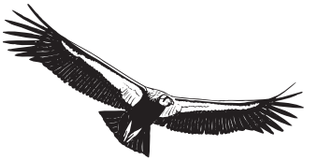

RESEARCH PAPERS

The Condor 113(1):7–23

COMPARATIVE STRUCTURE AND ORGANIZATION OF CANOPY BIRD ASSEMBLAGES IN HONDURAS AND BRAZIL

DAVID L. ANDERSON[1] AND LUCIANO N. NAKA

Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803

Abstract. Birds of the forest canopy are an integral component of bird communities of neotropical forests but remain largely unstudied, inhibiting any broad characterization of their assemblages. We present the first description of a canopy-bird assemblage from Middle America and, on the basis of >11 000 detections in lowland rainforests in Honduras and Amazonian Brazil, compare two distant canopy-bird assemblages. The richness of canopy birds at the two sites was similar despite the much higher richness of forest birds in Brazil. Furthermore, abundance distributions differed significantly: in Honduras the assemblage was dominated by a small number of superabundant species and had fewer rare species, whereas in Brazil it had fewer abundant species and was thus more even. Omnivores and insectivores dominated the assemblages in terms of species richness, but omnivores were numerically more abundant. Species of forest edges and open habitats, sometimes considered an important component of forest-canopy avifauna, were underrepresented at both sites in comparison to null expectations drawn from the pool of species in each region. Long-distance migrants were more important in Honduras, where they constituted a third of canopy birds, yet species richness of migrants did not differ from a null expectation. Finally, we present a baseline classification of the core constituent species of bird assemblages in the canopy of lowland neotropical rainforests.

Key words: birds; Brazil; community structure; core canopy species; forest canopy; Honduras; lowland neotropical rainforest.

Estructura y Organización Comparativa de Ensambles de Aves del Dosel en Honduras y Brasil

Resumen. Las aves del dosel del bosque son un componente integral de las comunidades de aves de los bosques neotropicales pero continúan en gran medida desconocidas, impidiendo cualquier caracterización amplia de sus ensambles. Presentamos la primera descripción de un ensamble de aves del dosel de Centroamérica y, sobre la base de >11 000 detecciones en los bosques lluviosos de tierras bajas de Honduras y la Amazonía de Brasil, comparamos dos ensambles distantes de aves del dosel. La riqueza de aves del dosel en los dos sitios fue similar a pesar de que en Brasil la riqueza de aves de bosque es mucho mayor. Más aún, las distribuciones de abundancia difirieron significativamente: en Honduras el ensamble fue dominado por un pequeño número de especies súper abundantes y tuvo menos especies raras, mientras que en Brasil presentó menos especies abundantes y fue por ende más equitativo. Los omnívoros e insectívoros dominaron el ensamble, pero los omnívoros fueron numéricamente más abundantes. Las especies de los bordes del bosque y de los ambientes abiertos, a veces consideradas un componente importante de la avifauna del dosel del bosque, estuvieron sub-representadas en ambos sitios en comparación con las expectativas nulas derivadas de las especies existentes en la región. Las especies migratorias de larga distancia fueron más importantes en Honduras, donde representaron un tercio de las aves del dosel, aunque la riqueza de especies de aves migratorias no difirió de una expectativa nula. Finalmente, presentamos una clasificación de base de las especies que constituyen el núcleo de los ensambles de aves en el dosel de los bosques lluviosos neotropicales de tierras bajas.

INTRODUCTION

Bird communities of tropical forests are famously diverse, with 250 species co-occurring at single 100-ha sites in Amazonia and over 180 species at single 100-ha sites in southern Middle America (Terborgh et al. 1990, Robinson et al. 2000). Although birds that frequent the forest canopy often constitute 40–50% of the species richness in these communities (Terborgh et al. 1990, Cohn-Haft et al. 1997), the difficulty of accessing the canopy has hindered studies of upper forest lev-

Manuscript received 6 January 2010; accepted 23 September 2010.
[1]E-mail: danders.lsualum@gmail.com

The Condor, Vol. 113, Number 1, pages 7–23. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2011.100007

els, so few published studies have focused directly on canopy bird assemblages and their ecology (Greenberg 1981, Loiselle 1988, Walther 2002, Naka 2004). Despite the limited work on canopy birds, we know that they are an important component of forest bird communities and of the forest ecosystem. Canopy birds include important functional groups such as top predators, seed dispersers, and pollinators (Nadkarni and Matelson 1989, Howe 1996, Blake and Loiselle 2000, Holbrook and Smith 2000, Anderson 2001), and it has been argued that the loss of species in these groups following forest disturbance can have severe consequences for the forest ecosystem (da Silva et al. 1996, Loiselle and Blake 2002, Laurance et al. 2006).

As biodiversity is eroded through the continued effect of humanity in lowland neotropical rainforests, it will be essential to understand the processes that maintain and structure biological communities of forest ecosystems so that current levels of biodiversity can be preserved as much as possible. One way to elucidate patterns of diversity and the processes that create and maintain high levels of diversity in the tropics is through a comparison of similar systems at geographically distant locations (Pitman et al. 2001, Stevens and Willig 2002). Despite the use of this approach to examine bird communities in lowland neotropical rainforests (Karr et al. 1990, Robinson et al. 2000), no comparative study that focuses specifically on canopy birds has been published.

Ground-based methods alone are insufficient for the study of canopy birds (Anderson 2009). To date, only three studies have used canopy-based methods to describe entire bird assemblages in neotropical forest canopies: two in southern Middle America, at La Selva, Costa Rica (Loiselle 1988), and Barro Colorado Island, Panama (Greenberg 1981), and one in central Amazonian Brazil (Naka 2004). Although these studies have allowed us a preliminary understanding of canopy bird assemblages, some issues remain unresolved. One key question is whether canopy bird assemblages are dominated by forest birds (Loiselle 1988, Naka 2004) or by species associated with open habitats such as edges or clearings (Greenberg 1981). The harsh environment of the two-dimensional forest canopy is similar to open habitats in that it receives more direct sunlight and is subject to greater diurnal fluctuations of temperature and humidity, greater seasonal variation in water potential, and greater overall wind turbulence than is the forest interior (Endler 1993, Koch et al. 2004, Madigosky 2004). As a consequence, we may expect canopy bird assemblages to be dominated by species that tend to occur in open habitats (Walther 2002, Burney and Brumfield 2009). Second, no consensus has been reached as to the trophic organization of canopy assemblages in lowland neotropical forests (Greenberg 1981, Loiselle 1988, Naka 2004). Because food resources in the forest canopy are highly variable over space and time (Frankie et al. 1974, Levey et al. 1994, Foster 1996, Leigh 1999), we may expect a high proportion of diet generalists, vagile species, and migrants in the canopy, able to exist on or track a variable and unpredictable diet. Finally, identifying the constituent vertebrate species of any given habitat is a fundamental step in field ecology used to characterize habitats and the ecosystems they constitute. The characterization of the core constituent species of the lowland neotropical forest canopy, and differentiating this group from visitors from other forest strata or neighboring habitats, have remained elusive and unquantified.

The major goal of our study was to present a broad characterization of canopy bird assemblages in lowland neotropical rainforests. We begin with the first description of a canopy bird assemblage from northern Middle America and use these data as a basis for comparisons with a canopy bird assemblage in central Amazonia similarly censused by means of canopy-based methods. In particular, we address the following questions: (1) What are the similarities or differences in the structure and composition of canopy bird assemblages in Honduras and Brazil, in particular as related to species richness, species abundances, composition of dietary guilds, and predominance of edge-living species and long-distance migrants at the respective sites? (2) Does species richness of habitat and diet generalists and of migrants in canopy bird assemblages differ from random expectations drawn from regional pools of species? (3) Which genera and species may be considered the core constituents of the assemblages in forest canopies in the humid lowlands of the neotropics?

METHODS

STUDY AREAS AND BIRD CENSUSES

We studied canopy birds at two lowland rainforest sites, one in Pico Bonito National Park in northern Honduras (DLA), the other in central Amazonia near Manaus, Brazil (LNN), during two independent research projects. Detailed descriptions of the study areas and census methods are in Anderson (2009) and Naka (2004). Briefly, both sites lie at elevations below 350 m. Forest structure is similar, characterized by a closed canopy reaching to approximately 35 m, with abundant epiphytes and lianas. Annual rainfall averages 2900 and 2400 mm for Pico Bonito and Manaus, respectively, and is seasonal, with a pronounced dry season of approximately 3–5 months.

To make the data sets from the original studies more strictly comparable, we made minor changes to data summarization for the present study. We therefore provide a brief overview of census methods before discussing the standardization of data. The principal method for studying birds in Honduras and Brazil was censuses from canopy-based viewpoints, following the protocol of Loiselle (1988). In Brazil, canopy viewpoints consisted of three canopy towers separated by 10 to 45 km. Three censuses were made monthly from each tower over a complete annual cycle from November 1999 to November 2000. In Honduras censuses were made from 30 trees within a 100-ha plot from April 2006 to April 2007. Additional observations were obtained from 30 point-count stations along two ground transects. Canopy censuses began 30 min after sunrise and lasted 3 hr, during which we recorded all birds seen or heard in the forest canopy within 150 m of the observer (Loiselle 1988). The data used in analyses are the maximum number of individuals and species observed per

3-hr canopy census. For point counts from the ground in Honduras, numbers of individuals and species for all points covered in a single walked transect are summed. For Honduras only, we categorized all birds detected into one of four forest strata: (1) ground (soil, leaf litter, and fallen logs), (2) understory (the space from the ground to 2 m), (3) midstory (the space between the understory and canopy), and (4) canopy (the sum of all tree crowns exposed to the sky above; Figure 1C in Bongers 2001). Our analyses exclude nocturnal species, aerial foragers (swifts, swallows), and scavengers (vultures) because these species were observed solely as flyovers.

