

THE HETEROGENEITY OF AMAZONIAN TREEFALL GAPS AND BIRD COMMUNITY COMPOSITION

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Abstract. It is widely recognized that the physical disturbances created by treefall gaps influence animal communities in tropical forests. However, how the bird community is affected by the internal heterogeneity of gaps is still unstudied. Twenty-five treefall gaps were sampled for their understory and canopy bird assemblages in a mature Central Amazonian rain forest. Mist nets, binoculars, and tape recorders were used to sample the bird community. Environmental variables were chosen for their known influence on forest regeneration through variation in sunlight exposure (gap size, canopy openness, aspect, gap orientation, and elevation), and for representing gap dynamics (gap age and vegetation structure). The bird community attributes analyzed were species abundance, richness, and community composition. Species richness and relative abundance did not vary significantly according to gap characteristics. The gap variables that most influenced bird community composition were related to sunlight exposure, and frugivores and nectarivores were the most affected guilds. Insectivores were affected only by gap size while understory species were not affected at all. The results indicate that differences among treefall gaps in the Manaus region may have a stronger influence just on some species, as shown by changes in community composition only than on overall species abundance and richness. Among all groups, frugivorous and nectarivorous birds were shown to be the most affected guilds by gap environmental variables. As previously suggested, we bring more evidence showing that treefall gaps may indeed function as “keystone places” for birds for their role in sustaining frugivores and nectarivores in periods of fruit scarcity in the forest. *Accepted 15 January 2008.*

Key words: Amazon, birds, community ecology, frugivory, gaps, tropical rain forest.

INTRODUCTION

A variety of organisms inhabit treefall gaps or openings in intact forest (Schemske & Brokaw 1981, Wunderle *et al.* 1987, Levey 1988b, Restrepo *et al.* 1999, Fuller 2000, Guilherme & Cintra 2001). However, most previous studies have only compared species presence in gaps with nearby forest understory and have not related their occurrence to habitat variables within the gaps. This approach disregards the vast heterogeneity gaps show with respect to the amount of incident light, topographic, and edaphic conditions

(Whitmore 1989), factors that play a significant role in determining floristic composition and vegetation structure (Uhl 1982, Denslow 1987, Uhl *et al.* 1988, Whitmore 1989, Schnitzer & Carson 2001). So far, we know of no study that has addressed how the combined effects of such factors may influence the structure and composition of bird communities using treefall gaps.

In tropical rain forests usually only 1–3% of incident light from the sun reaches the forest floor (Chazdon & Fetcher 1984), but most tree species cannot complete their life cycle under these conditions (Schupp *et al.* 1989). Therefore treefall gaps are critical in driving forest regeneration (Popma *et al.* 1988,

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Levey 1990) and increasing local plant diversity (Uhl *et al.* 1988, Schnitzer & Carson 2001, Boudreau & Lawes 2005).

Through the course of regeneration different plant assemblages are found in gaps (Schnitzer & Carson 2001). In the gap phase, plants are mainly light-demanding species, whereas shade-tolerant species dominate in later phases (Whitmore 1989). The establishment, survival, and fruiting success of plants are also influenced by gap characteristics (Denslow 1987, Uhl *et al.* 1988, Whitmore 1989). For instance, soon after a tree falls, small openings are mostly occupied by advanced regeneration of plants, while larger ones are usually dominated by pioneer plants, which require much more light to grow and reproduce (Uhl *et al.* 1988, Whitmore 1989). The floristic composition found at any given gap thus varies according to gap characteristics and its successional stage, which result in different varieties and quantities of fruits available for consumers.

Birds are highly dependent on fruits of some pioneer species, such as *Cecropia* sp., especially during periods of food scarcity (Charles-Dominique 1986). Understory plants in gaps often show higher fruit production, longer fruiting periods, and they even have sweeter fruits than in adjacent mature forest (Levey 1988a, 1990). Moreover, densities of fruiting plants tend to increase with gap size (Levey 1988b). Also treefall gaps may harbor a greater density of insects than mature forest because of changes in microclimatic conditions and the increase in primary production (Malmborg & Willson 1988, Richards & Coley 2007). Consequently, many birds may be attracted to gaps in response to such increase in food availability (Blake & Hoppes 1986).

Previous studies conducted in the Neotropical region have indeed shown an increase in bird species richness and/or abundance in treefall gaps in comparison with forest sites (Schemske & Brokaw 1981, Wunderle *et al.* 1987, Levey 1988b, Wunderle *et al.* 2005). Many species in the above studies had strong preferences for either gap or forest environments, but most species favored gaps. If birds are thus attracted to treefall gaps, we hypothesized that they should also be affected by the internal heterogeneity of gaps. For instance, it is possible that frugivorous and nectarivorous birds are more attracted to larger and younger gaps, given their enhanced fruit and flower productivity (Levey 1988a). On the other hand, insectivorous birds may show preferences for smaller and more

closed gaps since many of these species avoid forest edges and open areas (Sick 1997, Laurance 2004).

