Research Article

Habitat structure influences the diversity, richness and composition of bird assemblages in successional Atlantic rain forests

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Abstract

This study evaluated the influence of vegetation structure on bird diversity, guilds, and the richness and composition of species in different successional stages of the subtropical Atlantic rain forest. Much of the land that was formerly agricultural in the Brazilian Atlantic rain forest region is now given over to secondary forests. The habitat structure of these successional forests vary and are influenced by time, historical use and local variables, all of which affect bird assemblies. Sampling of bird species was carried out through audio-visual point counts conducted in forests varying from six years after abandonment to old-growth areas. Forests in which the point counts were conducted were further classified into initial, intermediate and advanced stages according to 11 vegetation structural variables, through cluster analyses. The study found that bird richness and diversity were similar between initial and intermediate stages, but higher in advanced areas. Bird species composition differed between the initial and advanced stages, whereas the guild composition of initial forests differed in both intermediate and advanced stages. Late successional forests had more heterogeneous habitats, and some species and guilds were found only in this stage. However, bird diversity and species and guild composition were similar in intermediate and advanced forests, emphasizing the importance of successional forests for conservation efforts, especially when they are located near old-growth forests and conservation units. The recovery patterns of the successional forests studied indicate a great potential for the natural regeneration of the Atlantic rain forest, at least in areas where slash-and-burn agriculture was the previous landuse.

Keywords: avifauna; habitat modification; secondary forests; vegetation structure.

RESUMO

Este estudo avaliou a influência da estrutura da vegetação sobre a diversidade, riqueza e composição de espécies e guildas de aves em florestas sucessionais na Mata Atlântica subtropical. Grande parte das áreas agrícolas que cobriam as regiões da Mata Atlântica são atualmente florestas secundárias, podendo variar em estrutura de habitat conforme o histórico de uso e variáveis locais, influenciando as assembleias de aves. A amostragem da avifauna foi realizada pelo método áudio-visual em pontos de escuta em florestas com seis anos de regeneração após o abandono a áreas antigas. Florestas em cada ponto de escuta foram posteriormente classificadas em estágios inicial, intermediário e avançado de acordo com 11 variáveis estruturais da vegetação, através da análise de agrupamento. A riqueza e diversidade de aves foram similares entre os estágios inicial e intermediário, mas maiores no estágio avançado. A composição de espécies diferiu somente entre os estágios inicial e avançado, enquanto a composição de guildas do estágio inicial diferiu dos estágios intermediário e avançado. Florestas tardias foram mais heterogêneas em termos de habitat, e algumas espécies de aves e guildas foram registradas somente neste estágio. Todavia, diversidade e composição de espécies e guildas foram similares entre as florestas em estágio médio e avançado, enfatizando a importância das florestas secundárias para fins de conservação, principalmente quando próximas de áreas em estágio avançado e de unidades de conservação. Os padrões de recuperação observados nestas florestas sucessionais indicam o grande potencial de regeneração natural da Mata Atlântica, pelo menos em áreas onde a agricultura de coivara era o uso da terra.

Palavras chave: avifauna, estrutura da vegetação, florestas secundárias, modificação do habitat.

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Introduction

Human disturbance is one of the most significant drivers of habitat change [1]. The use and subsequent abandonment of areas once covered by natural forests start the process of succession. This produces secondary forests which have varied habitat structures, influenced by historical and local variables [2]. In the Neotropics, secondary forests occur widely on former farmland, particularly in areas where slash-and-burn subsistence agriculture has been practiced [3, 4]. Although many animal species need large areas of primary forest for survival [5], secondary forests are important for a wide range of species, especially when they occur close to old-growth forests which serve as population sources [6]. Secondary forests also have seasonally abundant fruit resources which result in temporary increases in frugivore species populations [7]. It has been suggested that these forests play a relevant role in bird conservation because bird species richness recovers more quickly after anthropogenic disturbance than species composition does [8]. Therefore, it is essential that the potential of successional forests as assets in the conservation of subtropical and tropical forest species is better understood [6], not least because they are becoming increasingly widespread [1].

The Brazilian Atlantic rain forest is now highly fragmented with remnants in different successional stages. However, it still retains a considerable portion of its former biodiversity [9], and is known worldwide as a priority area for conservation [10]. Therefore, it is important to know how fauna responds to the habitat modifications imposed by humans, if conservation initiatives focusing on this biome are to be successful. Although many studies have described relationships between habitat structure and bird assemblages and their guilds [11–14], as well as between disturbances or succession and avifauna [8, 12, 15, 16], few studies have been carried out in the Brazilian Atlantic rain forest [17]. In this biome, most remnants of successional forests are highly fragmented within an agricultural matrix [18], where species assemblies are likely to be affected by how the patches are connected [9]. The area where we conducted our study is a mosaic of successional forests which are interconnected. Previously, the matrix had predominantly been slash-and-burn agriculture and, at the time of our study, distinct forest stages were intermingled with old-growth forest and conservation units. The main objective of our study was to test the influence

of vegetation structure on bird assemblages, focusing particularly on bird diversity, richness and the composition of species and guilds in areas of the forest at different successional stages.

Bird abundance and species composition vary in response to different degrees of change in vegetation structure [19]. Considerable variation in species composition may occur along successional gradients, and many species are restricted to either initial or advanced stages [13, 20]. As vegetation structure influences microhabitat, diet, and body size, guilds can be used as predictors of the effects of habitat modification or of the conservation status of forest remnants. Terrestrial insectivores and large canopy frugivores, for example, are sensitive to habitat change [21]. However, factors such as the richness and abundance of birds may be similar in different stages of forest regeneration [15]. Our study therefore examined the influence of habitat structure on bird assemblages in areas at different regeneration stages since slash-and-burn agriculture had been abandoned. Our hypotheses were (1) that successional forests with more heterogeneous habitats have greater bird richness and diversity; and (2) the species and guild composition of bird assemblages differ in different forest successional stages because of the habitat specificity of some species and guilds.

Methods

Study Area

The study area is located in southern Brazil, in the Maquiné River basin (29º35'S, 50º16'W), Maquiné municipality, northeast of the state of Rio Grande do Sul (Fig. 1). This river basin is the southernmost distribution point of the Brazilian Atlantic rain forest *stricto sensu* [22]. The sampling areas were submontane rain forest and were restricted to altitudes between 125 and 450 meters above sea level. The climate is subtropical humid, with a mean annual temperature of 18°C, 1400 to 1800 mm of annual rainfall and no periods of drought.