To facilitate comparisons at the assemblage level, we assigned all bird species to one of six major feeding guilds: (1) raptors, (2) nectarivores (exclusively hummingbirds), (3) frugivores (diet includes a substantial portion of fruit at least during some seasons, seeds not destroyed but presumably dispersed; Moermond and Denslow 1985), (4) granivores (seeds destroyed; parrots), (5) insectivores, and (6) omnivores (species that regularly feed on fruits, insects, nectar, and sometimes small vertebrates). We omit the guild insectivore-omnivore (Naka 2004) and include those species within the omnivore guild. Assignment to guild is based in part on Stiles and Skutch (1989), Terborgh et al. (1990), and Robinson et al. (2000), combined with our own personal observations.

STATISTICAL ANALYSES

One of our primary objectives was to distinguish the "core" members of the canopy assemblage, species that regularly breed in, winter in, or migrate through the forest canopy, from those species that are not characteristic of the forest canopy and that occur as visitors from lower levels of the forest, as visitors from nonforest habitats, or as vagrants (Remsen 1994). For Honduras, we used census data to quantify birds' preference for the canopy stratum with the method of Neu et al. (1974), which compares the observed frequency of use of a given resource or habitat with an expected frequency derived from the available proportion of that resource or habitat. To maintain a 95% confidence level, we used Bonferonni's adjustment to set confidence limits around the observed frequency of detection in the canopy stratum for species with ≥4 detections. A significant preference for the canopy was indicated by expected values below the 95% confidence limits for the observed values (Haney and Solow 1992, da Silva et al. 1996), and we refer to species that met this criterion as the core canopy species. Furthermore, we assigned numeric values (ground = 0, understory = 1, midstory = 2, canopy = 3) to the four strata defined in Honduras so that we could calculate a stratum average for each species. These procedures could not be applied to Brazil, where detections below the forest canopy were not recorded. Instead, we adopted the list by Cohn-Haft et al. (1997) of residents having the forest canopy as their preferred habitat. Because the methods for defining core canopy species in Honduras and Brazil differ, we attempt no quantitative comparisons of core canopy species (e.g., richness, abundance distributions) at the two sites.

We rarified rates of species accumulation to compare species richness in canopy assemblages. Rarefaction curves are derived from repeated and random resampling of the pool of observations and plotting the average number of species represented by n individuals; they are therefore a statistical representation of species-accumulation curves (Gotelli and Colwell 2001, Magurran 2004). We calculated Chao 1 and Chao 2 nonparametric estimators (Magurran 2004) to estimate species richness from each study area. Chao 1 is an abundance-based estimator that relies on the number of species represented by a single individual to estimate species richness, whereas Chao 2 is an incidence-based estimator that uses the number of species detected in a single sample to estimate richness. For these calculations we used EstimateS version 7.5 (Colwell 2005).

We used the inverse of the Simpson index ($1/d$) to characterize the evenness of species in Honduras and Brazil (Smith and Wilson 1996, Magurran 2004). First, we calculated this index for the data from Honduras and Brazil, respectively, as an approximation of evenness for the overall assemblage of canopy birds. We then used a randomization procedure to obtain confidence limits around the overall values. Specifically, we bootstrapped individual daily censuses until we obtained a sample that contained the same number of censuses as constituted the original empirical sample. We repeated this process 1000 times to obtain 95% confidence limits around the index of diversity. Bootstrapping and randomization were done in R (R Development Core Team 2008).

We used a new approach to determine the 20 dominant canopy species in Honduras and Brazil, a recurrent theme in descriptions of avian assemblages (Loiselle 1988, Karr et al. 1990, Robinson et al. 2000, Naka 2004). Ideally, dominance is described in terms of the relative density of individuals and biomass (Terborgh et al. 1990, Robinson et al. 2000, MacKenzie et al. 2006), although various proxies have been used in the absence of these data, including percentage of overall detections (Blake 2007), total number of detections (Loiselle 1988), mean number of individuals detected per census (Naka 2004), and frequency of detection (Naka 2004). To standardize comparisons of the two sites, we used a procedure that takes into account two such measures of relative abundance: frequency of observation and average number of individuals per observation. Specifically, we multiplied the mean number of individuals per survey and the proportion of surveys in which a species was detected and ranked species by the product. This measure more accurately accounts for the difference between species that are observed regularly in small numbers and species observed infrequently but in larger numbers, usually in single-species flocks.

We compared the observed composition of dietary guilds, numbers of edge species, and numbers of migrant species in each group of core canopy species with null distributions drawn from each regional pool of species through a randomization procedure. At each site we conservatively defined edge species as those found in both continuous forests and forest edges, in gardens, or in semi-open and nonforest habitats.

We made these determinations primarily on the basis of personal experience and Stotz et al. (1996). To assemble each regional pool of species we considered all species of possible occurrence in the canopy of primary forest, exluding terrestrial, aquatic, and aerial species as well as regional species not known to frequent primary forests. For Honduras we considered those species found below 350 m in Pico Bonito National Park (Bonta and Anderson 2002), and for Brazil we considered species listed by Cohn-Haft el al. (1997) as occurring in the Biological Dynamics of Forest Fragments Project (BDFFP) north of Manaus. We used a bootstrapping procedure to randomly draw a number of species from a given regional pool equal to the number of species in the region's group of core canopy species. We then tallied the number of edge species, migrants, and species in each dietary guild and repeated this procedure 1000 times to obtain confidence estimates around a randomly generated assemblage composition. We inferred a result to be significant when the observed values fell above or below 95% of the null values.

For some analyses we desired a balanced comparison of equal survey effort in Brazil (117 canopy censuses) and Honduras (56 canopy censuses). For this purpose we narrowed the Brazil data set to 56 censuses by selecting those censuses whose Julian dates most closely matched those of the corresponding canopy censuses in Honduras. Analyses that used this restricted data set are noted below.

DENSITY ESTIMATION

Previous studies have shown that the great variety of social systems of tropical birds necessitates that a variety of methods be used to estimate population densities, that correcting for observation biases in avian communities with such high species richness is complex and not possible for all species present, and that relationships between the true population density of a species and estimates derived from such methods remain unclear (Terborgh et al. 1990, Robinson et al. 2000). We acknowledge that our comparison of distinct avifaunas of distant sites will introduce bias in density estimation. We emphasize that an attempt at correcting density estimates for a limited number of species under these circumstances would not fully rectify the problem of detection biases in the assemblages under consideration, nor would it allow us to fully address the structure of whole avian assemblages as proposed. Finally, an additional focus of our study was a comparison with the results of the two remaining canopy-based studies of canopy bird assemblages from Panama (Greenberg 1981) and Costa Rica (Loiselle 1988) for which no corrections would be possible. We instead adhere to the use of detections as a proxy for population density (Greenberg 1981, Loiselle 1988, Karr et al. 1990, Robinson et al. 2000, Naka 2004, Blake 2007), and we restrict our comparisons of the data to broad analyses of general patterns that we believe reflect taxonomic and functional patterns of real assemblages and broad-scale biogeographic patterns that are the result of structuring mechanisms operating at the assemblage level.

RESULTS

NUMBERS OF DETECTIONS AND SPECIES

From April 2006 to April 2007 DLA conducted 83 censuses in Honduras (56 canopy censuses and 27 ground transects), resulting in 2538 detections of 118 species in the canopy (Table 1). In Brazil, LNN conducted 117 censuses from November 1999 to November 2000, resulting in 9194 detections of 145 species observed in the canopy (Table 1). Our combined data set totals >11 000 detections of canopy birds.

The rarefaction curve for all canopy species in Brazil is asymptotic, indicating that sampling was adequate for the questions posed by the study (Fig. 1a). The all-canopy species curve for Honduras has the same shape as the left side of the Brazil curve but is truncated before it reaches the graduated tail of the asymptote (Fig. 1a), indicating that sampling was also reasonably complete. More importantly, the curves for core canopy species in both Honduras and Brazil reached asymptotes, signaling that sampling of this group was complete and that few core species remained to be added.

TABLE 1. Number of species and detections (by sight or sound) from the canopy stratum at Pico Bonito National Park, Honduras, and Manaus, Brazil.

			Number of species/number of detections	
Method	Censuses	Census hours[b]	All canopy species	Core canopy species
Honduras				
Ground	27	66.7 (2.4 ± 0.56)	36/300	31/294
Trees	56	168 (3 ± 0)	118/2238	66/2114
Total	83	234.7	118/2538	66/2408
Brazil				
Towers (all surveys)	117	351 (3 ± 0)	145/9194	107/8814
Towers (reduced set)[a]	56	168 (3 ± 0)	138/4575	107/4360

[a]Sample size reduced to equal number of censuses in Honduras.
[b]Numbers represent total census hours, with mean ± 1 SD in parentheses.

