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A BIOACÚSTICA COMO FERRAMENTA ADICIONAL PARA O ESTUDO DA ESTRUTURA E DINÂMICA DE UMA COMUNIDADE DE AVES EM MATA ESTACIONAL SEMIDECIDUAL

São Carlos – SP
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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos/SP, como parte dos requisitos necessários para obtenção do título de Doutora em Ciências, área de concentração Ecologia e Recursos Naturais.

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Resumo

O estudo da estrutura e dinâmica de comunidades de aves em fragmentos florestais é de grande importância para a conservação dos mesmos. A classificação da comunidade de acordo com suas categorias tróficas e estratos é uma forma eficiente de se acessar a o estado da mata, visto que a sensibilidade à fragmentação varia de uma espécie para a outra de acordo com seus hábitos alimentares, área de forrageamento e estratos ocupantes, elementos que podem ser perdidos ou alterados na redução de uma porção original. Adicionalmente, as manifestações acústicas de uma comunidade, combinadas com esses dados ecológicos, podem nos fornecer informações adicionais. Visto que as aves que cantam em uma mesma faixa de frequência estão sujeitas a interferência acústica se estiverem vocalizando no mesmo intervalo temporal, os horários de vocalização e variáveis vocais podem refletir padrões de distribuição das espécies. Além disso, a composição acústica de um habitat fragmentado, está sempre sujeita a alterações, visto que espécies generalistas tendem a se estabelecer ambientes mais degradados com altas proporção de áreas de borda da mata. Com isso, o objetivo deste trabalho foi de se acessar as dinâmicas de distribuição de uma assembleia de aves de uma mata semidecidual em relação à ecologia das espécies e variáveis vocais. A coleta se deu através de pontos de escuta de 15 minutos durante um ano e todos os pontos foram gravados. A presença de espécies sensíveis e especialistas como *Habia rubica*, *Pyriglena leucoptera* e *Crypturellus undulatus*, indicou estar o fragmento em estado de conservação adequado para abrigar essas espécies. A baixa abundância de espécies generalistas, como *Tangara sayaca* e *Tyrannus melancholicus*, também contribuem para essa definição, visto que tendem a se estabelecer em áreas mais degradadas. A partir da caracterização da comunidade de acordo com três variáveis vocais espectrais e estratos ocupantes, verificamos que espécies de co-ocorrência significativa nos pontos de escuta possuem dispersão tanto nas características vocais quanto nos estratos ocupados. Adicionalmente, também realizamos um estudo de caso da ocorrência e dinâmicas de atividade vocais entre duas espécies (*Myiothlypis flaveola* e *Basileuterus culicivorus*) que foram observadas vocalizando sequencialmente. A co-ocorrência significativa e estratégias para evitar a sobreposição dos cantos sugerem que a relação interespecífica seja vantajosa para pelo menos uma das espécies. Esses resultados nos mostram que os sinais acústicos têm importância fundamental na distribuição das espécies em um fragmento e podem ser uma ferramenta a mais para a verificação da estrutura e qualidade dos habitats.

Palavras-chave: Nicho acústico, Neotropical, Comunidades, Interação interespecífica.

Abstract

Understanding the dynamics and structure of bird communities in forest fragments provide us important data for conservation. The classification of the community regarding trophic categories and strata is one of the most effective methods to access the status of a given area, whereas sensitivity to fragmentations varies among species regarding their foraging habits, foraging area and occupying strata, and these elements could be lost or altered in smaller fragments. Additionally, the acoustic features of a given community associated with ecological data can provide further information. Since birds that sing in the same frequency band undergo acoustic interference when singing in the same temporal interval, the time of singing and vocal characteristics may reflect distribution patterns of species. Furthermore, because generalist species tend to establish in more fragmented areas, the acoustic community of these habitats tends to suffer constant alterations. Thus this study aimed to access the dynamic and distribution of a bird assemblage in a semi-deciduous forest regarding the ecology and vocal characteristics of the species. Data collection occurred during a year through point counts method, and recordings were made for every sample. The presence of sensitive and specialists' species such as *Habia rubica*, *Pyriglena leucoptera*, and *Crypturellus undulatus*, and the low abundance of generalists' species such as *Tangara sayaca* and *Tyrannus melancholicus* indicated that this area, that was not previously sampled, presents suitable conservation status to harbor these species. With community characterization based on three vocal spectral variables and occupying strata, we verified that species with significant co-occurrence across the point counts, present more dispersed songs and strata. Also, we carried out a case study regarding the occurrence and vocal activity dynamics of two species (*Myiothlypis flaveola* and *Basileuterus culicivorus*) that were registered singing shortly after the other. The significant co-occurrence and the strategies to avoid song overlap suggest that the interspecific interaction may benefit at least one of the species. These results demonstrate that the bioacoustics have fundamental importance regarding species distribution in a fragmented area and could be used as an additional tool to assess the structure and status of habitat.

Keywords: Acoustic niche, Neotropical, Communities, Interspecific interactions.

