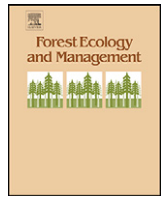




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## Bird use of logging gaps in a subtropical mountain forest: The influence of habitat structure and resource abundance in the Yungas of Argentina

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## ABSTRACT

Selective logging is one of the main economical activities in tropical and subtropical forests. While most of the effects of this activity on bird communities have been studied by comparing exploited vs. non-exploited areas; the use of human-created treefall gaps by birds is relatively unknown. We studied habitat structure, resource abundance (fruits, flowers and arthropods) and bird activity in logging gaps of different age (1-year-old and 10- to 20-year-old) in a mountain forest (Yungas) of northwest Argentina in both dry and wet seasons. In less than a year after creation, short herbs colonize logging gaps increasing the abundance of arthropods in the ground and the activity of understory insectivores. During dry seasons recently created gaps become an important source of resources for understory frugivores-insectivores. Later on in succession logging gaps are invaded by exotic graminoid vegetation and tall herbs (dispersed through extraction tracks) which can impede the colonization and development of pioneer trees and natural regeneration. Probably as a consequence of a high abundance of fruits and flowers in the understory and a very low abundance of these resources in the canopy, old gaps were mainly used by understory frugivores-insectivores while arboreal frugivores were rare. Because arboreal frugivores disperse most tree seeds in tropical and subtropical forests, the low activity of this guild in logging gaps contribute to the low observed regeneration. Sustainable timber harvest in tropical and subtropical forests should include gap and logging track management to minimize the invasion by exotic graminoid vegetation and facilitate natural succession.

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### 1. Introduction

The creation of forest gaps by treefalls in temperate and tropical ecosystems enhances species coexistence by increasing spatial heterogeneity and decreasing competitive exclusion (Schemske and Brokaw, 1981; Schnitzer and Carson, 2001; Faccio, 2003). Canopy openness increases light incidence and modify microclimatic conditions allowing the establishment and development of vegetation in the understory and pioneer trees which produce fleshy fruits and flowers consumed by birds (Blake and Hoppes, 1986; Levey, 1988; Feisinger et al., 1998; Wunderle et al., 2005). Also, as a consequence of changes in vegetation structure and composition, arthropods abundance tends to be high in gaps compared to forest interior (Blake and Hoppes, 1986; Linhart et al., 1987). Natural gaps represent an important habitat patch

exploited by birds in both tropical and temperate forest (Schemske and Brokaw, 1981; Blake and Hoppes, 1986; Levey, 1988; Feisinger et al., 1998; Fuller, 2000; Wunderle et al., 2005).

Selective logging is one of the principal human disturbances in tropical and subtropical forests. Despite its economical importance, governmental and private controls and regulations are, almost, non-existent (Putz, 2000; Fredericksen and Putz, 2003). Studies evaluating the effects of selective logging on bird communities and populations in tropical and subtropical forests showed heterogeneous responses; while some species disappear or decrease in abundance (particularly understory insectivores), others increase in abundance (Thiollay, 1992; Mason, 1996; Marsden, 1998; Robinson and Robinson, 1999; Aleixo, 1999; Fredericksen and Putz, 2003; Wolmann, 2003). Only a few studies evaluated bird use of logging gaps at a small scale (Fredericksen et al., 1999).

The Yungas of Argentina represents the southern limit of the tropical Andes ecosystem, one the world hotspot of biodiversity (Myers et al., 2000), which extends from 400 to 2500 m a.s.l.

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(Cabrera and Willink, 1980). Lowland premontane forest is the most disturbed sector in the Yungas and currently less than 20% of this forest is protected in Argentina (Grau and Brown, 2000). Selective logging is one of the main economical activities in the Yungas of Argentina; however, no study has evaluated the effects of this activity on bird communities. In this context, our objective was to study the use of logging gaps by birds in a premontane forest in relation to the structure of vegetation and resource abundance.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in a premontane forest of north-western Argentina ( $23^{\circ} 47'S$ ;  $64^{\circ} 47'W$ ; Fig. 1). Total precipitation is 1400 mm and is highly seasonal, with 80% concentrated between November and April (Cabrera and Willink, 1980). Because bird community composition changes with altitude (Blake and Rougès, 1997), we focused in the premontane forests between 490 and 560 m a.s.l. Native forest in the study area is exploited in cycles of 10–20 years between harvests; the most recent harvest was in 2000. Logging treefall gaps (mainly old gaps) were dominated by isolated individuals of pioneer tree species including *Croton* spp., *Urera baccifera* and *Anadenanthera colubrinae*. The most abundant species of interior forest in the study area included several species of the Myrtaceae family and *Trichilia hieronymi*.

### 2.2. Sampling design and bird surveys

Bird activity, vegetation structure and composition and resource abundance (arthropods, fruits and flowers) were sampled during both wet (January–February) and dry (July–August) seasons in 2001. We randomly selected ten logging gaps (five 10- to 20-year-old and five recent gaps less than 1-year-old) and 10 interior forest sites. Selected sampling sites were at least 200 m apart to ensure independence. Logging gaps were identified, in most cases, by the remaining stumps and the presence of extraction tracks. Average size of gaps was 211 m<sup>2</sup> (113–412 m<sup>2</sup>) for recent gaps and 308 m<sup>2</sup> (212–530 m<sup>2</sup>) for old gaps. Because five old gaps and five interior forest sampling sites were destroyed by extraction tracks created between wet and dry seasons, we sampled only five recent gaps and five interior sites in dry season.

