

Trophic structure and composition of an understory bird community in a succession gradient of Brazilian Atlantic forest

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RESUMO. Estrutura trófica e composição de uma comunidade de aves de sub-bosque em um gradiente de sucessão na Mata Atlântica. O presente estudo investigou a estrutura trófica e a composição de uma comunidade de aves de sub-bosque da Mata Atlântica em um gradiente de sucessão florestal. Três áreas em diferentes estágios de sucessão foram selecionadas em um fragmento florestal de 605 ha, localizado na Bacia do Alto Rio Doce, no sudeste do Brasil. Em cada uma dessas áreas, quatro parcelas de 800m² foram marcadas e cinco redes de neblina foram instaladas em cada parcela, entre os meses de fevereiro a agosto de 2004. As espécies de aves foram agrupadas em seis categorias tróficas de acordo com o seu principal item alimentar. Durante o período amostrado, foram capturados 371 indivíduos pertencentes a 54 espécies de aves. Os insetívoros foram a categoria trófica mais abundante e rica em espécies em todas as áreas estudadas. A floresta secundária mais antiga (80 anos) diferiu significativamente das florestas mais recentes (40 e 20 anos) devido a maior abundância de pequenos insetívoros e a baixa abundância de onívoros e grandes insetívoros. No grupo dos pequenos insetívoros, a composição de espécies diferiu entre a floresta de 80 anos e as de 40 e 20 anos, enquanto que a composição dos onívoros e dos frugívoros não mudou entre as áreas de diferentes idades. Estes resultados sugerem que a área de estudo está em bom estado de conservação e que mesmo as florestas de 40 e 20 anos já estão em um estágio mais avançado de sucessão. Assim, o estágio de sucessão florestal afetou a organização trófica e a composição de espécies nas categorias tróficas, mesmo dentro de uma floresta contínua.

PALAVRAS-CHAVE. perturbação, guildas alimentares, redes de neblina, floresta secundária, floresta tropical.

ABSTRACT. This study compared trophic structure and community composition of the understory Atlantic Forest avifauna in a forest succession gradient. Three areas in different stages of forest succession were selected within a 605 hectare forest fragment, located in the Upper Doce River valley of southeastern Brazil. In each of these areas four 800 m² plots were demarcated and five mist nets were located in each plot, between February and August 2004. Bird species were grouped into six trophic categories according to their main food preferences. We captured a total of 371 birds of 54 species. Insectivores were both the most abundant and the richest trophic category in all study sites. The old-aged secondary forest site (80 years old) differed significantly from the two younger ones (40 and 20 years old) due to the greater abundance of small insectivores and the lower abundance of omnivores and large insectivores. In the small insectivores group, species composition differed between the 80 years old forest and 40 and 20 years old forests; while omnivores and frugivores species composition did not change among different-aged areas. These results suggest that the study area is in good conservation state and that even the 40 and 20 years old forests are already in a more advanced succession stage. Thus, the stage of forest succession affects the trophic organization and species composition within trophic categories, even within a continuous forest.

KEY WORDS. disturbance, feeding guilds, mist nets, secondary forest, tropical forests.

INTRODUCTION

Understory birds are good indicators of disturbance and forest succession in tropical forests since they respond to changes in local vegetation structure (BARLOW *et al.* 2002, PEARMAN 2002). Bird species feed on a wide variety of resources and can be grouped into trophic categories according to their feeding preferences (e.g. WILLIS 1979, KARR *et al.* 1990). Many previous studies have classified birds into trophic categories to examine the relationship between changes in avian community structure and anthropogenic disturbance (DALE *et al.* 2000, WATSON *et al.* 2004, HODGSON *et al.* 2007) and forest succession stage (ALEIXO 1999, BORGES & STOUFFER 1999, PEARMAN 2002). The bird trophic categories or guilds can be altered according to changes in forest and floristic structure during succession (BLANKERPOOR 1991, KELLER *et al.* 2003).

Specialized insectivores and canopy frugivores are usually associated with areas in late successional phases, while granivores, omnivores and generalist insectivores are more abundant in areas of early and middle stages of succession (RAMANN *et al.* 1998, BORGES 2007, GRAY *et al.* 2007). Such findings can provide information on community organization and inform predictions concerning avifauna recolonization in succession areas, facilitating comparisons between communities that differ in species composition. Since animal species conservation plans are usually achieved through habitat management, it is important to understand the relationship between different avian trophic categories and the stages of forest succession.