SUMÁRIO

1. Introdução Geral

1.1 Fragmentação ambiental e a comunidades de aves

A perda ambiental e a consquente fragmentação do habitat são resultados de processos históricos de perturbação de vegetações originais, onde inúmeros fatores interagiram ao longo do tempo (MacArthur & Whitmore 1979; Whitmore 1997). A fragmentação florestal é uma das principais ameaças à biodiversidade nos neotrópicos (Whitmore 1997; Primack & Rodrigues 2001; Tabarelli & Gascon 2005), e, na maioria das vezes, é decorrente de atividades antrópicas, onde a vegetação original é substituída por áreas urbanas ou destinadas à agricultura (Vitousek et al. 1998; Foley et al. 2005; Venter et al. 2006;). A modificação ou remoção de grandes áreas de vegetação natural resulta em um mosaico de fragmentos isolados ao longo da paisagem, cada qual com sua estrutura e dinâmica dependentes do histórtico de perturbações, tamanho da área, forma, entorno e grau de isolamento da porção original (MacArthur & Whitmore 1979; Gascon et al. 1999; Villard et al. 1999; Gimenes & Anjos 2003; Kupfer et al. 2006). Por serem menores do que a vegetação original, fragmentos florestais abrigam uma riqueza menor de espécies e populações menores, podendo comprometer a regeneração natural e a sustentação dos mesmos (Harris 1984; Bierregaard et al. 2001; Tabarelli & Gascon 2005). Além disso, a não necessária perda em área mas sim de componentes ambientais (e. g. espécies e estratos vegetais), pode tornar o habitat inóspito para espécies mais sensíveis (Bender et al. 1998; Cerqueira et al. 2003). Fatores como dependência florestal (e consequentemente a impossibilidade de sobrevivência em bordas), intolerância a mudanças ambientais dentro dos fragmentos, tamanho populacional naturalmente baixo, capacidade de dispersão limitada, baixas taxas de sobrevivência anual, alto nível de especialização e necessidade de grandes áreas devido ao tamanho corporal, podem caracterizar espécies como vulneráveis ou sensíveis (Willis 1974; Leck 1979; Karr 1990; Aleixo & Vielliard 1995; Bierregaard & Stouffer 1997; Alexandrino et al. 2016).

O grupo das aves é um dos mais bem estudados do reino animal, e muitas informações sobre sua ecologia estão disponíveis na literatura (Verner 1981; Morrison 1986; Gregory & Strien 2010). Por este motivo, é possível delinear os níveis de sensibilidade das espécies de acordo com suas categorias tróficas, ocupação de estrato, tamanhos populacionais e locais de nidificação. Portanto, a presença, ausência e abundância de determinadas espécies podem refletir a qualidade de um fragmento florestal (Gentilli 1992; Tellería et al. 1992; Marques & Anjos 2014). Além disso, pelo fato da maioria das aves possuir hábitos diurnos e vocalizar com frequência, são um grupo de fácil detecção e amostragem em campo (Gardner et al. 2008), são excelentes bio indicadoras, e são constantemente utilizadas em estudos para avaliação ambiental (i. e. Aleixo & Vielliard 1995; Stotz et al. 1996; Gimenes & Anjos 2003; Marques & Anjos 2014).

Espécies que necessitam de hábitats e itens alimentares específicos são mais diversas e abundantes em ambientes bem preservados, e, paralelamente, espécies generalistas tendem a se estabelecer em fragmentos mais degradados (Cerqueira et al. 2003; Devictor et al. 2008; Carrara et al. 2015). Portanto, o levantamento da comunidade de aves em uma área e a posterior classificação das espécies de acordo com suas categorias tróficas e estratos é uma das formas mais eficientes de se acessar a qualidade ambiental (Gray et al. 2007). Por exemplo, a presença de insetívoros foliares dependentes, como *Synallaxis ruficapilla*, indica a presença de microhabitats encontrados em áreas maiores e ambientes bem preservados; ou a presença de frugívoros terrestres de grande porte, como *Crypturellus undulatus* e *Penelope superciliaris*, indica a disponibilidade e distribuição de alimentos ao longo do ano; ou a presença de espécies seguidoras de formiga, como *Pyriglena leucoptera*, indica a possível presença de determinadas espécies de formiga e área suficiente para forrageamento (Willis & Oniki 1978), sendo uma das primeiras categorias a desaparecer com a fragmentação. Alternativamente, a presença e abundância de algumas espécies podem indicar a baixa qualidade de conservação de uma área, como *Pitangus sulphuratus*, *Tyrannus melancholichus* e *Tangara sayaca* apresentam uma alta plasticidade e capacidade de se adaptarem em ambientes antropizados, e, com isso tendem, a aumentar suas distribuições geográficas e se instalar aonde as vegetações originais foram suprimidas (Sick 1997).