We used the point count method with fixed radius (20-m) to estimate bird species abundance in gaps and interior forest (Bibby et al., 1998). We recorded all heard individuals during a 10-min period between sunrise and 3 h later (7:30–10:30 h in wet season and 8:00–11:00 h in dry season). To increase the reliability of samples, all point counts were sampled 6 days but visit order was systematically changed (Bibby et al., 1998). We only considered aural records because of differences in visual detectability between gaps and forest interior. All point counts were performed by the same observer. However, to validate aural species identification, the principal observer and another trained observer simultaneously sampled the same bird point counts for 3 days in wet



Fig. 1. Regional distribution of the Southern Andean Yungas in South America and detailed study area in the Yungas of Argentina.

seasons. On each bird point count, both observer independently identified birds. Total records and records for each species obtained by both observers were correlated. Relative activity, or habitat use by birds, was estimated as the number of records for each species per sampling point in the 6 sampling days. The median value and the 10–90% percentiles of the relative activity were calculated for gaps and forest interior (10 replicates in wet season and five in dry season) and for old and recent gaps (5 replicates) on each season.

### 2.3. Vegetation and resources sampling

On each sampling site, we estimated vegetation cover in a 5 m × 5 m plot using an adaptation of the interception line method (Morrison et al., 1998). We extended a 5 m line at ground level, 0.1 and 1.0 m and measured the length of litter, dicotyledonous herbs and graminoid vegetation touching the line. This line was extended north–south and west–east and coverage measurements were averaged. We visually estimated percentage cover of low, medium and high arboreal stratum in a 35 mm lens focused at 2, 5 and 10 m in the four cardinal directions (Vides-Almonacid, 1992). Diameters at breast height (dbh) of trees larger than 2 cm dbh were measured in plots.

We estimated the abundance of fruits and flowers in plots by counting all individual woody plants with fleshy fruits and flowers in the understory and arboreal stratum (over 1.5 m). For each individual we visually estimated its percentage cover within the plot. Total fleshy fruits and flowers abundance per plot and strata (understory and arboreal) was calculated as the sum of the relative cover of individuals. All sampling sites and the main logging track were mapped using a GPS. The minimum distance between each sampling site and the main logging track was calculated in a Geographical Information System (GIS).

Arthropods were sampled using pitfall traps of 450 cm<sup>3</sup> (10 cm high and 7 cm diameter) (Southwood, 1978). Traps were located 2.5 m apart from central sampling point in the four cardinal directions, buried 10 cm in the ground and filled 3/4 with 70% ethylic alcohol (340 cm<sup>3</sup>). Traps were covered for 24 h to avoid digging problems, after which uncovered traps collected arthropods for 72 h. Arthropods were identified to order level or, in some cases, to family level.

### 2.4. Data analysis

Vegetation structure, resource abundance, and bird- and guild activity were compared between gaps and forest interior and between old and recent gaps using a non-parametric Mann–Whitney tests. Cluster analysis using foraging strata and diet composition was performed to aggregate species into feeding guilds. Foraging strata was calculated from 284 visual records from 90 h of observation in which we could identify the feeding bird. Observations were casual and performed during bird point counts (between sunrise and 10 a.m.) in this study and a previous study in the same location (Zurita and Zuleta, unpublished data). Foraging strata were defined as: (1) ground (species feeding mainly in litter), (2) understory (feeding in herbs and shrubs below 1.5 m), (3) low-medium canopy (feeding on trees between 1.5 and 10 m), (4) high canopy (feeding on trees canopy over 10 m) and (5) trunks. Diet composition was obtained from previous studies in the Yungas (Blake and Rougès, 1997; Rougès and Blake, 1999; Malizia, 2001). Species were considered insectivores and/or frugivores based on the presence/absence of food items (arthropods, fruits teguments and seeds) in fecal samples and field observations. A principal components analysis (PCA) was per-

formed to study the relation between vegetation variables and resources distribution. Multivariate axes of the PCA were correlated to resource abundance (fruits/flowers and arthropods) using an  $\alpha = 0.05$  (error type I). Arcsine transformation of variables measuring vegetation cover was used in the PCA. Resource abundance and guilds activity were related using Spearman non-parametric correlation tests. The activity of ground and understory guilds were correlated with resource abundance in the understory (cover of plants with fruits/flowers in the understory and average abundance of arthropods) and the activity of arboreal guilds with cover of arboreal plants with fleshy fruits/flowers.

## 3. Results

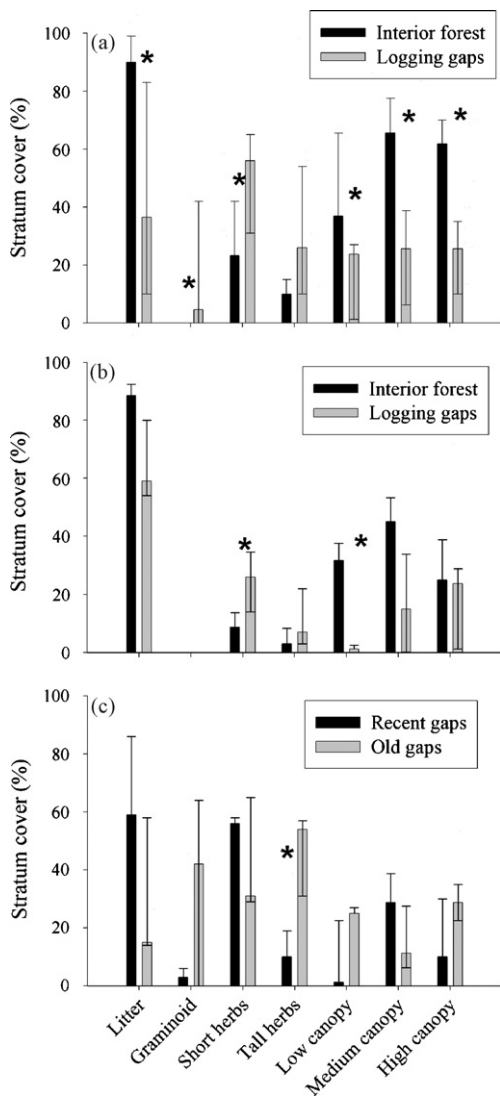
### 3.1. Habitat structure and resource abundance