Therefore in this study we aimed to investigate how bird species richness, abundance, and community composition are related to gap attributes. The gap attributes examined were some of those known to influence the regeneration process, such as gap size, canopy openness, aspect, gap orientation, and elevation (Brokaw & Scheiner 1989, Lieberman *et al.* 1989, Poulson & Platt 1989, Webb *et al.* 1999, Catterall *et al.* 2001), as well as some resulting from the gap dynamic process itself, such as gap age and vegetation structure. These components could influence the availability of fruit, flowers and insects (Levey 1988b, 1990, Malmborg & Willson 1988, Hill *et al.* 2001), and consequently each bird guild may respond differently to changes in food supply. Here, we examined how frugivores, nectarivores, and insectivores, occupying both the canopy and the understory, were influenced by a gradient of gap internal heterogeneity. To our knowledge this is the first study conducted in a Neotropical forest examining the relationship between bird community composition, including canopy species, and forest-gap internal heterogeneity.

METHODS

Study area. Fieldwork was conducted in the Reserva Florestal Adolpho Ducke (Ducke Reserve), located 30 km from the city of Manaus, Amazonas, Brazil (2°55'–03°01'S, 59°53'–59°59'W). The average annual rainfall is around 2300 mm, with the dry season extending from June to November, and the peak of the rainy season from February to March (MME 1978). Local topography is gently rugged, with only 100 m difference in elevation between river level and hill-top. The dominant vegetation is classified as Amazon *terra firme* forest, an ombrophilous mature forest, in which the canopy is 30–40 m high and emergent trees rise up to 55 m (Ribeiro *et al.* 1999). There is a trail system consisting of 18 parallel trails, eight km long and one km apart, nine of which are oriented north-south and nine are oriented east-west, forming a grid that covers 6400 ha of the reserve. This trail system is separated from the edge of the forest for at least 1000 m. Every 100 m along the trails there are PVC poles marking the position and local altitude in relation to the Amazon river level. For this study we chose an area of 400 ha, in which the sampled gaps were distributed uniformly.

Bird surveys. We sampled birds in each treefall gap for two days using mist nets, binoculars, and a tape recorder. Each gap was sampled once between October and November 2002 and a second time in July and August 2003. Nets were opened from 06:00h until 12:00 h. To minimize their exposure to sunlight, we placed seven to eight nets along the east side of the gap edge. There were no pre-existing trails within the gaps and we tried to cause minimal disturbance to the vegetation by using 6-m length nets (2.5 m high, 36 mm mesh), which are easier to set than the usual 12-m ones. Nets were checked every hour and all birds captured were banded, with numbered aluminum bands supplied by the Center of Research for Conservation of Wild Birds (CEMAVE – IBAMA), and released.

While operating mist nets in a gap we simultaneously recorded birds in the gap using binoculars and a tape recorder. We occupied the place that provided the best view of the entire gap and recorded only birds that perched, foraged, or rested within the gap area, thus excluding those that only flew over the area (which could be just passing by and not utilizing the gap). Vocalizations were recorded only when it was not possible to visually identify the species using the gap and were used for later identification. We did not use playback since this method could attract birds that would otherwise not enter the gaps. We wore inconspicuous clothes and kept as quiet as possible during visualizations. We conducted a pilot study prior to the sampling in which we noticed that many birds were comfortable at close proximity (e.g. 1–2 m) to us and continued to forage for many minutes; therefore we believe that our presence did not interfere with bird behavior.

Data obtained using these complementary sampling methods were lumped together for statistical analysis. If we recorded a species using more than one method, saw or heard a bird on different days, or for whatever reason doubted that it was a different individual, we registered it only once. Therefore our analyses are based on a conservative estimate of bird abundance. Although the methods we used differ in their ability to detect individuals, we compared bird abundances only between our studied gaps, which were sampled with the same amount of effort, and did not attempt to make comparisons with results from other study sites.

We divided the bird assemblage into four groups according to their usual microhabitat association (un-

derstory and canopy) and trophic guild (frugivorous/nectarivorous, insectivorous/omnivorous). Microhabitat information came from Cohn-Haft *et al.* (1997), and guild information from Willis (1977).

Treefall gaps. We sampled birds in 25 treefall gaps, which we defined as “a hole in the forest extending through all levels down to an average height of 2 m above ground” (Brokaw 1982), “its extension including the area limited by lateral trunks” (Barton 1984). Gaps were chosen for being located within 50 m of a trail, separated by at least 150 m and being larger than 12 m in diameter.

For each gap we recorded seven characteristics. We estimated gap size by measuring the larger and smaller axes and then calculating the area using the formula for an ellipse (Gap area = $\pi * \text{larger axis}/2 * \text{smaller axis}/2$). We recorded canopy openness using a Spherical Crown Densiometer (Concave – Mode C – Robert E. Lemonn, Forest Densiometer). We made four readings (N, S, W, and E) from the center of each gap and used the mean value in the analyses. We recorded the aspect of the terrain with a clinometer and gap orientation by using a compass positioned in the direction of the fallen bole.

We measured the diameter at breast height (DBH) of all tree stems (excluding palms, herbs and lianas) in a 2 x 10-m plot along the length of the fallen bole and calculated the mean, which we used as an index relative to gap age. Low values indicated younger gaps and high values indicated older ones. We quantified the vegetation structure, represented by foliage height profiles, in an 8–12-m long transect (depending on gap size) parallel to the fallen bole. At 1-m intervals along the transects, we sampled two points on each side of the person measuring the vegetation (2 m apart) by holding a 2-m tall round pole in a vertical position from the ground. The height of the vegetation touching the pole was recorded and later categorized into four height intervals: 0–50, 51–100, 101–150, 151–200 cm. The number of records in each interval was divided by the sum of sampling points to obtain one standardized value for each interval. The values obtained for each vegetation structure height profile were used in a principal components analysis (PCA), which resulted in one value for each gap representing the four height classes. This ordination procedure was undertaken using the PATN statistical package (Belbin 1992) and the resulting PCA-axis was used as the explanatory variable in the regression models. The elevation (local altitude)

values were recorded by an engineering company based in Manaus (Andrade Construção e Comércio), which obtained them with the use of a theodolite.