The Atlantic Forest is one of the most fragmented and endangered tropical forests in the world (MYERS *et al.* 2000, RIBEIRO *et al.* 2009). Furthermore, it supports one of the highest

rates of endemism on the planet (SILVA *et al.* 2004). This biome has 1020 bird species, 188 of which are endemic and 112 are in risk of extinction (MARINI & GARCIA 2005). The upper Doce River valley is a region in southeastern Brazil where the Atlantic Forest is now highly fragmented and most of these fragments are formed by secondary forests (MACHADO & FONSECA 2000, METZGER *et al.* 2009). The only avifaunal studies conducted in this region have been restricted to community and species conservation status assessments (GOERCK 1997, ALEIXO 1999, MACHADO & FONSECA 2000, RIBON *et al.* 2003, ANJOS 2006, FARIA *et al.* 2006, MENDONÇA *et al.* 2009, BANKS-LEITE *et al.* 2010, ANJOS *et al.* 2011). Studies on bird trophic organization within gradients of succession in the tropical rain forests are increasing (STOFFER *et al.* 2006, BARLOW *et al.* 2007, GRAY *et al.* 2007, ANSELL *et al.* 2011, LOURES-RIBEIRO *et al.* 2011), but are rare in the Atlantic Forest. Since it is important to understand how ecological communities are structured in secondary forest, the aim of this research was to compare trophic structure and composition of understory birds in a gradient of forest succession stages in a Brazilian Atlantic Forest fragment.

METHODS

Study sites

Field work was carried out at Estação de Pesquisa e Desenvolvimento Ambiental de Peti (hereafter Peti) (19°52'23" to 19°54'27" S and 43°20'51" to 43°23'28" W), at municipality Santa Bárbara, state Minas Gerais, in southeastern Brazil. This reserve is a 605 ha forest fragment at an altitude of 600-800 m. The region has a marked climatic regime, underscored by a well-defined rainy season from October to March and a dry season from May to September and the mean annual temperature is 21.7° C (ANTUNES 1986).

Peti is located within the Atlantic Forest domain in the upper Doce River valley, with physiognomies of seasonal semideciduous montane forest, although there are patches of savana (NUNES & PREDALLI 1995, LOPES *et al.* 2009). This forest fragment is isolated by a matrix of eucalyptus plantations (*Eucalyptus* spp.), pastures and areas of exposed soil due to the mining that surrounds part of dam hydroelectric power station, managed by Companhia Energética de Minas Gerais (CEMIG). It is a mosaic of secondary forest of different successional stages, because it was logged at different times in the past for charcoal, prior to the establishment of the hydroelectric (NUNES & PREDALLI 1995). After the logging, the area was protected from human activities, allowing a process of natural regeneration (NUNES & PREDALLI 1995).

Three areas in different successional stages, in which the last logging happened in approximately 80, 40 and 20 years ago, were chosen to carry out this study. Old-aged secondary forest (80 years old), designated A (or "Barragem"), had a taller canopy, the largest basal area, the lowest relative density, a floristic composition richer in species and more rare species than other secondary forest stages. Euphorbiaceae was the most important family, especially due to high relative density value of *Aparisthium cordatum*, *Mabea fistulifera* and *Pogonophora schomburgkiana* (LOPES *et al.* 2009). This area also had higher

moisture due to the proximity of the hydroelectric dam spillway and had several access trails where large quantities of bamboo (*Merostachys kunthii*) were founded at the edges (LOPES *et al.* 2009). Middle-aged secondary forest (40 years old), designated B (or "Usina") had a relative density and canopy height intermediate between the 80 years old forest and the 40 and 20 years old forests, although it had the lowest species richness and basal area. Fabaceae was the most important family and the species with major importance value were: *Mabea fistulifera*, *Cupania ludowigii* and *Macherium villosum* (LOPES *et al.* 2009). Young-aged secondary forest (20 years old), designated C (or "Bom Será") had a lower canopy and the highest relative density, although its species richness and basal area were intermediate between the other older areas. Fabaceae was the most important family and the species with major importance value were: *Melanoxylon brauna*, *Pogonophora schomburgkiana* and *Astronium fraxinifolium* (LOPES *et al.* 2009).

A previous study conducted in Peti between the years 2002 and 2004 recorded 231 bird species, belonging to 57 families, of which 33 species were endemic to the Atlantic Forest and one was endemic to the Cerrado biome. This represent 33% of all 682 bird species recorded for the Atlantic Forest of east Brazil (FARIA *et al.* 2006).

Understory birds sampling

Within each of the three areas, four 800 m² plots (10 x 80 m) were marked at least 100 m apart to represent the sampling units (blocks).

Birds were captured with five mist nets (2.5 m height, 12 m length and 32 mm mesh, arranged in a line in each plot. Understory birds were sampled monthly from February to August 2004, from sunrise to noon, until we had sampled a total of 840 net-hours per area (2520 net-hours total). All captured birds were identified with field guides (RIDGELY & TUDOR 1989, 1994, SOUZA 2002) and marked with a numbered aluminum band provided by the Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE/IBAMA) and released. Taxonomic order and scientific names followed the Comitê Brasileiro de Registros Ornitológicos (CBRO 2011).