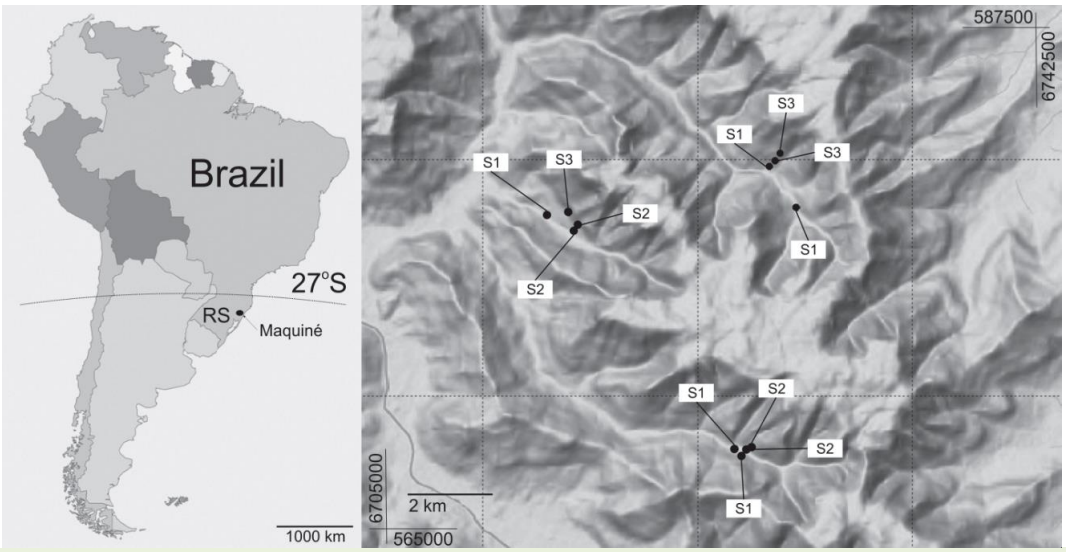

Fig. 1. Maquiné municipality in Rio Grande do Sul (RS) state, Brazil (left), and sample design in three valleys (right). Sampling unit labels are according to the cluster groups that considered 22 structural variables of sampling plots. S1 – structural stage 1: includes three point counts in initial areas and two in intermediate areas (defined according to the abandonment time; see methods); S2 – structural stage 2: includes one intermediate and two advanced; S3 – structural stage 3: includes three in advanced areas.

The landscape is a mosaic of secondary forests in different successional stages, with large areas covered by vegetation in initial stages of regeneration (22% of the land cover in the Maquiné river basin), intermediate stages (35%), and late stages (20%). All the forest stages originated from abandoned slash-and-burn agriculture. Old-growth forest was restricted to deep valleys, and 10% of the area was still used for agriculture [23, 24]. From the original vegetation cover of this river basin, approximately 70% was cleared for agriculture [24] and, at the time of the study, a large portion was regenerating naturally. Further details about the floristic and forest features of distinct successional stages can be found in Zanini *et al.* [23]. See also the results of habitat characterization below.

Sampling and data collection

The survey was carried out in three valleys approximately five km apart. One valley was within a conservation area (*Reserva Biológica da Serra Geral*). Areas were selected according to how long the forest had been regenerating, identified through interviews with local residents regarding the historical use of the land and the date of abandonment [23]. Field expeditions for physiognomic evaluations were also carried out. Sampling was then stratified by valley: sampling areas (three in each valley) were selected according to the date of abandonment (Fig. 1): initial (six to 10 years), intermediate (15 to 22 years) and advanced (more than 40 years). One of the nine sampling areas was an old-growth forest that had not been cleared, but had probably undergone selective logging during the past century.

For the quantitative survey of the avifauna we used the point count method [25] for sampling units (SU). For initial and intermediate stage areas, we undertook one point count, whereas for advanced areas we performed two. Initial and intermediate patches were too small to warrant more than one point count, whereas advanced forests were larger and more heterogeneous in terms of regeneration characteristics. Therefore, we intensified the sampling in such forests in order to better determine the relationship between bird assemblies and all the forest regeneration structures in the region. This design resulted in three SUs for initial stage forests, three for intermediate, and six for advanced, classified according to the date of abandonment. We also reclassified the forest stages according to structural characteristics measured in the field. Each SU had a 20 m fixed radius and the minimum distance between SUs was 100 m. Time spent sampling each point was 10 min. The 12 SUs were surveyed eight times between January and April 2010, resulting in 96 sampling events. Sampling was carried out between January and April because climate events (repeated floods) prevented us from sampling before, although the breeding season (spring/summer) is between September and early March [26, 27] and would be a more favorable time for bird sampling. Between March and April birds are less active, and some species migrate to northern Brazil [26] whereas others can still be found because of altitudinal migration [28]. As a result, new species were registered in the last sampling events leading to an increase in 'rare' species in our data (see data analyses).

Surveys started 15 minutes after dawn and lasted for three hours. Each valley was sampled in one day, and we alternated the sampling sequence of stages within a valley. Each SU was sampled in all possible time intervals in order to take into account the effect of time of day on bird activity. All individuals seen and/or heard were documented, except for those that only flew over the area. The bird assembly was described by recording the number of birds per species for each SU in each sampling event. We used this method in order to compare bird assembly patterns in different stages of successional forests. The data also reflects to what extent each species uses the local resources.

Bird species were further classified into guilds based on food preference, following Willis [29], Motta-Junior [30], Sick [26], Aleixo [17], and Anjos [31], and foraging strata, following Willis [29], Stotz *et al.* [32], Sick [26], and Aleixo. Four strata were considered: ground (up to approximately one meter high),

understory (from one meter to five meters), intermediate (trees between five meters and 15 meters) and canopy [17]. We used scientific nomenclature in accordance with the classifications established by the Brazilian committee of ornithological records [33].

To characterize the habitat and reclassify the SUs into structural stages, each successional area was described according to several vegetation structure variables provided by another study carried out on the same sites [23], which was part of a long-term project on permanent plots. Our SUs were in permanent plots, which were 0.25 ha for the initial and intermediate successional stages and 0.5 to 1 ha for the advanced stages. Randomly placed circular sub-plots of 100 m^2 were used to characterize the vegetation of each SU, with three in each 0.25 ha plot. In these sub-plots, we measured the habitat structural variables of the forest's upper stratum (tree specimens with DBH≥10 cm; DBH = diameter at breast height) and of the intermediate stratum (ligneous specimens with 1 cm<DBH<10 cm). For each stratum, we used 11 structural variables (Table 1). The structural variables were chosen to represent a wide range of vertical structures, tree density, and habitat complexity, measurements used to classify forest successional stages [2]. More detailed descriptions of plant species characterizing successional stages in these and adjacent areas of the Maquiné River basin can be found in Zanini *et al.* [23].

Table 1. Structural variables used to characterize the forest habitat of sampling areas where bird assemblages were described.

Structural variables	Labels	
	Upper stratum	Intermediate stratum (understory)
Individuals.m^2	Uni	Ini
Species.m^2	US	IS
Sum of basal area ($cm^2.m^2$)	Uba	Iba
Variance of basal area	UbaV	IbaV
Mean height (m)	Umh	Imh
Maximum height (m)	Umah	Imah
Height variance	UhV	IhV
Standing dead individuals.m^2	UdeN	IdeN
Basal area of standing dead individuals ($cm^2.m^2$)	UdeB	IdeB
Abundance of zoochorous species.m^2	UzoA	IzoA
Richness of zoochorous species.m^2	UzoS	IzoS

Data analysis

To sort the SUs according to habitat structure, the matrix containing the SUs were described by structural variables and then cluster analyses were carried out, based on the Gower index for similarity between SUs and the incremental sum of squares as criteria for clustering [34]. The significance of clustering groups was tested using the bootstrap resampling method [35, 36]. The resulting groups (structural stages) were used to test for differences in richness, diversity, and the composition of bird

assemblages. The same matrix underwent a principal coordinate analysis (PCA) to summarize the information from the structural variables and in order to describe the structural complexity of each SU and its respective cluster group.