Statistical analyses. First we conducted a Spearman rank-correlation to check for colinearity among the explanatory variables, undertaken in the Systat 8.0 program (Wilkinson 1997). Then we tested for spatial autocorrelation in bird species composition among gaps using a Mantel test with 999 randomizations in the RT statistical package.

The effects of gap environmental variables on bird species richness or relative abundance were investigated using multiple linear regression analysis in Systat. We built two regression models in which species richness and abundance of the total assemblage and guilds were analyzed. In the first model, we included gap size, canopy openness, aspect, and compass orientation, while gap age, altitude, and vegetation structure were included in the second model.

To investigate the effects of gaps on bird assemblage composition we ran a hybrid multidimensional scaling analysis (HMDS) using the Bray-Curtis dissimilarity index in PATN. Two ordinations were done, one using species abundance values (quantitative data), which gives more weight to abundant species (e.g. *Phaethornis superciliosus*, *Glyphorhynchus spirurus*, *Pipra pipra*), and another using species presence-absence (qualitative data), which gives more weight to rare species. When used on presence-absence data, the Bray-Curtis index is known as the Sørensen distance measure (Legendre & Legendre 1998). The Bray-Curtis coefficient has been recommended and used in ecological gradient studies (Minchin 1987, MacNally 1994), with plants (Magnus-

son *et al.* 1999, Costa *et al.* 2005), insects (Lima *et al.* 2000), and birds (Cintra 1997, Guilherme & Cintra 2001, Cintra & Sanaïotti 2005). After calculating the stress value for each ordination, we decided to make all ordinations on two axes, as an adequate amount of variation was captured without losing too many degrees of freedom.

To test for the effects of gap characteristics on the bird assemblage composition (represented by the two HMDS-axes), we used multivariate regression analyses available in the GLM procedure in Systat. Multivariate regressions are functionally similar to simple or multiple regressions as they also search for linear relationships among response and explanatory variables. The difference is that they allow the use of more than one response variable. Multivariate regressions do not automatically generate a value of significance, which was later assessed by the use of an *a posteriori* Pillai-Trace test, as this measure has been shown to be less sensitive to deviations from assumptions than other multivariate statistics (Olson 1976, Johnson & Field 1993). We carried out the same analyses on each assemblage separately (canopy, understory, frugivorous/nectarivorous and insectivorous/omnivorous).

RESULTS

A total of 410 birds, representing 105 species of 26 families, was heard, seen, or captured (1818 net-hours). Although we had a low number of net-hours (around 72 net-hours per gap) and capture rate (only 131 birds captured in total), we believe this method provided us with valuable information on the understory bird-use of gaps. These birds are generally inconspicuous and difficult to be detected; without mist

TABLE 1. Maximum and minimum values, mean, standard deviation, and percentage of variance (3) explained by the first component of PCA, for dependent and independent variables sampled in gaps.

Variables	Max	Min	Mean	SD	(%)3
Bird abundance	33	6	16.44	6.627	
Bird species richness	29	6	11.88	5.118	
Canopy openness (%)	62.4	6.24	26.79	13.57	–
Elevation (m)	111	46	83.5	21.4	–
Gap age	1.83	0.58	0.926	0.29	–
Slope of the terrain (degrees)	22	0	5	6.84	–
Gap orientation (degrees)	90	0	44	32.75	–
Gap size (m ²)	583	121	311	125	–
Vegetation structure (PCA)	–	–	–	–	72.101

TABLE 2. Multivariate regression analysis results for community composition of each analyzed assemblage. Qualitative and quantitative columns refer to ordinations performed on the matrix of species presence/absence and species abundance respectively. Values of Pillai-Trace represent the strength of multivariate regression results to which a probability value is assigned (analogous to the t value in simple regressions). Pillai-Trace values have no upper limit but minimum value is 0. Significant results are presented in bold.

	Total birds				Understory birds				Canopy birds			
	Qualitative Pillai- Trace	P	Quantitative Pillai- Trace	P	Qualitative Pillai- Trace	P	Quantitative Pillai- Trace	P	Qualitative Pillai- Trace	P	Quantitative Pillai- Trace	P
Canopy openness	0.274	0.041	0.044	0.655	0.028	0.764	0.022	0.810	0.280	0.044	0.120	0.296
Elevation	0.306	0.031	0.013	0.879	0.099	0.370	0.004	0.961	0.112	0.323	0.257	0.051
Gap age	0.142	0.232	0.088	0.419	0.029	0.757	0.082	0.444	0.085	0.432	0.026	0.781
Gap size	0.005	0.949	0.016	0.861	0.129	0.271	0.112	0.325	0.139	0.242	0.042	0.665
Compass orientation	0.296	0.036	0.003	0.972	0.145	0.226	0.011	0.905	0.065	0.526	0.111	0.326
Slope of the terrain	0.296	0.036	0.028	0.762	0.159	0.192	0.016	0.857	0.140	0.238	0.006	0.948
Vegetation structure	0.049	0.622	0.071	0.499	0.024	0.793	0.154	0.204	0.188	0.138	0.073	0.486