Bird species were grouped into six trophic categories according to their main food preferences following Willis (1979), KARR *et al.* (1990), ALEIXO (1999), LOPES *et al.* (2005) and MANHÃES *et al.* (2010). The trophic categories considered were: small insectivores (SI) – feed mainly on small insects; large insectivores (LI) – feed mainly on large insects and small vertebrates; frugivores (FR) – feed mainly on fruits and seeds; granivores (GR) – feed on grass seeds; nectarivores (NE) – feed mostly on nectar; and omnivores (OM) – feed on several items that include more than one trophic level. In this study the term trophic structure refers to the number of individuals in each trophic category.

Statistical analysis

Adequate sampling of understory bird communities from different-aged areas was verified by estimating the total number of species according to Jackknife and species accumulation curve (using mist nets, 840 net-hours per area)

using the program EstimateS v.5 (COLWELL 1997).

The G test was applied to testing the hypotheses of significant association between trophic categories (SI, LI, FR, NE, OM) to a particular successional stage, using the number of individuals in each trophic category. One of the assumptions of this test is that 20% of the samples may not have a sampling frequency lower than five (SOKAL & ROHLF 1995). Thus, the granivore trophic category was excluded from the analysis because it presented only two individuals in plot B4.

Species of the most representative trophic categories (SI, OM, FR) were compared among the three areas according to a non-metric multidimensional scaling multivariate analysis (NMDS) (CLARKE 1993). For this analysis, a matrix of similarity was constructed based on the Bray-Curtis Index, using species abundance in each trophic category per plot and area. The strength of ordination is evaluated by a measure of stress, which varies from 0 to 1, and where values between 0 and 0.20 are considered representative of the similarity between pairs of samples (CLARKE 1993).

Differences in species composition within the most representative trophic categories (SI, OM, FR) were assessed using the Analysis of Similarity (ANOSIM) and the contribution

(in similarity percentage) of each species to the differences in the community composition between the areas was ordered by the module SIMPER, with the program PRIMER, as suggested by CLARKE & WARWICK (1994). ANOSIM is a non-parametric permutations test that is analogous to an ANOVA for similarity matrices.

RESULTS

We recorded 371 birds, 54 species and 13 families (Tab. I), and we recaptured 71 individuals (19.14%). Families Thamnophilidae, Pipridae and Tyrannidae were the most representative in all areas. Species accumulation curves showed that the samples were representative of the understory bird community for all areas (Tab. II, Fig. 1). The species most frequently captured was *Pyriglena leucoptera* (VIEILLOT 1818, Thamnophilidae), with 15 individuals in area A, 25 in area B and 17 in area C, followed by *Drymophila ochropyga* (HELLMAYR 1906, Thamnophilidae), with 13 birds in area A, *Platyrinchus mystaceus* (VIEILLOT 1818, Tyrannidae), with 11 in area B, and *Lanio melanops* (VIEILLOT 1818, Thraupidae), with 8 birds in area C.

Table I. The number of registrations of birds in mist nets in three areas of different succession ages in Peti/Minas Gerais, Brazil. Trophic categories codes are: SI (small insectivores), LI (large insectivores), FR (frugivores), GR (granivores), NE (nectarivores), OM (omnivores).

