to determine if plots or months differed in species composition more than expected by chance. The significance of the ANOSIM test statistic is determined by comparison with values obtained by a Monte Carlo randomization procedure. ANOSIM was followed with an indicator-species analysis (Dufrêne and Legendre 1997, McCune and Grace 2002) to determine which species were particularly characteristic (indicative) of each plot. Indicator values were tested for significance with a Monte Carlo randomization procedure (McCune and Mefford 1999).

I used similar approaches to evaluate similarities and differences in community composition among sites in Central and South America (sites as above). First, I determined the percentage of detections accounted for by each species in the current study and the percentage of total density accounted for by each species in the studies that provided density estimates. Species percentages were combined to produce estimates at the genus level, which were combined to produce estimates at the family

TABLE 1.   Number of detections (Det.), number of species (Spp.), and estimated (Est.) number of species (estimated with program SPECRICH; Hines 1986) by year and month on two 100 ha plots, Tiputini Biodiversity Station, Ecuador.

	Harpia plot			Puma plot			Combined	
Sample	Det.	Spp.	Est. ± SE	Det.	Spp.	Est. ± SE	Spp.	Est. ± SE
2002								
February	1886	185	261 ± 19	1923	191	221 ± 8	227	259 ± 8
April	1662	165	201 ± 8	1692	172	207 ± 8	204	240 ± 9
2003								
February	2257	185	213 ± 7	2116	179	202 ± 7	215	239 ± 7
April	1759	166	189 ± 7	2254	177	204 ± 7	208	232 ± 7
2004								
February	2828	196	227 ± 8	2792	200	226 ± 7	227	247 ± 7
April	2546	180	202 ± 7	2382	183	205 ± 7	213	234 ± 6
2005								
February	2891	203	237 ± 8	2581	185	211 ± 7	228	273 ± 14

level. For each level of analysis, I used a Bray-Curtis ordination (McCune and Grace 2002) to graphically evaluate differences among sites. (Nonmetric multidimensional analyses only returned a one-dimensional solution so were not used in these comparisons.) I also used a Mantel test to evaluate the relationship between geographic distances (calculated from latitude and longitude of each site) and distances based on species, genus, and family composition.

All multivariate analyses were done with PC-ORD version 4 (McCune and Mefford 1999) or PRIMER version 5.2.9 (Clarke and Gorley 2002). The Sørensen measure was used to calculate distance matrices for multivariate analyses (see descriptions of distance measures in McCune and Grace [2002]).

RESULTS

NUMBERS OF DETECTIONS AND SPECIES

Number of detections per morning typically ranged from approximately 150 to 300, with 60 to 95 species; number of species per morning count was highly correlated with number of detections ($r = 0.93$ in Harpia, $r = 0.85$ in Puma). Total detections per sample ranged from approximately 1700 to 2900 in Harpia (165–203 species) and from 1700 to 2800 in Puma (172–200 species; Table 1). Number of species per sample for both plots combined ranged from 204 to 228. A total of 319 species were recorded in both plots combined (309 if birds simply flying overhead are omitted), with 285 in Harpia (280 without fly-overs) and 281 (278 without fly-overs) in Puma. Numbers exceed 300 in each plot if detections outside sample periods and species recorded only with mist nets are included. Further results do not include detections of birds flying over the plots unless otherwise indicated. Species-accumulation curves are virtually identical for both plots (Fig. 1a) and suggest that most, but not all, species were recorded (i.e., curves approach an asymptote). Similarly, abundance-rank curves are nearly identical for the two plots (Fig. 1b) and indicate strong equitability or evenness in the abundance relationships (Terborgh et al. 1990).

FAMILY COMPOSITION

A total of 43 families were represented on both plots combined (Table 2). Eurypygidae (*Eurypyga helias* [Sunbittern]) was not observed in Puma and Alcedinidae and Cathartidae were not seen in Harpia during regular observation periods. All are known to occur on both plots (JGB, pers. obs. outside of census periods). Thamnophilidae, Tyrannidae, and Thraupidae were represented by more than 20 species in each plot, with five or six additional families represented by more than 10 species (Fig. 2a). Suboscines accounted for five of the nine families represented by at least 10 species, oscines accounted for one (Thraupidae), and three nonpasserine families accounted for the others (Fig. 2a). The slope of the line between
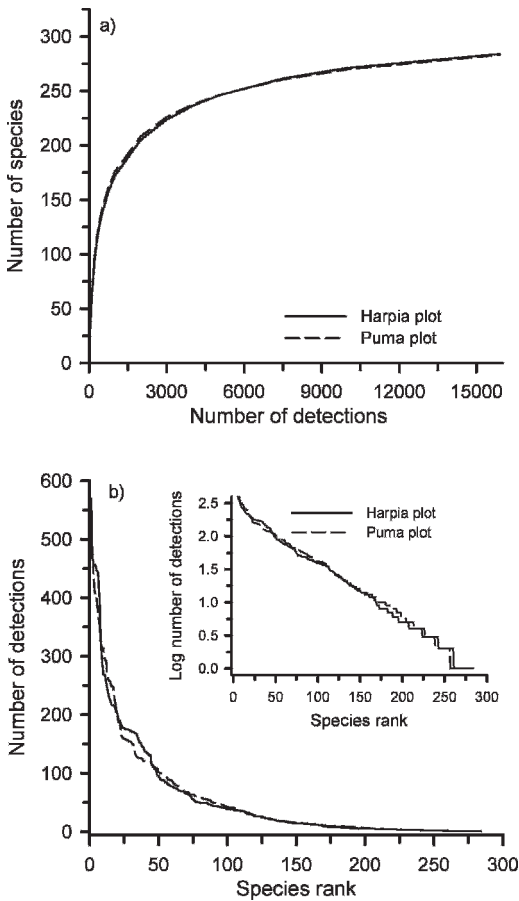
FIGURE 1. Species-accumulation (a) and rank-abundance (b) curves for the 100 ha Harpia and Puma plots, Tiputini Biodiversity Station, Ecuador, based on numbers of detections (by sight or sound) from February 2002 through February 2005.

Harpia and Puma was equal to 1.0, indicating that the same pattern of species richness per family held in both plots.

Thamnophilidae accounted for the greatest number of detections in both plots (Fig. 2b), more than 3.5 times as many as the next most common, Dendrocolaptidae and Pipridae. Dendrocolaptidae were equally represented in both plots, whereas Pipridae were slightly more common in Harpia. Ramphastidae, Psittacidae, Furnariidae, and Formicariidae were more common in Puma; the reverse was true for Columbidae, Picidae, and Cotingidae. Differences were particularly pronounced for Cotingidae (Fig. 2b) because of the large lek of

Lipaugus vociferans (Screaming Piha) in Harpia. The slope of the line between Harpia and Puma was close to 1.0.