To assess the response of bird species and guilds to changes in specific habitat structural parameters between SUs, we performed a canonical correspondence analysis (CCA) [37]. Structural variables that explained the variation were selected through the stepwise method and further tested by the Monte Carlo permutation method (using 999 random permutations).

Species richness and diversity patterns were compared between each clustering group. For species richness, we used a rarefaction analysis based on the number of records [38], to take into account the effect of differences in sampling effort. Species diversity was compared using the Hill series diversity profile, which correspond to different diversity indexes according to parameter a; from raw species richness (a = 0) to indices that give more weight to dominant species over rare ones [39]. Thus, comparisons between richness and equitability in each cluster group were possible, and the need for an arbitrary diversity index was avoided. Differences in species composition and guilds among cluster groups were tested through a multivariate variance analysis (MANOVA) with randomization (1000 permutations), based on chord distance as a measure of similarity between SUs [40]. We used the software Multiv [41] for PCA, MANOVA, and cluster analysis, PAST 1.84 [42] for rarefaction curves, and R [43] for the CCA and Hill series. In order to assess the influence of locally rare species in the observed patterns, assuming a potential bias of our sampling period, all analyses of the composition of bird species and guilds, richness, and diversity were repeated using the subset of the most frequent bird species (minimum record number = three).

Results

Habitat Structure

The cluster analyses of the SUs described by habitat structural variables revealed three distinct groups (hereafter referred to as structural stages) (see Appendix 1). Stages 1, 2, and 3 had five, four, and three SUs, respectively. Note that this reclassification of structural stages was used for all comparative analyses. Stage 1 comprised initial and intermediate areas (between six and 22 years), stage 2 intermediate and advanced (from 15 to more than 40 years), and stage 3 only advanced areas (one of more than 40 years and two of old-growth forest). This classification did not coincide completely with that defined according to the abandonment date: one SU of 22 years was grouped with initial areas in stage 1, and one SU of more than 40 years, previously considered advanced, was clustered into stage 2.

The PCA of the SUs described by habitat structural variables revealed 62% of explanation in the first two axes (Fig. 2). The first component expresses variation in habitat complexity, distinguishing SUs in initial structural stages from those of late successional stages. Areas on the left side of the scatter diagram represent forests with a higher complexity of habitat structure: upper and intermediate strata with higher individuals, larger basal areas and variances in height and basal area, greater tree richness and abundance in the upper stratum (both total and among zoochorous species), and a greater number (and size) of standing dead individuals sampled in this stratum. The SUs in the right quadrants show lower values for all of these variables, besides an understory with higher values of abundance and richness (total and among zoochorous species) and higher abundance and basal areas of standing dead individuals sampled in the intermediate stratum. The second component shows habitat variations between stages 2 and 3: intermediate/advanced forests (stage 2) showed a higher variance between the individuals' height and the abundance of zoochorous species in the understory, whereas stage 3 showed

larger proportions of total basal areas (for both strata) and a higher variance of basal areas for the upper stratum (due to the presence of bigger trees).

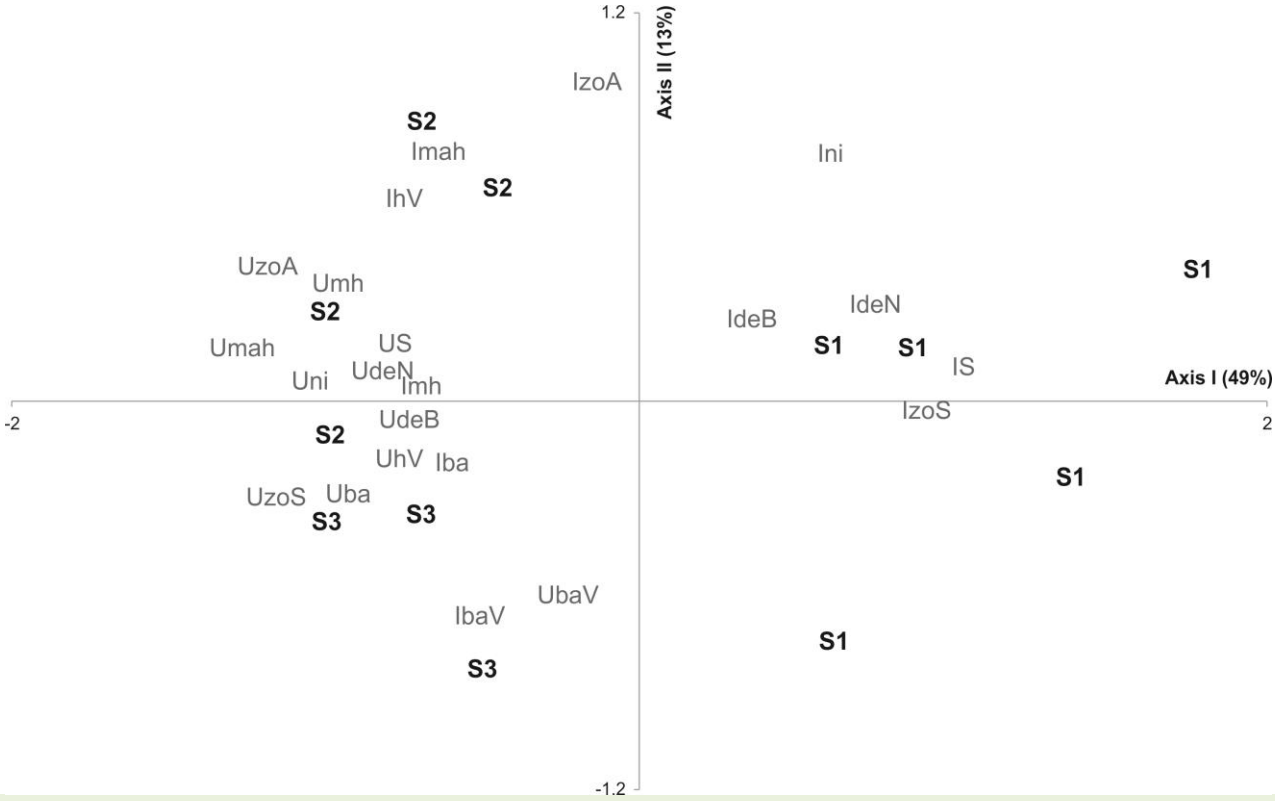

Fig. 2. Scatter diagram of sampling units described by habitat structural variables, represented by the first two ordination axes (PCA). See labels for environmental variables in Table 1. Labels for sampling units correspond to the cluster groups (Appendix 1) – S1: stage 1, S2: stage 2, and S3: stage 3.