We recorded 22 tree species growing in forest interior and 10 species in gaps (seven in old gaps and five in recent gaps). During wet season, cover of litter, the three arboreal strata (low, medium and high canopy), tree density (900 individual/ha vs. 150 individual/ha) and basal area (25.79 m<sup>2</sup>/ha vs. 0.17 m<sup>2</sup>/ha;  $n = 10$ ,  $p < 0.05$  in both cases) were higher in forest interior than in gaps (Fig. 2). Cover of short herbs and exotic graminoid vegetation were higher in gaps than in forest interior (Mann–Whitney,  $n = 10$ ,  $p < 0.05$  in all cases) (Fig. 2). In this season, old gaps differed from recent gaps in the high cover of tall herbs (Fig. 2) (Mann–Whitney,  $n = 5$ ,  $p < 0.05$ ). Tree density and basal area were similar between old and recent gaps (200 individual/ha vs. 100 individual/ha and 0.19 m<sup>2</sup>/ha vs. 0.16 m<sup>2</sup>/ha; Mann–Whitney,  $n = 5$ ,  $p > 0.1$  in both cases). In dry season, cover of low arboreal strata and short herbs were higher in forest interior compared to gaps (Mann–Whitney,  $n = 5$ ,  $p < 0.05$  in both cases) (Fig. 2). Graminoid vegetation cover was correlated with distance to the main logging track in old gaps but not in recent gaps ( $r = -0.97$ ;  $n = 5$ ,  $p < 0.01$  and  $r = -0.1$ ;  $n = 5$ ,  $p = 0.87$ , respectively (Fig. 3).

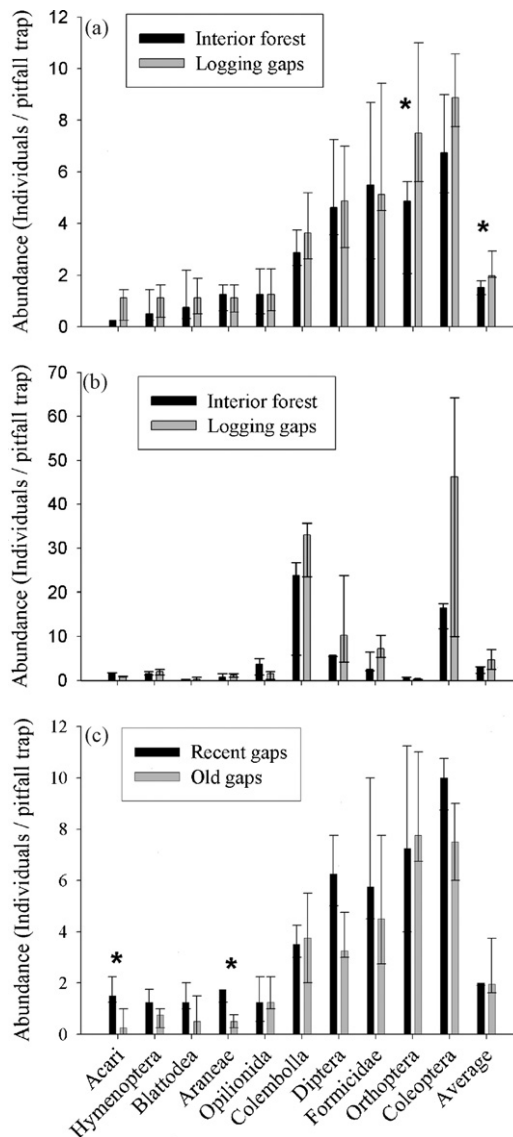
Cover of species in fruit and flower was higher in the understory of gaps compared to forest interior in wet (16% vs. 4%) and dry season (5% vs. 0%) (Mann–Whitney,  $n = 10$  and  $n = 5$ , respectively,  $p < 0.05$  in both cases). In the wet season cover of species in fruit and flower in the arboreal stratum was higher in forest interior than gaps (1% vs. 0%; Mann–Whitney,  $n = 10$ ,  $p < 0.05$ ). In this season, cover of species in fruit and flower was similar between old and recent gaps both in the understory (22% vs. 12%) and arboreal stratum (0% vs. 0%; Mann–Whitney,  $n = 5$ ,  $p > 0.1$  in both cases).

A total of 3550 arthropods (of 16 orders) were captured in pitfall traps in wet season and 3347 in dry season. In the wet season Coleoptera, Orthoptera, Hymenoptera (Formicidae) and Diptera were the most abundant taxa. In dry season, Collembola and Coleoptera were, by far, the most abundant taxa. Average abundance of arthropods and Orthoptera abundance were higher in gaps than in forest interior in wet season (Mann–Whitney,  $n = 10$ ,  $p < 0.05$ ). In dry season average abundance of arthropods between gaps and forest interior was similar (Mann–Whitney,  $n = 5$ ,  $p > 0.1$ ) (Fig. 4). Abundance of Araneae and Acari was higher in recent gaps than in old gaps (Mann–Whitney,  $n = 5$ ,  $p < 0.05$ ); nevertheless average abundance of arthropods was similar between gaps of different age (Mann–Whitney,  $n = 5$ ,  $p > 0.1$ ) (Fig. 4).

