Birds associated with treefall gaps in a lowland forest in southwestern Brazilian Amazonia

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ABSTRACT

Natural communities are dynamic systems in time and space. The spatial distribution of plants and animals tends to coincide with the availability of resources needed for the survival and reproduction of each species. Natural treefall gaps offer a number of resources that influence the distribution of birds within the forest. We compared the understory bird assemblages of natural treefall gaps (15 sampling points) with those found in the adjacent forest (15 points) in the Humaitá Forest Reserve in southwestern Brazilian Amazonia. We used mist-nets to sample birds and obtained 700 captures of 105 species. Species richness, number of individuals, and species composition were all similar between gaps and forest, although six species presented some degree of association with the gaps, and nine with the forest. Nectarivores preferred gaps significantly over forest, whereas insectivores and frugivores were distributed equally between gaps and forest. Vegetation height and density differed between gaps and forest, and influenced the distribution of bird species in the two environments. Fruit availability was positively correlated with frugivore abundance in gaps. Overall, 33.3% of the birds associated with the treefall gaps are from lower forest canopy, while the others are understory species. We showed that the use of natural gaps by birds in a fragmented landscape of the Amazon forest contributes to the environmental heterogeneity and succession dynamics following natural events of habitat disturbance.

KEYWORDS: tropical forests, Amazon region, forest fragment, understory

Aves associadas a clareiras naturais em uma floresta de terras baixas no sudoeste da Amazônia brasileira

RESUMO

As comunidades naturais são sistemas dinâmicos no tempo e no espaço. A distribuição espacial de plantas e animais coincide com a disponibilidade dos recursos necessários para a sobrevivência e reprodução de cada espécie. Clareiras naturais oferecem vários recursos que influenciam a distribuição de aves na floresta. Comparamos a assembleia de aves de sub-bosque de clareiras naturais (15 clareiras) com a encontrada na floresta adjacente (15 pontos) na Reserva Florestal Humaitá, no sudoeste da Amazônia brasileira. Amostramos aves com redes de neblina e contabilizamos 700 capturas de 105 espécies. A riqueza de espécies, o número de indivíduos e a composição de espécies foram semelhantes entre clareiras e floresta, mas seis espécies foram mais associadas com as clareiras e nove com a floresta. Os nectarívoros preferiram significativamente clareiras à floresta, enquanto os insetívoros e frugívoros distribuíram igualmente entre clareiras e floresta. A altura e a densidade da vegetação variaram significativamente entre clareiras e floresta e influenciaram a distribuição das espécies nos dois ambientes. A disponibilidade de frutos foi correlacionada positivamente com a abundância de frugívoros nas clareiras. Em geral, 33,3% das aves associadas às clareiras são espécies de sub-dossel e as demais de sub-bosque. Mostramos que o uso de clareiras pelas aves em uma paisagem fragmentada da Amazônia contribui para a heterogeneidade ambiental e a dinâmica de sucessão após eventos naturais de perturbação do habitat.

PALAVRAS-CHAVE: florestas tropicais, região amazônica, fragmentos florestais, sub-bosque

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INTRODUCTION

Biological communities in natural forests are formed by a mosaic of microhabitats and their associated organisms (Whittaker and Levin 1977). Environmental variability, resource availability, and the adaptive capacity of different organisms will determine the composition of local assemblages (Townsend et al. 2010). In natural communities, species assemblages tend to be similar in environments that have similar abiotic conditions, such as climate, soil, and water (Thompson and Sorenson 2000). Species will be favored distinctly by environmental conditions, including those created in novel environments (Sousa 1984), leading to the unequal spatial distribution of natural communities (Scheiner et al. 2000). Mosaics of environments and their associated biological communities are mediated by events such as landslides (Garwood et al. 1979), wildfires (Silva et al. 2015), and natural treefall in forests, coupled with the succession process (Thompson and Sorenson 2000).

In forest ecosystems, natural treefall, including events caused by wind, creates open spaces within the forest, known as treefall gaps (Baker et al. 2016). The gaps promote ecosystem dynamics, help shape the structure of natural communities and contribute to the heterogeneity in the composition of tropical forests (Brokaw 1985; Wunderle et al. 1987; Levey 1988; Hubbell et al. 1999; Busing and Brokaw 2002; Lima 2005; Schnitzer and Carson 2010; Maranho and Salimon 2015; Terborgh 2017).

Treefall gaps have higher sunlight incidence and higher density of plants with young leaves than adjacent forest, which attracts herbivorous arthropods (Richards and Coley 2007) and are referred to as nutrient hotspots due to their high rates of decomposition and mineralization (Scharenbroch and Bockheim 2008). In forests, many organisms are adapted specifically to the spectrum of conditions and resources provided by treefall gaps, resulting in high abundance and diversity, including butterflies (Pardonnet et al. 2013), spiders (Peres et al. 2014), snails (Alvarez and Willig 1993), bats (Crome and Richards 1988), amphibians (Strojny and Hunter 2010), small mammals (Beck et al. 2004), and birds (Schemske and Brokaw 1981; Levey 1990; Wunderle et al. 2005).