SPECIES COMPOSITION

Dominant species were similar in both plots. The two plots shared eight of the top 10 species, but in no case was the ranking the same for both plots (Table 3, Fig. 3). Similarly, 16 of the top 20 species were shared but had different rankings. The top 10 species accounted for 26% and 25% of all detections in Harpia and Puma, respectively; the top 20 accounted for 40% and 41%. Overall, the similarity between plots with respect to detections per species was less than that based on detections per family; the slope of the line between Harpia and Puma was less than 1.0 and there was considerably more scatter around the line (Fig. 3). Differences in number of detections between plots were relatively small for some common species (e.g., *Baryphthengus martii* [Rufous Motmot], *Capito auratus* [Gilded Barbet], *Glyphorynchus spirurus* [Wedge-billed Woodcreeper], *Thamnomanes caesius* [Cinereous Antshrike], *Cercomacra cinerescens* [Gray Antbird], and *Lepidothrix coronata* [Blue-crowned Manakin]), but differed substantially for others (Fig. 3, Table 3). For example, *Lipaugus vociferans* was virtually absent from Puma (only two records in ~16 000 detections) but had an extensive lek in Harpia that extended over more than 30 ha. In contrast, several oropendolas and macaws, two motmots, and several other species were recorded much more frequently in Puma (Fig. 3).

As a consequence of individual species differences, samples from the two plots were well separated in a nonmetric multidimensional scaling ordination (Fig. 4.). Separation was evident both by month (i.e., February vs. April; primarily along axis 1) and plot (axis 3). Thus, samples differed along both spatial and temporal scales. A two-way ANOSIM (plots and months) supported the significant separation of samples both by plot (Global $R = 0.76$, $P < 0.01$) and month (Global $R = 0.34$, $P < 0.05$).

Indicator-species analysis selected 20 species each as indicators of the two plots (Table 4), supporting results of the ordination and ANOSIM. In several cases, members of the same genus were indicators of opposite plots, frequently reflecting differences in habitat prefer-

TABLE 2.   Number of species and individuals detected (by sight or sound) on two 100 ha plots at Tiputini Biodiversity Station, eastern Ecuador, February and April, 2002–2005. Species observed flying overhead are included. Taxonomy follows Remsen et al. (2007), except as noted.

Family	Harpia plot		Puma plot	
	Species	Detections	Species	Detections
Tinamidae (tinamous)	7	181	6	213
Cracidae (guans)	4	113	3	131
Odontophoridae (New World quail)	1	21	1	41
Ardeidae (herons)	2	5	1	2
Cathartidae (New World vultures)	0	0	2	2
Accipitridae (hawks)	6	22	7	22
Falconidae (falcons)	9	113	7	162
Psophiidae (trumpeters)	1	43	1	40
Rallidae (rails)	2	4	2	19
Eurypygidae (sunbittern)	1	1	0	0
Columbidae (pigeons)	5	632	5	427
Psittacidae (parrots)	13	599	13	743
Cuculidae (cuckoos)	3	72	3	73
Strigidae (owls)	5	55	4	48
Nyctibiidae (potoos)	3	10	3	10
Caprimulgidae (nightjars)	1	37	2	5
Trochilidae (hummingbirds)	10	364	10	495
Trogonidae (trogons)	7	343	5	226
Alcedinidae (kingfishers)	0	0	1	1
Momotidae (motmots)	3	274	3	495
Galbulidae (jacamars)	3	90	3	70
Bucconidae (puffbirds)	9	239	7	268
Capitonidae (New World barbets)	2	524	2	502
Ramphastidae (toucans)	5	624	5	848
Picidae (woodpeckers)	11	546	12	419
Furnariidae (ovenbirds)	16	571	15	736
Dendrocolaptidae (woodcreepers)[a]	15	1004	13	1016
Thamnophilidae (antbirds)	36	3712	37	3612
Formicariidae (antpittas)	5	441	6	755
Conopophagidae (gnateaters)	1	15	1	7
Rhinocryptidae (tapaculos)	1	205	1	154
Tyrannidae (tyrant flycatchers)[b]	31	588	33	618
Cotingidae (cotingas)[c]	5	725	7	203
Pipridae (manakins)[d]	10	1127	9	806
Vireonidae (vireos)	5	289	4	209
Corvidae (jays)	1	46	1	112
Troglodytidae (wrens)	4	747	5	725
Polioptilidae (gnatcatchers)	3	120	2	62
Turdidae (thrushes)	3	234	3	219
Thraupidae (tanagers)[e]	26	719	25	754
Cardinalidae (cardinal grosbeaks)	3	213	4	123
Parulidae (wood-warblers)	2	18	1	28
Icteridae (blackbirds)	5	257	6	456
Totals	285	15 943	281	15 857