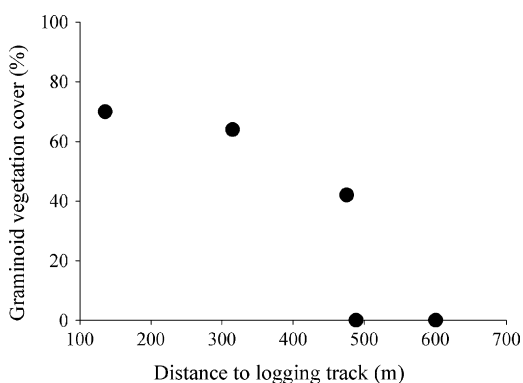
Three axis with eigenvalues over one were extracted from the PCA accounting for 75.8% of total variation in wet season ( $\lambda_1 = 2.7$ ,  $\lambda_2 = 1.5$  and  $\lambda_3 = 1.2$ ) and 74.2% in dry season ( $\lambda_1 = 2.5$ ,  $\lambda_2 = 1.5$  and  $\lambda_3 = 1.2$ ). In wet season data, the first axis explained 38% of the



**Fig. 2.** Median values (range 25–75 quartiles) of vegetation variables used to describe forest interior and logging gaps in wet (a) and dry (b) seasons in Yungas of Argentina. Old (10- to 20-year-old) and recent (1-year-old) gaps were also separated (c). Mann–Whitney test, \* $p < 0.05$ .



**Fig. 4.** Median values (range 25–75 quartiles) of arthropods abundance (average and the 10 principal taxonomic groups) in forest interior and logging gaps in wet (a) and dry (b) season in Yungas of Argentina. Old ( $\geq 10$ -year-old) and recent (1-year-old) were also separated (c). Mann–Whitney test, \* $p < 0.05$ .

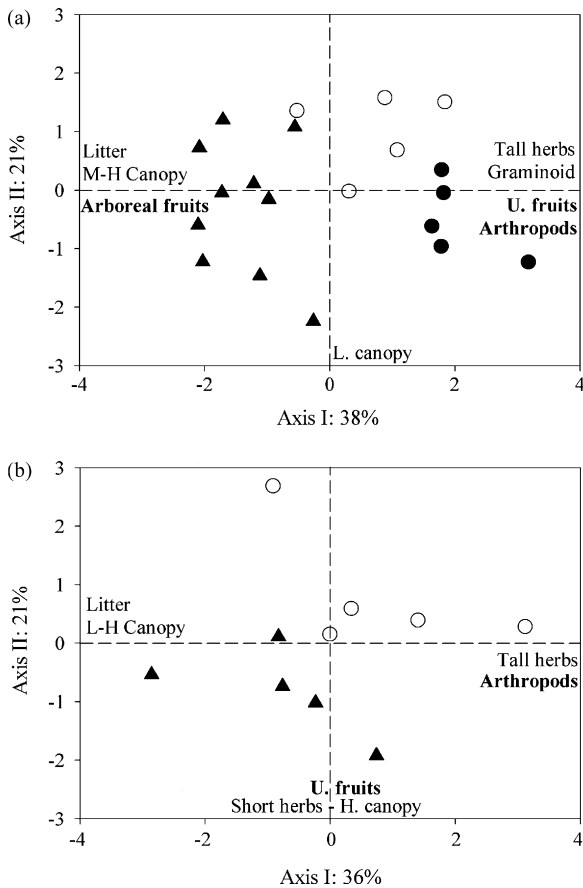


**Fig. 3.** Relationship between exotic graminoid vegetation cover and the distance to the main logging track (source of seeds) in old ( $\geq 10$ -year-old) logging gaps in Yungas of Argentina.

variation and separated gaps from forest interior sites. This axis was correlated to the cover of understory fruit and flower species ( $r = 0.77$ ,  $n = 20$ ,  $p < 0.01$ ), arthropods abundance ( $r = 0.51$ ,  $n = 20$ ,  $p = 0.02$ ) and marginally correlated to the cover of arboreal fruit and flower species ( $r = -0.41$ ,  $n = 20$ ,  $p = 0.07$ ) (Fig. 5). Axis II explained an additional 17.0% and partially separated old and recent gaps (Fig. 5). In dry season, the first axis explained 36% of total variation, partially separated gaps and forest interior sites and was correlated to the abundance of arthropods ( $r = 0.78$ ,  $n = 10$ ,  $p < 0.01$ ). Axis II explained an additional 21% and was correlated to the cover of understory fruit/flower species ( $r = -0.76$ ,  $p = 0.01$ ) (Fig. 5).

### 3.2. Bird use of logging gaps

The correlation of total bird records simultaneously obtained by the two independent observers was high ( $r = 0.81$ ;  $n = 780$ ;  $p < 0.01$ ); also correlations of total counts for individual species



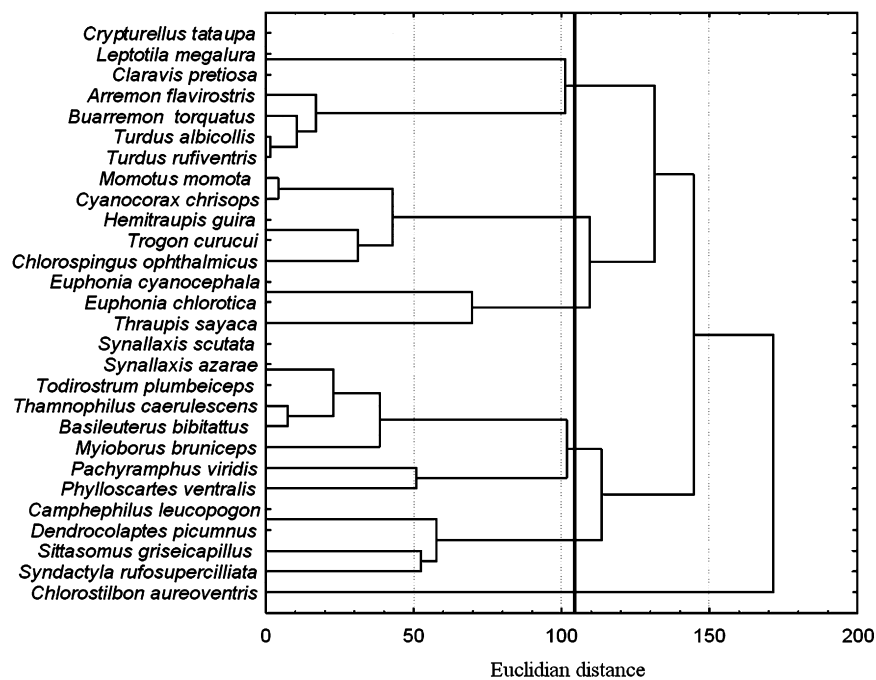
**Fig. 5.** Principal component analysis showing the location of forest interior (by solid triangles) and gaps (open circles: recent gaps, solid circles: old gaps) sampling sites in wet (a) and dry season (b) in relation to vegetation variables and resource abundance in Yungas of Argentina. H: High, M: Medium, L: Low, U: Understory.