	Frugivorous/nectarivorous birds				Insectivorous/omnivorous birds			
	Qualitative Pillai- Trace	P	Quantitative Pillai- Trace	P	Qualitative Pillai- Trace	P	Quantitative Pillai- Trace	P
Canopy openness	0.184	0.144	0.365	0.013	0.071	0.537	0.018	0.855
Elevation	0.037	0.700	0.199	0.121	0.267	0.072	0.237	0.100
Gap age	0.131	0.264	0.145	0.225	0.121	0.334	0.219	0.122
Gap size	0.011	0.903	0.309	0.030	0.331	0.033	0.138	0.282
Compass orientation	0.022	0.809	0.048	0.626	0.017	0.865	0.013	0.893
Slope of the terrain	0.019	0.832	0.474	0.002	0.038	0.722	0.020	0.845
Vegetation structure	0.262	0.048	0.043	0.659	0.016	0.875	0.081	0.486

net sampling we would hardly have had any record for this assemblage. Also, we could not just rely on bird vocalization since we could not be sure whether a bird was singing inside the gap or outside its boundaries unless we saw its location. However we observed birds in each gap for 10 hours, which also allowed us to make some records about bird behavior in gaps. Around 36% of species and 44% of birds were non-passeriformes. The three most abundant families and species recorded (captured, observed, or heard) were, respectively, Formicariidae, Ramphastidae, and Trochilidae, and *Ramphastos vitellinus* (23), *Caryothraustes canadensis* (22) and, *Phaethornis supersilius* (20) (Appendix).

The Spearman rank-correlation results showed that the environmental variables were not significantly related to each other (Table 1). Although this might seem counterintuitive, many sampled gaps were large but presented a closed canopy. First, because some of these large gaps were old and thus the canopy was already almost fully closed and second, because in many

occasions a large tree falls or breaks but nevertheless leaves many trees standing on its way. The Mantel test for spatial autocorrelation was not significant ($P = 0.26$), showing that bird species composition was not grouped by spatial proximity. We also never recaptured a bird previously captured in a different gap.

Species richness and relative abundance. None of the gap environmental variables was significantly related to species richness and relative abundance of birds, as revealed by the multiple linear regression results.

Entire bird assemblage. The two HMDS axes of bird community composition based on the presence-absence (qualitative) matrix were significantly related to canopy openness, gap orientation, elevation, and aspect, but none of the environmental variables was significantly related to the entire bird assemblage composition, based on abundance (quantitative) (Table 2). These results show that when considering the whole gap assemblage, the common species, such as *Pithys albifrons* and *Phaethornis supersilius*, are mostly pre-