Bird species	Trophic category	Area A (80 years)				Area B (40 years)				Area C (20 years)				Total
		A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4	
Columbidae														
<i>Geotrygon montana</i> (Linnaeus 1758)	FR	0	0	0	0	0	0	0	0	0	1	0	0	1
Trochilidae														
<i>Amazilia lactea</i> (Lesson 1832)	NE	0	1	0	0	0	0	3	1	1	1	0	0	7
<i>Aphantochroa cirrochloris</i> (Vieillot 1818)	NE	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Florisuga fusca</i> (Vieillot 1817)	NE	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Thalurania glaucopsis</i> (Gmelin 1788)	NE	1	0	0	1	1	0	0	0	2	0	0	0	5
<i>Phaethornis pretrei</i> (Lesson & Delattre 1839)	NE	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Phaethornis squalidus</i> (Temminck 1822)	NE	2	0	1	0	1	0	1	0	0	1	1	1	8
Picidae														
<i>Picumnus cirratus</i> (Temminck 1825)	IP	2	0	0	0	0	0	0	0	0	0	0	0	2
Thamnophilidae														
<i>Drymophila ochropyga</i> (Hellmayr 1906)	IP	3	3	1	6	0	1	0	0	0	0	0	0	14
<i>Dysithamnus mentalis</i> (Temminck 1823)	IP	2	0	0	2	1	2	0	2	0	2	0	0	11
<i>Formicivora serrana</i> (Hellmayr 1929)	IP	0	0	0	0	0	0	1	2	0	0	0	0	3
<i>Herpsilochmus atricapillus</i> (Pelzeln 1868)	IP	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Myrmeciza loricata</i> (Lichtenstein 1823)	IP	0	0	1	0	3	3	1	0	3	3	0	0	14
<i>Pyriglena leucoptera</i> (Vieillot 1818)	IG	4	2	5	4	1	6	9	9	6	2	4	5	57
<i>Thamnophilus caeruleus</i> (Vieillot 1816)	IG	0	0	0	0	0	0	1	2	0	0	0	0	3
<i>Thamnophilus ruficapillus</i> (Vieillot 1816)	IG	0	0	0	0	0	0	0	1	0	0	0	0	1
Conopophagidae														
<i>Conopophaga lineata</i> (Wied 1831)	IP	2	0	2	0	0	0	0	2	0	1	0	0	7
Rhinocryptidae														
<i>Eleoscytalopus indigoticus</i> (Wied 1831)	IP	1	0	0	0	0	0	0	0	0	0	0	0	1

Table 1. Continuation.

Bird species	Trophic category	Area A (80 years)				Area B (40 years)				Area C (20 years)				Total
		A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4	
Dendrocolaptidae														
<i>Sittasomus griseicapillus</i> (Vieillot 1818)	IP	1	0	0	3	1	1	1	1	1	2	0	0	11
<i>Xiphorhynchus fuscus</i> (Vieillot 1818)	IP	1	1	1	1	0	1	0	0	0	2	0	0	7
Furnariidae														
<i>Automolus leucophthalmus</i> (Wied 1821)	IG	0	0	0	0	1	0	1	1	1	1	0	0	5
<i>Synallaxis cinerascens</i> (Temminck 1823)	IP	0	0	0	0	2	2	0	0	1	0	1	0	6
<i>Synallaxis ruficapilla</i> (Vieillot 1819)	IP	0	0	0	2	0	0	0	0	0	1	1	0	4
<i>Xenops rutilans</i> (Temminck 1821)	IP	1	0	0	0	0	0	0	0	0	0	0	0	1
Pipridae														
<i>Chiroxiphia caudata</i> (Shaw & Nodder 1793)	FR	1	0	5	1	1	2	1	0	1	3	0	1	16
<i>Ilicura militaris</i> (Shaw & Nodder 1809)	FR	2	0	5	1	2	3	1	1	0	3	0	1	19
<i>Neopelma pallescens</i> (Lafresnaye 1853)	FR	0	0	0	0	0	0	0	4	0	0	0	0	4
<i>Manacus manacus</i> (Linnaeus 1766)	FR	1	0	0	1	0	0	2	2	0	0	0	2	8
Tityridae														
<i>Myiobius atricaudus</i> (Lawrence 1863)	IP	1	0	0	0	0	0	0	0	0	1	0	0	2
<i>Schiffornis virescens</i> (Lafresnaye 1838)	FR	0	0	0	0	0	2	0	0	0	1	0	0	3
Rhynchocyclidae														
<i>Corythopsis delalandi</i> (Lesson 1830)	IP	0	0	0	0	1	1	0	0	0	1	0	0	3
<i>Leptopogon amaurocephalus</i> (Tschudi 1846)	IP	1	0	0	0	1	1	2	0	2	0	0	0	7
<i>Mionectes rufiventris</i> (Cabanis 1846)	IP	3	0	0	0	0	0	0	0	0	0	0	0	3
<i>Poecilatriccus plumbeiceps</i> (Lafresnaye 1846)	IP	1	2	0	0	0	0	0	1	0	0	0	0	4
<i>Tolmomyias sulphurescens</i> (Spix 1825)	IP	1	0	2	1	0	0	0	0	1	0	0	0	5
Tyrannidae														
<i>Camptostoma obsoletum</i> (Temminck 1824)	IP	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Elaenia obscura</i> (d'Orbigny & Lafresnaye 1837)	IP	0	0	0	0	0	0	1	1	0	0	0	0	2
<i>Lathrotriccus euleri</i> (Cabanis 1868)	IP	2	1	1	1	0	0	0	0	1	1	1	0	8
<i>Phaeomyias murina</i> (Spix 1825)	IP	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Platyrinchus mystaceus</i> (Vieillot 1818)	IP	4	1	3	3	5	2	4	0	3	1	1	0	27
Vireonidae														
<i>Hylophilus poicilotis</i> (Temminck 1822)	IP	1	0	0	0	0	0	1	0	0	0	0	0	2
Turdidae														
<i>Turdus albicollis</i> (Vieillot 1818)	ON	0	0	0	0	1	0	1	1	0	0	2	0	5
<i>Turdus leucomelas</i> (Vieillot 1818)	ON	0	0	0	0	0	0	1	1	0	0	1	1	4
<i>Turdus rufiventris</i> (Vieillot 1818)	ON	0	0	0	0	0	0	1	2	0	0	1	0	4
Coerebidae														
<i>Coereba flaveola</i> (Linnaeus 1758)	NE	0	0	0	0	0	0	0	1	0	0	0	0	1
Thraupidae														
<i>Lanio melanops</i> (Vieillot 1818)	IP	2	0	1	2	0	1	1	3	1	5	0	2	18
<i>Saltator similis</i> (d'Orbigny & Lafresnaye 1837)	IP	0	0	0	1	0	0	0	1	1	0	1	0	4
<i>Tachyphonus coronatus</i> (Vieillot 1822)	FR	3	0	1	0	0	0	1	0	1	2	3	0	11
<i>Tangara cayana</i> (Linnaeus 1766)	IP	0	0	1	0	0	0	0	0	0	0	0	0	1
Emberezidae														
<i>Sporophila nigricollis</i> (Vieillot 1823)	GR	0	0	0	0	0	0	0	2	0	0	0	0	2
Parulidae														
<i>Basileuterus culicivorus</i> (Deppe 1830)	IP	0	0	0	1	0	3	0	0	1	0	0	1	6
<i>Basileuterus flaveolus</i> (Baird 1865)	IP	0	0	0	0	0	2	1	0	2	0	0	1	6
<i>Basileuterus hypoleucus</i> (Bonaparte 1830)	IP	3	2	2	2	3	1	2	2	2	1	0	1	21
<i>Geothlypis aequinoctialis</i> (Gmelin 1789)	IP	0	0	0	0	1	0	0	0	0	0	0	0	1