Ornithological surveys of forest fragments in southwestern Amazonia have revealed a high diversity of species, many of which are rare and/or endemic, with poorly-known ecological characteristics (Guilherme 2001, 2012, 2016; Rasmussen et al. 2005; Mestre et al. 2010). Our objective was to understand the influence of treefall gaps on the distribution of birds in a southwestern Amazonian forest. Specifically, we tested the hypotheses that (i) there are more species in treefall gaps relative to adjacent continuous forest due to their heterogeneity, and species composition and abundance differ between gaps and forest; (ii) some species have an intrinsic preference for gaps or forest; (iii) the vegetation structure and food resources (flowers and fruits) influence species richness, composition, and abundance of birds, so that trophic guilds of birds differ between gaps and forest; and (iv) the bird species associated with gaps are found in other specific forest strata.

MATERIAL AND METHODS

Study area

We conducted the study in the Humaitá Forest Reserve (HFR), a 2,000-ha forest fragment administered by Universidade Federal do Acre (UFAC), in Porto Acre, Acre state, southwestern Brazilian Amazonia (9º45’19’’S, 67º40’18’’W; Figure 1). HFR is covered by open terra firme rainforest, interspersed with palm stands and patches of Guadua bamboo, as well as alluvial forest, known locally as várzea (Acre 2010; IBGE 2012). The climate is humid tropical, with mean annual temperatures of 24–26 °C (Alvares et al. 2013), and mean annual rainfall of approximately 1,900 mm. The rainy season extends from October to April, and the dry season from May to September (Duarte 2006). See Pedroza et al. (2020) for details on the local bird fauna.

We considered two forest habitats in the HFR (Figure 2a): natural treefall gaps and undisturbed continuous forest (henceforth gap and forest). A gap is ‘a vertical opening in the forest extending through the canopy to within 2 m of the forest floor’ (Brokaw 1982). We calculated the area of the gaps based on their maximum length and width (Wunderle et al. 2005). We defined one sampling site randomly within each gap (Figure 2b, c) and a control site in the adjacent forest, located 50 m away from the nearest gap edge (sensu Levey 43 VOL. 51(1) 2021: 42 - 51
Overall we had 15 gap and 15 forest sites mapped in a GIS program (ArcMap, ESRI 2015).

We sampled birds with mist-nets 12 × 2.5 m and 36-mm mesh, from May to November 2018, between 05h30 and 17h30. At each site, we arranged two nets in either a straight line or in L or T configuration, to fit into the gap, with the same layout being used in the forest. We banded all the birds captured on one tarsus with a permanent metal ring engraved with a unique numerical code provided by the Brazilian government’s Centro Nacional de Pesquisa para Conservação das Aves Silvestres (CEMAVE/ICMBio) to EG’s project #1099, authorized by SISBIO license # 23269-1. We sampled each pair of gap-forest sites simultaneously on two consecutive days during four field sessions of 30 days, with intervals of 20–34 days between sessions. Overall, we sampled each site on eight days. We adopted the bird species nomenclature of Gill and Donsker (2019).

We classified each species as frugivore, insectivore, nectarivore, omnivore, or piscivore (sensu Wilman et al. 2014). Regarding the forest stratum in which the species typically forages, each species captured in the gaps was classified as terrestrial, understory, mid-story, canopy or secondary-growth species, based on Henriques et al. (2003) and Schulenberg et al. (2010). Terrestrial birds forage primarily on the ground, understory birds at heights of up to 5 m in shrubs and small trees, mid-story birds above 5 m and below the canopy, and secondary-growth birds exploit regenerating habitats.

We estimated the structure of vegetation in the gap and forest sites using the method of Wunderle et al. (2005). We obtained vegetation height profiles from two parallel transects, one located on each side of the mist-net, every 1 m along each transect using a 3-m pole as a reference scale. We recorded the presence or absence of vegetation touching the pole within each height interval. The height intervals (in meters) were: 0–0.5, 0.51–1, 1.01–2, 2.01–3, 3.01–4, 4.01–6, 6.01–8, 8.01–10, 10.01–12, 12.01–15, 15.01–20, and > 20. An estimate of percentage cover was based on these data for each height interval. We evaluated the density of the vegetation for all gap and forest site using a modified version of the method of Levey (1988). We demarcated an area of 48 m² between the transects, within which we counted the number of trunks, shrubs, branches, and stems with a diameter ≥ 7 mm. We determined the absolute density of the plants in the plots using the formula of Freitas and Magalhães (2012). We quantified plants bearing flowers and/or fruits within the entire gap area below 10 m height (sensu Levey 1988). We collected a sample of each flowering or fruiting plant and we prepared exsiccates deposited and identified in the Laboratory of Botany and Plant Ecology (LABEV) at UFAC. Plant species nomenclature followed Daly and Silveira (2008) and Medeiros et al. (2014).