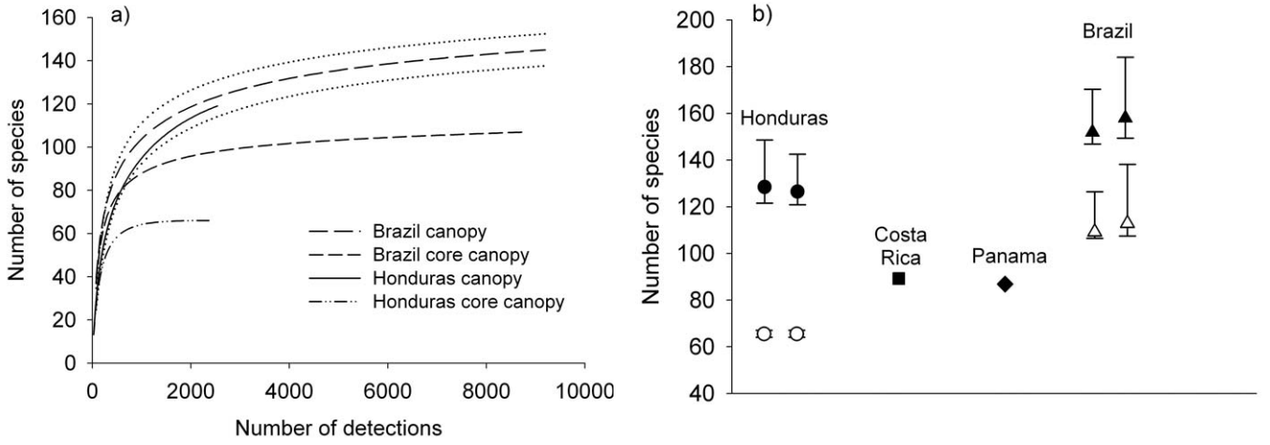

FIGURE 1. (a) Sample-based rarefaction curves for canopy bird assemblages in Honduras and Brazil. Curves for all canopy species and core canopy species are shown separately. Dotted line around the curve for Brazil depicts 95% confidence interval for all canopy species. (b) Estimates of species richness for all species observed in the canopy (solid shapes) and core canopy species only (hollow shapes) for Honduras and Brazil derived from Chao 1 and Chao 2 estimators, respectively. Shapes represent means and bars encompass 95% confidence intervals. Observed species richnesses in the canopy in Costa Rica and Panama are also shown.

Species richness of canopy bird assemblages in Honduras and Brazil appeared similar. The rarefaction curve for Honduras fell within the 95% confidence interval of the curve for Brazil, indicating that richness of the two sites did not differ significantly (Fig. 1a). Expected species richness for Honduras was approximately 130 species, or 20 species fewer than the 150 species expected for Brazil (Fig. 1b), although the difference was not statistically significant, on the basis of the level of sampling obtained. Observed species richness in Costa Rica and Panama was 86 and 84 species, respectively (Fig. 1b).

CORE CANOPY SPECIES

The core canopy species in Honduras were represented by 66 species, or 60% of all species observed in the canopy (Appendix). Twenty of these were observed exclusively in the canopy stratum, as represented by a stratum mean of 3.0 (Appendix). An additional 25 species were observed disproportionately more often in the canopy, as indicated by a stratum average of 2.9 or higher. Together these 45 species can be classified as canopy specialists. In Brazil, 107 species (74% of all species detected in the canopy) were core canopy species. A total of 49 genera encompassing 155 species were reported from the canopy at a minimum of three of the four sites (Honduras, Costa Rica, Panama, and Brazil). Historically, 25 genera occurred at all sites (*Ara* and *Amazona* having been extirpated from some), and three species (*Florisuga mellivora*, *Chlorophanes spiza*, *Cyanerpes cyaneus*) were observed at all sites (Table 2). Together, the grouping of core species in Honduras and Brazil in genera observed at a majority of the sites can be taken to represent the core allospecies that characterize bird assemblages of the canopy of these lowland neotropical rainforests. By family, richness of the Tyrannidae was greatest, with 13 genera and 35 species represented. The most species-rich genera were *Euphonia*, with eight species represented, and *Trogon*, *Dendroica*, and *Tangara*, each with seven species. Migrants were well represented, with high richness in the genera *Dendroica* and *Vireo* (four species).

SPECIES ABUNDANCES

The distribution of species' abundances in Honduras was significantly different from that in Brazil when sampling was restricted to 56 canopy censuses for each site (Kolmogorov–Smirnov test, $P < 0.001$). Three lines of evidence indicate that abundance distributions were more even in Brazil than in Honduras. First, three important differences in rank-abundance curves are noteworthy: (1) Honduras has more super-abundant species, (2) the middle portion of the Brazil curve lies completely above the Honduras curve, and (3) the tail of rare species is longer for Brazil (Fig. 2). Second, the 20 most abundant species make up a greater proportion of the canopy assemblage in Honduras than in Brazil (Table 3). In Honduras, the top 20 species accounted for 68.9% of all detections in the canopy, and seven species (*Hylophilus decurtatus*, *Psarocolius wagleri*, *Pyrilia haematotis*, *Ramphastos sulfuratus*, *Vireo olivaceus*, *Pteroglossus torquatus*, *Cyanerpes cyaneus*) each accounted for ≥4% of total detections. In Brazil the 20 most abundant species accounted for 48.5% of total detections, and only one species (*Brotogeris chrysopterus*) accounted for ≥4% of total detections. Third, results from bootstrapping analyses of the inverse of the Simpson evenness index revealed greater evenness in the canopy assemblage in Brazil (assemblage value 52.11; 95% confidence interval 46.93–56.26) and greater dominance in Honduras (assemblage value 24.92, 95% confidence interval 17.73–30.85).

TABLE 2. Constituents of the core canopy assemblage as represented by genera observed in the canopy of four lowland neotropical rainforests with published studies: Pico Bonito National Park, Honduras (this study), La Selva, Costa Rica (Loiselle 1988), Barro Colorado Island, Panama (Greenberg 1981), and Manaus, Brazil (Naka 2004). Only genera observed at ≥3 sites are included. Genera constituting part of the core canopy assemblage at the sites in Honduras (Ho) or Brazil (Br) are noted.

Genus	Core species	No. species	No. sites
Leucopternis	Ho, Br	3	3
Patagioenas	Ho, Br	4	3
Amazona[a]	Br	2	3
Ara[a]	Br	2	1
Brotogeris	Br	2	3
Pionus	Br	3	4
Piaya	Ho, Br	2	4
Florisuga	Ho, Br	1	4
Heliothryx	Ho	2	4
Thalurania	Ho, Br	2	3
Trogon	Ho, Br	7	4
Notharchus	Ho, Br	3	4
Pteroglossus	Ho, Br	2	4
Ramphastos	Ho, Br	4	4
Selenidera	Ho, Br	2	3
Campephilus	Ho	3	4
Celeus	Ho, Br	4	3
Melanerpes	Ho	2	4
Xiphorhynchus	Ho	5	3
Attila[b]	Ho, Br	1	2
Contopus	Ho	3	3
Mionectes	Ho	3	3
Myiarchus	Ho	4	4
Myiodynastes	Ho	2	3
Myiopagis	Br	3	3
Ornithion	Ho, Br	3	3
Pachyramphus	Br	5	3
Rhytipterna	Br	2	3
Tityra	Ho, Br	3	4
Tolmomyias	Ho, Br	3	4
Zimmerius	Ho, Br	2	4
Cotinga	Ho, Br	4	3
Hylophilus	Ho, Br	3	4
Vireo	Ho, Br	5	3
Vireolanius	Ho, Br	2	3
Polioptila	Ho, Br	2	4
Dendroica	Ho	7	4
Vermivora	Ho	1	3
Chlorophanes	Ho, Br	1	4
Cyanerpes	Ho, Br	4	4
Dacnis	Br	3	4
Tachyphonus	Br	4	3
Tangara	Br	7	3
Caryothraustes	Ho, Br	2	3
Piranga	Ho	3	3
Thraupis	Br	3	3
Icterus	Ho, Br	2	4
Psarocolius	Ho, Br	3	4
Euphonia	Ho, Br	8	4

[a]*Ara* and *Amazona* historically occurred at all sites but have been extirpated from some.
[b]*Attila spadiceus* is included because it was considered a core species for both Honduras and Brazil and occurred in high densities at both sites.

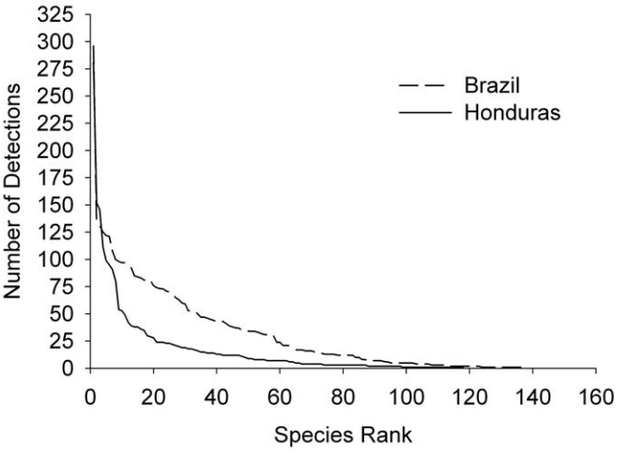

FIGURE 2. Rank-abundance curves based on number of detections by sight or sound of canopy birds in the Manaus study area, Brazil, November 1999–November 2000, and Pico Bonito National Park study area, Honduras, April 2006–April 2007. Data are derived from 56 canopy censuses at each site.

TROPHIC ORGANIZATION

In terms of species richness, the two dominant foraging guilds in Honduras were omnivores and insectivores, both of which had nearly four times as many species as any other guild (Fig. 3). Omnivores, however, dominated in terms of numerical abundance, constituting 49% of total detections in the canopy, followed by insectivores (23%) and nectarivores (12%). Granivores (10%), frugivores (7%), and diurnal raptors (1%) all accounted for 10% or fewer of total detections. The pattern for species richness in Brazil was similar, with omnivores and insectivores being the most species-rich guilds, although the pattern of relative abundance, when measured in terms of numbers of detections by guild, differed from the pattern found in Honduras. In Brazil, omnivores also were detected most often (41%), followed by insectivores (23%), granivores (20%), frugivores (14%), nectarivores (2%) and diurnal raptors (1%). Guild composition differed by site when compared at the level of all species detected in the canopy ($\chi_{5, 255} = 18.80$, $P = 0.0021$; Fig. 3a) and at the level of core canopy species ($\chi_{5, 163} = 13.88$, $P = 0.0164$; Fig. 3b). However, when species that had been extirpated from Honduras (*Ara macao*, *Amazona farinosa*, *A. autumnalis*) or whose populations were likely reduced through human persecution (*Buteogallus urubitinga*, *Harpagus bidentatus*, *Falco rufigularis*, *Pionus senilis*) were added to the analysis, the composition of dietary guilds within the set of core canopy species was indistinguishable ($\chi_{5, 170} = 4.99$, $P = 0.418$; Fig. 3c). This relationship held when nearctic migrants were excluded ($\chi_{5, 157} = 3.80$, $P = 0.579$; Fig. 3d), demonstrating that the similarity in guild composition between Honduras and Brazil was not affected by richness of migrants.