[a] Considered part of Furnariidae by Remsen et al. (2007).
[b] Includes *Tityra* and *Pachyramphus*, placed in incertae sedis by Remsen et al. (2007).
[c] Includes *Laniocera*, placed in incertae sedis by Remsen et al. (2007).
[d] Includes *Schiffornis* and *Piprites*, placed in incertae sedis by Remsen et al. (2007).
[e] Includes *Habia* and *Euphonia*, placed in incertae sedis and Fringillidae, respectively, by Remsen et al. (2007).
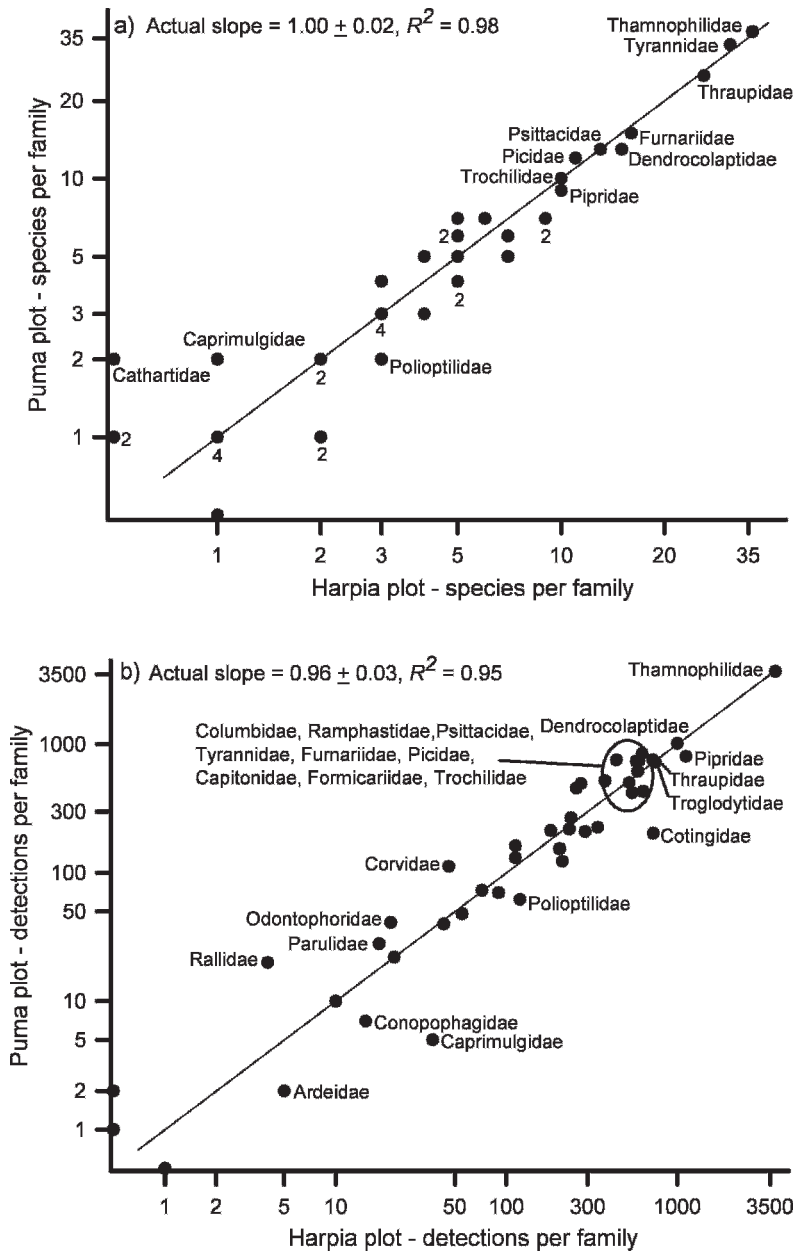
FIGURE 2.   Number of (a) species and (b) detections (by sight or sound) per family in the Harpia and Puma plots, Tiputini Biodiversity Station, Ecuador. Straight line indicates a 1:1 relationship between values for the two plots. The actual slope of the regression between the two plots is given. Numbers by points indicate number of families represented by that point.

ences. For example, *Pipra pipra* [White-crowned Manakin] and *P. erythrocephala* [Golden-headed manakin] both were indicators of Harpia, whereas *P. filicauda* [Wire-tailed Manakin] was characteristic of Puma; *Xiphorhynchus ocellatus* [Ocellated Woodcreeper] was more common in Harpia and *X. elegans* [Elegant Woodcreeper] in Puma.

COMPARISONS WITH OTHER NEOTROPICAL SITES

Differences in species dominance relationships were most pronounced between South American and Central American sites (Table 3). The 10 most abundant species in South American sites accounted for 17% (Peru) to 26% (Tiputini, Ecuador) of individuals (Peru) or observations (Ecuador), with the top two species accounting for less than 5% each. In contrast, the top 10 species accounted for 42% of all individuals, with ~7% and 6% accounted for by the top two species, respectively, in Panama. Level of similarity in number of species per family varied across Neotropical sites as well. Similarity was actually greatest (slope closest to 1.0) between the Puma plot (this study) and the site in Peru, largely because of very similar numbers of species in Thamnophilidae, Tyrannidae, and Thraupidae. Similarity also was high between Puma and the Yasuní site and between Puma and French Guiana, but in both cases slopes were less than 1.0, reflecting greater numbers of species in Puma in several of the most species-rich families (Fig. 5). Differences were most pronounced between Ecuador and Panama; the slope of the regression line was much less than 1.0, reflecting the fact that most families were represented by more species in Ecuador.

Differences in community composition followed a similar pattern, except that similarities were greatest among all three sites in Ecuador (Harpia, Puma, and Yasuní; Fig. 6). Differences between the Panama site and all South American sites were large and approximately the same in all pairwise comparisons. Differences in composition followed a similar pattern when comparisons were based on genera and families, but level of difference decreased at each step (Fig. 6). Correlations between geographic distance and composition were not significant, based on Mantel tests, and decreased with level of comparison (species level: $r = 0.62$, $P = 0.10$; genus level: $r = 0.51$, $P = 0.15$; family level: $r = 0.10$, $P = 0.75$). Lack of correlation, particularly at the species and genus levels, reflected the influence of Panama, which, although geographically closer to Ecuador (Fig. 6), was different at all levels of comparison. When Panama was omitted from the comparison, correlations with distance were stronger (species level: $r = 0.84$, $P < 0.05$; genus

level: $r = 0.73$, $P < 0.05$; family level: $r = 0.26$, $P = 0.16$).

DISCUSSION

OVERVIEW

Many tropical forest bird communities are very diverse (e.g., >160 species with overlapping territories or areas of use; Terborgh et al. 1990), whereas other habitats or regions are less so (Borges 2004). Central Amazonian communities, for example, typically support fewer species and individuals than do sites in western Amazonia (Bierregaard 1990, Robinson and Terborgh 1990), although such differences may be less pronounced when comparisons are restricted to terre firme forest (Cohn-Haft et al. 1997). Similarly, Central American sites support fewer species than western Amazonian sites (but perhaps more individuals), as least partially as a consequence of historical influences on distribution and species richness of certain families and genera (Robinson et al. 2000, Ricklefs 2002). Large-scale, biogeographical comparisons (Terborgh et al. 1990, English 1998, Robinson et al. 2000) shed light on factors (e.g., regional and historical) that may limit the species pool of a region and thereby influence the number of species that have the potential to co-occur within a given area of study (e.g., 100 ha study plots in lowland forest).

At smaller scales, the patchy distribution of many tropical species can have a strong influence on the composition and richness of species within a given study plot (Terborgh et al. 1990, Tuomisto et al. 1995, Pitman et al. 1999, Robinson et al. 2000, Valencia et al. 2004). Turnover in species identities from one area to the next (i.e., beta diversity) may contribute substantially to the overall species richness of a region (gamma diversity; Whittaker 1972, see also Thiollay 2002). Documentation of such turnover may be important for conservation (Tuomisto et al. 2003); the greater the turnover or change from one site to another, the more sites (or total area) may be needed to ensure preservation of the full complement of species. Yet, there have been few attempts to document or determine beta diversity in tropical bird communities (Young et al. 1998, Thiollay 1999, 2002, Blake and Loiselle 2000).