were high and significant in all cases ( $r > 0.7$ ,  $p < 0.05$ ) showing observer reliability on species identification.

Based on feeding strata and diet composition (cluster analysis) birds were grouped into six feeding guilds: (1) ground granivores–insectivores: species feeding seeds and arthropods in ground litter, (2) understory frugivores–insectivores: species feeding fruits and arthropods on herbs and shrubs below 1.5 m, (3) understory insectivores: species feeding only arthropods on herbs and shrubs below 1.5 m, (4) arboreal frugivores–insectivores: species feeding fruits and arthropods on trees over 1.5 m, (5) nectarivores: species feeding nectar in flowers and (6) bark insectivores: species feeding arthropods on trunks (Appendix A and Fig. 6).

In wet season 22 species were recorded, 20 in forest interior and 15 in gaps (14 in old gaps and 10 in recent gaps; Tables 1 and 2). In this season, the activity of ground granivores–insectivores was higher in forest interior than in gaps while the activity of understory insectivores tended to be higher in gaps compared to forest interior (Mann–Whitney,  $n = 10$ ,  $p < 0.05$  and  $p = 0.07$ , respectively) (Table 1). In dry season 19 species were recorded, 18 in recent gaps and 13 at the interior forest. In this season, the activity of guilds was similar between forest interior and gaps (Table 1). Within gaps, the activity of arboreal frugivores–insectivores and nectarivores was higher in old gaps compared to recent gaps while understory frugivores–insectivores tended to be more active in recent gaps compared to old gaps (Mann–Whitney,  $n = 5$ ,  $p < 0.05$ ,  $p < 0.05$  and  $p = 0.07$ , respectively).

In wet season, the activity of ground granivores–insectivores and understory frugivores–insectivores was related to cover of plants with fleshy fruits/flowers in the understory ( $r = 0.54$ ,  $n = 20$ ,  $p = 0.01$  and  $r = 0.48$ ,  $n = 20$ ,  $p = 0.03$ ) but not to arthropods abundance ( $r = -0.09$ ,  $n = 20$ ,  $p = 0.68$  and  $r = -0.31$ ,  $n = 20$ ,  $p = 0.17$ ). The activity of understory insectivores and nectarivores was not related to arthropods abundance and cover of plants with fleshy fruits/flowers in the understory ( $r = -0.41$ ,  $n = 20$ ,  $p = 0.07$  and  $r = 0.05$ ,  $n = 20$ ,  $p = 0.81$ , respectively). Finally, the activity of



**Fig. 6.** Cluster analysis for 28 species based on foraging stratum and diet composition in Yungas of Argentina.

**Table 1**  
Median values (range 10–90%) of species and guilds activity in forest interior and logging gaps in a premontane forest of Yungas, Argentina