Data analysis

Our sampling units were 15 gaps compared to 15 forest sites. To compare species richness between gap and forest, after confirming the normality of the data (Sokal and Rohlf 1995),...
RESULTS

Total sampling effort was 3,916 h. We captured 700 birds belonging to 105 species and 26 families (Supplementary Material, Table S1). We banded 531 individuals and recaptured 144. We captured a similar number of individuals in gaps (366) and forest (334), with no significant difference between habitats ($\chi^2 = 1.4, df = 1, p = 0.22$). Species richness was similar between gaps and forest, 81 and 80 species, respectively ($t = 0.66, df = 14, p = 0.52$). The species rarefaction curve did not present a tendency to stabilize, with an estimated total of 101 species for the gaps and 103 for the forest. The composition of the bird assemblages did not vary significantly between gaps and forest (PERMANOVA: $F = 1.40, df = 1, p = 0.09, stress = 0.25$).

We detected an association with gaps or forest in 15 species (Table 1), corresponding to 14.2% of the 105 recorded species. We classified three (20%) of these species as habitat specialists, two of which were specialized in gaps, and one in forest (Table 1). Four species (26.6%) were associated with gaps and eight (50%) with forest (Table 1). The capture frequency of species with some degree of habitat association was similar between gaps and forest ($\chi^2 = 1.81, df = 1, p = 0.17$). The recapture data (Figure 3) indicate that Thalurania furcata, Sciaphylax hemimelaena, Xenops minutus, Lepidothrix coronata, Pipra fascicula and Micrastur oleraeus moved either between gaps or between gap and forest (Table 2).

Table 1. Specialist and associate bird species in treefall-gap and forest sampling sites in the Humaitá Forest Reserve, southwestern Brazilian Amazonia. N captures = number of individual captures. The frequency and p values are derived from IndVal tests. Guilds: I = insectivore; F = frugivore; N = nectarivore; O = omnivore. The trophic guild classification followed Wilman et al. (2014).

| Species                          | N captures | Frequency | IndVal test value | p   | Guild |
|----------------------------------|------------|-----------|-------------------|-----|-------|
| Hypocollyris peruviana           | 14         | 40        | 0.37              | 0.03| I     |
| Oryzoborus angolensis            | 12         | 2         | 0.51              | 0.01| F     |
| Sittasomus gresiacapillus        | 8          | 4         | 0.26              | 0.41| I     |
| Thamnomanes schistogynus         | 10         | 4         | 0.28              | 0.30| I     |
| Sciaphylax hemimelaena           | 16         | 7         | 0.27              | 0.30| I     |
| Pipra fascicula                 | 35         | 30        | 0.35              | 0.84| F     |
| Thamnomanes ardesiacus           | 0          | 7         | 0.40              | 0.01| I     |
| Sclerauchen caudatoculus         | 5          | 6         | 0.21              | 1.00| I     |
| Dendrocincla merula             | 10         | 20        | 0.44              | 0.05| I     |
| Dendrocincla fuliginosa          | 5           | 11        | 0.27              | 0.30| I     |
| Glypopteryx spinus               | 3           | 9         | 0.30              | 0.18| I     |
| Islaea hauwelli                  | 15         | 16        | 0.24              | 0.86| I     |
| Onciornis saltinis              | 9           | 16        | 0.29              | 0.40| I     |
| Wintersornis poecilinotus        | 7           | 15        | 0.36              | 0.11| I     |
| Phlegopsis nigraculata           | 6           | 12        | 0.31              | 0.22| I     |
Nectarivores (9%) were significantly more frequent in the gaps than in the forest ($\chi^2 = 4.41$, df = 1, $p = 0.03$, 33 captures in gaps and 18 in forest) (Figure 4). Most frequent nectarivores in the gaps were *Glaucis hirsutus* ($\chi^2 = 4.40$, df = 1, $p = 0.03$) and *T. furcata* ($\chi^2 = 5.40$, df = 1, $p = 0.01$). The frugivores were distributed evenly between gaps and forest ($\chi^2 = 0.66$, df = 1, $p = 0.41$, 62 captures in gaps and 56 in forest) and represented 17.8% of the total captures (Figure 4). Overall, 56.4% of the frugivores captured in gaps were *Pipra fasciicauda*, while 25% of the frugivores captured in forest were *M. oleagineus*. The distribution of insectivores was also similar between gaps and forest ($\chi^2 = 0.66$, df = 1, $p = 0.41$, 62 captures in gaps and 56 in forest) and represented 17.8% of the total captures (Figure 4). Overall, 56.4% of the frugivores captured in gaps were *Pipra fasciicauda*, while 25% of the frugivores captured in forest were *M. oleagineus*. The distribution of insectivores was also similar between gaps and forest ($\chi^2 = 0.58$, df = 1, $p = 0.44$, 256 captures in gaps and 240 in forest). This guild was represented by the largest number of species (74), and contributed 70.2% of the captures in the gaps and 71.8% in the forest (Figure 4). The most abundant insectivores were *Myrmotherula axillaris* (7.5% of total insectivores captured), *Ileria hauxwelli* (6.2%), and *Dendrocincla merula* (6%). *Sciaphylax hemimelaena* and *Thamnomanes schistogynus* were captured more in gaps than forest (Table 1), contributing 4.4% and 1.2%, respectively, of the insectivores captured. Omnivores (5.4% of the captures) were represented by seven species, and had a similar distribution in gaps and forest ($\chi^2 = 1.68$, df = 1, $p = 0.19$, 11 captures in gaps and 18 in forest). *Ramphocelus carbo* contributed 38% of the omnivores captured, with 36.4% of the individuals captured in gaps and 38.9% in forest. We captured piscivores only in the forest ($\chi^2 = 2$, df = 1, $p = 0.15$, N = 2), two typical forest-dwelling species of the family Alcedinidae, *Chloroceryle aenea* and *Chloroceryle inda*.