Bird richness, diversity and composition

We recorded 86 bird species (there were two we could not identify), distributed among 27 families (Appendix 2). Thraupidae (10 species) and Tyrannidae (nine species) were the best represented families with regard to species number. The CCA showed a significant relationship (P = 0.02) between bird species composition and seven selected structural variables (Fig. 3). The right side of the CCA scatter diagram shows segregation between species restricted to areas with higher structural complexity (for example the Green-throated Euphonia *Euphonia chalybea,* the Short-tailed Antthrush *Chamaeza campanisona,* the Gray-hooded Flycatcher *Mionectis rufiventris,* the Brown Tinamou *Crypturelus obsoletus,* and the Scaly-headed Parrot *Pionus maximiliani*), as well as species found in areas in the initial structural stage (for example the Chestnut-headed Tanager *Pyrrhocoma ruficeps,* the Rufous-browed Peppershrike *Cyclarhis gujanensis,* the Green-winged Saltator *Saltator similis,* and the Gray-bellied Spinetail *Synallaxis cinerascens*). Rarefaction showed that species richness was higher in stage 3, despite the lower number of records generated, compared to stages 1 and 2 (Fig. 4). Confidence intervals between stages 1 and 2 overlapped, indicating that richness did not differ between SUs in these stages. Diversity was also higher in stage 3 but only in comparison to stage 1, as shown throughout the Hill series (Fig. 5). Stage 2 did not differ from any other stage. Multivariate variance analysis revealed

significant differences in bird species composition between stages 1 and 3 (P = 0.02), but not between stages 1 and 2 (P = 0.08) or 2 and 3 (P = 0.16).

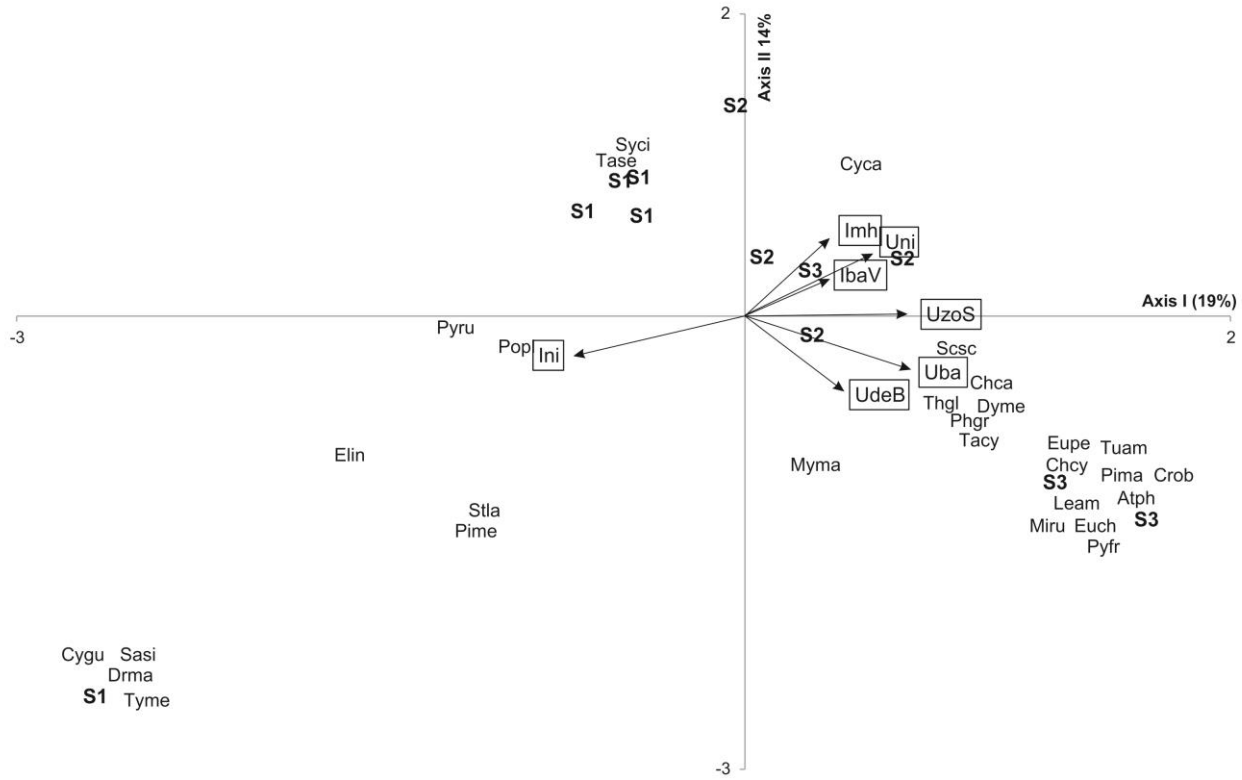

Fig. 3. Ordination diagram of the canonical correspondence analysis (CCA) relating avifauna to habitat structural variables in sampling units. Species with the highest correlation values with the first two axes are shown. Species labels: Atph *Attila phoenicurus*, Chca *Chamaeza campanisona*, Chcy *Chlorophonia cyanea*, Crob *Crypturellus obsoletus*, Cyca *Cyanocorax caeruleus*, Cygu *Cyclarhis gujanensis*, Drma *Drymophila malura*, Dyme *Dysithamnus mentalis*, Elin *Eleoscytalopus indigoticus*, Euch *Euphonia chalybea* , Eupe *Euphonia pectoralis*, Leam *Leptopogon amaurocephalus*, Miru *Mionectes rufiventris*, Myma *Myiodynastes maculatus,* Phgr *Phyllomyias griseocapilla*, Pima *Pionus maximilianus*, Pime *Pipraeidea melanonota*, Popl *Poecilotriccus plumbeiceps*, Pyru *Pyrrhocoma ruficeps*, Pyfr *Pyrrhura frontalis*, Sasi *Saltator similis*, Scsc *Sclerurus scansor,* Stla *Stephanoxis lalandi,* Syci *Synallaxis cinerascens*, Tacy *Tangara cyanoptera* Tase *Tangara seledon*, Thgl *Thalurania glaucopis*, Tuam *Turdus amaurochalinus*, Tyme *Tyrannus melancholicus.* Labels for environmental variables: first letter corresponds to stratum (U: upper stratum; I: Intermediate); second letter corresponds to structural variables (ni: number of individuals; mh: mean plant height; baV: variance of basal area; zoS: richness of zoochorous species; ba: sum of basal area; deB: basal area of standing dead individuals). Labels for sampling units: S1 - stage 1 (initial/intermediate); S2 - stage 2 (intermediate /advanced); S3 - stage 3 (advanced).