TABLE 3. The twenty dominant species recorded from the forest canopy in Pico Bonito National Park, Honduras, and Manaus, Brazil. Dominance rankings are derived from a relative-abundance index, calculated as the product of the mean number of detections per census and the percentage of censuses in which a species was detected (see text). Species are listed in descending order of relative abundance.

Species	% total detections	Mean no. detections	% surveys	Relative-abundance index
Honduras				
Hylophilus decurtatus	8.9	2.7	90.4	246.04
Psarocolius wagleri	12.6	3.9	39.8	155.64
Pyrilia haematotis	7.5	2.3	45.8	106.64
Ramphastos sulfuratus	5.0	1.5	65.1	100.76
Vireo olivaceus	4.4	1.4	57.4	78.41
Polioptila plumbea	3.3	1.0	59.0	61.20
Pteroglossus torquatus	4.0	1.2	36.1	44.96
Cyanerpes cyaneus	4.0	1.2	34.9	43.04
Tityra semifasciata	2.5	0.8	32.5	25.39
Dendroica petechia	1.7	0.5	46.6	23.86
Psilorhinus morio	2.1	0.7	33.7	22.22
Ornithion semiflavum	1.6	0.5	43.4	21.69
Piranga rubra	1.5	0.5	35.6	16.07
Melanerpes pucherani	1.5	0.5	32.5	15.47
Thalurania colombica	1.4	0.4	34.9	14.91
Aratinga nana	2.1	0.6	20.5	13.24
Piaya cayana	1.2	0.4	32.5	11.90
Euphonia gouldi	1.2	0.4	26.5	10.02
Piranga olivacea	1.0	0.3	28.6	8.71
Vireolanius pulchellus	1.3	0.4	21.7	8.46
Total	68.9			
Brazil				
Brotogeris chrysopterus	7.3	5.7	79.5	455.2
Dacnis cayana	2.8	2.2	86.3	191.8
Galbula dea	2.5	1.9	93.2	180.8
Zimmerius gracilipes	2.2	1.8	97.4	170.7
Herpsilochmus dorsimaculatus	2.3	1.8	90.6	160.3
Ramphastos tucanus	2.3	1.8	80.3	146.3
Vireolanius leucotis	2.0	1.6	92.3	144.4
Hylophilus muscicapinus	1.9	1.5	86.3	130.6
Terenura spodioptila	1.9	1.5	82.9	123.3
Patagioenas plumbea	1.9	1.5	81.2	120.8
Tangara punctata	2.1	1.6	74.4	120.8
Cyanerpes cyaneus	2.3	1.8	67.5	119.5
Tachyphonus cristatus	2.0	1.5	76.9	119.0
Tolmomyias assimilis	1.7	1.4	84.6	114.3
Chlorophanes spiza	1.9	1.5	76.1	111.8
Lamprospiza melanoleuca	2.0	1.6	70.1	110.2
Tangara chilensis	2.8	2.2	49.6	108.0
Amazona autumnalis	2.6	2.1	47.9	98.2
Xipholena punicea	1.7	1.4	70.1	95.8
Pionus menstruus	2.4	1.9	48.7	92.4
Total	48.5			

Omnivores were overrepresented in both canopy assemblages when compared with null expectations drawn from regional species pools (Table 4). In addition, raptors were underrepresented in Honduras, whereas granivores were overrepresented and insectivores were underrepresented in Brazil in comparison to the null expectation (Table 4).

HABITAT AFFILIATIONS

Edge species were not an important component of either canopy assemblage. In both Honduras and Brazil the number of core canopy species that are characteristic of edges and open habitats was significantly less than the null expectation based on species drawn from each regional pool (Table 4).

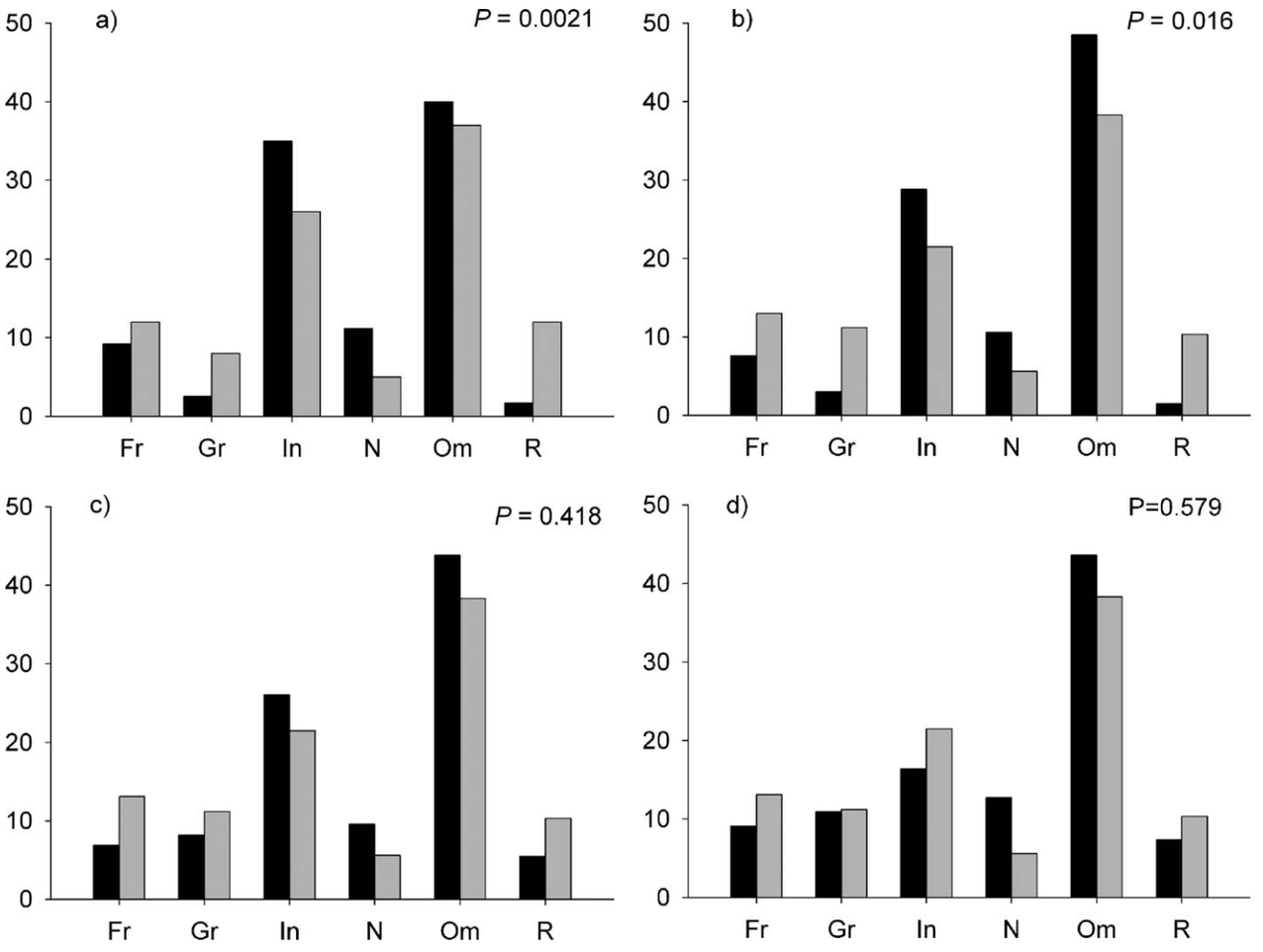

FIGURE 3. Percent composition of canopy bird assemblages by guild in Pico Bonito National Park, Honduras, and Manaus, Brazil. (a) All birds observed in the canopy, (b) core canopy species only, (c) core canopy species including those extirpated from Honduras, (d) core canopy species excluding nearctic migrants. Black bars are for Honduras, gray bars Brazil. Guild abbreviations represent frugivores (Fr), granivores (Gr), insectivores (In), nectarivores (N), omnivores (Om), and raptors (R).

TABLE 4. Observed vs. expected (95% confidence interval) species richness of feeding guilds and edge species in the canopy assemblages of Honduras and Brazil. Expected values were derived from random draws from regional pools of species in each country. Cases where observed species richness is significantly greater or less than expected values are indicated by "<" and ">," respectively. Note in particular the prevalence of omnivores.

	Honduras			Brazil		
Comparison	No. species observed	Significance	No. species expected	No. species observed	Significance	No. species expected
Guilds						
Insectivore	18		17–30	23	<	33–49
Frugivore	5		2–10	11		7–18
Granivore	2		0–5	11	>	2–9
Nectarivore	8		1–9	7		2–9
Raptor	1	<	2–10	11		5–14
Omnivore	32	>	18–31	45	>	27–41
Edge species	16	<	17–29	14	<	21–35

TABLE 5. Distribution of canopy bird species in Pico Bonito National Park, Honduras, and Manaus, Brazil, by residency status.