The height ($W = 2$, $p = 0.001$) and density ($W = 108$, $p = 0.001$) of the vegetation varied significantly between gaps and forest. We counted 3,218 plants in the gap plots (214.5 ±

**Table 2.** Movements of recaptured individuals of six bird species between treefall-gap and forest sampling sites in the Humaitá Forest Reserve, in southwestern Brazilian Amazonia, showing the distance travelled between locations. Sampling site indicates the codes of the specific sampling site (see Figure 2), where G = gap and F = forest. Distance = linear distance traveled calculated using Google Earth Pro.

| Species               | Sampling site | Days between captures | Distance (m) |
|-----------------------|---------------|-----------------------|--------------|
|                       | 1st capture   | 2nd capture          | 3rd capture  |
| Thalurania furcata    | G1            | G4                    | 2            |
| Xenops minutus        | G1            | G4                    | 142          |
| Sciaphylax hemimelaena| G1            | G4                    | 40           |
| Mionectes oleagineus  | F3            | G11                   | 4            |
| Lepidothrix coronata  | G9            | F9                    | G10          |
| Pipra fasciicauda     | G15           | F14                   | 13           |
| Pipra fasciicauda     | F6            | G7                    | 171          |
| Pipra fasciicauda     | F1            | G1                    | F1           |
| Pipra fasciicauda     | F6            | G6                    | F6           |
| Pipra fasciicauda     | F9            | G10                   | 83           |
| Pipra fasciicauda     | F14           | G15                   | 19           |
40.7; 117 - 284) and 2,588 in the forest plots (172.5 ± 46.4;
68 - 300). The gaps had a high percentage of plants less than
2 m high, with a much lower percentage of plants over 3 m
in height (Figure 5). Less than 1% of the plants in the gaps
were over 20 m high. The gaps had a mean size of 238.1 m²
(range: 104–437.4 m²).

The pRDA explained 72.5% of the total variation in bird
species abundance in relation to vegetation structure. The bird
assemblages were influenced by the vegetation structure (F =
1.75, df = 2, p = 0.001; adjusted R² = 0.112). The first pRDA
axis indicated a negative correlation (-81.7%) of the variation
in total abundance with the height of the vegetation and also
indicated a negative correlation (-55.7%) between vegetation
density and the occurrence of some bird species. The second
axis indicated that 43.5% of this variation is explained by the
density of the vegetation.

We recorded 19 plants bearing flowers or fruit, representing
13 genera and 12 botanical families (Supplementary Material,
Table S2). Abundance (r = 0.06, p = 0.02) and richness (r =
0.49, p = 0.05) of frugivore birds and fruit supply in the gaps
showed a moderate positive relationship. However, we found
no relationship between the number of flowering plants and
the abundance (r = -0.3, p = 0.25) and richness (r = -0.2, p
= 0.31) of nectarivores.

The two gap-specialist birds were recorded in the forest
understory (100%), and the only forest specialist in the sub-
canopy (Table 1). Species associated with gaps were recorded
in almost all strata (Table 1), primarily in the understory
(71.4%) and sub-canopy (57.1%). Forest-associated species
were recorded primarily in the understory (75%), and sub-
 canopy and forest floor both 37.5%.

Two species that we classified as gap-associated were
recorded primarily in the forest sub-canopy: Sittasomus
griseicapillus and T. schistogynus. Three (37.5%) of the
eight species associated with the forest also were recorded
preferentially in the sub-canopy: Dendrocincla fuliginosa,
 Glyphorhynchus spirurus, and I. hauxwelli.

DISCUSSION
Species richness and composition, and bird
abundance

Bird species richness did not vary significantly between
gap and forest because most species were captured in the two
types of habitat, as recorded in forests of Puerto Rico and Costa
Rica (Wunderle et al. 1987; Levey 1988). Thus we could not
confirm our assumption that bird assemblages in gaps and
forest were different, as reported in Panama and Malaysia
(Schemske and Brokaw 1981; Rosely et al. 2007). In the
HFR, the availability of food resources in gaps was probably
to similar to that of the forest, contributing to the similarity in
the bird assemblages, in contrast with the pattern suggested
by Blake and Hoppes (1986) and Martin and Karr (1986).