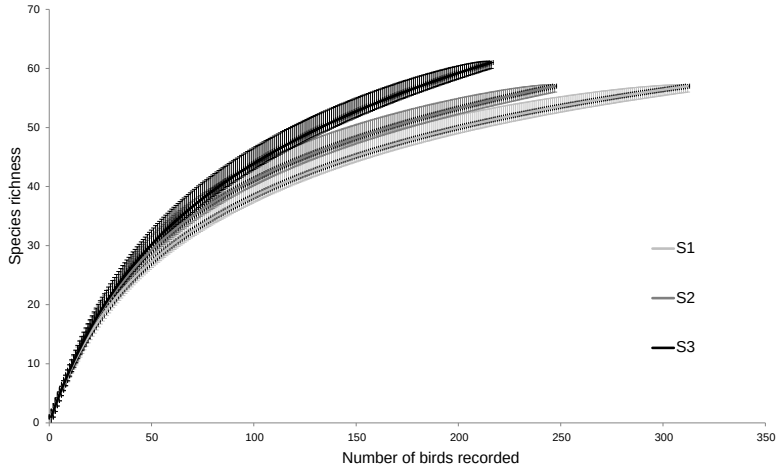

Fig. 4. Rarefaction curves of bird species richness in the three structural stages, defined in cluster analysis. Labels for structural stages: S1 - stage 1 (initial/intermediate); S2 - stage 2 (intermediate/advanced); S3 - stage 3 (advanced).

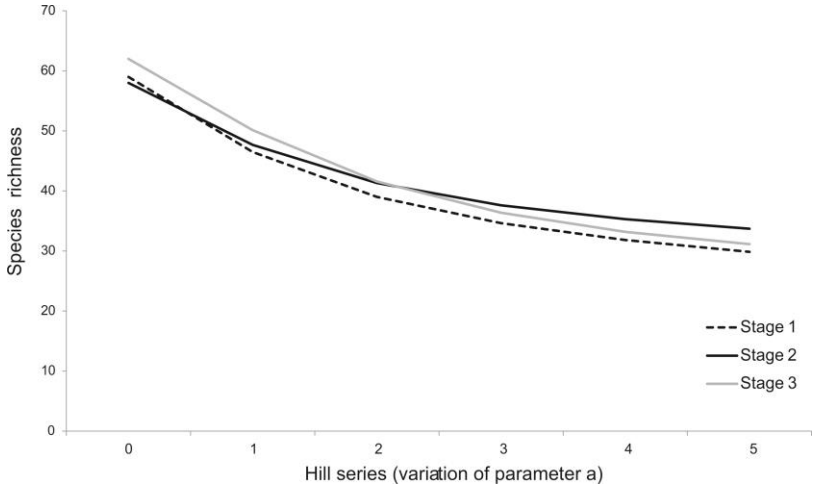

Fig. 5. Diversity profiles for the three structural stages defined in cluster analysis, using the Hill series. Labels for structural stages: S1 - stage 1 (initial/intermediate); S2 - stage 2 (intermediate/advanced); S3 - stage 3 (advanced).

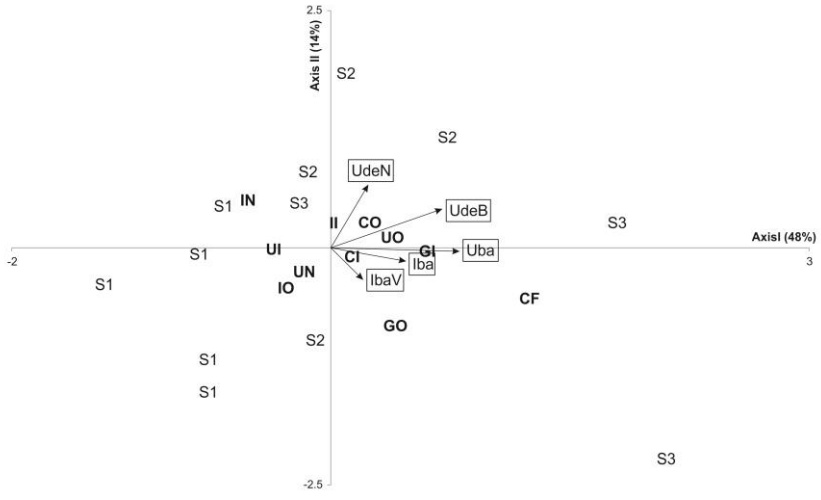

Fig. 6. Ordination diagram of the canonical correspondence analysis (CCA) relating bird guilds (bold) to habitat structural variables (boxes) in sampling units (S1-3). Guilds labels: GI ground insectivore; II intermediate stratum insectivores; UI understory insectivores; CI canopy insectivores; GO ground omnivores; UO understory omnivores; IO intermediate stratum omnivores; CO canopy omnivores; CF canopy frugivores; UN understory nectarivores; IN intermediate stratum nectarivores. Labels for environmental variables: first letter corresponds to stratum (U: upper stratum; I: Intermediate); second letter corresponds to structural variables (deN: standing dead individual; deB: basal area of standing dead individuals; ba: sum of basal area; baV: variance of basal area). Labels for sampling units: S1 - stage 1 (initial/intermediate); S2 - stage 2 (intermediate/advanced); S3 - stage 3 (advanced).

Foraging guilds

We grouped the 86 species into 11 guilds: ground insectivores (four species), intermediate stratum insectivores (six), understory insectivores (25), canopy insectivores (five), ground omnivores (three), understory omnivores (nine), intermediate stratum omnivores (seven), canopy omnivores (17), canopy frugivores (six), understory nectarivores (three), and intermediate stratum nectarivores (one) (see Appendix 2).

Canonical correspondence analysis of guilds showed a significant relationship ($P < 0.001$) with five habitat structural variables (Fig. 6). The diagram distinguishes SUs in initial structural stages from advanced areas according to guild composition, and reflects guild turnover along the first axis, from stages 1 to 3. We did not find guilds exclusive to any single stage, except for canopy frugivores, which were restricted to stage 3. However, the right side of the diagram shows six guilds that were more closely associated with those habitat variables that represent higher structural complexity (stages 2 and 3): canopy frugivores, omnivores and insectivores, ground insectivores and omnivores, and understory omnivores. Guilds grouped on the diagram's left side, such as intermediate stratum omnivores and nectarivores, understory nectarivores and insectivores, were associated with forest areas with lower structural complexity. Results from the MANOVA regarding guild composition revealed significant differences between stage 1 and the other two stages ($P= 0.01$), but not between stages 2 and 3 ($P = 0.34$).

Removing rare bird species

Among the 86 species sampled, 46 species did not reach the minimum of three records (hereafter called rare species). Thus, we reran all analyses with only the remaining 40 species. As expected, diversity and richness results shifted with the removal of rare species: stage 2 became more diverse than stages 1 and 3, but these two stages did not differ from each other, and all three stages did not differ in terms of rarefied richness. However, patterns of species and guild composition were alike. Therefore, MANOVAs of species and guild composition comparing structural stages had the same results across the entire species set: significant differences in species composition between stages 1 and 3 ($P = 0.01$), but not between stages 1 and 2 ($P = 0.06$) or 2 and 3 ($P = 0.28$). In relation to guild composition, we found significant differences between stage 1 and the other two stages ($P = 0.01$), but not between stages 2 and 3 ($P = 0.45$). The general pattern of guilds and species revealed in the CCAs analysis was also similar to that found in the whole species set (Appendix 3).