1.2 Composição acústica da comunidade

A estrutura e dinâmica de comunidades geralmente são estudadas de acordo com características em relação ecologia e morfologia das espécies presentes (Emerson & Gillespie 2008), no entanto, características vocais podem estar associadas (Groning & Hochkirch 2008; Cardoso & Price 2010), e dados bioacústicos de uma determinada comunidade podem nos fornecer importantes para a conservação das espécies e dos ambientes (ver Laiolo 2010). A comunicação acústica das aves ocorre através de cantos e chamados (Catchpole & Slater 2008), e essas vocalizações transmitem informações essenciais para o reconhecimento de conspecíficos, escolha de parceiros e disputas territoriais (Bradbury & Vehrencamp 1998; Catchpole & Slater 2008). A transmissão e entrega das mensagens carregadas por sinais sonoros depende da interferência acústica ambiental (Endler 1992; Duellman & Pyres 2013), que está diretamente ligada à composição vegetal dos diferentes hábitats e aos sons de fundo, tanto abióticos (e. g. vento) quanto bióticos (e. g. cantos e vocalizações de outras espécies) (Wollerman & Wiley 2002). Espécies da mesma comunidade, enfrentam as mesmas pressões ambientais de seleção natural, o que pode resultar na convergência de determinadas características vocais que são favorecidas em determinados habitats (Keddy 1992; Weiher et al. 1998). Por exemplo, pelo fato de sons de baixa frequência atingirem distâncias mais longas em vegetações fechadas do que sons mais agudos, espécies florestais normalmente apresentam cantos mais graves do que habitantes de áreas abertas (Morton 1975; Badyeav & Leaf 1997). Espécies que cantam na mesma faixa de frequência estão sujeitas a sofrer interferência acústica caso vocalizem no mesmo intervalo temporal (Miller 1982), e, em consequência, algumas espécies podem evitar a emissão de sinais acústicos enquanto a outra estiver vocalizando (Planqué & Slabbekoorn 2008). Portanto, alternativamente à convergência dos caracteres por pressões ambientais da vegetação, os sinais acústicos podem ser mais dispersos na mesma comunidade como resultado da competição interespecífica, com a seleção favorecendo os sinais mais contrastantes com os sons de fundo (Brumm & Slabbekoorn 2005; Price 2008).

A competição entre aves que cantam na mesma faixa de frequência é mais forte entre espécies que também ocupam os mesmos estratos florestais. Luther (2009) observou que aves que vocalizam no mesmo intervalo temporal possuem cantos mais diversificados e ocupam diferentes estratos. Além disso, diferentes alturas da floresta também podem funcionar para evitar a aglomeração de sons semelhantes, uma vez que a propagação do som difere do chão para o dossel (Marten et al. 1977; Ellinger & Hodl 2003; Luther 2009).

1.3 Dinâmicas e interações acústicas interespecíficas

A interferência acústica pode causar o mascaramento de sinais e consquentemente falhas na comunicação (Wiley 1994; Brumm & Slabbekoorn 2005; Duellman & Price

2013). Como exemplos desses erros, podemos destacar repostas a sinais heteroespecíficos (e possível hibridização de espécies próximas filogeneticamente), e o gasto de energia para uma emissão sonora que não será processada pelo recebedor (Endler 1992). Espécies que habitam a mesma comunidade e vocalizam na mesma faixa de frequência estão sujeitas a sobreposições espectrais e consquentes interferências acústicas (Planqué & Slabbekoorn 2008). A partição do espaço acústico, definida pela divisão dos horários da manhã por espécies que vocalizam em frequências similares, é uma possível estrategia para evitar esse fenômeno (Luther 2009). Adicionalmente, dinâmicas a curto prazo também já foram observadas, nas quais espécies coordenam suas emissões, em um mesmo intervalo temporal, para evitar a sobreposição dos cantos (Ficken et al. 1974; Popp & Ficken 1985). Por espécies próximas filogeneticamente possuírem mais chances de hibridizarem, alguns trabalhos demonstraram que o canto de espécies simpátricas evoluiu de forma divergente afim de se evitar a comunicação interespecífica e a consquente hibridizição (Miller 1982; Kroodsma & Canady 1985; Seddon 2005).

1.4 Capítulos da tese

O primeiro capítulo da tese descreve a comunidade de aves de uma mata estacional semidecidual, no qual busquei caracterizar as espécies de acordo com suas categorias tróficas e estratos para poder assim avaliar o status do fragmento. Adicionalmente, comparei metodologias mensais e quinzenais de pontos de escuta, por meio das quais investiguei a eficiência de se coletar os dados duas vezes por mês. No segundo capítulo, coletei e mensurei as variáveis vocais das aves do fragmento, e, juntamente com dados sobre a ecologia (estrato de forrageamento), verifiquei se a distribuição das espécies nos pontos de escuta tinha relação com a dispersão desses caracteres. No terceiro capítulo, realizei um estudo de caso entre duas espécies próximas filogeneticamente que foram observadas cantando em sequência, e avaliei as possíveis vantagens desse comportamento e o significado e relação com a comunidade.

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CAPÍTULO 1

BIRD COMMUNITY STRUCTURE IN A SEMI DECIDUOUS FOREST FRAGMENT IN THE STATE OF SÃO PAULO

Ana Luiza Camargo Catalano

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Bird community structure in a semi-deciduous forest fragment in the State of São Paulo

Abstract. Habitat loss is a result of forest fragmentation caused by anthropogenic activities that replace natural vegetation for agricultural and urban areas. The reduction and alteration of a forest patch may turn the environment inhospitable to some species (specialists) and adequate to others (generalists). Because many bird species are sensitive to forest fragmentation regarding their trophic categories or foraging stratum, we sampled a bird community in a semideciduous fragment not previously studied to access the environment conditions. We established 15 sample points across the fragment and visits occurred twice per month. We recorded all 15-minute point counts to confirm species identification. A total of 127 species were recorded, 115 of which through quantitative acoustic censuses. The sample represented 16.5% of all birds of São Paulo State and four threatened species. Most of the species were considered scarce or rare, according to their frequency of occurrence, and 27 species were considered as abundant or common in the fragment (FO > 50%). Insectivores were the major trophic category followed by frugivores/nectarivores. Specialists and sensitive birds were recorded in this fragment such as *Pyriglena leucoptera*, an ant-follower, *Crypturellus undulatus*, a large frugivore, and high punctual index of abundance (PIA) of microhabitat dependent species, such as *Synallaxis ruficapilla*, indicate a considerable conservation quality of the habitat. Also, we concluded that acoustic censuses sampled twice per month provide a significant increase in monthly bird richness per and increases the chance of recording migrant and errant species.