TABLE 3.   Percentage of detections and rank (in parentheses) for the 10 most frequently detected species in Tiputini, Ecuador (separately by plot) and other Neotropical sites (Yasuní, Ecuador: English [1998], Peru: Terborgh et al. [1990], French Guiana (FG): Thiollay [1994], Panama: Robinson et al. [2000]). Species (and rank) are shown for Ecuador if the species was in the 10 most frequently detected in either plot or if the species was one of the top 10 species in one or more of the other countries. For Tiputini, results are based on all detections; for the other sites, results are based on estimated number of individuals per 100 ha. A "+" sign indicates presence at a given site but not in the top 10 at the site indicated. Taxonomy follows Remsen et al. (2007), except as noted.

Family Species	Harpia	Puma	Yasuní	Peru	FG	Panama
Tinamidae						
Crypturellus bartletti (Barlett's Tinamou)	<0.1 (230)	<0.1 (220)		1.4 (7)		
Columbidae						
Patagioenas plumbea (Plumbeous Pigeon)	2.9 (2)	2.3 (8)	+	+	+	
Psittacidae						
Brotogeris cyanoptera (Cobalt-winged Parakeet)	0.8 (44)	0.6 (50)	+	1.7 (5)		
Trochilidae						
Phaethornis malaris (Great-billed Hermit)	1.1 (24)	2.0 (9)	1.4 (8)	+		
Trogonidae						
Trogon melanurus (Black-tailed Trogon)	0.6 (53)	0.4 (74)	+	1.4 (7)	+	
Motmotidae						
Baryphthengus martii (Rufous Motmot)	1.7 (10)	2.6 (5)	+			+
Capitonidae						
Capito auratus (Gilded Barbet)	2.8 (5)	2.6 (4)	+	+	+	
Ramphastidae						
Ramphastos tucanus (White-throated Toucan)	1.9 (9)	2.3 (7)	+	+	+	
Dendrocolaptidae[a]						
Glyphorynchus spirurus (Wedge-billed Woodcreeper)	2.9 (3)	2.3 (6)	4.7 (1)	+	3.4 (2)	+
Xiphorynchus guttatus (Ocellated Woodcreeper)	2.5 (7)	3.1 (1)	+	+		+
Thamnophilidae						
Thamnophilus atrinucha (Western Slaty-Antshrike)						6.6 (1)
Thamnophilus murinus (Mouse-colored Antshrike)	1.7 (11)	1.6 (16)	+		+	
Thamnomanes ardesiacus (Dusky-throated Antshrike)	1.5 (13)	1.2 (21)	1.9 (4)	1.4 (7)	+	
Thamnomanes caesius (Cinereous Antshrike)	2.8 (6)	3.1 (2)	1.4 (8)		+	
Myrmotherula fulviventris (Checker-throated Antwren)						5.1 (4)
Myrmotherula erythrura (Rufous-tailed Antwren)	0.7 (48)	0.8 (39)	1.7 (6)			
Myrmotherula brachyura (Pygmy Antwren)	1.3 (20)	2.0 (10)	+	1.4 (7)	+	+
Myrmotherula hauxwelli (Plain-throated Antwren)	0.4 (67)	0.5 (67)	1.9 (4)	+		
Myrmotherula axillaris (White-flanked Antwren)	1.0 (35)	0.8 (36)	+	1.4 (7)	+	3.7 (6)
Myrmotherula menetriesii (Gray Antwren)	0.4 (74)	0.3 (93)	1.4 (8)	1.6 (6)	+	
Microrhopias quixensis (Dot-winged Antbird)	0.1 (173)	0.1 (181)	+	+	+	5.3 (3)
Cercomacra cinerascens (Gray Antbird)	3.6 (1)	2.7 (3)	+	1.8 (4)	4.6 (1)	
Hypocnemis cantator (Warbling Antbird)	1.1 (27)	1.8 (12)	+	+	1.7 (9)	
Myrmoborus myotherinus (Black-faced Antbird)	1.4 (16)	1.6 (14)	+	2.1 (3)		

TABLE 3.   Continued.

Family Species	Harpia	Puma	Yasuní	Peru	FG	Panama
Myrmeciza ferruginea (Ferruginous-backed Antbird)					2.1 (4)	
Pithys albifrons (White-plumed Antbird)	0.3 (82)	0.3 (106)	+		1.8 (6)	
Hylophylax naevius (Spot-backed Antbird)	1.2 (22)	0.8 (41)	2.4 (3)	+	1.7 (9)	
Hylophylax poecilinotus (Scale-backed Antbird)	1.1 (34)	1.0 (30)	1.5 (7)	+	1.8 (6)	
Phaenostictus mcleannani (Ocellated Antbird)						3.0 (8)
Formicariidae						
Formicarius analis (Black-faced Antthrush)	1.1 (29)	1.9 (11)	+	1.4 (7)	+	+
Tyrannidae						
Zimmerius vilissimus (Paltry Tyrannulet)						3.4 (7)
Mionectes oleagineus (Ochre-breasted Flycatcher)	0.2 (113)	0.2 (111)	+	+		1.8 (10)
Oncostoma olivaceum (Southern Bentbill)						5.0 (5)
Hemitriccus zosterops (White-eyed Tody-Tyrant)	0.3 (87)	0.1 (181)		+	1.9 (5)	
Platyrinchus coronatus (Golden-crowned Spadebill)	0.3 (77)	0.3 (86)	+	+	1.8 (6)	+
Cotingidae						
Lipaugus vociferans (Screaming Piha)	2.9 (4)	<0.1 (215)	+	+	+	
Pipridae						
Tyranneutes virescens (Tiny Tyrant-Manakin)					2.2 (3)	
Lepidothrix coronata (Blue-crowned Manakin)	2.1 (8)	1.7 (13)	2.8 (2)	+		+
Pipra fasciicauda (Band-tailed Manakin)				2.3 (2)		
Pipra mentalis (Red-capped Manakin)						3.0 (9)
Vireonidae						
Hylophilus decurtatus (Lesser Greenlet)						5.6 (2)
Turdidae						
Turdus albicollis (White-necked Robin)	0.6 (53)	0.8 (40)	+	+	1.7 (9)	
Thraupidae						
Coereba flaveola (Bananaquit)[b]						1.7 (9)
Icteridae						
Cacicus cela (Yellow-rumped Cacique)	0.1 (128)	0.4 (85)	+	2.6 (1)		
Top 10 species, % of total	25	26	21	17	23	42

[a] Considered part of Furnariidae by Remsen et al. (2007).
[b] Placed in incertae sedis by Remsen et al. (2007).