Discussion

Our study demonstrated that variations in habitat features among structural stages influence patterns of species richness, abundance and composition of bird assemblages in the subtropical Brazilian Atlantic rain forest, similar to what Tews *et al.* [14] observed for several other animal groups (i.e, ants, butterflies, birds, rodents...). Nevertheless, studies focusing solely on avifauna remain scarce for the subtropical Atlantic Forest. More specifically, our study found that richness and diversity were higher in late successional forests (stage 3), where two of the three SUs were old-growth forest that had never undergone clear-cutting, but had probably been affected by selective logging within the past century. We believe that the greater structural heterogeneity found in this successional stage enabled a higher number of species to coexist, probably by providing more diverse resources [44]. Aleixo [17] found that selective logging changed bird assemblage composition, but not richness and diversity in a primary Atlantic rain forest. The intermediate structural stage (stage 2) presented similar species and guild composition and diversity as stage 3 in our study, which could be explained by the landscape context of the areas. The similarity between intermediate and advanced successional stages could increase when

the areas are contiguous [6], and our sampling sites were located inside a mosaic of successional forests, mostly connected to each other by secondary forests at varied successional stages. Furthermore, our study areas were situated close to a large conservation unit area, which may have acted as a source of species and resources.

Features of the landscape, such as those we mentioned above, potentially increase the value of having secondary forests of various ages. Forests in the initial successional stage (less than 20 years of regeneration) may act as foraging sites for some bird species, supplying food resources for diets based on fruits and insects [45, 46]. However, despite the spatial proximity between initial and advanced areas, a few bird species were recorded exclusively in stage 3 areas. Indeed, we found significant differences between the species composition of these stages. Likely, stage 1 areas do not possess the structural complexity required to attract exclusive taxa.

The difference in the guild composition found between the initial structural stage and stages 2 and 3 may reflect guild turnover between stages, probably caused by availability of resource originating from different habitat structures. Understory nectarivores and insectivores, and intermediate stratum omnivores were the guilds more associated with initial and intermediate successional forests. Raman *et al.* [13] also found that understory insectivores and omnivores tend to occur in intermediate stage forests, although they are usually absent in initial successional stages in the Amazon forest [15, 47]. Pinotti *et al.* [48] found that earlier tropical forests present higher total food availability regarding arthropods and fruits, which should influence many insectivorous and frugivorous species. In our study, there was a higher incidence of zoochorous species and a higher number of standing dead trees in the understory of initial areas, which probably influenced the occurrence of those guilds in the initial stage. Also, the understory insectivore was the guild with the most species, presenting many generalists (for example, the Euler's Flycatcher *Lathrotriccus euleri,* the Rufous-capped Spinetail *Synallaxis ruficapilla,* the Buff-browed Foliage-gleaner *Syndactyla rufosuperciliata,* and the Variable Antshrike *Thamnophilus caerulescens).* The predominance of generalist species is likely the reason for the association between this guild and areas with lower structural complexity.

The influence of habitat structure modification on guilds was also demonstrated in naturally occurring gaps in the primary tropical rain forest [49, 50]. Guilds are sensitive to habitat change and some only occur in old-growth forests [21], therefore we were surprised not to find differences in guild composition between stages 2 and 3, especially because we sampled two old-growth forests in stage 3. Additionally, we did not register guilds exclusive of a single stage, with the exception of the canopy frugivores in stage 3. Studies carried out in the Americas and Asia have demonstrated that frugivores and insectivores respond negatively to habitat alteration (reviewed by Gray *et al.* [16]). In studies carried out in the Amazon forest [15, 47], the omnivores' guild was more closely associated with stages 2 and 3. Large-tree users and terrestrial understory birds are also strongly influenced by local forest structure [51], and the terrestrial insectivores are the guild which recovers most slowly in the Amazon rain forest [52].

Our sampling included a transitional period (from the breeding season to the non-breeding season) and, consequently, new species were registered in the later sampling events. The analyses performed without species that were sighted less than three times, which we labeled rare, changed the pattern of bird diversity and richness according to the structural stages: stage 2 became more diverse than the other two stages, and richness did not differ between the stages. Given this result, it is possible to conclude that species that are rare locally seem to be using the late successional forests out of preference [15,53]. However, the patterns of species and guild composition did not change when rare species were removed

from the analyses. Therefore, we can conclude that the number of rare species and the sampling period did not influence the general patterns we have found.

Implications for conservation

This study has provided insights into the potential of successional secondary subtropical rain forests as suitable habitats for bird assemblages. Most forest areas, which were at different stages of post-abandonment regeneration, also had different vegetation structural complexity. However, some areas where regeneration was more advanced were grouped together according to their structure of upper and intermediate strata, which is probably a result of different historical land use, local processes of species colonization, and abiotic conditions [2]. The land use history and context also influences fauna recovery [7].

Although the Brazilian Atlantic rain forest is highly fragmented, it is still seen worldwide as a priority area for conservation [10]. We could not compare our structural stages with undisturbed reference areas, because there were no such areas available near the study site (or their topology simply precludes studies such as ours from be carried out). Nevertheless, our results showed that bird assemblages in secondary forests at an intermediate structural stage were similar to those in advanced structural stages, with regard to diversity and the composition of species and guilds. However, we would like to emphasize that our advanced stages showed some species and guilds that occurred only, or predominantly, in this stage. Such species are highly sensitive to habitat modification, and we assume that they would also occur in primary undisturbed forests.

Conservation units with old-growth forests are very important, but the protection status of secondary forests, especially when surrounded by advanced and old-growth forest areas, needs to be improved. The proportion of secondary vegetation continues to increase, and many old-growth forest birds are found in these regenerating forests [54]. Secondary forests of all ages provide heterogeneous habitats, maximize beta diversity conservation [55], and also act as buffers for cores of older forest remnants.

The impact of the recovery patterns of successional forests on birds (this study) and plants [23] indicate the great potential of the natural regeneration (passive restoration) of the Atlantic rain forest, at least in landscape where slash-and-burn agriculture had previously been practiced. Our study provides baseline data showing that successional secondary subtropical rain forests are important assets for conservation efforts that focus on this biome.