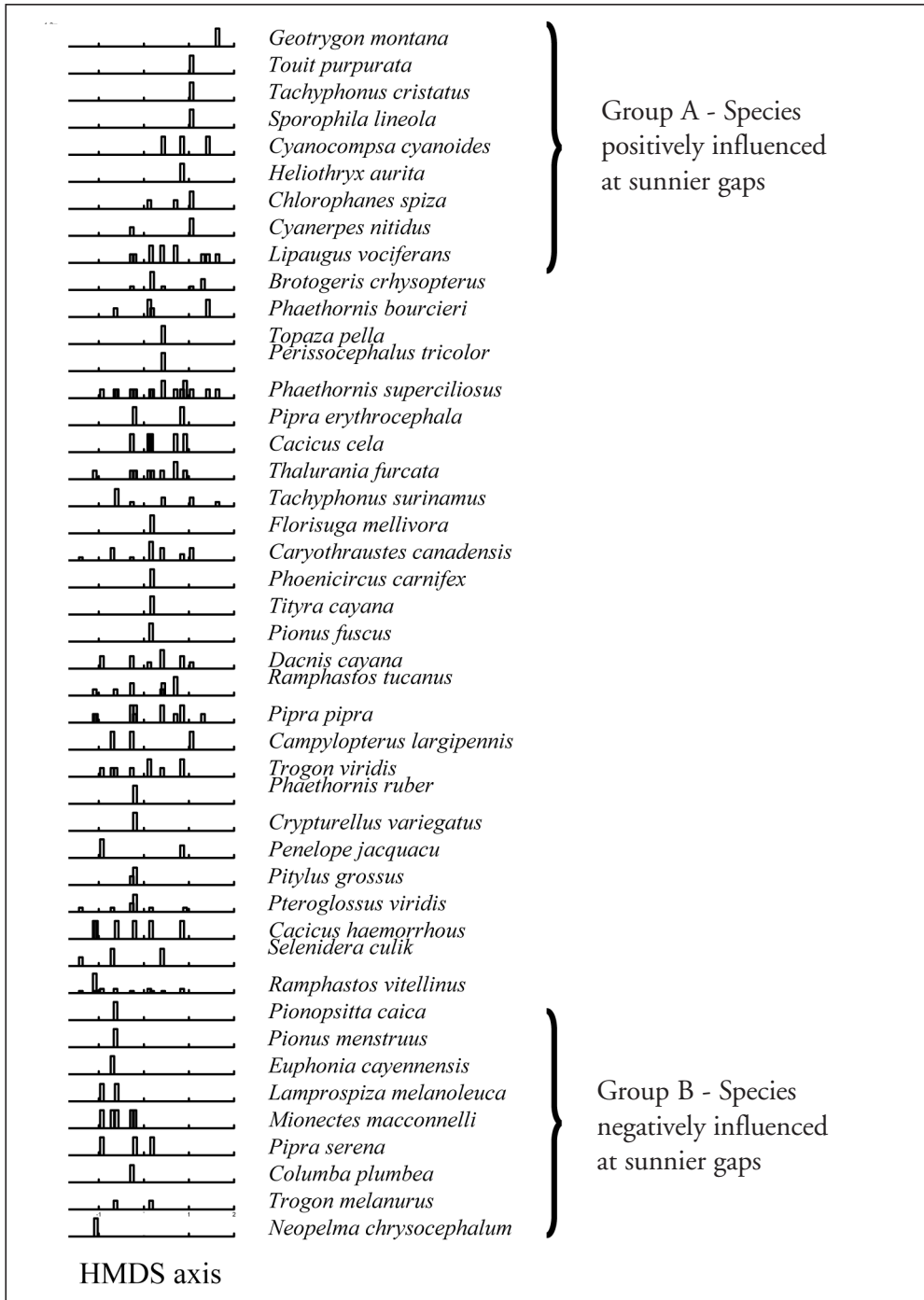


FIG. 1. Distribution of bird species along the MDS1 axis, which represents the gradient of gap size, canopy openness, and slope of the terrain. The ordination of the gaps was based on species abundance.

sent everywhere and do not account for differences in community composition. Instead it was the presence of less abundant species that were affected by gap orientation, elevation, and aspect such as the preference of *Geotrygon montana* and *Tachyphonus cristatus* for gaps located in flat areas and close to streams.

Frugivorous and nectarivorous birds. Community composition based on qualitative data was significantly related to gap vegetation structure, while the community composition based on quantitative data was significantly related to canopy openness, gap size, and aspect (Table 2).

For a better understanding of how these changes took place, we analyzed how each species was influenced by the heterogeneity of treefall gaps. If we only had one variable significantly influencing community composition, such as gap size, we could have tested how the abundance of each species is related to that specific gradient or variable. In this case, however, it was the effect of three variables together (canopy openness, gap size, and aspect) that influenced the frugivorous assemblage composition. In such a case, where the idea is to analyze the joint effect of more than one variable on community composition, Legendre & Legendre (1998) suggest using the ordination axis as a surrogate of this environmental gra-

dient. Figure 1 shows the frugivorous and nectarivorous species ordered by their relative abundance (bars) along the gradient of canopy openness, gap size, and aspect, represented there by the HMDS axis (MDS1). The right-hand side of the HMDS axis represents wider and sunnier gaps and the left-hand side smaller darker gaps. Considering the species on the upper end of the figure (*Geotrygon montana*, *Touit purpuratus*, *Tachyphonus cristatus*, *Sporophila lineola*, *Cyanocopsa cyanooides*, *Heliothryx auritus*, *Chlorophanes spiza*, *Cyanerpes nitidus*, *Lipaugus vociferans*) as a group of birds influenced by this gradient of light incidence inside the gap, we can see that their pooled abundance increased with canopy openness ($R^2 = 0.51$, $df = 23$, $P = 0.024$, Fig. 2), but tended to be negatively related to the slope of the terrain ($R^2 = 0.51$, $df = 23$, $P = 0.092$, Fig. 2). On the other hand, the overall abundance of species at the lower end of this same gradient distribution (*Pionopsitta caica*, *Pionus menstruus*, *Euphonia cayennensis*, *Lamprospiza melanoleuca*, *Mionectes macconnelli*, *Pipra serena*, *Columba plumbea*, *Trogon melanurus*, *Neopelma chrysocephalum*) was negatively correlated with species at the upper end (Spearman rank correlation, $r = -0.59$, $P = 0.001$, Fig. 3), showing that where some species are present others tend to be absent. Figures 1 and 3

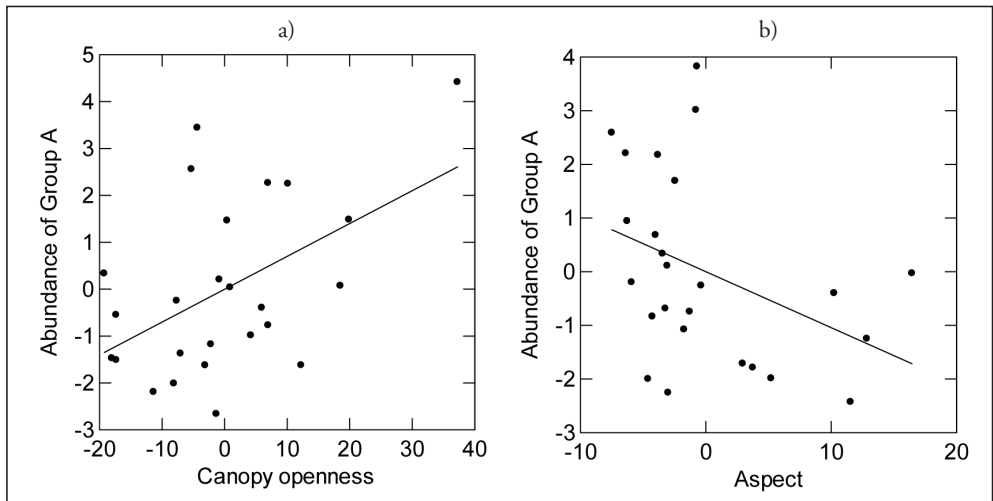


FIG. 2. Abundance of Group A, present at the upper end of species distribution (Fig. 1), in relation to (a) canopy openness and (b) aspect. The group consisted of *Geotrygon montana*, *Touit purpuratus*, *Tachyphonus cristatus*, *Sporophila lineola*, *Cyanocopsa cyanooides*, *Heliothryx auritus*, *Chlorophanes spiza*, *Cyanerpes nitidus*, *Lipaugus vociferans*. Members of group A can be seen on Figure 1. Canopy openness and aspect are in different scales since they are the partial values obtained from a multiple regression.

also show that this community is not nested; instead some species prefer one side of the gradient while others prefer the opposite side, which is one of the reasons why richness and abundance were not affected by the gap variables. The number of species in these groups was chosen by their relatively narrow representation on this environmental gradient.