	No. species (% of total)	
Residency status	Honduras	Brazil
Breeding residents	89 (75)	134 (92)
Migrants	29 (25)	11 (8)
Nearctic	24 (20)	4 (3)
Resident	19 (16)	4 (3)
Transient	5 (4)	—
Austral	1 (1)	3 (2)
Also breeding	—	2 (1)
Austral + nearctic	—	1 (1)
Austral + nearctic + resident	—	1 (1)
Elevational	2 (2)	—
Vagrants	2 (2)	—
Total no. species	118	145

MIGRATORY STATUS

In Honduras, the number of long-distance migrants that were core canopy species did not differ statistically from the null expectation. However, migrants appear to be a relatively important component of the canopy assemblage there, accounting for 19 core canopy species (29%, Table 5) and four of the top 20 species (Table 3). Long-distance migrants were relatively less important in Brazil, where only 11 species were observed in the canopy (8% of all core canopy species) and none of the top 20 species was a long-distance migrant. Brazil's 11 species of migrants likewise did not differ from the null expectation.

DISCUSSION

OVERVIEW

Difficulty of access into the forest canopy has hindered the study of canopy bird assemblages as well as attempts to unify concepts on their structure and organization. Our study takes several steps to make such an attempt possible. First, we describe for the first time a canopy bird assemblage from northern Middle America, thereby broadening our perspective of canopy birds in lowland neotropical rainforests. Second, we compare canopy bird assemblages of distant neotropical forests, on the basis of similar canopy-based censuses in Honduras and Brazil. These sites are particularly useful for such a comparison because they share a similar climate and forest structure yet offer relatively independent biogeographic histories, being separated by over 2000 km. Most importantly, we took three steps designed to clarify previously unresolved arguments on the composition of canopy bird assemblages: (1) by categorizing bird observations in Honduras into distinct strata we achieved a quantitative definition of the core canopy birds at that site; (2) we assessed the relative importance of dietary guilds and of edge species and migrants in Honduras and Brazil by comparing the observed composition of these groups with expectations based on species drawn randomly from each regional pool; and (3) by reclassifying data sets from Costa Rica and Panama by similar criteria, we are able to broadly characterize bird assemblages of lowland neotropical rainforest canopies.

SPECIES RICHNESS AND ABUNDANCE

The species diversity of forest birds is notably higher in Amazonia than in Middle America at levels of both local (alpha) and regional (gamma) diversity (Karr et al. 1990, Terborgh et al. 1990, Blake 2007). Although we observed 27 more species in the canopy in Brazil than in Honduras, the overall richness of the canopy assemblages of the two sites did not differ significantly. Furthermore, if we include six species extirpated from the study site in Honduras (*Ara macao*, *Amazona farinosa*, *A. autumnalis*) or reduced below detectable levels by persecution (*Spizaetus ornatus*, *S. tyrannus*, *S. melanoleucus*), the difference between the sites in observed richness is 14%. Given that overall richness of forest birds is approximately 35% higher in Brazil, the similarity in species richness in the forest canopy is notable. The higher richness of migrants in Honduras, roughly three times that in Brazil, partially explains this finding. Especially notable was the greater richness of the family Parulidae, represented by 11 more species in Honduras than in Brazil, and the families Tyrannidae, Vireonidae, and Cardinalidae, which together contributed 15 species of migrants. Additionally, the number of hummingbird species observed in the canopy in Honduras was twice that observed in Brazil (14 vs. 7), despite equal species richness at the regional level. We suspect that in Honduras the high number of individual flowering trees in the canopy (principally *Vochysia guatemalensis* and *Symphonia globulifera*) may have attracted a greater diversity of hummingbird species into the canopy. During peak flowering, as many as eight individuals of seven species were observed in the canopy during a single 3-hr census, whereas in Brazil the median number of both species and individuals observed per census was one. This difference may be due to factors intrinsic to the Honduras site, because a similarly high richness of hummingbirds was not observed in Costa Rica (five species) or Panama (seven species).

Nonetheless, the additional migrants and hummingbirds in Honduras do not completely account for the similarity to Brazil in species richness. Clearly, in Brazil a smaller proportion of the regional forest species occurs in the canopy stratum. One plausible explanation is that differences in stratification result from the difference in taxonomic composition of the local avifaunas. At the Brazil site, the families Tinamidae, Cracidae, Furnariidae, Thamnophilidae, Formicariidae, Pipridae, and Troglodytidae, are all dominated by species of lower and middle forest strata, and richness of these families is more than double their richness in Honduras. In contrast, the few families with similar (Trochilidae, Vireonidae)

or greater (Parulidae, Cardinalidae) species richness in Honduras are weighted with species of the upper forest strata, or with migrants, which seem to be more important locally in the canopy than at lower levels. Therefore, we suggest that taxonomic differences in the regional avifaunas explain in large part the similarity of richness in the canopy in Honduras and Brazil.

Despite this similarity in species richness, patterns of species abundance differed markedly. Our findings that the Middle American canopy was dominated by a few superabundant species and that species' abundances were distributed more evenly in Amazonia are consistent with the findings reported by Robinson et al. (2000) for sites in Panama and Amazonian Peru. Robinson et al. described an "oligarchy" of eight common species, six from the understory and two from the canopy (*Hylophilus decurtatus* and *Zimmerius vilissimus*), that accounted for a disproportionate number (36%) of individuals at the Panama site. Likewise, in Honduras the seven most abundant canopy species each accounted for ≥4% of all detections and a combined 46% of all detections in the canopy, whereas in Brazil only a single species reached comparable abundance. Finally, the overall pattern of more rare species than common ones observed in both the Honduras and Brazil canopies mirrors results from other lowland sites in neotropical forest (Pearson 1977, Karr et al. 1990, Terborgh et al. 1990, Thiollay 1994b, Robinson et al. 2000).

RICHNESS OF MIGRANTS

The importance of migrants in the canopies of lowland neotropical forests deserves special recognition. Even in Brazil, where the proportion of austral to nearctic migrants is greater, migrants are observed disproportionately more often in the canopy than in the understory (Bierregaard 1990, Stotz et al. 1992). Moreover, few migrant forest birds are true ground-dwellers, and the majority inhabits mid- to upper forest strata. Of 36 passeriform species that are long-distance migrants to the Honduras study site, only six occur principally on the ground or in the understory (*Seiurus aurocapilla*, *Parkesia noveboracencis*, *P. motacilla*, *Oporornis formosus*, *Wilsonia citrina*, *Hylocichla mustelina*). Therefore, the annual influx of migrants to tropical forests adds disproportionately to the midstory and canopy. Finally, the pool of migrant species available to colonize the canopy is substantially greater in Honduras than in Brazil (Kelly and Hutto 2005), thereby disproportionately weighting the Honduras canopy with this group.

TROPHIC ORGANIZATION

Little consensus has been reached on the trophic organization of bird assemblages in the canopy of lowland neotropical rainforests. One confounding factor is that assignments to dietary guilds are not consistent among studies. In Honduras, omnivores and insectivores dominated the canopy in terms of species richness, whereas omnivores dominated in terms of numerical abundance. When we reclassified species' assignments to dietary guilds from previous studies by similar criteria, and restricted analyses to true forest species by eliminating aerial foragers and scavengers, the pattern that emerged was similiar at all four neotropical sites studied thus far. In Costa Rica, Panama, and Brazil, omnivores and insectivores were the most species-rich groups, with slightly higher richness in the omnivore guild for three of four forests. Similarly, omnivores predominated in numerical abundance at all sites. In the understory of lowland neotropical rainforests this patterns seems to be reversed. In Costa Rica species richness of insectivores was three times greater than that of omnivores, and abundance of individual insectivores twice as high (Blake and Loiselle 2001). In Brazil, 80% of the abundance of individuals and 69% of the biomass of understory species were of insectivores (Bierregaard 1990). The greater importance of omnivory in rainforest canopies contrasts with the greater predominance of insectivory in rainforest understories. This phenomenon may be related to the greater temporal and spatial unpredictability of canopy resources, which could favor diet generalists or vagile species like migrants able to take advantage of diverse resources over broad areas (Martin 1985).

HABITAT AFFILIATIONS

Another topic that has remained unsettled is whether the canopy of lowland neotropical rainforests is dominated by scrub species, as reported for Panama by Greenberg (1981), or forest species, as observed by Loiselle (1988) and Naka (2004). Our analyses for Honduras and Brazil showed that edge species are underrepresented in the forest canopy at both sites in comparison to the regional pool of species available to colonize the canopy. Although differences in observed and expected values for Honduras were low, we emphasize that the pattern of low importance of edge species found in both assemblages contrasts with previous suggestions that edge species should dominate the canopy stratum (Greenberg 1981, Walther 2002, Burney and Brumfield 2009). We propose that the occurrence of scrub species in the canopy at the site studied in Panama was due to the proximity of secondary forest and open habitats to the canopy tower. By comparison, the proportion of scrub species Naka (2004) observed in the canopy surrounding the tower at Reserva Ducke, situated on the outskirts of Manaus and surrounded on three sides by open, agricultural and human-disturbed habitats, was greater than at two towers in the midst of uninterrupted primary forest. Of further note, some of the most common species Greenberg (1981) reported from the canopy in Panama are commonly associated with gardens or forest edges, notably *Coereba flaveola*, which was only rarely observed in the canopy in Brazil and never in Costa Rica or Honduras, despite being found in neighboring secondary forests and open habitats.

CORE SPECIES OF LOWLAND NEOTROPICAL RAINFOREST CANOPIES

Many species occur in the forest canopy as occasional visitors from lower forest strata or as vagrants from nonforest habitats, thus complicating a characterization of the core canopy assemblage. Having quantified the core canopy species for Honduras and compensated for methodological differences in previous studies, we are able to present a broad-scale characterization of the assemblage's constituent genera. The species in the 25 genera that, at least historically, occurred at all sites should be taken as the nucleus of the core species or allospecies most likely to be found in neotropical canopies. The remaining 24 genera observed at a minimum of three sites complete the roster of core canopy constituents. Some general observations on this group are worth noting. In terms of species richness, the Tyrannidae are the predominant family in the canopy, with twice as many species as any other family. Other important families include the Thraupidae (18 species in our sample) and Psittacidae (9 species). Extirpations notwithstanding, the canopy typically includes seed predators that are large (*Ara*), medium (*Amazona*), and small (*Brotogeris*, *Pionus*). Although neotropical forest raptors are diverse in size and diet, the medium-sized species in the closely related genera *Leucopternis* and *Pseudastur* (Raposo do Amaral et al. 2009) that prey largely on reptiles and amphibians (Thiollay 1994a) appear to represent the core carnivores of the canopy. The genus *Euphonia* is particularly well represented in the canopy, with approximately 30% of known species observed just in our sample.