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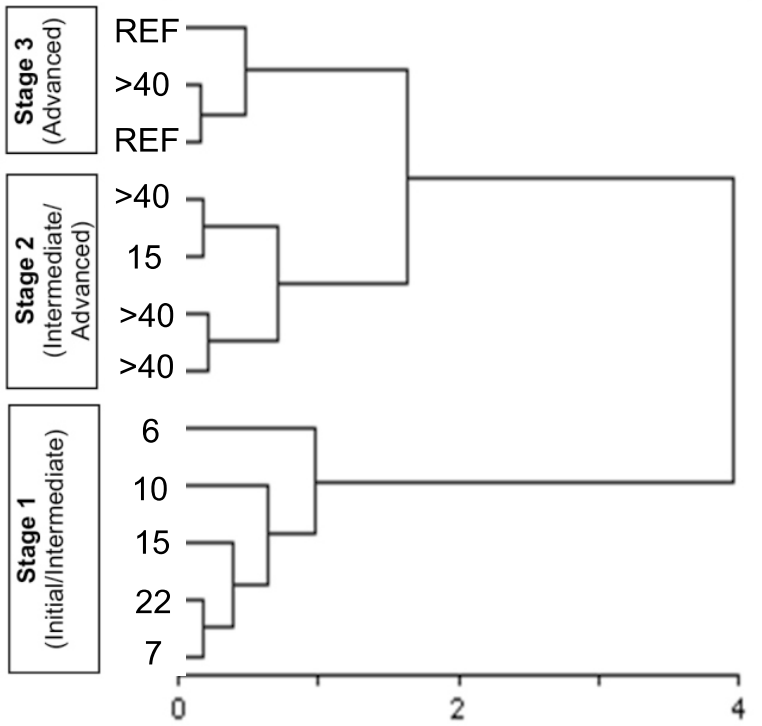
APPENDICES



Appendix 1. Cluster analysis of sampling units (SUs) described by habitat structural variables. The SU labels are defined according to post-abandonment time. Stage 1 comprises initial and intermediate areas (6-22 years), stage 2 intermediate and advanced areas (from 15 to more than 40 years), and stage 3 only advanced areas (more than 40 years and 2 SUs affected only by selective logging).

Appendix 2. Species registered in the listening points and their respective guilds, in each structural stage. Labels for structural stages: stage 1 - initial/intermediate; stage 2 - intermediate/advanced; stage 3 - advanced. Guild labels: GI ground insectivore; II intermediate stratum insectivores; UI understory insectivores; CI canopy insectivores; GO ground omnivores; UO understory omnivores; IO intermediate stratum omnivores; CO canopy omnivores; CF canopy frugivores; UN understory nectarivores; IN intermediate stratum nectarivores.

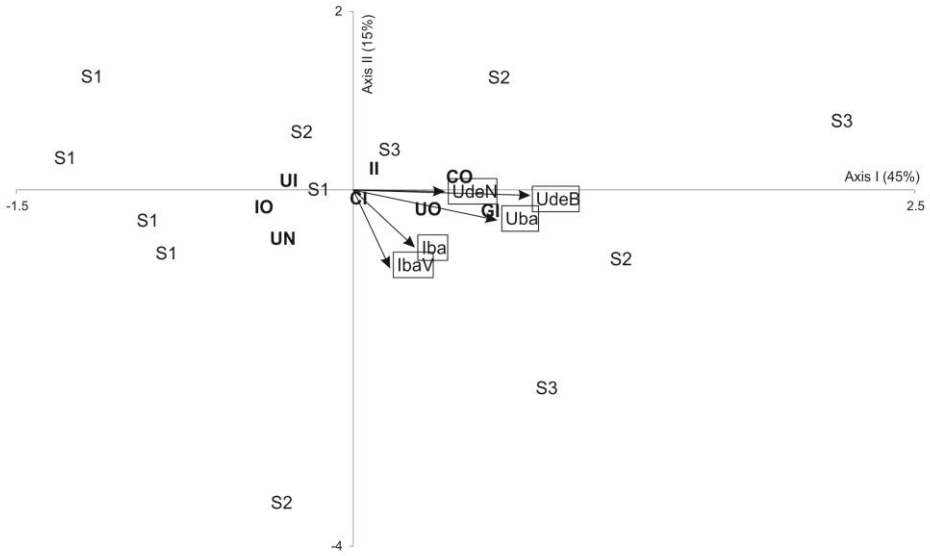
Family	Species	Common name	Stage 1	Stage 2	Stage 3	Guild
Tinamidae						
	Tinamus solitarius (Vieillot, 1819)	Solitary Tinamou	X		X	GI
	Crypturellus obsoletus (Temminck, 1815)	Brown Tinamou			X	GI
Columbidae						
	Leptotila rufaxilla (Richard & Bernard, 1792)	Gray-fronted Dove	X	X		GI
Trochilidae						
	Phaethornis eurynome (Lesson, 1832)	Scale-throated Hermit	X	X	X	UN
	Stephanoxis lalandi (Vieillot, 1818)	Plovercrest	X	X		IN
	Thalurania glaucopis (Gmelin, 1788)	Violet-capped Woodnymph	X		X	UN
	Hummingbird (unidentified)		X	X	X	
Trogonidae						
	Trogon surrucura (Vieillot, 1817)	Surucua Trogon		X	X	CO
	Trogon rufus (Gmelin, 1788)	Black-throated Trogon		X	X	CO
Picidae						
	*Picumnus temminckii (*Lafresnaye, 1845)	Ochre-collared Piculet	X		X	II
	Veniliornis spilogaster (Wagler, 1827)	White-spotted Woodpecker	X	X		UI
	Piculus aurulentus (Temminck, 1821)	Yellow-browed Woodpecker	X		X	II
Psittacidae						
	Pyrrhura frontalis (Vieillot, 1817)	Maroon-bellied Parakeet			X	CF
	Pionus maximiliani (Kuhl, 1820)	Scaly-headed Parrot			X	CF
	Triclaria malachitacea (Spix, 1824)	Blue-bellied Parrot	X	X		CF
Thamnophilidae						
	Dysithamnus mentalis (Temminck, 1823)	Plain Antvireo		X	X	UI
	Thamnophilus caerulescens (Vieillot, 1816)	Variable Antshrike	X	X	X	UI
	Hypoedaleus guttatus (Vieillot, 1816)	Spot-backed Antshrike			X	II

	Batara cinerea (Vieillot, 1819)	Giant Antshrike	X		X	UI
	Mackenziaena severa (Lichtenstein, 1823)	Tufted Antshrike		X		UI
	Myrmoderus squamosus (Pelzeln, 1868)	Squamate Antbird		X		GI
	Pyriglena leucoptera (Vieillot, 1818)	White-shouldered Fire-eye	X	X	X	UI
	Drymophila malura (Temminck, 1825)	Dusky-tailed Antbird	X			UI
Conopophagidae						
	Conopophaga lineata (Wied, 1831)	Rufous Gnateater	X	X	X	UI
Grallariidae						
	Hylopezus nattereri (Pinto, 1937)	Speckle-breasted Antpitta	X	X	X	GI
Rhinocryptidae						
	Eleoscytalopus indigoticus (Wied, 1831)	White-breasted Tapaculo	X			UI
	Scytalopus speluncae (Ménétriès, 1835)	Mouse-colored Tapaculo			X	UI
Formicariidae						
	Chamaeza campanisona (Lichtenstein, 1823)	Short-tailed Antthrush		X	X	GI
Scleruridae						
	Sclerurus scansor (Ménétriès, 1835)	Rufous-breasted Leaftosser	X	X	X	GI
Dendrocolaptidae						
	Sittasomus griseicapillus (Vieillot, 1818)	Olivaceous Woodcreeper	X	X	X	II
	Xiphorhynchus fuscus (Vieillot, 1818)	Lesser Woodcreeper	X	X	X	UI
	Campylorhamphus falcularius (Vieillot, 1822)	Black-billed Scythebill			X	UI
	Lepidocolaptes falcinellus (Cabanis & Heine, 1859)	Scalloped Woodcreeper	X	X	X	II
	Dendrocolaptes platyrostris Spix, 1825	Planalto Woodcreeper	X	X		UI
	Xiphocolaptes albicollis (Vieillot, 1818)	White-throated Woodcreeper		X		UI
Furnariidae						
	Anabacerthia amaurotis (Temminck, 1823)	White-browed Foliage-gleaner		X	X	UI
	Philydor atricapillus (Wied, 1821)	Black-capped Foliage-gleaner		X		UI
	Philydor rufum (Vieillot, 1818)	Buff-fronted Foliage-gleaner	X	X	X	II
	Heliobletus contaminatus (Berlepsch, 1885)	Sharp-billed Treehunter	X	X	X	CI