Insectivorous and omnivorous birds. Only gap size affected community composition based on qualitative data (Table 2), showing that some of the rare species tend to avoid large gaps while others are positively correlated with gap size. Based on quantitative data, none of the gap environmental variables affected the assemblages (Table 2), as common species such as *Pithys albifrons*, *Glyphorhynchus spirurus*, and *Hypocnemis cantator*, do not make a distinction between gaps of different sizes, or other traits.

Understory birds. The understory bird community composition was not significantly related to any of the gap environmental variables (Table 2).

Canopy bird. Community composition based on the qualitative data matrix was significantly related to forest canopy openness, whereas the bird assemblage based on the quantitative matrix was significantly related only to elevation (Table 2). These results show that some canopy species such as *Ramphastos vittelinus* and *Caryothraustes canadensis* tended to use gaps more often on hill-tops than on valleys.

DISCUSSION

Considering that birds are attracted to treefall gaps (Schemske & Brokaw 1981, Restrepo *et al.* 1999, Fuller 2000, Wunderle *et al.* 2005), that gaps are so heterogeneous (Whitmore 1989) and that this heterogeneity influences resource availability (Levey 1988b), we believed we would find that gap characteristics influenced bird species richness and abundance. It is possible that we were unable to detect such changes because our sampling effort was not large enough to truly represent the bird assemblage, or because the sampled gaps did not differ enough in size or in other attributes that affect regeneration. Indeed, we did not perform a high number of net-hours, especially considering that capture rate was low, at approximately 7.20 individuals in every 100 net-hours. Nevertheless, this is within the average capture rate for this region (6.04 individuals per 100 net-hours; R. Cintra, *unpublished manuscript*), and if we wanted to achieve the same number of captured individuals as Levey (1988b) we would have to perform more than 22 000

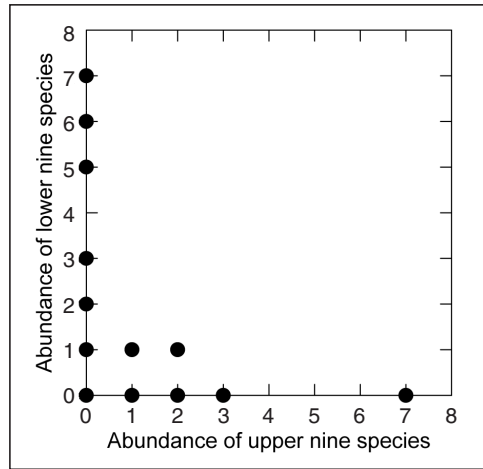


FIG. 3. Plot of summed abundance of lower against upper nine species present in the distribution of species along the gradient of treefall gaps, showing negative correlation between both groupings (Spearman correlation = -0.571).

net-hours, nearly three times more than he did. For this reason we preferred to extend our observations, which also allowed us to make records on bird behavior.

We also tried to sample the widest range of gaps present in the Ducke Reserve. For example, in our study gap area varied from 121 to 583 m² (Table 1), and within this size range Brokaw (1982) reported changes in the survivorship of many light-demanding plants. There was a tenfold difference in canopy openness between gaps (6.24–62.4%) and gap age varied from recently fallen trees to gaps filled with 20-m *Cecropia* trees (Table 1). So it was probably not due to the short sampling effort or a lack of variation in gap characteristics that variation in species richness and abundance were not significant.

While comparing gap and non-gap areas, some authors also perceived changes in community composition in gaps that differed in size, age, or other characteristics. On the other hand, none of them reported variation in captures, or bird richness, due to these characteristics (Schemske & Brokaw 1981, Levey 1988b). Fuller (2000) addressed the influence of vegetation structure, floristic composition, and gap size on singing birds in Poland. When non-gap areas were included in the analysis, he found that species richness and number of individuals were both influ-

enced by some of these variables. But when analyzing only gap sites, he encountered differences solely in bird community composition.

According to Denslow (1987), most plant species are broadly distributed along environmental gradients among gaps. But the distribution and abundance of many others, including some ecologically and morphologically similar species, are affected at a finer scale. This means that most of the plant community is able to use any kind of gap, but part of it shows a tendency to occupy specific gaps. Cintra *et al.* (2006) showed this trend for birds in the Ducke Reserve. They found that two congeneric species of woodcreepers (*Dendrocincla merula* and *D. fuliginosa*), which are broadly distributed in the reserve, were differently affected by elevation and tree density, suggesting that although both species overlap in distribution they have different preferences in forest microhabitats. Schemske & Brokaw (1981) found different community composition between gaps and forest sites and also believe that there should be considerable overlap between forest and gap bird assemblages. In our study, for instance, the community composition of frugivorous and nectarivorous birds was related to canopy openness and elevation. Almost 60% of the bird species in this assemblage were not affected by these environmental variables, as they were evenly distributed along the gradient (Fig. 1). Nevertheless, approximately 20% of this assemblage (nine species) was composed of species that have their abundance positively related to canopy openness and elevation (Fig. 2), and another 20% tended to be negatively related to these variables. In other words, in gaps where some species tended to appear others tended to disappear (Fig. 3), therefore bird abundance and richness remained stable. It was one response counteracting the other.