Habitat preferences

We identified species specialized in the exploitation of
either treefall gaps or continuous forest and others that were
associated with both environments, i.e., species that have some
degree of affinity with one habitat, but are not dependent on
this environment in the way specialists are. This indicates that
a minimal degree of differentiation exists between gap and
forest bird assemblages. However, as the gaps found within a
given forest will typically present different stages of maturation
(Brokaw 1985), we would expect to find an overlap between
the bird assemblages in gaps and forest. We suggest that few

Figure 4. Overall abundance of bird individuals of each trophic guild captured
in treefall gap and forest sites in the Humaitá Forest Reserve, southwestern
Brazilian Amazonia. Fru = Frugivore; Ins = Insectivore; Nec = Nectarivore; Omn =
Omnivore; Pis = Piscivore.

Figure 5. Vegetation height profiles of the 15 gap and 15 forest sites sampled in
the Humaitá Forest Reserve, southwestern Brazilian Amazonia. The bars indicate
the mean ± standard error of the percentage cover in each height class.
forest species have specific adaptations for the exploitation of gap environments at an early stage of regeneration. This would account for the fact that we recorded only two species that were associated strongly with the treefall gaps in the HFR.

In the HFR, we captured only a few individuals of *Arreremon taciturnus* and *Cyanocorax rorisschildii*, which are associated clearly with Amazonian treefall gaps (Schulenberg et al. 2010). It seems likely that these species may have a preference for larger gaps than those found in the HFR, or occur locally at very low densities. Overall, most species classified as specialists in both habitats in the HFR preferred gap environments, as found in other tropical forests (Schemske and Brokaw 1981; Wunderle et al. 2005). The HFR and El Verde in Puerto Rico had relatively few species associated with gaps. In some tropical forests, species richness and total captures are much higher in gaps than in forest (Levey 1988; Wunderle et al. 2005).

**Habitat specialist birds**

We captured individuals of *Thamnomanes ardesiacus* only in the forest, probably because this species inhabits primarily the understory of *terra firme* forest (Zimmer and Isler 2003) and, in the HFR, it seems likely that it avoids gaps. *Hypocnemis peruviana* was associated with gaps in the HFR, a behavior well documented in the Peruvian Amazon (Schulenberg et al. 2010) and also observed for *Hypocnemis cantator* (currently Spix’s Warbling-antbird *Hypocnemis striata*, Isler et al. 2007) in the Tapajós National Forest (Wunderle et al. 2005). By contrast, *Oryzoborus angolensis* normally inhabits open areas, natural grassland beyond the forest edge, and secondary forest (Rising and Jaramillo 2011). It is a gap specialist in the HFR. Gaps in the early stages of regeneration offer a range of resources (such as seeds) capable of maintaining this species within the forest, as is the case with its congeners *Sporophila aurita* (*S. corvina*) in Costa Rica (Levey 1988) and *Sporophila lineola* in Brazil (Banks-Leite and Cintra 2008), both known to colonize continuous forest by exploiting gaps efficiently.

**Bird movement between gaps and forest**

We showed the actual use of gaps by birds which were recaptured in different gaps in the HFR. This reveals that the birds are moving systematically to these environments to forage, rather than just ranging randomly. The movements of *Pipra fasciicauda* and *Lepidothrix coronata* between gaps indicate that they play an important role in dispersing seeds from the forest to gaps and also between gaps (Murray 1988; Snow 1981; Loiselle and Blake 1990; Marini 1992; Piratelli and Mello 2001; Oliveira and Dario 2018).

We observed that *Sciaphylax hemilemaena* and *Xenops minutus*, which are common in secondary growth (Laurance et al. 2004), frequently forage in forest edges or gaps in the HFR. *Sciaphylax hemilemaena* was observed almost daily in the edges of the study gaps (J.L., personal obs.). Probably edge insectivores, birds that exploit gaps, and some frugivores move within the forest via these environments (Laurance et al. 2004). This behavior appears to be advantageous for many bird species, especially where the forest has undergone significant fragmentation (Lees and Peres 2009). Our results indicate that these movements do occur, and that this pattern may be frequent among all species associated with gaps in the HFR.

**Distribution of trophic guilds**

The number of plants flowering and fruiting in gaps was low in the HFR throughout the study period. We observed the nectarivores *Amazilia lactea*, *Chlorostilbon mellisugus* and *Phaethornis ruber* foraging constantly within the gaps (J.L. personal obs.), but they were rarely captured. This indicates that, while these species were present in the gaps, our capture method may have been inadequate for the effective sampling of the members of this guild. The low capture rates of frugivores and nectarivores were likely related to the relative scarcity of food resources in the gaps during the study period (Gentry and Emmons 1987), which coincided with the dry season in the study region, which lasts from May to October (Duarte 2007). The same pattern was recorded in Puerto Rico and central Amazonia (Wunderle et al. 1987; Henriques et al. 2003). Despite the low capture rates, the positive correlation we observed between fruit availability and frugivore abundance corroborates the hypothesis that resource availability attracts these birds to the gaps (Willson et al. 1982; Blake and Hoppes 1986; Gomes et al. 2011).