In conclusion, although we were able to address previously unanswered questions about the structure and organization of canopy bird assemblages, much remains to be learned about this understudied group of birds. As previously shown by Anderson (2009), ground methods alone are not adequate for canopy birds. We argue that the use of canopy-based methods at tropical field stations and other sites of continuous scientific research are essential for the accurate representation of long-term population trends, especially of secretive and rare or declining canopy species. Data thus derived from across a broader geographical range of lowland neotropical forests should help solidify our understanding of canopy bird assemblages and allow intensive analyses designed to reveal intrinsic differences in the structure and organization of bird assemblages in the top of the forest with those in the forest interior.

ACKNOWLEDGMENTS

In Honduras, we are indebted to field assistants Luis Soto, Mike Beard, and Juan Gomez. The Corporación Hondureña de Desarrollo Forestal kindly granted research permits. Funding and material support were provided by the U.S. Agency for International Development's Manejo Integrado de Recursos Ambientales (MIRA) project, the Cleveland Zoological Society's Small Grants Program, the Explorers Club, Eagle Optics, Louisiana State University Museum of Natural Science Big Day Fund, Louisiana State University BioGrads, Global Forest Science (GF-18-2008-266) and U.S. Fish and Wildlife Service Neotropical Migratory Bird Conservation Act funds administered by the Gulf Coast Bird Observatory. Logistical support was provided by the MIRA project and Fundación Pico Bonito. In Brazil, we thank the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Ecology Department for providing logistical and financial support (PPI 1-3200) throughout the project. We are specially indebted to Renato Cintra, Jeff Chambers, Mario Cohn-Haft, Niro Higuchi, and the many rangers who assisted LNN in the field. LNN was fully supported by a fellowship from the Brazilian Research Council (CNPq). J. Sebastian Tello, S. Wong, and K. Harms provided assistance with statistical analyses. This manuscript benefited from comments by J. V. Remsen, Jr., P. Stouffer, and two anonymous reviewers.

LITERATURE CITED

Anderson, D. L. 2001. Landscape heterogeneity and diurnal raptor diversity in Honduras: the role of indigenous shifting cultivation. Biotropica 33:511–519.

Anderson, D. L. 2009. Ground versus canopy methods for the study of birds in tropical forest canopies: implications for ecology and conservation. Condor 111:226–237.

Bierregaard, R. O. Jr. 1990. Species composition and trophic organization of the understory bird community in a central Amazonian terra-firme forest, p. 217–236. *In* A. H. Gentry [ed.], Four neotropical rainforests. Yale University Press, New Haven, CT.

Blake, J. G. 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. Condor 109:237–255.

Blake, J. G., and B. E. Loiselle. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. Auk 117:663–686.

Blake, J. G., and B. E. Loiselle. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. Auk 118:304–326.

Bongers, F. 2001. Methods to assess tropical rain forest canopy structure: an overview. Plant Ecology 153:263–277.

Bonta, M., and D. L. Anderson. 2002. Birding Honduras: a checklist and guide. EcoArte, Tegucigalpa, Honduras.

Burney, C. W., and R. T. Brumfield. 2009. Ecology predicts levels of genetic differentation in neotropical birds. American Naturalist 174:358–368.

Cohn-Haft, M., A. Whittaker, and P. C. Stouffer. 1997. A new look at the "species poor" central Amazon: the avifauna north of Manaus, Brazil. Ornithological Monographs 48:205–235.

Colwell, R. K.[online]. 2005. EstimateS: statistical estimation of species richness and shared species from samples, version 7.5. <http://purl.oclc.org/estimates> (1 October 2009).

Da Silva, J. M. C., C. Uhl, and G. Murray. 1996. Plant succession, land management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conservation Biology 10:491–503.

Endler, J. A. 1993. The color of light in forests and its implications. Ecological Monographs 63:1–27.

Foster, R. B. 1996. The seasonal rhythm of fruitfall on Barro Colorado Island, p. 151–172. *In* E. G. Leigh, Jr., A. S. Rand and D. M. Windsor [eds.], The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC.

Frankie, G. F., H. G. Baker, and P. A. Opler. 1974. Phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881–919.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

GREENBERG, R. 1981. The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. Biotropica 13:241–251.

HANEY, J. C., AND A. R. SOLOW. 1992. Testing for resource use and selection by marine birds. Journal of Field Ornithology 63:43–52.

HOLBROOK, K. M., AND T. B. SMITH. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. Oecologia 125:249–257.

HOWE, H. F. 1996. Fruit production and animal activity in two tropical trees, p. 189–199. *In* E. G. LEIGH JR., A. S. RAND, AND D. M. WINDSOR [EDS.], The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC.

KARR, J. R., S. K. ROBINSON, J. G. BLAKE, AND R. O. BIERREGAARD JR. 1990. Birds of four neotropical forests, p. 237–269. *In* A. Gentry [ED.], Four neotropical forests. Yale University Press, New Haven, CT.

KELLY, J. F., AND R. L. HUTTO. 2005. An east–west comparison of migration in North American wood warblers. Condor 107:197–211.

KOCH, G. W., S. C. SILLETT, G. M. JENNINGS, AND S. D. DAVIS. 2004. The limits to tree height. Nature 428:851–854.

LAURANCE, W. F., H. E. M. NASCIMENTO, S. G. LAURANCE, A. ANDRADE, J. E. L. RIBEIRO, J. P. GIRALDO, T. E. LOVEJOY, R. CONDIT, J. CHAVE, K. E. HARMS, AND S. D'ANGELO. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy Sciences 103:19010–19014.

LEIGH, E. G. JR. 1999. The seasonal rhythm of fruiting and leaf flush and the regulation of animal populations., p. 149–169. *In* E. G. J. Leigh [ED.], Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York.

LEVEY, D. J., T. C. MOERMOND, AND J. S. DENSLOW. 1994. Frugivory: an overview, p. 282–294. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn [EDS.], La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago.

LOISELLE, B. A. 1988. Bird abundance and seasonality in a Costa Rican lowland forest canopy. Condor 90:761–772.

LOISELLE, B. A., AND J. G. BLAKE. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical forest, p. 397–406. *In* D. J. Levey, W. R. Silva, and M. Galetti [EDS.], Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Wallingford, UK.

MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling Elsevier Academic Press, Amsterdam.

MADIGOSKY, S. R. 2004. Tropical microclimate considerations, p. 24–48. *In* M. D. Lowman and H. B. Rinker [EDS.], Forest canopies. Elsevier Academic Press, Burlington, MA.

MAGURRAN, A. E. 2004. Measuring biological diversity. Blackwell Science, Malden, MA.

MARTIN, T. E. 1985. Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant diversity? Journal of Tropical Ecology 1:157–170.

MOERMOND, T. C., AND J. S. DENSLOW. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithological Monographs 36:865–897.

NADKARNI, N. M., AND T. J. MATELSON. 1989. Bird use of epiphyte resources in neotropical trees. Condor 91:891–907.

NAKA, L. N. 2004. Structure and organization of canopy bird assemblages in central Amazonia. Auk 121:88–102.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545.

PEARSON, D. L. 1977. A pantropical comparison of bird community structure on six lowland forest sites. Condor 79:232–244.

PITMAN, N. C. A., J. W. TERBORGH, M. R. SILMAN, P. NÚÑEZ V., D. A. NIELL, C. E. CERÓN, W. A. PALACIOS, AND M. AULESTIA. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82:2101–2117.

R DEVELOPMENT CORE TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAPOSO DO AMARAL, F., F. H. SHELDON, A. GAMAUF, E. HARING, M. REISING, AND L. F. SILVEIRA. 2009. Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). Molecular Phylogenetics and Evolution 53:703–715.

REMSEN, J. V. JR. 1994. Use and misuse of bird lists in community ecology and conservation. Auk 111:225–227.

ROBINSON, W. D., J. D. BRAWN, AND S. K. ROBINSON. 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. Ecological Monographs 70:209–235.

SMITH, B., AND J. B. WILSON. 1996. A consumer's guide to evenness indices. Oikos 76:70–82.

STEVENS, R. D., AND M. R. WILLIG. 2002. Geological ecology at the community level: perspectives on the diversity of New World bats. Ecology 83:545–560.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.

STOTZ, D. F., R. O. BIERREGAARD JR., M. COHN-HAFT, P. PETERMANN, J. SMITH, A. WHITTAKER, AND S. V. WILSON. 1992. The status of North American migrants in central Amazonian Brazil. Condor 94:608–621.

STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER III, AND D. K. MOSKOVITS. 1996. Neotropical birds: ecology and conservation University of Chicago Press, Chicago.

TERBORGH, J., S. K. ROBINSON, T. A. PARKER III, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213–238.

THIOLLAY, J.-M. 1994a. Family Accipitridae, p. 52–205. *In* J. del Hoyo, A. Elliot. and J. Sargatal [EDS.], Handbook of the birds of the world, volume 2: New World vultures to guineafowl. Lynx Edicions, Barcelona.

THIOLLAY, J.-M. 1994b. Structure, density and rarity in an Amazonian rainforest bird community. Journal of Tropical Ecology 10:449–481.

WALTHER, B. A. 2002. Grounded ground birds and surfing canopy birds: variation of foraging stratum breadth observed in neotropical forest birds and tested with simulation models using boundary constraints. Auk 119:658–675.