Species/Guilds	Activity (individuals recorded in 6 sampling days)			
	Wet season		Dry season	
	Forest	Gaps	Forest	Gaps
Ground G-I	1.0 (1.0–2.0)*	0.0 (0.0–1.2)	0.0 (0.0–0.6)	–
<i>Crypturellus tataupa</i>	0.0 (0.0–1.0)	0.0 (0.0–1.2)	0.0 (0.0–0.6)	–
<i>Leptotila megalura</i>	0.0 (0.0–1.0)*	–	–	–
<i>Claravis pretiosa</i>	0.0 (0.0–1.1) <sup>®</sup>	–	–	–
Understory F-I	3.0 (0.9–5.0)	3.0 (2.0–5.0)	4.0 (1.4–6.0)	6.0 (4.0–7.0)
<i>Arremon flavirostris</i>	2.0 (0.9–5.0)	2.0 (1.9–5.0)	4.0 (1.4–6.0)	5.0 (3.4–6.6)
<i>Buarremon torquatus</i>	–	–	–	0.0 (0.0–0.6)
<i>Turdus albicollis</i>	–	–	–	0.0 (0.0–0.6)
<i>Turdus rufiventris</i>	0.0 (0.0–2.0)	0.0 (0.0–1.0)	–	1.0 (0.0–2.6)*
Understory I	12 (11–15)	14 (12–19) <sup>®</sup>	18 (14–23)	19 (16–21)
<i>Synallaxis scutata</i>	1.0 (0.0–3.2)	1.0 (0.0–4.5)	4.0 (0.4–6.2)	3.0 (1.0–4.6)
<i>Synallaxis azarae</i>	–	0.0 (0.0–0.1)	–	–
<i>Thamnophilus caeruleus</i>	0.5 (0.0–1.0)	0.5 (0.0–2.1)	0.0 (0.0–0.6)	0.0 (0.0–2.8)
<i>Poecilatriccus plumbeiceps</i>	1.0 (0.0–5.1)	0.0 (0.0–1.0)	7.0 (2.0–8.6)	5.0 (4.0–7.2)
<i>Basileuterus bivittatus</i>	5.0 (3.0–11.1)	8.0 (5.0–10.0)	8.0 (3.4–9.0)	7.0 (5.8–9.6)
<i>Pachyrhamphus viridis</i>	–	–	0.0 (0.0–1.0)	0.0 (0.0–1.2)
<i>Phylloscartes ventralis</i>	2.0 (0.9–6.1)	3.0 (1.9–6.2)	–	0.0 (0.0–2.2)
<i>Myioborus bruniceps</i>	–	–	1.0 (0.0–2.0)	1.0 (0.4–2.2)
Arboreal F-I	1.5 (0.0–6.4)	0.0 (0.0–3.2)	1.0 (0.0–1.0)	1.0 (0.0–1.0)
<i>Momotus momota</i>	0.0 (0.0–0.1)	–	–	–
<i>Cyanocorax chrysops</i>	1.0 (0.0–5.4)	0.0 (0.0–3.2)	1.0 (0.0–1.6)	0.0 (0.0–2.2)
<i>Hemithraupis guira</i>	–	0.0 (0.0–0.1)	–	–
<i>Chlorospingus ophthalmicus</i>	–	–	–	0.0 (0.0–0.6)
<i>Trogon curucui</i>	0.0 (0.0–1.0)	–	–	–
<i>Euphonia cyanocephala</i>	0.0 (0.0–0.1)	–	–	–
<i>Euphonia chlorotica</i>	0.0 (0.0–1.0)	–	–	–
<i>Thraupis sayaca</i>	–	–	–	0.0 (0.0–0.6)
Nectarivores	0.0 (0.0–1.0)	0.0 (0.0–1.1)	0.0 (0.0–1.0)	0.0 (0.0–0.6)
<i>Chlorostilbon lucidus</i>	0.0 (0.0–1.0)	0.0 (0.0–1.1)	0.0 (0.0–1.0)	0.0 (0.0–0.6)
Bark I	4.5 (1.9–9.2)	4.5 (1.8–7.4)	5.0 (5.0–6.0)	6.0 (5.0–6.0)
<i>Camphephilus leucopogon</i>	0.0 (0.0–0.1)	–	–	–
<i>Dendrocolaptes picumnus</i>	0.5 (0.0–3.1)	0.5 (0.0–1.0)	1.0 (0.0–1.0)	0.0 (0.0–0.6)
<i>Sittasomus griseicapillus</i>	0.0 (0.0–0.1)	1.0 (0.2–2.0)*	–	–
<i>Syndactyla rufosuperciliata</i>	3.0 (1.8–7.0)	3.5 (0.9–4.5)	5.0 (4.0–8.0)	5.0 (3.4–5.6)
Recorded species	20	15	13	18

Ground G-I: feeding seeds and arthropods in ground litter; Understory F-I and Understory I: feeding arthropods and/or fruits in shrubs below 1.5 m; Arboreal F-I: feeding arthropods and fruits on trees over 1.5 m; Nectarivores: feeding nectar in flowers; Bark I: feeding arthropods on trunks. (–) Not recorded. Mann–Whitney: (\*)  $p < 0.05$ , (®)  $p = 0.07$ .

arboreal frugivores–insectivores was not related to the cover of arboreal plants with fleshy fruits/flowers ( $r = -0.33$ ,  $n = 20$ ,  $p = 0.15$ ). In dry season, the activity of guilds was not related to resource abundance (both cover of plants with fleshy fruits/flowers and arthropods abundance) ( $n = 10$ ,  $p > 0.1$  in all cases).

#### 4. Discussion

As expected, vegetation structure and composition differed between forest interior and logging gaps. The hole in the canopy created by a tree extraction facilitates a rapid colonization and development of vegetation in the understory, as observed in natural gaps of tropical and temperate ecosystems (Blake and Hoppes, 1986; Levey, 1988). However, the characteristics of this understory in logging gaps were different from those observed in natural gaps.

After being created, understory cover in natural gaps decreases with the colonization and development of pioneer trees following a general pattern of natural succession (Schemske and Brokaw, 1981; Levey, 1988; Fuller, 2000). In contrast, in logging gaps arboreal species establishment was very slow, probably because of the high cover of exotic

graminoid vegetation. These graminoid species are probably dispersed from the central track through secondary extraction tracks (as showed in Fig. 3). Only few, small individuals of pioneer species – such as *U. baccifera* and *Croton* spp. – were found in gaps; these species are common in recent logging gaps and disturbed areas (Park et al., 2005). The arrest of tree regeneration in logging gaps as a consequence of an excessive growth of native species (including herbs, lianas and bamboo) or invasive exotic species has been found in other tropical and subtropical forests (Veblen, 1989; Hartshorn, 1989; Frederickson and Mostacedo, 2000; Fagan and Peart, 2004). The interruption of natural succession in logging gaps was also evident when comparing the structure of ground arthropods communities, which remains similar in gaps of different ages and different to those of forest interior. Interesting exceptions were taxa within the class Arachnida (Araneae and Acari) that were much more abundant in recent gaps.