Table II. Summary of abundance (number of individuals), species richness (number of species), and richness species estimated (according to Jackknife) in three areas of different succession ages in Peti/Minas Gerais, Brazil.

Forest category	Abundance	Richness	Richness estimated
A (80 years)	125	32	34.9 (± 1.9)
B (40 years)	146	43	44.9 (± 1.9)
C (20 years)	100	32	32

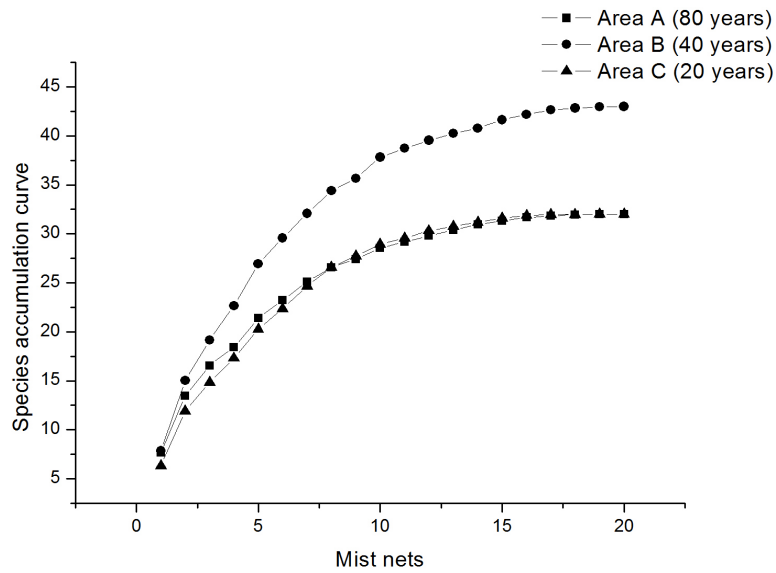


Figure 1. Species accumulation curve per mist net (840 net-hours per area) from three areas of different succession ages in Peti/Minas Gerais, Brazil.

Trophic structure differed significantly among the three areas (G Test, $G = 17.942$, $df = 8$, $p = 0.022$) (Fig. 2). These differences were found between areas A and C (Test G, $G = 15.90$, $df = 4$, $p = 0.003$). Between A and B we found a marginal value (G Test, $G = 9.173$, $df = 4$, $p = 0.057$), but not between B and C (G Test, $G = 2.484$, $df = 4$, $p = 0.648$) (Fig. 2). Among the six trophic categories, small insectivores were the most abundant in all areas (Fig. 2). Granivores were present only in plot B4, where grass cover was about 40%.