The present study is the first to compare bird communities in two 100 ha plots located in close proximity (i.e., species turnover at a local scale). Previous comparisons (e.g., Ecuador vs. Peru and French Guiana: English 1998, Panama vs. Peru: Robinson et al. 2000) have dealt with plots separated by distances of >1000 km. Such comparisons have revealed striking differences and similarities in species richness (e.g., similar between Peru and French Guiana; different between Peru and Panama), abundance-rank relationships, and other aspects of community structure (e.g., trophic relationships). Overall, differences are most pronounced between Central and South American sites, largely reflecting biogeographic history and large-scale processes (Robinson et al. 2000). Differences among Amazonian sites vary with level of comparison (e.g., family level vs. species level; structure vs. composition) and reflect extent of geographic separation. In this study, replicate plots were located ~1.5 km apart at the closest point. Thus, bird communities would have developed with similar large-scale, long-term histories, but with different smaller-scale, ecological timeframe processes
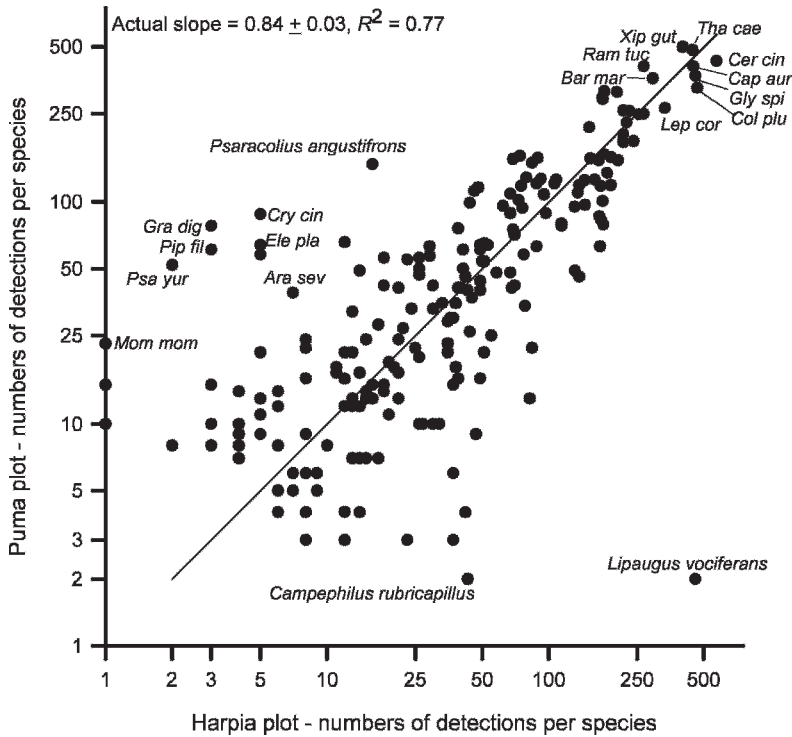
FIGURE 3.   Number of detections per species in two 100 ha plots, Tiputini Biodiversity Station, Ecuador. Some of the most common species or species more common in one plot than the other are indicated by the first three letters of the genus and species names: *Ara severa* (Chestnut-fronted Macaw), *Baryphthengus martii* (Rufous Motmot), *Capito auratus* (Gilded Barbet), *Cercomacra cinerescens* (Gray Antbird), *Patagioenas plumbea* (Pumbeous Pigeon), *Crypturellus cinereus* (Cinereous Tinamou), *Electron platyrynchum* (Broad-billed Motmot), *Glyphorynchus spirurus* (Wedge-billed Woodcreeper), *Grallaria dignissima* (Ochre-striped Antpitta), *Lepidothrix coronata* (Blue-crowned Manakin), *Momotus momota* (Blue-crowned Motmot), *Pipra filicauda* (Wire-tailed Manakin), *Psaracolius bifasciatus* (Olive Oropendola), *Ramphastos tucanus* (White-throated Toucan), *Thamnomanes caesius* (Cinereous Antshrike), and *Xiphorhynchus guttatus* (Buff-throated Wood-creeper). Straight line indicates a 1:1 relationship between values for the two plots. The actual slope of the regression between the two plots is given.

(e.g., gaps created by trees falling, wind storms, habitat variation, and species interactions) that often produce differences in current species distribution and abundance patterns. Consequently, differences in composition and structure would not reflect biogeographical or other historical processes. In the following, I review some of the results of these comparisons, focusing on similarities and differences at the between-plot scale. Such comparisons ignore, for the present, spatial and temporal variation in species distribution and abundance at the within-plot scale.

SPECIES RICHNESS AND DOMINANCE

Overall patterns of species richness, number of detections, and abundance-rank relationships

were, for all practical purposes, the same in both plots. Species totals for the two plots differed by $<1\%$ and total number of detections by $<0.5\%$, with $\sim 16\,000$ detections in each plot. Species richness per plot was comparable to that of other studies in Amazonia. In their pioneering study, Terborgh et al. (1990) reported a total of 319 species in 97 ha of mature floodplain forest in Peru, with 245 species considered resident (i.e., with densities of ≥ 0.5 pairs per ha; actual numbers given in their appendix show 227 species at that density, with an additional 18 at 0.25 pairs per ha). The Peruvian plot is bordered by the Manu River, Cocha Cashu (oxbow lake), swamp forest, and mature forest. Presence of these habitats, particularly the aquatic ones, accounts for some
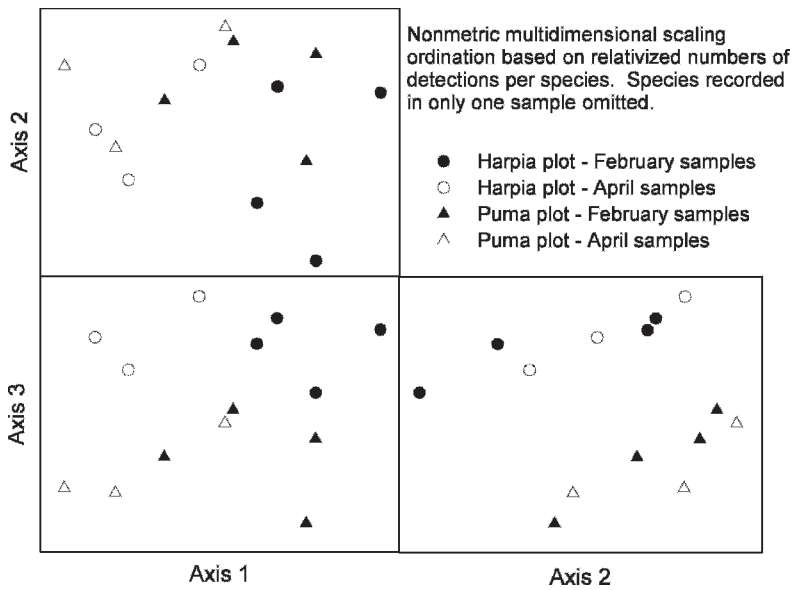
FIGURE 4.   Nonmetric multidimensional scaling ordination based on number of detections per species per sample on two 100 ha plots at Tiputini Biodiversity Station, Ecuador. Axes reflect differences in relative number of detections per species between plots and among samples. Axis 1 largely reflects differences in composition between February and April; axis 2 partially reflects differences between plots but also differences among years in samples from Harpia; axis 3 largely reflects differences between plots.

of the differences between Peru and Ecuador. For example, one of the most abundant species in the Peruvian site was *Cacicus cela* (Yellow-rumped Cacique; Icteridae), with a colony at the lake margin; similarly, occurrence of *Opisthocomus hoazin* (Hoatzin; Opisthocomidae) reflects the presence of the lake. In a similar study, Thiollay (1994) reported total species richness of 268 species on 100 ha in French Guiana; 245 species were considered resident (220 with densities of ≥ 0.5 pairs per 100 ha, almost the same as in Peru). Closer to the site of the present study, English (1998) found 284 species (221 in ''measurable densities'') at a 100 ha site approximately 30 km from Tiputini (Yasuní Research Station, Yasuní National Park).