Fuller (2000), among other authors (Schemske & Brokaw 1981, Levey 1988b), suggested that the bird preference for treefall gaps is due to a higher resource concentration in gaps compared with closed forest areas. We did not measure resource abundance directly, but our observations support these ideas. About 76% of all birds recorded in gaps were seen in foraging activities, whether for fruits or insects. Indeed, we observed large birds, such as toucans, descending to the understory and foraging for extended periods of time (up to 15 minutes). Nonetheless, even though mixed-species flocks have been considered to preferentially use treefall gaps (Stouffer and Bierregaard 1995), we only observed three flocks foraging in gaps during the entire sampling period.

Most studies are consistent in proposing gaps as areas where fruits are found in high concentration and predictability (Levey 1988a, 1990, Malmberg & Willson 1988). But much controversy surrounds the insect community response. Some studies have found that gaps harbor a higher biomass or concentration of insects (Malmberg & Willson 1988, Richards & Coley 2007), while others have found either similar or lower abundance/richness of insects in gaps compared with closed forest (Shelly 1988, Feener & Schupp 1998). Although we recorded approximately the same number of species foraging for insects and fruits (18 *vs.* 19 species), a considerably smaller number of individuals were foraging for insects rather than for fruits (26 *vs.* 40 individuals). Our results also showed that insectivorous and understory bird species were poorly related to gap heterogeneity. For instance, the Warbling antbird, *Hypocnemis cantator*, which is an understory insectivorous bird considered to be a gap specialist (Sick 1997), was not related to any environmental variable of gaps, although it was found in nearly 40 percent of gaps. Levey (1988b) also had similar results, as in Costa Rica insectivorous birds did not show any preference for gaps. However, other studies from the Neotropical region have shown higher abundance of insectivorous species in gaps, with some species strongly attracted to them (Schemske & Brokaw 1981, Wunderle *et al.* 2005).

On the other hand, frugivorous and nectarivorous birds appear to be more predictable in their responses to gaps. In Costa Rica, nectarivores and frugivores were significantly more abundant in gaps, comprising approximately 80% of all gap specialists, and frugivore abundance in gaps and non-gap areas was correlated with the number of fruiting plants (Levey 1988b). In eastern Amazonia, birds of these guilds were captured more frequently in gaps than in forest, even though they are scarce in the forest understory (Wunderle *et al.* 2005). In our study, frugivorous and nectarivorous species were influenced by the highest number of environmental variables (gap size, canopy openness, slope, and vegetation structure). For example, species that are known as gap specialists, such as *Tachyphonus cristatus* and *Cyanocopsa cyanooides*, tended to appear in larger and more open gaps, while more sensitive species such as *Pipra serena* and *Neopelma chrysocephalum* tended to appear on the opposite side of the gradient (Fig. 1). Although hummingbirds were not affected by any characteristics of gaps, they also showed a tendency to be in more open and larger gaps (Fig. 1).

In conclusion, our results support the idea that bird species are tracking differences in environmental characteristics of treefall gaps in the Manaus region, mostly through variation in their assemblage composition. It is possible that richness and abundance could also be influenced by gap traits, but we did not have any evidence of this. Even though Wunderle *et al.* (2005) also conducted their study in the Amazon forest, 500 km from Manaus, their findings differed greatly from ours, which were actually more similar to those from Costa Rica (Levey 1988b) and Poland (Fuller 2000). Thus, at least with the information available, it appears to be difficult to propose a general pattern of the influence of treefall gap on bird communities. Although we did not measure resource abundance directly, our observations and results also indicate that treefall gaps might function as “keystone places” (Levey 1990) for birds in the Manaus region for their role in sustaining frugivores and nectarivores in periods of fruit scarcity in the forest. Considering the frugivorous bird assemblage is influenced by gap characteristics, particular bird species may be bringing particular seeds to particular gaps. The regeneration process in Neotropical rain forests is likely to be affected by this differential behavior among bird species.

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APPENDIX. Birds recorded in Ducke Reserve, Brazil. N = relative abundance. M = method of observation with o – visually observed, v – vocalization recorded, c – captured.