The non-metric multidimensional scaling analysis (NMDS) and the Analysis of Similarity (ANOSIM) based on species composition and abundance of small insectivores (SI) suggests that the study area is divided into two groups (Global $R = 0.337$; $p = 0.003$), which one group consisting of area A and the second of areas B and C, which did not differ. On the other hand, the species composition of frugivore (FR) and omnivore (OM) were not separated in groups, being similar among the three study areas (Tab. III, Fig. 3).

Twenty species of small insectivores were responsible for the dissimilarity between areas A and B, 17 species were responsible for the dissimilarity between areas A and C (see Tab. IV for species that contributed to these differences).

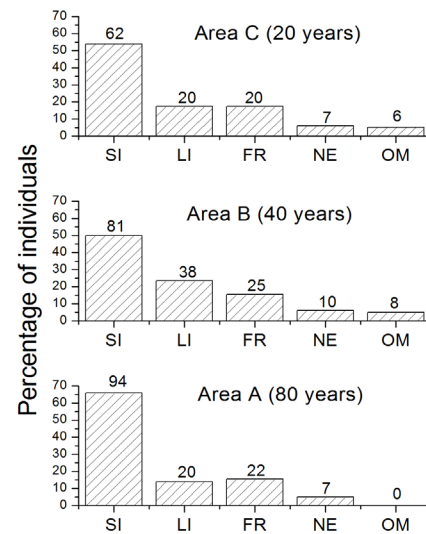


Figure 2. Proportion of individual birds recorded in trophic categories between areas of different succession ages (G Test, $G = 17.942$, $df = 8$, $p = 0.022$). Trophic categories codes are: SI (small insectivores), LI (large insectivores), FR (frugivores), GR (granivores), NE (nectarivores), OM (omnivores). The number above the bars corresponds to the number of individuals in each trophic category.

Table III. Results from analysis of similarity (ANOSIM) between areas of different succession ages by using species composition and abundance of each trophic category (small insectivores, large insectivores and frugivores). ANOSIM was conducted on the similarity matrix based on the Bray-Curtis similarity index.

Trophic categories	Similarity between areas	R	P
Small insectivores	A - B	0.813	0.029
	A - C	0.573	0.029
	B - C	0.063	0.343
Large insectivores	A - B	0.672	0.029
	A - C	- 0.010	0.571
	B - C	0.219	0.143
Frugivores	A - B	- 0.125	0.857
	A - C	- 0.177	0.914
	B - C	- 0.052	0.629

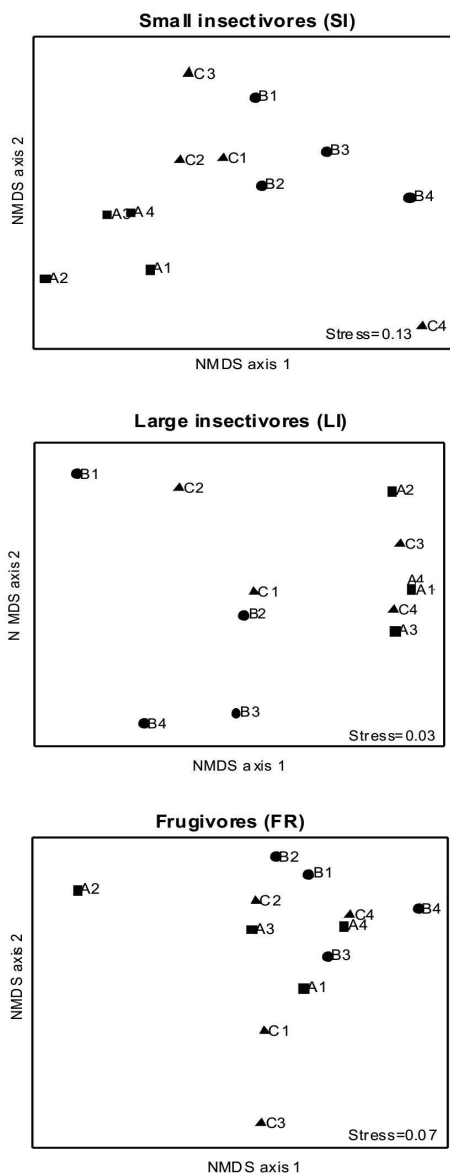


Figure 3. Ordination of areas of different succession ages based on a non-metric multidimensional scale (NMDS), using data on bird abundance in each trophic category (small insectivores, omnivores and frugivores). Areas of different ages of succession codes are: Old-aged secondary forest (A1, A2, A3, A4), middle-aged secondary forest (B1, B2, B3, B4), young-aged secondary forest (C1, C2, C3, C4).

Table IV. Small insectivores species that consistently made the highest contributions to between-areas community dissimilarity (SIMPER).