In contrast to results from South America, species richness was less on a 104 ha plot in Panama (Robinson et al. 2000). Of 252 total species, 181 were considered resident (152 with >0.5 pairs per 100 ha). Presence of migratory species (45 latitudinal, three altitudinal) accounted for a substantial proportion of the remaining species and highlights one of the differences between sites in Central and South America. Migrants accounted for a very small fraction of species and detections at Tiputini, for example.

Differences between South America and Central America also were evident in dominance relationships. Abundance-rank curves for the two plots in the present study indicated strong equitability in abundances among species, similar to results from Yasuní and Peru, but very different from Panama, where several species accounted for a much greater proportion of the total number of individuals (Terborgh et al. 1990, English 1998, Robinson et al. 2000).

FAMILY COMPOSITION

Both plots at Tiputini were dominated by the same families in terms of species and detections. As was true in other Amazonian forests (Bierregaard 1990, Terborgh et al. 1990, Thiollay 1994), suboscines, particularly Thamnophilidae, Tyrannidae, Dendrocolaptidae, Furnariidae, and Pipridae, accounted for many of the most species-rich or abundant families, with oscines (Thraupidae) and nonpasserines (Trochilidae, Psittacidae) also important. Differ-

TABLE 4. Species selected as indicators of either the Harpia or Puma plot, based on indicator-species analysis (Dufrêne and Legendre 1997). Species are ordered by significance of indication; lower *P*-value indicates higher degree of association with that plot.

Harpia Plot		Puma Plot	
Species	*P*	Species	*P*
Hemitriccus zosterops (White-eyed Tody-Tyrant)	0.002	*Crypturellus cinereus* (Cinereous Tinamou)	0.002
Hylophylax naevius (Spot-backed Antbird)	0.002	*Electron platyrhynchum* (Broad-billed Motmot)	0.002
Hypocnemis hypoxantha (Yellow-browed Antbird)	0.002	*Grallaria dignissima* (Ochre-striped Antpitta)	0.002
Lipaugus vociferans (Screaming Piha)	0.002	*Psarocolius angustifrons* (Russet-backed Oropendola)	0.002
Nyctiphrynus ocellatus (Ocellated Poorwill)	0.002	*Ara macao* (Scarlet Macaw)	0.006
Microbates cinereiventris (Half-collared Gnatwren)	0.004	*Ramphastos vitellinus* (Channel-billed Toucan)	0.006
Schiffornis turdina (Thrush-like Schiffornis)	0.005	*Pteroglossus pluricinctus* (Many-banded Aracari)	0.007
Xiphorhynchus ocellatus (Ocellated Woodcreeper)	0.006	*Ara severa* (Chestnut-fronted Macaw)	0.008
Campephilus rubricollis (Red-necked Woodpecker)	0.008	*Pipra filicauda* (Wire-tailed Manakin)	0.015
Tyranneutes stolzmani (Dwarf Tyrant-Manakin)	0.008	*Cercomacra serva* (Black Antbird)	0.017
Pipra pipra (White-crowned Manakin)	0.009	*Campephilus melanoleucos* (Crimson-crested Woodpecker)	0.018
Tinamus guttatus (White-throated Tinamou)	0.010	*Phaethornis malaris* (Great-billed Hermit)	0.021
Phoenicircus nigricollis (Black-necked Red-Cotinga)	0.012	*Momotus momota* (Blue-crowned Motmot)	0.026
Saltator grossus (Slate-colored Grosbeak)	0.012	*Synallaxis rutilans* (Ruddy Spinetail)	0.039
Pipra erythrocephala (Golden-headed Manakin)	0.017	*Cyanocorax violaceus* (Violaceous Jay)	0.042
Conopophaga peruviana (Ash-throated Gnateater)	0.024	*Myrmotherula ornata* (Ornate Antwren)	0.044
Celeus grammicus (Scale-breasted Woodpecker)	0.035	*Hypocnemis cantator* (Warbling Antbird)	0.045
Trogon rufus (Black-throated Trogon)	0.036	*Xiphorhynchus elegans* (Elegant Woodcreeper)	0.046
Jacamerops aureus (Great Jacamar)	0.042	*Ancistrops strigilatus* (Chestnut-winged Hookbill)	0.050
Frederickena unduligera (Undulated Antshrike)	0.055	*Psarocolius bifasciatus* (Olive Oropendola)	0.051