Keywords. Habitat loss, Guild, Trophic category, Stratification.

Introduction

Habitat loss and forest fragmentation are results of historical processes of vegetation disturbance in which countless factors interacted over time (MacArthur & Whitmore 1979). Although it can be a result of natural processes, habitat fragmentation occurs mainly as an outcome of anthropogenic activity, where original vegetation is replaced due to agricultural conversion and urbanization (Czech et al. 2000; Kerr & Cihlar 2004; Venter et al. 2006). The drastic change of natural habitats to human-dominated forms, or to downsize original vegetation, renders the environment inhospitable to some species (e. g. specialist forest-dependent species) (Borgella & Gavin 2005). Yet, these changes can favor the establishment and population growth of generalist species, thus causing an ecological imbalance (Primack 1993; Devictor et al. 2008; Desrochers et al. 2011; Carrara et al. 2015). Therefore, the richness and abundance of species on a given locality indicate the status of the habitat, providing information to trace conservation strategies (Guldemond & van Aarde 2010; Alexandrino 2016, but see Telles & Dias 2010; Marques & Anjos 2014; Campos et al. 2018 for examples).

Birds are frequently used as bioindicators for many reasons. First, it is a well-studied group and extent information about ecological aspects of many families, genera and species are understood (Verner 1981; Morrison 1986; Gregory & Strien 2010); Second, the relationship among bird communities and other groups (i. e. plants) and territory have been demonstrated (Keast 1990; Petty & Avery 1990); Third, they occupy different levels of the ecological pyramid in different environments (Bunce et al. 1981); Fourth, because of acoustic communication, they are easily detected and identified, allowing rapid data collection (Haila 1985; Gardner et al. 2008).

The presence, absence, and abundance of bird species that are sensitive to fragmentation on given community work as indicators of the conservation status. Henle et al. (2004), suggest 12 traits that predict bird sensitivity: population size; population fluctuation and storage effect; dispersal power; reproductive potential; annual survival; sociality; body size; trophic position; ecological specialization, microhabitat and matrix use; disturbance and competition sensitive traits; rarity; and biogeographic position.

Because more than 80% of the original vegetation in São Paulo state has been substituted due to human activity (Câmara 2018), and it is important to assess information concerning the remaining portion of unaltered areas (Alexandrino 2016), the aim of this study was to characterize the bird community of a semideciduous forest patch not previously sampled and studied in São Paulo. Thus, we evaluated if the fragment has representative rates of richness and abundance of sensitive species. Additionally, we compared the effectiveness of monthly and biweekly quantitative surveys.

Material and Methods

Study area

The study was conducted in a stationary semi-deciduous forest within the Paraíso Farm which is situated in the municipality of São Carlos, in São Paulo state, Brazil (25º59’08.8”S, 47º50’09.2”W, 845 – 870 m of elevation). The climate of the area is classified (Köppen) as a transition from Cwa_i - Aw_i (dry winter warm climate to tropical with humid summer and dry winter) (Tolentino 1967). The farm occupies an area of 195 ha in total, with 77 ha belonging to the forest fragment. The fragment is mainly surrounded by sugar cane and corn plantations and pasture areas (Fig. 1).