Species	N	MR	Species	N	MR
Tinamidae			Capitonidae		
<i>Crypturellus variegatus</i>	1	o	<i>Capito niger</i>	4	o
Falconidae			Ramphastidae		
<i>Daptrius americanus</i>	1	v	<i>Pteroglossus viridis</i>	10	o
Cracidae			<i>Selenidera culik</i>	5	o
<i>Penelope jacquacu</i>	5	o	<i>Ramphastos vitellinus</i>	23	o,v
Columbidae			<i>Ramphastos tucanus</i>	10	o,v
<i>Columba plumbea</i>	3	o,v	Picidae		
<i>Geotrygon montana</i>	1	o	<i>Melanerpes cruentatus</i>	1	o
Psittacidae			<i>Veniliornis cassini</i>	2	c,o
<i>Protogeris chrysopterus</i>	11	o,v	<i>Piculus flavigula</i>	1	o
<i>Touit purpuratus</i>	1	v	<i>Celeus undatus</i>	4	o,v
<i>Pionopsitta caica</i>	1	o	<i>Celeus torquatus</i>	2	o
<i>Pionus menstruus</i>	5	o	<i>Campephilus rubricollis</i>	3	o
<i>Pionus fuscus</i>	1	o	Dendrocolaptidae		
Cuculidae			<i>Dendrocincla fuliginosa</i>	5	c,v
<i>Piaya melanogaster</i>	3	o	<i>Deconychura longicauda</i>	3	c
Trochilidae			<i>Deconychura stictolaema</i>	2	c
<i>Phaethornis superciliosus</i>	20	c,o	<i>Sittasomus griseicapillus</i>	3	c
<i>Phaethornis bourcierii</i>	6	c,o	<i>Glyphorhynchus spirurus</i>	15	c
<i>Phaethornis ruber</i>	1	o	<i>Hylexestates perrotii</i>	1	o
<i>Florisuga mellivora</i>	1	o	<i>Xiphorhynchus pardalotus</i>	1	c
<i>Thalurania furcata</i>	11	c,o	<i>Lepidocolaptes albolineatus</i>	1	v
<i>Topaza pella</i>	1	v	Furnariidae		
<i>Heliothryx auritus</i>	1	o	<i>Sclerurus mexicanus</i>	1	c
Trogonidae			<i>Sclerurus rufigularis</i>	1	c
<i>Trogon melanurus</i>	4	o,v	Formicariidae		
<i>Trogon viridis</i>	9	o,v	<i>Cymbilaimus lineatus</i>	4	c,v
Momotidae			<i>Frederickena viridis</i>	2	c
<i>Momotus momota</i>	1	o	<i>Thamnophilus murinus</i>	1	c
Bucconidae			<i>Thamnomanes ardesiacus</i>	3	c
<i>Notharchus macrorhynchus</i>	2	o	<i>Thamnomanes caesius</i>	1	v
<i>Monasa atra</i>	5	o,v	<i>Mymotherula guttata</i>	1	c
Galbulidae			<i>Mymotherula gutturalis</i>	4	c
<i>Galbula albirostris</i>	4	c,o	<i>Herpsilochmus stictocephalus</i>	1	v
<i>Galbula dea</i>	6	o,v	<i>Cecomacra cinerascens</i>	1	v
<i>Jacamerops aurea</i>	2	o	<i>Cercomacra tyrannina</i>	2	c
			<i>Hypocnemis cantator</i>	11	c,o,v
			<i>Percnostola rufifrons</i>	1	c
			<i>Schistocichla leucostigma</i>	1	c
			<i>Myrmeciza ferruginea</i>	1	v
			<i>Pithys albifrons</i>	19	c

Appendix continued

Species	N	MR	Species	N	MR
<i>Gymnopithys rufigula</i>	4	c,v	Muscicapidae (Turdinae)		
<i>Hylophylax poecilinota</i>	2	c	<i>Turdus albicollis</i>	3	c,o
Tyrannidae			Vireonidae		
<i>Myopagis gaimardii</i>	1	o	<i>Cycularbis gujanensis</i>	2	v
<i>Myopagis caniceps</i>	1	v	<i>Vireolanius leucotis</i>	1	v
<i>Mionectes macconnelli</i>	6	c	<i>Hylophilus muscicapinus</i>	2	v
<i>Lophotriccus vitoriosus</i>	1	v	<i>Hylophilus ochraceiceps</i>	1	v
<i>Hemitriccus zosterops</i>	1	v			
<i>Tolmomyias poliocephalus</i>	2	o	Emberizidae (Emberizinae)		
<i>Platyrinchus coronatus</i>	3	c	<i>Volatinia jacarina</i>	2	o
<i>Platyrinchus platyrhynchos</i>	3	c	<i>Sporophila lineola</i>	1	o
<i>Attila spadiceus</i>	1	v	(Cardinalinae)		
<i>Myiarchus tuberculifer</i>	1	v	<i>Caryothraustes canadensis</i>	22	o,v
<i>Conopias parva</i>	2	v	<i>Cyanocompsa cyanooides</i>	3	o,v
<i>Tityra cayana</i>	1	o	<i>Pitylus grossus</i>	3	o,v
Pipridae			(Thraupinae)		
<i>Neopelma chrysocephalum</i>	1	c	<i>Lamprospiza melanoleuca</i>	8	o
<i>Pipra pipra</i>	13	c,o	<i>Tachyphonus cristatus</i>	1	o
<i>Pipra serena</i>	4	c	<i>Tachyphonus surinamus</i>	10	o
<i>Pipra erythrocephala</i>	2	c	<i>Euphonia cayaensis</i>	1	v
Cotingidae			<i>Dacnis cayana</i>	11	o
<i>Phoenicircus carnifex</i>	1	o	<i>Chlorophanes spiza</i>	4	o
<i>Lipaugus vociferans</i>	11	o,v	<i>Cyanerpes nitidus</i>	3	o
<i>Perissocephalus tricolor</i>	1	o	(Icterinae)		
Troglodytidae			<i>Cacicus cela</i>	6	o,v
<i>Microcerculus bamba</i>	1	c	<i>Cacicus haemorrhous</i>	6	o,v