ences existed between plots in the representation of some families, particularly those with few species or individuals, but the overall relationship indicated similar community composition at the family level. Patterns seen at Tiputini closely matched those at Yasuní, reflecting the close proximity and similar conditions at the two sites. Patterns also were very similar between Ecuador and Peru. Thamnophilidae, Tyrannidae, and Thraupidae were the most species-rich families in both countries. Deviations from a 1:1 relationship were evident for a few families; Accipitridae, for example, were better represented (or better sampled) in Peru, whereas Furnariidae were more important in Ecuador. Differences in number of species per family were more pronounced, but still very similar, between Ecuador and French Guiana. Apparent differences may, at least partially, reflect the fact that Thiollay (1994) listed only residents and omitted an additional 20 species that were recorded on the plot; inclusion of those species could alter the results slightly.
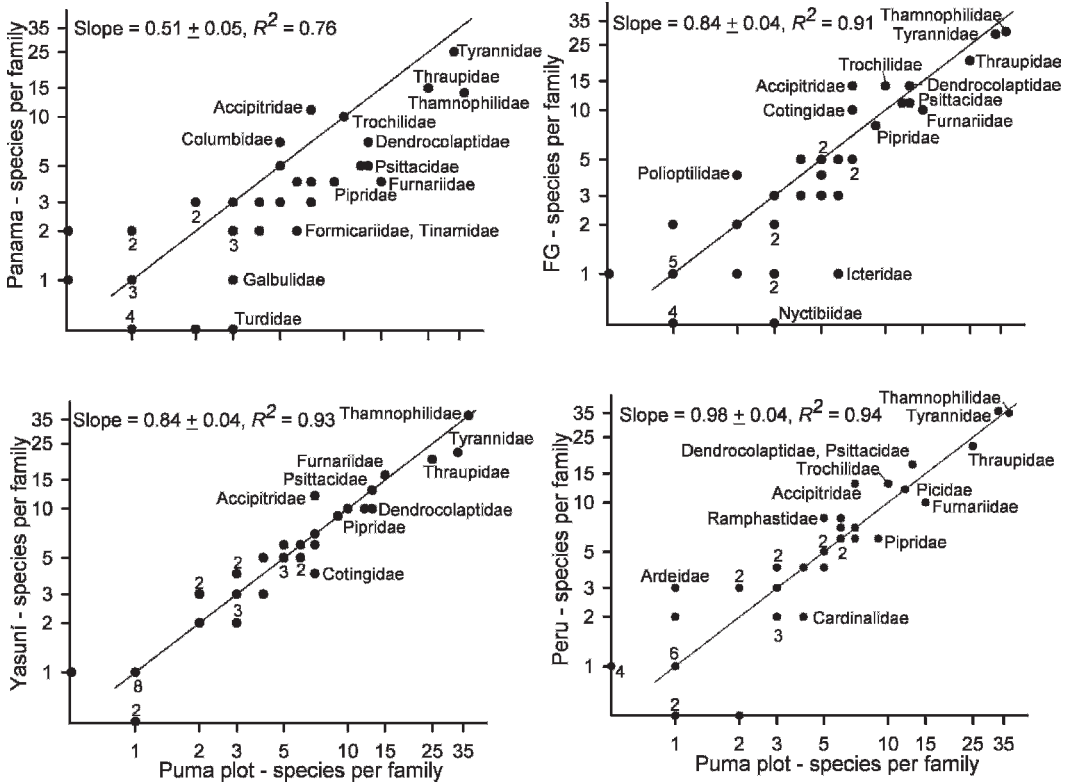
FIGURE 5.   Number of species per family in Puma Plot, Tiputini Biodiversity Station, Ecuador, compared to species per family on 100 ha study plots from Pipeline Road, Panama (data from Robinson et al. [2000]), Nouragues Research Station, French Guiana (data from Thiollay [1994]), Yasuní Research Station, Ecuador (data from English [1998]), and Cocha Cashu Biological Station, Peru (data from Terborgh et al. [1990]); species identified as migrants or vagrants at a given site were not included in results for that site. Straight lines indicate a 1:1 relationship between values for the two sites; the actual slope of the regression between pairs of sites is given. Numbers by points indicate number of families represented by that point.

The overall close similarity among Amazonian bird communities is in strong contrast to the large difference in species richness per family between Ecuador and Panama. Although Tyrannidae and Thraupidae are still among the most species-rich, Thamnophilidae, for example, are much less important in Panama than in Ecuador. Overall, the relationship between Ecuador and Panama differed strongly from 1:1, reflecting the fact that most shared families were represented by more species in Ecuador than in Panama.

SPECIES COMPOSITION

Differences between plots were most evident when examined at the individual species level. Of 309 total species (excluding species that simply flew over the plots), 292 were observed

at least twice (i.e., could be recorded in both plots). Of these, 13% were observed in only one plot (19 restricted to Harpia, 19 to Puma). Of species represented by at least 10 detections, 33 were detected more than twice as often in Harpia and 48 in Puma; 8 were detected five times more often in Harpia and 15 in Puma. Many of the species with large differences between plots are large or conspicuous, so it is unlikely that they were overlooked on one plot but not the other. The most extreme example is that of *Lipaugus vociferans*, which had a large lek in Harpia but was virtually absent from Puma. The two records from Puma likely represented individuals from a lek approximately 300–400 m outside the Puma plot. Given the distance over which one can hear this species (the common name Screaming Piha
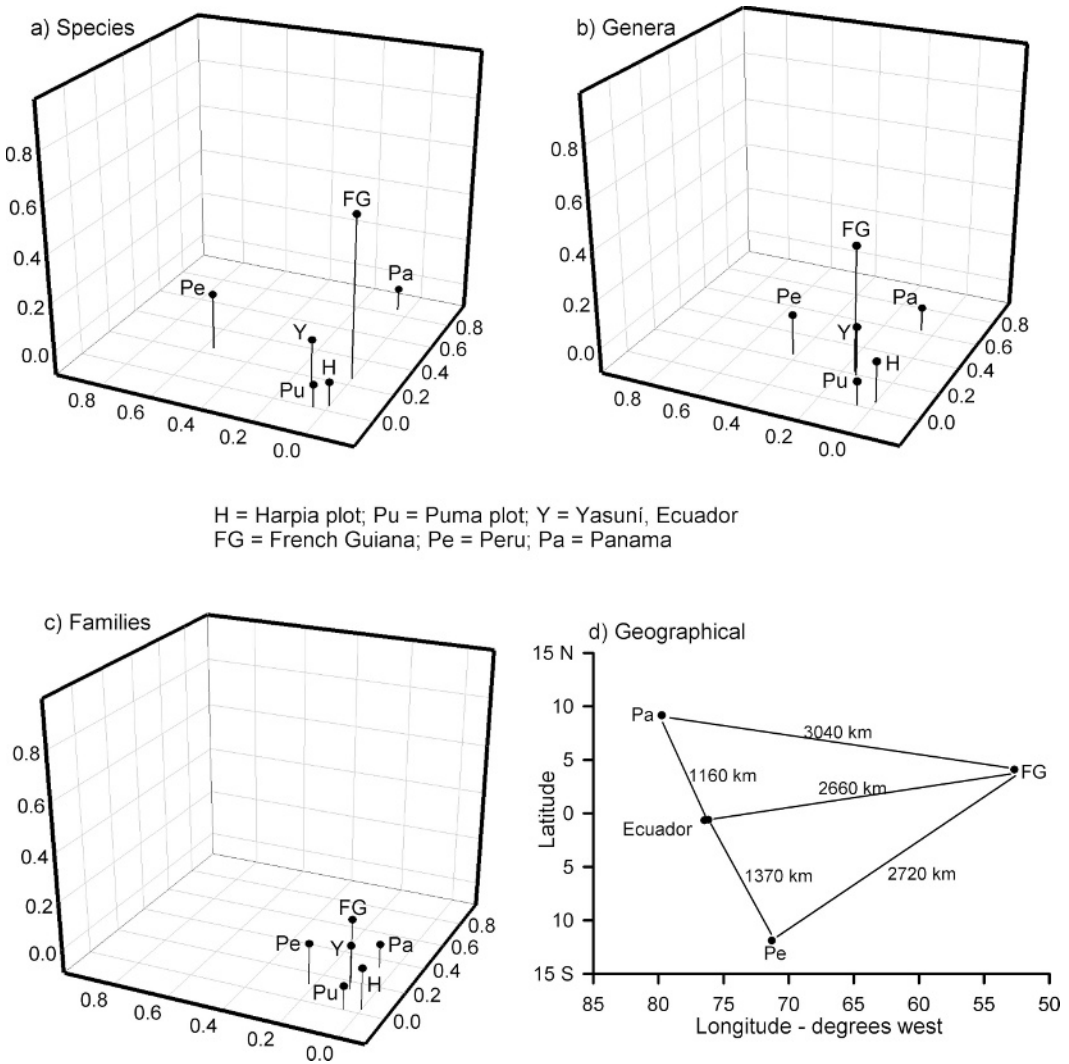
H = Harpia plot; Pu = Puma plot; Y = Yasuní, Ecuador
FG = French Guiana; Pe = Peru; Pa = Panama