Differences on vegetation structure and composition between logging gaps of different age and forest interior influence the abundance of resources used by birds. Similar to natural gaps (Schemske and Brokaw, 1981; Blake and Hoppes, 1986; Levey, 1988; Wunderle et al., 2005); the high abundance of resources in

**Table 2**

Median values (range 10–90 %) of species and guilds activity in old ( $\geq 10$ -year-old) and recent (1-year-old) logging gaps in a premontane forest of Yungas, Argentina

Species/guilds	Activity (individuals recorded in six sampling days)	
	Old gaps	Recent gaps
Ground G-I	0.0 (0.0–0.6)	0.0 (0.0–2.2)
<i>Crypturellus tataupa</i>	0.0 (0.0–0.6)	0.0 (0.0–2.2)
Understory F-I	2.0 (2.0–3.0)	4.0 (2.4–5.0) <sup>®</sup>
<i>Arremon flavirostris</i>	2.0 (1.4–2.0)	4.0 (2.4–5.0)*
<i>Turdus rufigiventris</i>	1.0 (0.0–1.0)*	–
Understory I	14.0 (12.4–17)	15.0 (11.8–19.0)
<i>Synallaxis scutata</i>	1.0 (0.0–1.6)	4.0 (1.0–7.0) <sup>®</sup>
<i>Synallaxis azarae</i>	–	0.0 (0.0–0.6)
<i>Thamnophilus caeruleus</i>	0.0 (0.0–1.0)	2.0 (0.0–2.6)
<i>Poecilatriccus plumbeiceps</i>	1.0 (0.0–1.0)*	–
<i>Basileuterus bivittatus</i>	8.0 (5.4–9.2)	9.0 (5.4–9.6)
<i>Phylloscartes ventralis</i>	5.0 (3.4–7.2)*	2.0 (1.4–2.6)
Arboreal F-I	1.0 (0.4–4.2)*	–
<i>Cyanocorax chrysops</i>	1.0 (0.0–4.2)*	–
<i>Hemithraupis guira</i>	0.0 (0.0–0.6)	–
Nectarivores	1.0 (0.0–1.6)*	–
<i>Chlorostilbon lucidus</i>	1.0 (0.0–1.6)*	–
Bark I	3.0 (0.8–8.6)	6.0 (4.0–7.0)
<i>Dendrocolaptes picumnus</i>	0.0 (0.0–0.6)	1.0 (0.4–1.0) <sup>®</sup>
<i>Sittasomus griseicapillus</i>	1.0 (0.0–1.6)	2.0 (0.4–2.0)
<i>Syndactyla rufosuperciliata</i>	2.0 (0.4–7.0)	4.0 (2.4–4.0)
Recorded species	14	10

Ground G-I: species feeding seeds and arthropods in ground litter; Understory F-I and Understory I: species feeding arthropods and/or fruits in shrubs below 1.5 m; Arboreal F-I: species feeding arthropods and fruits on trees over 1.5 m; Nectarivores: species feeding nectar in flowers; Bark I: species feeding arthropods on trunks. (–) Not recorded. Mann–Whitney: (\*)  $p < 0.05$ , (<sup>®</sup>)  $p = 0.07$ .

the understory (such as fruits, flowers and arthropods) of logging gaps is probably a consequence of understory vegetation development. Particularly, arthropods taxa feeding on understory vegetation, such as Orthoptera and Coleoptera, and highly consumed by understory insectivores birds were abundant in logging gaps. Understory insectivores have been found to decrease in abundance in exploited areas (Thiollay, 1992; Mason, 1996); however, this study and others studies shows that species in this guild intensively exploit resources of logging gaps (Fredericksen et al., 1999). This apparent contradictory result shows that mechanisms producing patterns of species abundance may differ at different scales and reflects the interaction between micro-habitat use within an area and changes in abundance between different areas (Wunderle, 2006). The decrease in abundance of understory insectivores in exploited areas is probably a consequence of an increase in predation pressures and nest parasitism and not a consequence of changes in arthropods abundance (Burke et al., 2004). However, at a smaller scale, logging gaps act as a source of resources for species in this guild explaining the highly observed activity. We found a direct relation between the activity of understory frugivores guilds and the abundance of understory fruits in wet season; however, we were not able to find a similar relation between the activity of understory insectivorous guilds and the average abundance of arthropods. In one side, average abundance of arthropods combining all taxa is probably a rough estimation of arthropods availability because birds usually feed more often some particular taxa (Blake and Rougès, 1997). In the other side, total abundance of fleshy fruits and flowers is probably a good estimator of fruit availability for birds. Another possible explanation is that arthropods are not a limiting resource for birds in this forest.

The use of logging gaps by ground granivore–insectivores was particularly low; in spite of the high abundance of arthropods and fruits in the understory. Only *Crypturellus tataupa* was recorded in gaps, while the other two species in this guild – *Claravis pretiosa* and *Leptotila megalura* – were only recorded at forest interior. Species in this guild are particularly susceptible to predation because of their large size and foraging habits (Schupp et al., 1999); one reason for the limited use of gaps by terrestrial birds may be that predation may be more common in logging gaps.

Old gaps tend to be exploited by a large number of understory frugivores–insectivores and nectarivores in wet season when fruits and flowers in the understory are in high abundance; however, during this season species in these guilds were rare in recent gaps. Recent gaps became an important source of resources for understory frugivores during dry season due to the high seasonality on fruit production in the southern Yungas (Malizia, 2001). Contrary to observations in natural gaps, arboreal frugivores were rare in logging gaps probably as a direct consequence of the scarcity of tree regeneration in logging gaps, even after 10 years. We were not able to find important statistical differences in resource abundance and bird activity between old and recent gaps. However, it is important to consider the low number of replicates (five old gaps and five recent gaps) and the low power of statistical test when interpreting these results.

As is true for most tropical and subtropical forests, selective logging in the Yungas is mostly “opportunistic” and governmental regulations and policies do not effectively regulate the intensity of the extraction (Putz, 2000). In natural conditions, gap formation is a continuous process that generates patches on different regeneration phases (Grau, 2002); in this system old gaps act as a source of pioneer trees that colonize recently created gaps. This spatial and temporal variability is not present in logged areas since logging gaps are created at discrete intervals of time. Areas are usually exploited during a short period of time and abandoned for several years. Also logging gaps are avoided by arboreal frugivores which increases gap isolation because seeds of pioneer trees are dispersed at lower rates (Murray, 1988; Restrepo, 1999).