Average dissimilarity	Species	% Contribution	% Cumulative
	Small insectivores		
A–B = 61%	<i>D. ochropyga</i>	9.07	9.07
	<i>M. loricata</i>	5.86	14.94
	<i>L. euleri</i>	5.46	20.39
	<i>T. sulphurescens</i>	4.85	25.25
	<i>L. amaurocephalus</i>	4.69	29.93
	<i>L. fuscus</i>	4.64	34.57
	<i>C. lineata</i>	4.50	39.08
	<i>S. cinerascens</i>	4.33	43.41
	<i>B. flaveolus</i>	4.21	47.62
	<i>D. mentalis</i>	3.98	51.60
A–C = 63%	<i>D. ochropyga</i>	11.38	11.38
	<i>P. mystaceus</i>	6.76	18.14
	<i>B. flaveolus</i>	6.13	24.27
	<i>M. loricata</i>	5.75	30.02
	<i>L. fuscus</i>	5.64	35.67
	<i>C. lineata</i>	5.08	40.75
	<i>T. melanops</i>	4.97	45.72
	<i>T. sulphurescens</i>	4.91	50.63
	<i>P. mystaceus</i>	8.45	8.45
	<i>M. loricata</i>	6.82	15.28
B–C = 54%	<i>T. melanops</i>	6.29	21.57
	<i>S. cinerascens</i>	5.90	27.46
	<i>B. hypoleucus</i>	5.86	33.32
	<i>D. mentalis</i>	5.26	38.58
	<i>L. amaurocephalus</i>	5.00	43.58
	<i>B. culicivorus</i>	4.99	48.57
	<i>S. griseicapillus</i>	4.51	53.08
	Large insectivores		
A–B = 41%	<i>P. leucoptera</i>	39.86	39.86
	<i>A. leucophthalmus</i>	36.21	76.07
	<i>T. caerulescens</i>	17.52	93.59
	<i>T. ruficapilla</i>	6.41	100.00
A–C = 19%	<i>P. leucoptera</i>	52.43	52.43
	<i>A. leucophthalmus</i>	47.57	100.00
	<i>P. leucoptera</i>	48.91	48.91
B–C = 33%	<i>A. leucophthalmus</i>	22.37	71.28
	<i>T. caerulescens</i>	21.01	92.29
	<i>T. ruficapilla</i>	7.71	100.00
	Frugivores		
A–B = 59%	<i>I. militaris</i>	22.48	22.48
	<i>C. caudata</i>	22.29	44.77
	<i>M. manacus</i>	16.77	61.54
	<i>T. coronatus</i>	14.70	76.24
	<i>S. virescens</i>	12.59	88.83
	<i>N. pallescens</i>	11.03	99.86
	<i>G. montana</i>	0.14	100.00
A–C = 63%	<i>T. coronatus</i>	32.12	32.12
	<i>I. militaris</i>	23.06	55.18
	<i>C. caudata</i>	21.92	77.10
	<i>M. manacus</i>	15.39	92.48
	<i>G. montana</i>	3.83	96.32
	<i>S. virescens</i>	3.68	100.00
	<i>T. coronatus</i>	22.78	22.78
B–C = 62%	<i>I. militaris</i>	21.25	44.03
	<i>C. caudata</i>	15.84	59.87
	<i>M. manacus</i>	15.12	74.99
	<i>S. virescens</i>	11.68	86.67
	<i>N. pallescens</i>	10.02	96.70
	<i>G. montana</i>	3.30	100.00

DISCUSSION

This study showed that trophic structure of understory birds at Peti differed along the gradient of forest succession and some trophic categories of understory birds would be more associated to the stage of forest succession than others. The 80 years old forest differed from the 40 and 20 years old forests due to the greater abundance of small insectivores and the lower abundance of omnivores and large insectivores. This result is consistent with the study of GRAY *et al.* (2007) that analyzed data from 57 published studies that investigated the response of tropical bird to forest disturbance and found that insectivore and frugivore abundance decreased and granivore abundance increased following disturbance. Similarly, birds of different foraging guilds were affected by forest disturbance in eastern Tanzania with ground insectivores most adversely affected (NEWMARK 2006). In the non-disturbed area, insectivores comprised 29%, while in the low and moderately disturbed areas, they represented 13% and 15%, respectively (NEWMARK 2006). Thus, some studies have related changes in the trophic structure of understory birds to forest succession age (BLANKESPOOR 1991, RAMAN *et al.* 1998) and to forest disturbance (BARLOW *et al.* 2007, BORGES 2007).