FIGURE 6.   Percentage of detections or individuals per (a) species ($n = 575$), (b) genus ($n = 274$), or (c) family ($n = 47$) were used to illustrate differences in community composition among sites in Central and South America, based on a Bray-Curtis ordination. The *x*-axis largely separates the Panama site from all others; the *y*-axis reflects differences between Peru and other sites; the *z*-axis separates French Guiana from other sites. Scales are the same in all three figures to illustrate how differences among sites decrease from species to genus to family-level comparisons. Geographic distances (d) were calculated from latitude and longitude; the three sites in Ecuador overlap at a single point, given the scale of the figure. Data from current study based on numbers of detections; data from other sources based on estimated numbers of individuals: Yasuní, Ecuador (English 1998); Peru (Terborgh et al. 1990); French Guiana (Thiollay 1994); Panama (Robinson et al. 2000).

provides an indication), it is unlikely that the pronounced difference in number of detections does not reflect a real difference in abundance. Other species apparently more abundant in Harpia than in Puma included a large woodpecker (*Campephilus rubricollis* [Red-necked Woodpecker]) and a second large cotingid

(*Phoenicircus nigricollis* [Black-necked Red-Cotinga]); both have far-carrying vocalizations or sounds. On the other hand, species such as *Microbates cinereiventris* (Half-collared Gnatwren), *Hypocnemis hypoxantha* (Yellow-browed Antbird), *Hemitriccus zosterops* (White-eyed Tody-Tyrant), and *Schiffornis turdina*

(Thrush-like Schiffornis) are relatively small and do not have exceptionally loud vocalizations, but still were detected much more often in Harpia. Differences in numbers of detections for these and other species likely reflected real differences in abundance related to habitat differences between the two plots. *Hypocnemis* and *Hemitriccus*, for example, favored hilly areas with ridges (Hilty and Brown 1986, Ridgely and Greenfield 2001; JGB, pers. obs.), which were more characteristic of Harpia than of Puma.

In Puma, three of the more frequently detected species were large psittacids (*Ara chloroptera* [Blue-and-green Macaw], *A. severa* [Chestnut-fronted Macaw], and *Amazona amazonica* [Orange-winged Parrot]), three were large icterids (*Psaracolius bifasciatus* [Olive Oropendola], *P. angustifrons* [Russet-backed Oropendola], and *Clypicterus oseryi* [Casqued Oropendola]), and two were motmots (*Electron platyrynchum* [Broad-billed Motmot] and *Momotus momota* [Blue-crowned Motmot]); all are conspicuous and hard to miss when present. Presence of nesting colonies of two of the oropendolas accounts for much of the difference in these species. Other species more common in Puma also reflect habitat differences. For example, *Pipra filicauda*, *Grallaria dignissima* (Ochre-striped Antpitta), and *Schistocichla leucostigma* (Spot-winged Antbird) were all much more commonly encountered in Puma and all were typically associated with streams or other moist areas (Hilty and Brown 1986, Ridgely and Greenfield 2001; JGB, pers. obs.). Such habitats were more common in Puma, which was flatter overall and had more permanent streams and swampy areas than were present in Harpia. In contrast, *Pipra erythrocephala* and *P. pipra* were more common in Harpia; both were associated with steeper topography (either ridgetops or slopes; Loiselle et al. 2007).

Thus, although the overall pattern of species composition was similar in the two plots, reflecting their close proximity and shared history, significant differences likely exist in the abundance of many individual species. Such differences reflect smaller-scale, ecological processes (e.g., differences in habitats between the plots and differences in patterns of habitat selection among species). Although not described here, notable differences also existed at the within-plot scale in species distributions, which reflected small-scale variation in habitat, including both vegetation and topography.

When compared to other Neotropical sites with ~100 ha plots, Tiputini was, not surprisingly, most similar to the geographically close and ecologically similar site at Yasuní (English 1998). This was true whether comparisons were based on species, genus, or family. Most species occurred at both sites and five species were among the 10 most abundant (or detected) at each, despite differences in sampling methods. Similarity in species composition was lowest between Tiputini and Panama (Robinson et al. 2000), reflecting different histories and, likely, differences in forest structure. Differences between Central and South American sites were not simply related to distance, as differences among sites in South America were less pronounced even when geographic separation was more than twice as great. Differences among sites within South America, in contrast, did, at least partially, reflect geographic separation. Although actual species identity often differed among sites, all were dominated by suboscines. Similarly, although individual species often differed, many of the same genera were among the most abundant at all or almost all sites (e.g., *Phaethornis*, *Myrmotherula*, *Thamnophilus*, *Platyrinchus*, and *Pipra*). As a consequence, when comparisons were made at higher taxonomic levels (genus and family), differences among sites were much less pronounced but still related somewhat to distance.

In summary, the oligarchic dominance hypothesis of Pitman et al. (2001) posits that tree communities in Amazonian forests largely are dominated by a similar or related set of families, genera, and, to a lesser extent, species. Bird communities, in general, are also dominated by a similar set of families, although actual species composition differs among plots located far apart. At a smaller scale, plots located close together not only are dominated by a similar set of families but also share, to a much greater extent, the same set of species. Important differences exist in species distribution and abundance and reflect small-scale differences in habitat structure and availability. Other species differ between plots for other, as yet unknown, reasons. The great similarity between the two plots in the current study suggests that, at least from the perspective of

these aspects of community structure, a single plot is likely to provide a good picture of the overall pattern for a region, but does not provide a good picture of local-scale beta diversity patterns that can contribute to the overall pattern of diversity.

ACKNOWLEDGMENTS

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