In the HFR, *P. fasciicauda* was the most abundant frugivore, and was the species most captured in gaps, especially at the sites with a higher concentration of fruiting plants of the families Rubiaceae and Olacaceae. Fruits of *Siparuna, Heisteria, Cissus, Psychotria*, and *Costus* are components of the diet of many Neotropical frugivorous birds (Snow 1981), and gaps function as a “key habitat” for the maintenance of populations of frugivorous birds during periods of fruit shortage (Levey 1990). Manakins specialize in eating small fruit (Snow 1981), in particular those of Melastomataceae and Rubiaceae (*Piratelli and Mello* 2001). Melastomataceae are pioneer species (Mentz and Oliveira 2004) that grow and fruit quickly, taking advantage of the greater input of sunlight in gaps in the forest (Uhl et al. 1988; Brokaw 1985). This may explain why *P. fasciicauda* was the most abundant frugivore in gaps in the HFR.

One gap specialist in the HFR was an insectivore. The high species richness and the abundance of individuals in comparison with other trophic guilds (Wunderle et al. 2005; Neto et al. 2017) corroborate the hypothesis that high concentrations of seedlings and young leaves in early regrowth likely attracts many invertebrates to the gaps (Richards and Coley 2007). Insectivores may be less sensitive to the marked microclimate variation between gap and forest (Wunderle et al. 2006). The even distribution of insectivores in gaps and forest in the HFR can be related to the active foraging behavior.
of these birds, which move constantly through the forest in search of prey, often in mixed-species flocks dominated by insectivores (Munn and Terborgh 1979), which are common in the HFR (Pedroza et al. 2020), in both gaps and forest (J.L. personal obs.). For example, Thamnomanes schistogynus brings together a number of other species that form high-density, mixed-species flocks that forage together (Munn 1985). This accounts for the capture of a large number of insectivores in the gaps when T. schistogynus was present.

Influence of vegetation structure and forest strata

In the HFR, species influenced by the vegetation structure of the gaps used the sites with denser vegetation and taller plants, i.e., they prefer gaps at an intermediate or advanced stage of regeneration (Banks-Leite and Cintra 2008). In this stage, the vegetation of gaps generally is relatively dense, offering more substrates for potential food resources such as invertebrates (Didham et al. 1996). The greater height of the vegetation in these gaps also creates different strata that are exploited by a greater variety of bird species, especially insectivores (Felton et al. 2008). Advanced regrowth in gaps thus allows some bird species that normally occupy the highest forest strata to exploit this newly-formed environment. Surprisingly, most of the species that were common in gaps inhabit the sub-canopy and canopy in forest (Schulenberg et al. 2010).

Tachyphonus luctuosus, Veniliornis affinis and Piculus leucolaemus, which all inhabit the forest sub-canopy and canopy, usually were observed in gaps foraging in mixed-species flocks (J.L. personal obs.). Forest sub-canopy birds are more commonly found in gaps in comparison with canopy birds, given the greater proximity of this stratum to the gap vegetation (Walther 2002). The movement of species from higher forest strata to the understory reflects vertical mobility, as observed in birds in many different rainforests (Schemske and Brokaw 1981; Wunderle et al. 1987; Wunderle et al. 2005). Given this, the occurrence of different species at the level of the mist-nets will vary among forest types (Levey 1988). In the HFR, this reflects a real preference for the gap environment in sub-canopy species, as observed by Schemske and Brokaw (1981) in a tropical forest in Panama, rather than just a tendency to occur in this environment as a random consequence of their movement patterns in the higher strata.

CONCLUSIONS

The assemblage of understory birds found in natural gaps was similar in species composition and richness to that of the adjacent forest in southwestern Brazilian Amazonia. Yet we identified species that specialize in the use of natural gaps, and others that are closely associated with these environments, but are not dependent on them. Natural gaps are exploited by birds from different strata of the forest, ranging from the ground to the sub-canopy and canopy. The different stages of gap maturation attract an ample diversity of birds that are fundamental to the regeneration and restoration of the forest environment. We suggest that the association of birds with natural forest gaps establishes a link that likely ensures pollination, seed dispersal, and pest control, and guarantees the heterogeneity and resilience of the forest environment following local impacts.

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Lima & Guilherme. Birds associated with treefall gaps in a lowland forest in southwestern Brazilian Amazonia.