APPENDIX. All bird species observed on the 100-ha study site at Pico Bonito National Park, Honduras, April 2006–April 2007. Species observed in the canopy and those designated as core canopy species are noted, as well as species observed outside of standardized survey times.

Family and species	Residency status[a]	Canopy status[b]	Feeding guild[c]	Stratum mean ± SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. detections (%)	Mean no. individuals	No. surveys (%)
Tinamidae							
Tinamus major	R	study	F				
Crypturellus boucardi	R	study	O				
Cracidae							
Ortalis vetula	R	study	O				
Penelope purpurascens	R	canopy	F	—	3 (0.1)	<0.05	2 (2.4)
Crax rubra	R	study	F				
Odontophoridae							
Rhynchortyx cinctus	R	study	G				
Cathartidae							
Coragyps atratus	R	aerial, out	S				
Cathartes aura	R	aerial	S				
Accipitridae							
Harpagus bidentatus	R	aerial	RD				
Leucopternis albicollis	R	noct	RD	3 ± 0.0	13 (0.5)	0.2	10 (12)
Buteogallus urubitinga	R	canopy	RD	—	3 (0.1)	<0.05	3 (3.6)
Spizaetus tyrannus	R	aerial	RD				
Spizaetus ornatus	R	aerial	RD				
Falconidae							
Micrastur semitorquatus	R	study	RD				
Falco rufigularis	R	canopy, out	RD				
Columbidae							
Patagioenas flavirostris	R	canopy	F	—	1 (0)	<0.05	1 (1.2)
Patagioenas nigrirostris	R	**core**	F	2.9 ± 0.3	16 (0.6)	0.2	12 (14.5)
Claravis pretiosa	R	canopy	F	—	2 (0.1)	<0.05	1 (1.2)
Leptotila cassini	R	study	F				
Geotrygon albifacies	EM	study	F				
Geotrygon montana	R	study	F				
Psittacidae							
Aratinga nana	R	**core**	G	3 ± 0.2	53 (2.1)	0.6	17 (20.5)
Pyrilia haematotis	R	**core**	G	3 ± 0.1	191 (7.5)	2.3	38 (45.8)
Pionus senilis	R	canopy	G	—	2 (0.1)	<0.05	1 (1.2)
Cuculidae							
Piaya cayana	R	**core**	I	2.7 ± 0.5	30 (1.2)	0.4	27 (32.5)
Coccyzus americanus	NMT	canopy	I	—	3 (0.1)	<0.05	2 (3.7)
Coccyzus minor	R	study	I				
Strigidae							
Lophostrix cristata	R	noct	RN				
Glaudicium griseiceps	R	noct	RN				
Ciccaba virgata	R	noct	RN				
Caprimulgidae							
Nyctidromus albicollis	R	noct	I				
Caprimulgus vociferus	NMR	noct	I				
Nyctibiidae							
Nyctibius grandis	R	noct	I				
Apodidae							
Streptoprocne zonaris	R	aerial	I				
Chaetura pelagica	NMT	aerial	I				
Chaetura vauxi	NMR	aerial	I				
Panyptila cayennensis	R	aerial	I				

(*continued*)

APPENDIX. Continued.

Family and species	Residency status[a]	Canopy status[b]	Feeding guild[c]	Stratum mean ± SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. detections (%)	Mean no. individuals	No. surveys (%)
Trochilidae							
Phaethornis longirostris	R	canopy	N	—	1 (0)	<0.05	1 (1.2)
Phaethornis striigularis	R	study	N				
Campylopterus hemileucurus	R	canopy	N		1 (0)	<0.05	1 (1.2)
Florisuga mellivora	R	**core**	N	3 ± 0.1	20 (0.8)	0.2	14 (16.9)
Colibri delphinae	R	canopy	N	—	1 (0)	<0.05	1 (1.2)
Anthracothorax prevostii	R	canopy	N	—	1 (0)	<0.05	1 (1.2)
Klais gumeti	R	canopy	N	—	1 (0.2)	<0.05	1 (1.2)
Lophornis helenae	R	**core**	N	3 ± 0.0	4 (0.2)	0.1	3 (3.6)
Thalurania colombica	R	**core**	N	2.8 ± 0.4	35 (1.4)	0.4	29 (34.9)
Hylocharis eliciae	R	**core**	N	3 ± 0.2	11 (0.4)	0.1	8 (9.6)
Amazilia candida	R	**core**	N	2.9 ± 0.3	22 (0.9)	0.3	19 (22.9)
Amazilia cyanocephala	R	canopy	N	—	1 (0)	<0.05	1 (1.2)
Amazilia tzacatl	R	**core**	N	3 ± 0.0	7 (0.3)	0.1	7 (8.4)
Eupherusa eximia	EM	study	N				
Heliothryx barroti	R	core	N	2.6 ± 0.9	4 (0.2)	0.1	4 (4.8)
Tilmatura dupontii	EM	**core**	N	3 ± 0.0	5 (0.2)	0.1	5 (6)
Trogonidae							
Trogon massena	R	**core**	O	2.7 ± 0.5	9 (0.4)	0.1	8 (9.6)
Trogon caligatus	R	**core**	O	2.6 ± 0.5	16 (0.6)	0.2	15 (18.1)
Trogon rufus	R	canopy	O	—	2 (0)	<0.05	2 (2.4)
Trogon collaris	R	canopy	O	2.4 ± 0.5	7 (0.1)	0.1	5 (6)
Momotidae							
Hylomanes momotula	R	study	I				
Momotus momota	R	study	O				
Electron carinatum	R	canopy	O	—	3 (0.1)	<0.05	3 (3.6)
Bucconidae							
Notharchus hyperrhynchus	R	**core**	I	3 ± 0.0	7 (0.3)	0.1	3 (3.6)
Galbulidae							
Galbula ruficauda	R	canopy	I	2.6 ± 0.5	4 (0.2)	0.1	4 (4.8)
Ramphastidae							
Aulacorhynchus prasinus	R	**core**	F	3 ± 0.0	5 (0.2)	0.1	3 (3.6)
Pteroglossus torquatus	R	**core**	F	2.9 ± 0.3	102 (40)	1.2	30 (36.1)
Selenidera spectabilis	R	canopy	F	—	3 (0.1)	<0.05	3 (3.6)
Ramphastos sulfuratus	R	**core**	F	3 ± 0.2	127 (5)	1.5	54 (65.1)
Picidae							
Picumnus olivaceus	R	canopy	I	—	1 (0)	<0.05	1 (1.2)
Melanerpes pucherani	R	**core**	O	2.9 ± 0.3	39 (1.5)	0.5	27 (32.5)
Picoides fumigatus	R	**core**	I	2.7 ± 0.5	13 (0.5)	0.2	12 (14.5)
Celeus castaneus	R	**core**	O	2.8 ± 0.4	5 (0.2)	0.1	4 (4.8)
Campephilus guatemalensis	R	canopy	I	—	1 (0)	<0.05	1 (1.2)
Furnariidae							
Xenops minutus	R	canopy	I	2.7 ± 0.5	4 (0.2)	0.1	4 (4.8)
Sclerurus guatemalensis	R	study	I				
Glyphorhynchus spirurus	R	canopy	I	—	2 (0.1)	<0.05	2 (2.4)
Dendrocincla anabatina	R	study	I				
Dendrocincla homochroa	R	study	I				
Xiphocolaptes promeropirhynchus	R	canopy	I	—	2 (0.1)	<0.05	2 (2.4)
Dendrocolaptes sanctihomae	R	canopy	I	—	3 (0.1)	<0.05	2 (2.4)
Xiphorhynchus susurrans	R	canopy	I	—	2 (0.1)	<0.05	2 (2.4)
Xiphorhynchus flavigaster	R	**core**	I	2.6 ± 0.6	8 (0.3)	0.1	8 (9.6)
Lepidocolaptes souleyetii	R	study	I				

(*continued*)

APPENDIX. Continued.