	Syndactyla rufosuperciliata (Lafresnaye, 1832)	Buff-browed Foliage-gleaner	X	X	X	UI
	*Synallaxis ruficapilla (*Vieillot, 1819)	Rufous-capped Spinetail	X	X	X	UI
	Synallaxis cinerascens (Temminck, 1823)	Gray-bellied Spinetail	X			UI
Pipridae						
	Chiroxiphia caudata (Shaw & Nodder, 1793)	Swallow-tailed Manakin	X	X	X	UO
Tityridae						
	Schiffornis virescens (Lafresnaye, 1838)	Greenish Schiffornis	X	X		UO
	Tityra cayana (Linnaeus, 1766)	Black-tailed Tityra		X		CO
	Pachyramphus polychopterus (Vieillot, 1818)	White-winged Becard	X	X	X	CO
	Pachyramphus validus (Lichtenstein, 1823)	Crested Becard	X	X	X	CO
Platyrinchidae						
	Platyrinchus mystaceus (Vieillot, 1818)	White-throated Spadebill	X	X	X	UI
Rhynchocyclidae						
	Mionectes rufiventris (Cabanis, 1846)	Gray-hooded Flycatcher			X	UO
	Leptopogon amaurocephalus (Tschudi, 1846)	Sepia-capped Flycatcher			X	UI
	Phylloscartes ventralis (Temminck, 1824)	Mottle-cheeked Tyrannulet	X	X	X	CI
	Tolmomyias sulphurescens (Spix, 1825)	Yellow-olive Flycatcher	X	X	X	II
	Poecilotriccus plumbeiceps (Lafresnaye, 1846)	Ochre-faced Tody-Flycatcher	X	X	X	UI
Tyrannidae						
	Phyllomyias virescens (Temminck, 1824)	Greenish Tyrannulet	X	X		CI
	Phyllomyias griseocapilla (Sclater, 1862)	Gray-capped Tyrannulet		X	X	CO
	Attila phoenicurus (Pelzeln, 1868)	Rufous-tailed Attila			X	CI
	Myiarchus swainsoni (Cabanis & Heine, 1859)	Swainson's Flycatcher	X			IO
	Myiodynastes maculatus (Statius Muller, 1776)	Streaked Flycatcher	X		X	CO
	Tyrannus melancholicus (Vieillot, 1819)	Tropical Kingbird	X			CI
	Myiophobus fasciatus (Statius Muller, 1776)	Bran-colored Flycatcher	X			UI
	Lathrotriccus euleri (Cabanis, 1868)	Euler's Flycatcher	X	X	X	UI

Vireonidae						
	Cyclarhis gujanensis (Gmelin, 1789)	Rufous-browed Peppershrike	X			IO
	Vireo chivi (Vieillot, 1817)	Chivi Vireo	X	X		CO
	Hylophilus poicilotis (Temminck, 1822)	Rufous-crowned Greenlet	X	X	X	IO
Corvidae						
	Cyanocorax caeruleus (Vieillot, 1818)	Azure Jay		X		CO
Turdidae						
	Turdus amaurochalinus (Cabanis, 1850)	Creamy-bellied Thrush			X	UO
	Turdus albicollis (Vieillot, 1818)	White-necked Thrush	X	X	X	UO
Parulidae						
	Setophaga pitiayumi (Vieillot, 1817)	Tropical Parula	X	X	X	CI
	Basileuterus culicivorus (Deppe, 1830)	Golden-crowned Warbler	X	X	X	UI
	Myiothlypis leucoblephara (Vieillot, 1817)	White-browed Warbler	X	X	X	UI
Icteridae						
	Cacicus chrysopterus (Vigors, 1825)	Golden-winged Cacique		X	X	CO
Thraupidae						
	Saltator similis (d'Orbigny & Lafresnaye, 1837)	Green-winged Saltator	X			IO
	Saltator fuliginosus (Daudin, 1800)	Black-throated Grosbeak			X	IO
	Pyrrhocoma ruficeps (Strickland, 1844)	Chestnut-headed Tanager	X			UI
	Tachyphonus coronatus (Vieillot, 1822)	Ruby-crowned Tanager	X	X	X	IO
	Lanio melanops (Vieillot, 1818)	Black-goggled Tanager		X	X	UO
	Tangara seledon (Statius Muller, 1776)	Green-headed Tanager	X			CO
	Tangara cyanoptera (Vieillot, 1817)	Azure-shouldered Tanager	X	X	X	CO
	Tangara sp.		X	X	X	
	Pipraeidea melanonota (Vieillot, 1819)	Fawn-breasted Tanager	X	X		CO
	Hemithraupis ruficapilla (Vieillot, 1818)	Rufous-headed Tanager	X	X	X	CO
	Species 1 (unidentified)		X	X	X	
Cardinalidae						
	Habia rubica (Vieillot, 1817)	Red-crowned Ant-Tanager		X	X	UO
Fringillidae						

Euphonia chalybea (Mikan, 1825)	Green-throated Euphonia		X	CF
Euphonia pectoralis (Latham, 1801)	Chestnut-bellied Euphonia		X	CF
Chlorophonia cyanea (Thunberg, 1822)	Blue-naped Chlorophonia	X	X	CF



Appendix 3. Ordination diagram of the canonical correspondence analysis (CCA) relating bird guilds (using eight guilds; 40 species) to habitat structural variables in sampling units. Guilds labels: GI ground insectivore; II intermediate stratum insectivores; UI understory insectivores; CI canopy insectivores; UO understory omnivores; IO intermediate stratum omnivores; CO canopy omnivores; UN understory nectarivores. Labels for environmental variables: first letter corresponds to stratum (U: upper stratum; I: intermediate); second letter corresponds to structural variables (deN: standing dead individual; deB: basal area of standing dead individuals; ba: sum of basal area; baV: variance of basal area). Labels for sampling units: S1 - stage 1 (initial/intermediate); S2 - stage 2 (intermediate/advanced); S3 - stage 3 (advanced).