Trophic structure of understory birds at Peti was primarily composed by insectivorous species. This trophic category is often the most abundant and species rich in many different types of habitat, such as Cerrado (PIRATELLI & BLAKE 2006, MANICA *et al.* 2010), Amazon Forest (TERBORGH *et al.* 1990, LAURANCE 2004) and Atlantic Forest (GOERCK 1997, LOURES-RIBEIRO *et al.* 2011). Most of the small insectivores recorded are dependent on forested habitats (MALDONATO-COELHO & MARINI 2000, FARIA *et al.* 2006) and are relatively sensitive to environmental disturbance (STOTZ *et al.* 1996). Also, insectivorous species have always been reported as the most sensitive group in the Neotropics (STOUFFER *et al.* 2006, BARLOW *et al.* 2007, BANKS-LEITE *et al.* 2010) and specialized insectivorous bird are more closely associated with primary forest (BORGES 2007).

In this study was possible to observe that small insectivorous species composition and abundance changed with the age of forest succession. These species could have been affected by the changes in vegetation structure across areas with different successional stages. It has already been shown that insectivore abundance is indirectly associated with vegetation characteristics (CRAIG & BEAL 2001, GABBE *et al.* 2002) and is very sensitive to several types of disturbance, as habitat loss and habitat fragmentation (HAUGAASEN *et al.* 2003, LAURANCE 2004, BANKS-LEITE *et al.* 2010). However, MANHÃES & DIAS (2011) concluded that spatial distribution of understory insectivorous birds is better explained by habitat type rather than the presence of prey. The three different-aged areas were about 1500 meters away from each other in a straight line, located in a reserve comprising 605 hectares of continuous forest. So, these data show that the replacement in species composition occurs over relatively short distances, although the distance itself is not the main reason for this variation.

The greatest abundance of large insectivores was found

in 40 years old forest and they were represented by three species: *Myrmeciza loricata* (LICHTENSTEIN 1823, Thamnophilidae), *Pyriglena leucoptera* and *Thamnophilus ruficapillus* (VIEILLOT 1816, Thamnophilidae). These species depend on forested habitats (MALDONATO-COELHO & MARINI 2000), but are less sensitive to environmental disturbance (STOTZ *et al.* 1996), as they are mostly found in habitats altered by human activity, such as early secondary forest. *Pyriglena leucoptera* was the most abundant species in three areas in different successional stages. Since it is an army-antfollower, its home range depends heavily on the dynamic distribution of its food resources (HANSBAUER *et al.* 2008, FARIA & RODRIGUES 2009). Because these small insects are dispersing over large areas in different habitat types, *P. leucoptera* is probably compelled to follow them at large scales compared to the other species (BOSCOLO & METZGER 2009).

The greatest abundance of omnivores was found in the 40 and 20 years old forests and the composition of species was similar among three areas. This trophic category was represented by eleven species and most of these species are less sensitive to environmental disturbance, being more abundant in early successional stages (JOHNS 1991, BORGES & STOUFFER 1999). Omnivores are correlated to the abundance of shrubs, tending to be favored by disturbed habitats (MOTTA-JUNIOR 1990). Granivores were found only in stands at early stages of succession, where high densities of grasses and shrubs were recorded. This trophic category is more abundant and species rich in early successional stages (JOHNS 1991, BORGES & STOUFFER 1999) and are associated with open areas and grasses composition (BLAKE *et al.* 1990, SICK 1997). GRAY *et al.* (2007) investigated the response of bird foraging guilds to different intensities of forest disturbance and found that the abundance and species richness of granivores increased after disturbance.

Frugivores were equally abundant due to the similarity in composition of species in different successional stages. *Chiroxiphia caudata*, *I. militaris* and *M. manacus* were the most abundant species in three areas, although the capture proportions were different. However, other studies have shown that Pipridae feed on native plants in the understory as Melastomataceae, common in early secondary forest (LOISELE & BLAKE 1994, BORGES & STOUFFER 1999). This is probably due to different criteria to categorize the stages of regeneration. For example, the young secondary forest of this study (20 years old) corresponds to the oldest secondary forests in the Brazilian Amazon (BORGES 2007). Thus, several studies have shown that understory frugivores and nectarivores are more abundant in young secondary forests, because they present more plants with soft fruits, like Melastomataceae and Rubiaceae to frugivores (ANDRADE & RUBIO-TORGLER 1994, BERSIER & MEYER 1994), and attractive flowers as *Heliconia* to nectarivores (ANDRADE & RUBIO-TORGLER 1994, PEARMAN 2002).

These results suggest that the study area is in good conservation state and the 40 and 20 years old areas are already in a more advanced succession stage. Our results also show that areas in different stages of succession, even in a continuous forest, have a different trophic organization and species composition in the bird community. Since the trophic groups of birds respond differently to changes in the gradient of vegetation

succession, is likely that the availability of food resources would be also affected by the process of forest regeneration, which deserves to be investigated in further studies.

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