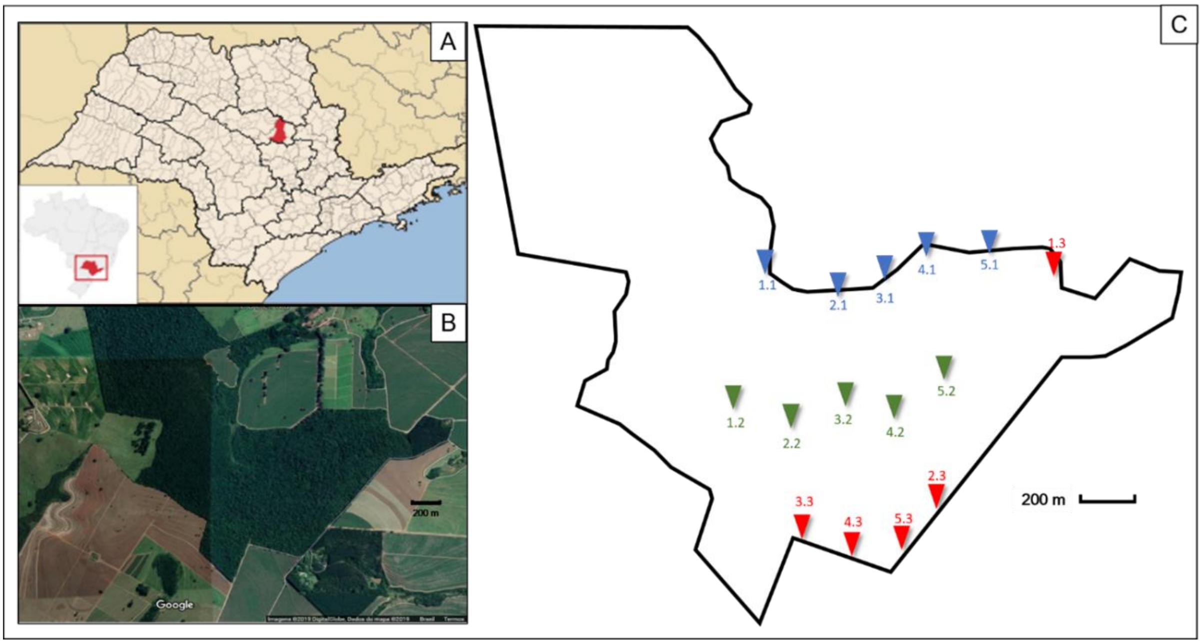

Figure 1. Maps of (A) Brazil, State of São Paulo (and the city of São Carlos highlighted), (B) forest fragment of the Paraíso Farm and (C) the 15 established sample points.

Sample design and data collection

The field visits started a month prior to the data collection in order to establish the tracks and the sampling points. Since no other work was previously carried out in this fragment, the delimitations of the paths inside the forest were traced assisted by the biology laboratory technician from UFSCar, totalizing 15 sampling points within the forest: two paths on the edge, with five points each, and one path on the interior, with five points. In order to reduce the probability of territorial overlap and registering the same individual, all points had a minimum distance of 200 m from each other.

Since we wanted to document the bird community of the fragment, only quantitative surveys were made, although some species that were active on the surroundings were registered for the elaboration of the species' list. For this purpose, we chose the point counts method, developed by Blondel et al. (1970) and adapted by Vielliard and Silva (1990). The data collection occurred twice a month from May/2017 to April/2018 (12 months). We visited each path on different days in order to cover the same and most active period of the morning, totaling 72 visits, and 360 sample plots. The surveys were held from 6:00 AM to 10 PM with 15-minute duration point counts, summing up 90 hours of observation throughout the year. The sampling order of the points was previously randomized before each field trip to avoid tendencies in data collection. We used 8x25 binoculars (Nikon SporstarEx 8.2º) for bird identification and recorded every point count with a Marantz Professional PMD661 MKII recorder and a directional microphone Sennheiser ME66, for comparisons and confirmation.

Definition and classification of the community

We used two indexes to assess the status of the fragment: Frequency of Occurrence (FO) of species and Punctual Index of Abundance (PIA) of each species and also for the community (Vielliard & Silva 1990). The FO determines the proportion of the number of visits that a species was registered concerning the total number of visits and was defined according to Rodrigues et al. (2005) in this paper: "abundant" when registered in 75 to 100% of the visits; "common" when registered in 50 to 74% of the visits; "scarce" when detected in 25 to 49% of the visits; "rare" when detected in less than 24% of the visits and "occasional" when a species was registered once. The PIA estimates the proportion of a species in a given community (number of contacts/total number of samples). The list of bird species was elaborated according to the systematic order and nomenclature suggested by the Brazilian Committee of Ornithological Records (CBRO 2015).

The feeding guilds and foraging strata of each species were determined according to Wilman et al. (2014), and sensitivity classification was based on Parker et al. (1996).

Comparing monthly surveys with biweekly surveys

The acoustics censuses were held twice per month, hence every sample point was visited every 15 days. We accessed the total richness per month and also per sample. Hence, we compared the mean values of the number of species in the two monthly samples with the total monthly richness. We also checked for species that would have been lost if the samples were carried out once per month.

Results

Bird community

A total of 127 bird species, distributed in 39 families, were recorded in 5790 contacts during the 12 months of data collection (see Table 1). The order Passeriformes was represented by 21 families, and Non-Passeriformes were distributed in 15 orders and represented by 19 families (Fig. 2).