Family and species	Residency status[a]	Canopy status[b]	Feeding guild[c]	Stratum mean ± SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. detections (%)	Mean no. individuals	No. surveys (%)
Thamnophilidae							
Thamnophilus atrinucha	R	canopy	I	—	3 (0.1)	<0.05	3 (3.6)
Thamnistes anabatinus	R	canopy	I	—	3 (0.1)	<0.05	2 (2.4)
Microrhopias quixensis	R	canopy	I	2.2 ± 0.6	7 (0.3)	0.1	3 (3.6)
Cercromacra tyrannina	EM	study	I				
Gymnopithys leucaspis	R	study	I				
Formicariidae							
Formicarius analis	R	study	I	—			
Tyrannidae							
Ornithion semiflavum	R	**core**	O	3 ± 0.0	41 (1.6)	0.5	36 (43.4)
Myiopagis viridicata	R	canopy	I	—	3 (0.1)	<0.05	3 (3.6)
Mionectes oleagineus	R	**core**	O	2.6 ± 0.6	13 (0.5)	0.2	12 (14.5)
Leptopogon amaurocephalus	R	canopy	I	2.6 ± 0.5	4 (0.2)	0.1	3 (3.6)
Zimmerius vilissimus	R	**core**	O	3 ± 0.0	26 (1)	0.3	20 (24.1)
Oncostoma cinereigulare	R	study	I				
Rhynchocyclus brevirostris	R	study	I				
Tolmomyias sulphurescens	R	**core**	O	3 ± 0.0	7 (0.3)	0.1	7 (8.4)
Platyrinchus cancrominus	R	study	I	—			
Onychorhynchus coronatus	R	study	I	—			
Terenotriccus erythrurus	R	canopy	I	—	2 (0.1)	<0.05	2 (2.4)
Myiobius sulphureipygius	R	study	I	—			
Contopus cooperi	NMT	canopy	I	—	1 (0)	<0.05	1 (1.5)
Contopus spp.[e]	NMR	**core**	I	2.7 ± 0.6	17 (0.7)	0.2	14 (20.9)
Contopus sordidulus	NMR	study	I	—		—	
Contopus virens	NMT	study	I	—		—	
Empidonax spp.[f]	NMR	**core**	I	2.8 ± 0.4	15 (0.6)	0.2	14 (34.1)
Empidonax virescens	NMT	study	I	—		—	
Empidonax trailii	NMR	study	I	—		—	
Attila spadiceus	R	**core**	O	2.9 ± 0.3	23 (0.9)	0.3	21 (25.3)
Rhytipterna holyerythra	R	canopy	O	—	3 (0.1)	<0.05	3 (3.6)
Myiarchus tuberculifer	R	**core**	I	3 ± 0.0	18 (0.7)	0.2	13 (15.7)
Myiarchus crinitus	NMR	**core**	I	3 ± 0.0	4 (0.2)	0.1	3 (4.3)
Myiarchus tyrannulus	R	canopy	I	—	1 (0)	<0.05	1 (1.2)
Megarynchus pitangua	R	**core**	O	3 ± 0.0	16 (0.6)	0.2	7 (8.4)
Myiozetetes similis	R	canopy	O	—	3 (0.1)	<0.05	2 (2.4)
Myiodynastes luteiventris	AM	**core**	O	2.7 ± 0.5	9 (0.4)	0.1	6 (16.7)
Schiffornis turdina	R	canopy	O	—	2 (0.1)	<0.05	2 (2.4)
Pachyramphus major	R	canopy, out	I				
Pachyramphus aglaiae	R	canopy	I	—	3 (0.1)	<0.05	2 (2.4)
Tityra semifasciata	R	**core**	O	3 ± 0.0	64 (2.5)	0.8	27 (32.5)
Tityra inquisitor	R	canopy	O	—	2 (0.1)	<0.05	1 (1.2)
Cotingidae							
Cotinga amabilis	R	**core**	F	3 ± 0.0	21 (0.8)	0.3	14 (16.9)
Pipridae							
Manacus candei	R	canopy	F	—	3 (0.1)	<0.05	2 (2.4)
Pipra mentalis	R	canopy	F	—	1 (0)	<0.05	1 (1.2)
Vireonidae							
Vireo flavifrons	NMR	**core**	I	3 ± 0.0	14 (0.6)	0.2	13 (17.8)
Vireo gilvus	NMR	canopy	I	—	3 (0.1)	<0.05	2 (2.7)
Vireo philadelphicus	NMR	**core**	I	3 ± 0.0	8 (0.3)	0.1	5 (6.8)
Vireo olivaceus	NMT	**core**	O	2.9 ± 0.3	112 (4.4)	1.4	31 (57.4)
Hylophilus ochraceiceps	R	canopy	I	2.3 ± 0.4	7 (0.3)	0.1	3 (3.6)
Hylophilus decurtatus	R	**core**	O	3 ± 0.1	226 (8.9)	2.7	75 (90.4)
Vireolanius pulchellus	R	**core**	O	3 ± 0.0	32 (1.3)	0.4	18 (21.7)

(*continued*)

APPENDIX. Continued.

Family and species	Residency status[a]	Canopy status[b]	Feeding guild[c]	Stratum mean ± SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. detections (%)	Mean no. individuals	No. surveys (%)
Corvidae							
Psilorhinus morio	R	**core**	O	2.9 ± 0.4	54 (2.1)	0.7	28 (33.7)
Hirundinidae							
Stelgidopteryx serripennis	R	aerial	I				
Troglodytidae							
Thryothorus maculipectus	R	**core**	I	2.4 ± 0.6	23 (0.9)	0.3	15 (18.1)
Henicorhina leucosticta	R	study	I				
Microcerculus philomena	R	study	I				
Polioptilidae							
Ramphocaenus melanurus	R	canopy	I	2.1 ± 0.5	8 (0.3)	0.1	8 (9.6)
Polioptila plumbea	R	**core**	I	3 ± 0.1	85 (3.3)	1.0	49 (59)
Turdidae							
Myadestes unicolor	R	study	O				
Catharus ustulatus	NMR	**core**	O	2.7 ± 0.7	16 (0.6)	0.2	11 (15.1)
Hylocichla mustelina	NMR	canopy	O	—	1 (0)	<0.05	1 (1.4)
Turdus grayi	V	canopy	O	—	1 (0)		1 (1.2)
Turdus assimilis	EM	canopy	O	—	1 (0)	<0.05	1 (1.2)
Parulidae							
Oreothlypis peregrina	NMR	**core**	O	2.9 ± 0.3	14 (0.6)	0.2	8 (11.1)
Dendroica petechia	NMR	**core**	I	3 ± 0.0	6 (0.2)	0.1	6 (7.5)
Dendroica pensylvanica	NMR	**core**	O	3 ± 0.1	42 (1.7)	0.5	34 (46.6)
Dendroica magnolia	NMR	**core**	I	2.9 ± 0.3	20 (0.8)	0.2	19 (26)
Dendroica virens	NMR	**core**	I	3 ± 0.0	13 (0.5)	0.2	12 (16.4)
Dendroica fusca	NMT	canopy	O	—	3 (0.1)	<0.05	3 (5.6)
Dendroica castanea	NMT	**core**	O	2.9 ± 0.2	10 (0.4)	0.1	6 (8.7)
Dendroica cerulea	NMT	canopy, out	I				
Mniotilta varia	NMR	**core**	I	2.8 ± 0.4	13 (0.5)	0.2	12 (29.3)
Setophaga ruticilla	NMR	**core**	I	2.9 ± 0.3	13 (0.5)	0.2	13 (16.3)
Helmitheros vermivorum	NMR	canopy	I	—	2 (0.1)	<0.05	2 (2.7)
Seiurus aurocapilla	NMR	study	I				
Parkesia noveboracencis	NMR	study	I				
Parkesia motacilla	NMR	study	I				
Oporornis formosus	NMR	study	I				
Wilsonia citrina	NMR	study	I				
Wilsonia pusilla	NMR	canopy	I	—	1 (0)	<0.05	1 (1.4)
Wilsonia canadensis	NMT	canopy, out	I				
Myioborus miniatus	EM	canopy	I	—	1 (0)	<0.05	1 (1.2)
Basileuterus culicivorus	R	study	I				
Basileuterus fulvicauda	R	study	I				
Thraupidae							
Lanio aurantius	R	**core**	O	3 ± 0.0	9 (0.4)	0.1	7 (8.4)
Thraupis abbas	R	canopy	O	—	3 (0.1)	<0.05	2 (2.4)
Chlorophanes spiza	R	**core**	O	3 ± 0.0	28 (1.1)	0.3	10 (12)
Cyanerpes lucidus	R	**core**	O	3 ± 0.0	15 (0.6)	0.2	2 (2.4)
Cyanerpes cyaneus	R	**core**	O	3 ± 0.1	101 (4)	1.2	29 (34.9)
Cardinalidae							
Piranga rubra	NMR	**core**	O	3 ± 0.1	37 (1.5)	0.5	26 (35.6)
Piranga olivacea	NMT	**core**	O	2.9 ± 0.2	25 (1)	<0.05	12 (28.6)
Piranga leucoptera	R	canopy	O	—	2 (0.1)	<0.05	2 (2.4)
Habia rubica	R	study	O				
Habia fuscicauda	R	study	O				
Saltator coerulescens	R	study	O				
Caryothraustes poliogaster	R	**core**	O	2.8 ± 0.4	66 (2.6)	0.8	6 (7.2)
Pheucticus ludovicianus	NMR	canopy	O	—	2 (0.1)	<0.05	2 (3.1)
Cyanocompsa cyanoides	R	study	O	—			

(*continued*)

APPENDIX. Continued.

Family and species	Residency status[a]	Canopy status[b]	Feeding guild[c]	Stratum mean ± SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. detections (%)	Mean no. individuals	No. surveys (%)
Icteridae							
Quiscalus mexicanus	V	canopy	O	—	1 (0)		1 (1.2)
Icterus galbula	NMR	**core**	O	3 ± 0.0	19 (0.7)	0.2	14 (18.2)
Psarocolius wagleri	R	**core**	O	3 ± 0.2	321 (12.6)	3.9	33 (39.8)
Psarocolius montezuma	R	**core**	O	3 ± 0.0	13 (0.5)	0.2	9 (10.8)
Fringillidae							
Euphonia affinis	R	canopy	O	—	1 (0)	<0.05	1 (1.2)
Euphonia hirundinacea	R	**core**	O	2.9 ± 0.3	19 (0.7)	0.2	10 (12)
Euphonia gouldi	R	**core**	O	2.7 ± 0.5	31 (1.2)	0.4	22 (26.5)
Euphonia minuta	R	**core**	I	3 ± 0.0	7 (0.3)	0.1	4 (4.8)

[a]AM, austral migrant; EM, elevational migrant; NMR, nearctic migrant resident; NMT, nearctic migrant transient; R, resident; V, vagrant.
[b]Aerial, species observed solely as flyovers; canopy, species observed in the canopy; core, species considered part of the core canopy assemblage; out, species observed outside the boundaries of the plot or not during standardized surveys; noct, nocturnal species; study, species observed on the 100-ha plot but not in the canopy.
[c]F, frugivore; G, granivore; I, insectivore; N, nectarivore; RD, diurnal raptor; RN, nocturnal raptor; S, scavenger.
[d]Stratum means are given only for species represented by ≥4 individuals observed in the canopy.
[e] *Contopus sordidulus* and *C. virens* could not be distinguished reliably so were treated as a single species for analyses.
[f]*Empidonax virescens* and *E. traillii* could not be distinguished reliably so were treated as a single species for analyses.