| Family/Species | Gap | Forest | Guild | Stratum |
|----------------|-----|--------|-------|---------|
| **Columbidae** |     |        |       |         |
| Leptotila rufaxilla | 1   | F      | T, Fe |         |
| Geotrygon montana    | 1   | 4      | O     | T       |
| **Cuculidae** |     |        |       |         |
| Coccyca minuta      | 2   | 0      | I     | Sc, Fe  |
| **Trochilidae** |     |        |       |         |
| Glaucis hirsutus    | 9   | 2      | N     | S, Fe   |
| Threnetes leucuras  | 0   | 1      | N     | U, Fe, Sf |
| Phaethornis hispidus | 5   | 7      | N     | U, Sc   |
| Phaethornis bouchieri | 4   | 1      | N     | U       |
| Phaethornis ruber    | 3   | 2      | N     | U       |
| Campyloterus longipennis | 0   | 1      | N     | C, Fe   |
| Chlorostilbon melliugus | 1   | 0      | N     | Sc, Fe, Sf |
| Thalurania furcata   | 8   | 1      | N     | C, Tf   |
| Hylocharis cyanus    | 1   | 3      | N     | U, Sc, C |
| Amazilia lactea      | 2   | 0      | N     | Sc, Fe  |
| **Alcedinidae** |     |        |       |         |
| Chlorococcyx aenea   | 0   | 1      | P     | Fe      |
| Chlorococcyx inda    | 0   | 1      | P     | Fe      |
| **Momotidae** |     |        |       |         |
| Momotus momota      | 0   | 2      | O     | Sc      |
| **Galbulidae** |     |        |       |         |
| Galbula cayanaeula  | 2   | 1      | I     | Sc      |
| Galbula cyanescens  | 1   | 0      | I     | T, Fe   |
| **Bucconidae** |     |        |       |         |
| Nonnula scloteri     | 2   | 0      | I     | T, U    |
| Nonnula ruficollis   | 0   | 1      | I     | Fe      |
| Monasa nigraella     | 1   | 0      | I     | Sc, C   |
| Monasa morpheus      | 1   | 0      | I     | Sc, C   |
| **Ramphastidae** |     |        |       |         |
| Pteroglossus inscriptus | 1  | 0      | F     | C       |
| Pteroglossus manae   | 1   | 0      | F     | C       |
| Pteroglossus beauhamaezi | 0  | 1      | F     | C       |
| **Picidae** |     |        |       |         |
| Veniliornis passeninus | 2   | 0      | I     | Fe, Sf  |
| Veniliornis affinis  | 2   | 2      | I     | Sc, U   |
| Pileulus leucomelas  | 1   | 0      | I     | C       |
| Campethus rubicollis | 1   | 0      | I     | C, Sc   |
| **Furnariidae** |     |        |       |         |
| Sclerurus mexicanus  | 1   | 1      | I     | T       |
| Sclerurus caudatus   | 5   | 6      | I     | T       |
| Sittasomus gniccaepilus | 8  | 4      | I     | U, Sc   |
| Dendrocinclia merula | 10  | 20     | I     | U       |

| Family/Species | Gap | Forest |Guild | Stratum |
|----------------|-----|--------|------|---------|
| **Dendrocinclia fuliginosa** | 5   | 11     | I    | S, Sc   |
| **Dendrocolaptes piciceps** | 1   | 1      | I    | S, Sc   |
| **Dendrocolaptes cerithya** | 4   | 1      | I    | Sc      |
| **Cyanoptila cyanomelana** | 1   | 1      | I    | Sc      |
| **Campylorhamphus trochilirostris** | 0   | 3      | I    | Sc, U   |
| **Phrygalicyclus melanoleucus** | 1   | 2     | I    | U       |
| **Prionochilus guttatus** | 1   | 1      | I    | C, Sc   |
| **Leptopogon amaurocephalus** | 0   | 1      | I    | U       |
| **Leptopogon exilis** | 0   | 1      | I    | U       |
| **Leptopogon palustris** | 1   | 0      | I    | U       |
| **Leptopogon schistocercus** | 11  | 11     | I    | U       |
| **Leptopogon subulatus** | 1   | 0      | I    | Sc      |
| **Syrinichas pulchella** | 2   | 0      | I    | U       |

**Thamnophilidae**

| Family/Species | Gap | Forest | Guild | Stratum |
|----------------|-----|--------|-------|---------|
| Epinecrophyllia leucophaea | 1   | 3      | I    | U, Sc   |
| Epinecrophyllia ornata | 2   | 3      | I    | Sc, U   |
| Myrmotherula axillaris | 26  | 11     | I    | U, Sf, T, Fe |
| Myrmotherula longipennis | 3   | 0      | I    | U       |
| Diphanoeca cincta | 0   | 1      | I    | T       |
| Iserla hauckiulli | 15  | 16     | I    | U, Sc   |
| Thamnomanes ruficapillus | 0   | 7      | I    | Sc      |
| Thamnomanes schistogynus | 10  | 4      | I    | Sc      |
| Thamnophilus affinis | 11  | 11     | I    | U       |
| Thamnophilus schistaceus | 4   | 1      | I    | U       |
| Onelliornis salvinii | 9   | 16     | I    | T, U    |
| Rhampharhynchus melanosticta | 0   | 1      | I    | U       |
| Philepomus nigromaculatus | 6   | 12     | I    | U, T    |
| Willisonia pectoralis | 7   | 15     | I    | U       |
| Hypnornis peruvianus | 14  | 1      | I    | U, Fe, T, Sf |
| Hypnornis subflava | 2   | 0      | I    | U       |
| Scaphyphas heminoeca | 16  | 7      | I    | U, Sf, Fe |
| Myrmelastes hyperythrus | 0   | 2      | I    | U, Fe   |
| Myrmelastes humayothae | 1   | 0      | I    | U, Sf, Fe |
| Mymoborus myotherinus | 5   | 7      | I    | U       |