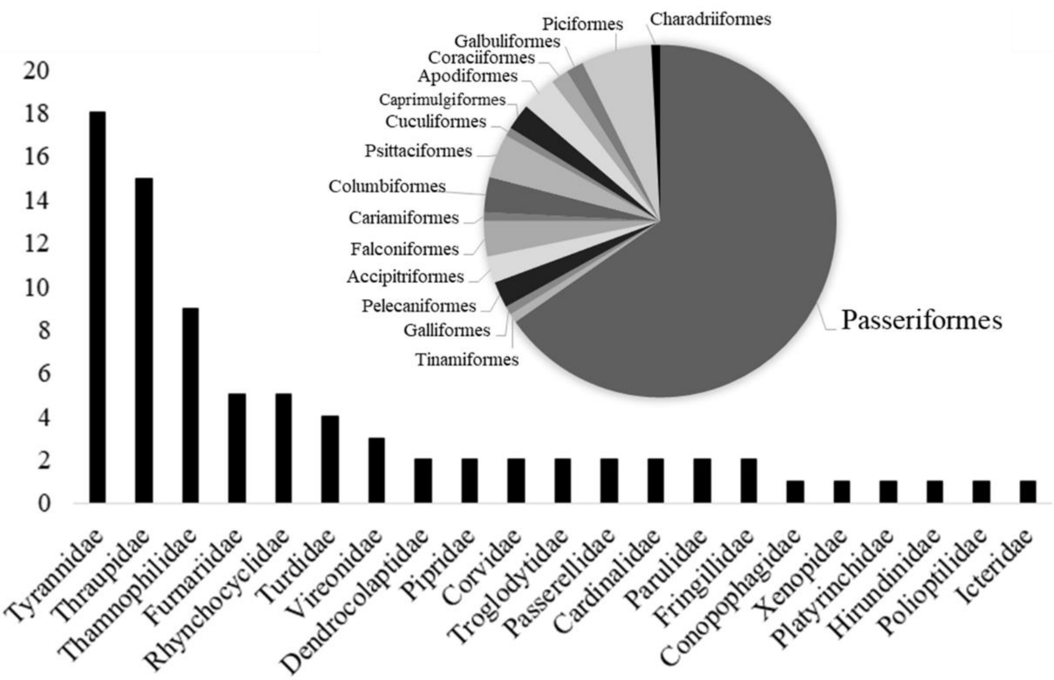

Figure 2. Box plots showing the number of species of each Passerine family, and a round chart representing all avian orders recorded.

The frequency of occurrence of the species ranged from 1.4% (recorded in one out of the 72 visits) to 91.7% (recorded in 66 out of the 72 visits). Because the main purpose of this study was to register the occurring species in the fragment, and surveys were only performed in the mornings, not many individuals were registered out of the point plots. The species registered qualitatively were mainly recorded when transitioning from a point to another or were vocalizing species from open areas outside the fragment but their songs usually reach long distances (i. e. *Cariama cristata*). Hence, there was an elevated number of “scarce” (FO 25-49%), “rare” (FO < 24%), and “occasional” (only one visit) species. There were 27 species that presented a FO higher than 50%, representing the “common” species group (13) and the “abundant” group (14) (see Table 2).

Table 1. Bird species recorded during qualitative and quantitative surveys at the Paraíso Farm, São Paulo, Brazil. FO – Frequency of Occurrence; PIA – Punctual Index of Abundance; TC – trophic categories; STRA – stratum. The trophic categories are represented by: F/N (frugivore/nectarivore), V/F/S (vertebrate/fish/scavenger), I (invertebrate), O (omnivore), P (plant/seed). The strata are represented by T (terrestrial), U (understory), M (midstory), and C (canopy) – based on Wilman et al. (2014).

Taxon	FO (%)	PIA	TC	STRA
TINAMIDAE				
Crypturellus undulatus (Temminck, 1815)	25	0.058	F/N	T
CRACIDAE				
Penelope superciliaris Temminck, 1815	4.2	0.008	F/N	T
ARDEIDAE				
Syrigma sibilatrix (Temmink, 1824)	5.6	0.014	V/F/S	T
THRESKIORNITHIDAE				
Mesembrinibis cayennensis (Gmelin, 1789)	5.6	0.014	I	T
Theristicus caudatus (Boddaert, 1783)	11.1	0.039	I	T
ACCIPITRIDAE				
Leptodon cayanensis (Latham, 1790)	1.4	0.008	O	C
Ictinia plumbea (Gmelin, 1788)	6.9	0.017	I	C

Rupornis magnirostris (Gmelin, 1788)	9.7	0.022	V/F/S	C
FALCONIDAE				
Caracara plancus (Miller, 1777)	1.4	-	V/F/S	T
Milvago chimachima (Vieillot, 1816)	1.4	-	V/F/S	T/C
Herpetotheres cachinnans (Linnaeus, 1758)	15.3	0.044	V/F/S	C
Micrastur semitorquatus (Vieillot, 1817)	11.1	0.022	V/F/S	M/C
CARIAMIDAE				
Cariama cristata (Linnaeus, 1766)	19.4	-	I	T
CHARADRIIDAE				
Vanellus chilensis (Molina, 1782)	6.9	-	I	T
COLUMBIDAE				
Columbina talpacoti (Temmink, 1811)	1.4	-	P/S	T
Columbina squammata (Lesson, 1831)	1.4	-	P/S	T
Patagioenas picazuro (Temminck, 1813)	88.9	0.697	P/S	C
Patagioenas cayennensis (Bonnaterre, 1792)	86.1	0.567	F/N	C
Zenaida auriculata (Des Murs, 1847)	1.4	-	P/S	M
Leptotila verreauxi Bonaparte, 1855	58.3	0.200	P/S	T/U
Leptotila rufaxilla (Richard & Bernard, 1792)	30	0.152	P/S	T
PSITTACIDAE				
Psittacara leucophthalmus (Statius Muller, 1776)	77.8	0.697	P/S	C
Brotogeris chiriri (Vieillot, 1818)	48.6	0.294	F/N	M
Pionus maximiliani (Kuhl, 1820)	29.2	0.106	P/S	C
Amazona amazonica (Linnaeus, 1766)	1.4	0.003	F/N	C
Amazona aestiva (Linnaeus, 1758)	11.1	0.042	O	C
CUCULIDAE				
Piaya cayana (Linnaeus, 1766)	4.2	0.008	I	C
CAPRIMULGIDAE				
Lurocalis semitorquatus (Gmelin, 1789)	2.8	-	I	C
Nyctidromus albicollis (Gmelin, 1789)	2.8	-	I	T
Hydropsalis parvula (Gould, 1837)	1.4	-	I	T
TROCHILIDAE				
Eupetomena macroura (Gmelin, 1788)	1.4	-	F/N	M
Thalurania glaucopis (Gmelin, 1788)	1.4	-	F/N	M
Hylocharis chrysura (Shaw, 1812)	26.4	0.061	F/N	U/M
Amazilia fimbriata (Gmelin, 1788)	20	0.100	F/N	U/C
ALCEDINIDAE				
Megaceryle torquata (Linnaeus, 1766)	1.4	0.003	V/F/S	U/C
MOMOTIDAE				
Baryphtengus ruficapillus (Vieillot, 1818)	68.1	0.219	I	U/M
GALBULIDAE				
Galbula ruficauda Cuvier, 1816	2.8	0.008	I	M
BUCCONIDAE				
Malacoptila striata (Spix, 1824)	2.8	0.006	I	U/M
RAMPHASTIDAE				
Ramphastos toco Muller, 1776	48.6	0.144	F/N	C