Gap creation during selective logging is a process affecting forests worldwide. As we showed in this study and others studies in tropical and subtropical forests, natural succession in logging gaps is, in many cases, arrested by the invasion of native or exotic species. Others factors, such as the low rate of seed dispersal to logging gaps and the elimination of a large proportion of adult trees (seed sources), contribute to delay natural succession in logging gaps. Particularly, the manual control of graminoid vegetation increases gap regeneration in Yungas (Marmol, 1995). A sustainable use of tropical and subtropical forests should include pre- and post-logging management policies, such as reduced impact logging, to accelerate gap regeneration. Also, a more detailed knowledge of bird predation and nest parasitism rates in logging gaps of different ages will increase the sustainability of this activity through fixing a minimum interval of time between harvest periods.

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## Appendix A

Foraging guilds based on foraging stratum (calculated from a number of direct observation (N) or bibliography (B)), and diet composition of birds (from bibliography) in Yungas of Argentina. Ground G-I: species feeding seeds and arthropods in ground litter; Understory F-I and Understory I: species feeding arthropods and/or fruits in shrubs below 1.5 m; Arboreal F-I: species feeding arthropods and fruits on trees over 1.5 m; Nectarivores: species feeding nectar in flowers; Bark I: species feeding arthropods on trunks.

Species/guilds	English name	N	Foraging stratum (%) <sup>a</sup>					Diet <sup>b</sup>			
			Gr	Un	L–M	H	Tr	I	F	S	N
Ground G-I		5	67	33	0	0	0	X	–	X	–
<i>Crypturellus tataupa</i>	Tataupa Tinamou	3	100	0	0	0	0	X	–	X	–
<i>Leptotila megalura</i>	White-faced Dove	2	50	50	0	0	0	X	–	X	–
<i>Claravis pretiosa</i>	Blue Ground-dove	B	50	50	0	0	0	–	–	X	–
Understory F-I		75	37	54	9	0	0	X	X	X	–
<i>Arremon flavirostris</i>	Saffron-billed Sparrow	24	79	21	0	0	0	X	–	X	–
<i>Buarremon torquatus</i>	Stripe-headed Brush-finch	18	44	39	17	0	0	X	–	X	–
<i>Turdus albicollis</i>	White-necked Robin	10	0	90	10	0	0	X	X	–	–
<i>Turdus rufiventris</i>	Rufous-bellied Thrush	23	26	65	9	0	0	X	X	–	–
Understory I		91	14	57	28	2	0	X	–	–	–
<i>Synallaxis scutata</i>	Ochre-cheeked Spinetail	12	58	42	0	0	0	X	–	–	–
<i>Synallaxis azarae</i>	Azara's Spinetail	1	0	100	0	0	0	X	–	–	–
<i>Thamnophilus caerulescens</i>	Variable Antshrike	7	14	72	14	0	0	X	–	–	–
<i>Poecilotriccus plumbeiceps</i>	Ochre-faced Tody-flycatcher	3	0	100	0	0	0	X	–	–	–
<i>Basileuterus bivittatus</i>	Two-banded Warbler	57	3	77	16	4	0	X	–	–	–
<i>Pachyramphus viridis</i>	Green-backed Becard	B	33	33	0	0	0	X	–	–	–
<i>Phylloscartes ventralis</i>	Mottle-cheeked Tyrannulet	1	0	0	100	0	0	X	–	–	–
<i>Myioborus brunneiceps</i>	Brown-capped Redstart	10	0	30	60	10	0	X	–	–	–
Arboreal F-I		80	1	11	55	33	0	X	X	–	–
<i>Momotus momota</i>	Blue-crowned Motmot	6	0	33	67	0	0	X	X	X	–
<i>Cyanocorax chrysops</i>	Plush-crested Jay	40	8	22	70	0	0	X	X	X	–
<i>Hemithraupis guira</i>	Guira Tanager	1	0	0	100	0	0	X	X	–	–
<i>Chlorospingus ophthalmicus</i>	Common Bush-tanager	23	0	0	78	22	0	X	X	–	–
<i>Trogon curucui</i>	Blue-crowned Trogon	3	0	0	100	0	0	X	X	–	–
<i>Euphonia cyanocephala</i>	Golden-rumped Euphonia	B	0	0	0	100	0	X	X	–	–
<i>Euphonia chlorotica</i>	Purple-throated Euphonia	B	0	0	0	100	0	X	X	–	–
<i>Thraupis sayaca</i>	Sayaca Tanager	7	0	29	28	43	0	X	X	–	–
Nectarivores		B	0	50	50	0	0	–	–	–	X
<i>Chlorostilbon lucidus</i>	Glittering-bellied Emerald	B	0	50	50	0	0	–	–	–	X
Bark I		33	3	7	11	0	79	X	–	–	–
<i>Campephilus leucopogon</i>	Cream-backed Woodpecker	B	0	0	0	0	100	X	–	–	–
<i>Dendrocolaptes picumnus</i>	Black-banded Woodcreeper	10	0	0	0	0	100	X	–	–	–
<i>Sittasomus griseicapillus</i>	Olivaceous Woodcreeper	5	0	0	40	0	60	X	–	–	–
<i>Syndactyla rufosuperciliata</i>	Buff-browed Foliage-gleaner	18	11	28	5	0	56	X	–	–	–

<sup>a</sup> Gr: ground, Un: Understory, L: low canopy; M: medium canopy; H: high canopy.

<sup>b</sup> Fru: fruits, Ins: insects; See: seeds; Nec: nectar.

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