**Formicariidae**

| Family/Species | Gap | Forest | Guild |
|----------------|-----|--------|-------|
| Formicarius calva | 2   | 4      | I    |

**Tyrannidae**

| Family/Species | Gap | Forest |
|----------------|-----|--------|
| *Corythia torquata* | 3   | 2      |
| *Monetes olivaceus* | 6   | 14     |
| *Leptopogon amaurocephalus* | 6   | 6      |
| *Hemitricus flammeus* | 4   | 2      |
| *Myiornis ecaudatus* | 1   | 0      |
| *Phlegopsis nigromaculata* | 6   | 12     |
| *Willisonia pectoralis* | 7   | 15     |
| *Hypnornis peruvianus* | 14  | 1      |
| *Hypnornis subflava* | 2   | 0      |
| *Scaphyphas heminoeca* | 16  | 7      |
| *Myrmelastes hyperythrus* | 0   | 2      |
| *Myrmelastes humayothae* | 1   | 0      |
| *Mymoborus myotherinus* | 5   | 7      |

**Furnariidae**

| Family/Species | Gap | Forest |
|----------------|-----|--------|
| *Sclerurus mexicanus* | 1   | 1      |
| *Sclerurus caudatus* | 5   | 6      |
| *Sittasomus gniccaepilus* | 8   | 4      |
| *Dendrocinclia merula* | 10  | 20     |
Table S1. Continued.

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Lathrotriccus euleri | 2   | 1      | I     | U       |
| Cnemotriccus fuscatus| 0   | 1      | I     | S, Fe, Sf |
| Rhytiphena simplex   | 2   | 1      | I     | Sc      |
| Ramphotragus megacephalus | 3 | 3   | I     | U, Sc   |
| Attila spadiceus      | 2   | 1      | O     | C, Sc   |

Pipridae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Lepidotrauchus coronata | 5 | 4 | F     | U, Sc   |
| Pipra fasciacauda     | 35  | 30    | F     | U       |
| Machaeropetron pyrocephalus | 3 | 0 | F     | Sc, U   |

Tityridae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Onychorhynchus coronatus | 2 | 4 | I     | U       |
| Terenotricula erythrurus | 5 | 6 | I     | Sc, U   |
| Laniocera hypopyma    | 1   | 2     | I     | Sc      |

Troglydytidae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Pheugopedius genibarbis | 5 | 1 | I     | U       |
| Cantorchilus leucotis | 0   | 1      | I     | U, Fe   |

Turdidae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Turdus amaurochalinus | 0   | 1      | F     | Fe, Sf  |
| Turdus ignobilis      | 0   | 1      | O     | Fe, Sf  |
| Turdus hauwelli       | 0   | 2      | O     | T, Sc   |

Passerellidae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Anremon taciturnus    | 4   | 1      | O     | U, Fe   |

Cardinalidae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Habia rubra          | 1   | 0      | I     | U, Fe   |
| Cyanocorvina rothschildi | 1 | 1  | F     | U       |

Thraupidae

| Family/Species       | Gap | Forest | Guild | Stratum |
|----------------------|-----|--------|-------|---------|
| Eucrateriae penicillata | 0 | 1 | I     | U, Sc   |
| Tachyphonus lucius | 2   | 0     | I     | Sc, Fe  |
| Ramphocelus carbo    | 4   | 7     | O     | Fe      |
| Thraupis palmarum    | 0   | 2     | F     | C, Fe   |
| Saltator grossus     | 1   | 0     | I     | Sc      |
| Saltator maximus     | 2   | 0     | I     | Sc      |
| Chrysobonus angolensis* | 12 | 2   | G     | T, U, Fe, Tf |

Table S2. Flowering and/or fruiting plant genera and species recorded in 15 treefall gaps from May 13th to November 19th, 2018, in the Humaitá Forest Reserve, southwestern Brazilian Amazonia. Botanical nomenclature follows Daly and Silva (2008) and Medeiros et al. (2014).

| Family             | Genus/Species                        | Status |
|--------------------|--------------------------------------|--------|
| Acanthaceae        | Pachystachys spicata (Ruiz and Pav.) Wassh | Flower |
| Arecaceae          | Geonoma lauriflora Mart.              | Fruit  |
| Bignoniaceae       | Anabidaea SP. DC.                     | Flower |
| Chrysobalanaceae   | Hirtella sp. L.                       | Flower |
| Costaceae          | Costus arabicus L.                    | Flower |
| Euphorbiaceae      | Pausandra trianae (Müll.Arg) Baill.   | Fruit  |
| Siparunaceae       | Siparuna guianensis Aubl.             | Fruit  |
| Myrtaceae          | Myrica sp. DC.                        | Flower |
| Olacaceae          | Heisteria nitida Spruce ex Engl.      | Fruit  |
| Rubiaceae          | Faramez sp. Aubl.                     | Fruit  |
| Rubiaceae          | Psychotria sp. L.                     | Flower |
| Violaceae          | Rinorea sp. Aubl.                     | Fruit  |
| Vitaceae           | Cissus sp. 1 L.                       | Flower |
| Vitaceae           | Cissus sp. 2 L.                       | Flower |