PICIDAE				
Picumnus albosquamatus d'Orbigny, 1840	59.7	0.208	I	M/C
Melanerpes candidus (Otto, 1796)	4.2	0.011	F/N	M/C
Veniliornis passerinus (Linnaeus, 1766)	30.6	0.111	I	C
Colaptes melanochloros (Gmelin, 1788)	1.4	0.014	I	T/C
Colaptes campestris (Vieillot, 1818)	5.6	0.011	I	T/C
Dryocopus lineatus (Linnaeus, 1766)	41.7	0.122	I	C
Campephilus robustus (Lichtenstein, 1818)	2.8	0.011	I	M
THAMNOPHILIDAE				
Dysithamnus mentalis (Temminck, 1823)	76.4	0.375	I	U/M
Herpsilochmus atricapillus Pelzeln, 1868	73.6	0.353	I	C
Thamnophilus doliatus (Linnaeus, 1764)	38.9	0.178	I	U/M
Thamnophilus pelzelni Hellmayr, 1924	4.2	0.011	I	U/M
Thamnophilus caerulescens Vieillot, 1816	81.9	0.536	I	U/M
Taraba major (Vieillot, 1816)	15.3	0.044	I	U
Mackenziaena severa (Lichtenstein, 1823)	33.3	0.097	I	U
Pyriglena leucoptera (Vieillot, 1818)	5.6	0.025	I	U
Drymophila ferruginea (Temminck, 1822)	6.9	0.017	I	U
CONOPOPHAGIDAE				
Conopophaga lineata (Wied, 1831)	88.9	0.547	I	U
DENDROCOLAPTIDAE				
Sittasomus griseicapillus (Vieillot, 1818)	68.1	0.311	I	M
Lepidocolaptes angustirostris (Vieillot, 1818)	27.8	0.067	I	U/M
XENOPIDAE				
Xenops rutilans Temminck, 1821	11.1	0.028	I	C
FURNARIIDAE				
Lochmias nematura (Lichtenstein, 1823)	1.4	0.003	I	T
Synallaxis ruficapilla Vieillot, 1819	91.7	0.628	I	U
Synallaxis frontalis Pelzeln, 1859	31.9	0.081	I	U
Synallaxis spixi Sclater, 1856	12.5	0.025	I	U
Automolus leucophthalmus (Wied, 1821)	34.7	0.106	I	U
PLATYRINCHIDAE				
Platyrhinchus mystaceus Vieillot, 1818	26.4	0.083	I	U
RHYNCHOCYCLIDAE				
Tolmomyias sulphurescens (Spix, 1825)	83.3	0.403	I	C
Todirostrum poliocephalum (Wied, 1831)	76.4	0.386	I	M/C
Todirostrum cinereum (Linnaeus, 1766)	18.1	0.044	I	U/C
Poecilotriccus plumbeiceps (Lafresnaye, 1846)	19.4	0.067	I	U
Leptopogon amaurocephalus Tschudi, 1846	12.5	0.031	I	U/M
TYRANNIDAE				
Euscarthmus meloryphus Wied, 1831	1.4	0.003	I	U
Camptostoma obsoletum (Temminck, 1824)	51.4	0.192	I	C
Elaenia flavogaster (Thunberg, 1822)	1.4	0.003	O	C
Elaenia spectabilis Pelzeln, 1868	1.4	0.003	O	C
Myiopagis caniceps (Swainson, 1835)	2.8	0.003	I	C
Myiarchus swainsoni Cabanis & Heine, 1859	18.1	0.056	I	M/C

Myiarchus ferox (Gmelin, 1789)	48.6	0.178	I	M/C
Myiarchus tyrannulus (Statius Muller, 1776)	4.2	0.008	I	M/C
Pitangus sulphuratus (Linnaeus, 1766)	61.1	0.244	O	T/C
Myiodynastes maculatus (Statius Muller, 1776)	43.1	0.147	O	M/C
Megarynchus pitangua (Linnaeus, 1766)	37.5	0.108	O	C
Myiozetetes cayanensis (Linnaeus, 1766)	4.2	0.006	I	C
Myiozetetes similis (Spix, 1825)	11.1	0.025	O	M/C
Tyrannus melancholicus Vieillot, 1819	2.8	0.008	I	C
Colonia colonus (Vieillot, 1818)	25	0.081	I	C
Myiophobus fasciatus (Statius Muller, 1776)	1.4	0.003	I	U
Cnemotriccus fuscatus (Wied, 1831)	33.3	0.097	I	U/M
Lathrotriccus euleri (Cabanis, 1868)	51.4	0.219	I	M
PIPRIDAE				
Antilophia galeata (Lichtenstein, 1823)	40.3	0.128	F/N	M/C
Chiroxiphia caudata (Shaw & Nodder, 1793)	45.8	0.158	F/N	U/M
VIREONIDAE				
Cyclarhis gujanensis (Gmelin, 1789)	90.3	0.464	I	M/C
Hylophilus amaurocephalus (Nordmann, 1835)	1.4	0.008	I	U/C
Vireo chivi (Vieillot, 1817)	44.4	0.314	I	C
CORVIDAE				
Cyanocorax cristatellus (Temminck, 1823)	30.6	0.078	O	M/C
Cyanocorax chrysops (Vieillot, 1818)	1.4	0.003	O	C
HIRUNDINIDAE				
Progne chalybea (Gmelin, 1789)	1.4	0.003	I	C
TROGLODYTIDAE				
Troglodytes musculus Naumann, 1823	36.1	0.097	I	T/U
Cantorchilus leucotis (Lafresnaye, 1845)	69.4	0.322	I	U
POLIOPTILIDAE				
Polioptila dumicola (Vieillot, 1817)	1.4	0.003	I	U/C
TURDIDAE				
Turdus rufiventris Vieillot, 1818	29.2	0.067	O	T/C
Turdus leucomelas Vieillot, 1818	91.7	0.706	I	T/C
Turdus amaurochalinus Cabanis, 1850	19.4	0.058	F/N	T/C
Turdus subalaris (Seebohm, 1887)	1.4	0.003	F/N	C
THRAUPIDAE				
Tangara sayaca (Linnaeus, 1766)	29.2	0.094	O	C
Tangara cayana (Linnaeus, 1766)	2.8	0.006	F/N	U/C
Conirostrum speciosum (Temminck, 1824)	1.4	0.006	I	C
Volatinia jacarina (Linnaeus, 1766)	8.3	0.022	O	T/U
Eucometis penicillata (Spix, 1825)	27.8	0.081	U/M	I
Coryphospingus cucullatus (Statius Muller, 1776)	2.8	0.006	O	T/U
Tachyphonus coronatus (Vieillot, 1822)	65.3	0.208	I	M/C
Ramphocelus carbo (Pallas, 1764)	50	0.192	O	U/C
Tersina viridis (Illiger, 1811)	2.8	0.006	F/N	C
Coereba flaveoa (Linnaeus, 1758)	80.6	0.447	F/N	C

Tiaris fuliginosus (Wied, 1830)	12.5	0.031	P/S	U/M
Sporophila caerulescens (Vieillot, 1823)	22.2	0.117	P/S	U
Saltator similis d'Orbigny & Lafresnaye, 1837	34.7	0.111	I	M/C
Saltator fuliginosus (Daudin, 1800)	65.3	0.467	I	C
*Thlypopsis sordida (*d'Orbigny & Lafresnaye, 1837)	13.9	0.031	O	U/C
PASSERELLIDAE				
Zonotrichia capensis (Statius Muller, 1776)	34.7	0.169	P/S	T/U
Arremon flavirostris Swainson, 1838	36.1	0.117	O	T
CARDINALIDAE				
Habia rubica (Vieillot, 1817)	12.5	0.033	I	U/M
Cyanoloxia brissonii (Lichtenstein, 1823)	1.4	0.006	F/N	U
PARULIDAE				
Basileuterus culicivorus (Deppe, 1830)	90.3	0.753	I	U/M
Myiothlypis flaveola Baird, 1865	91.7	0.497	I	T/U
ICTERIDAE				
Icterus pyrrhopterus (Vieillot, 1819)	1.4	0.003	O	C
FRINGILLIDAE				
Euphonia chlorotica (Linnaeus, 1766)	19.4	0.047	F/N	C
Euphonia violacea (Linnaeus, 1758)	4.2	0.008	F/N	C

Table 2. Frequency of occurrence (FO) classes percentage of bird species (May 2017 to April 2018).

	FO classes (%)				Total
	<24	25 - 49	50 - 74	75 - 100	
species (%)	55	24	10	11	100
species number	70	30	13	14	127

The classification regarding trophic categories was performed according to Wilman et al. (2004) as follows: Frugivores and nectarivores (F/N), plant and seed eaters (P/S), omnivores (O), invertebrate diet (I) and vertebrate, fish and scavenger diet (V/F/S). The bird assemblage was mostly represented by birds with an invertebrate diet (55%), followed by frugivores and nectarivores (17%) and omnivores (14%). The other categories (P/S and V/F/S) summed up 14% of the birds in the fragment. In Non-Passeriformes, insectivores were represented by 40% of the species followed by frugivores (22%). Thus, the invertebrate category is mostly concentrated in the Passeriformes order (63%). Birds were also classified according to foraging strata in the following categories: canopy, midstory, understory, and ground dwellers, and some species presented two of these categories for definition (according to Wilman et al. 2014). The canopy was the most occupied stratum (68 species), followed by the understory (45 species), the midstory (37), and, finally, the ground stratum (28). All strata were mostly represented by insectivores (invertebrate diet), but only in understory and midstory strata it surpassed 50%. The ground stratum presented the most balanced distribution across the different trophic categories (Fig. 3).

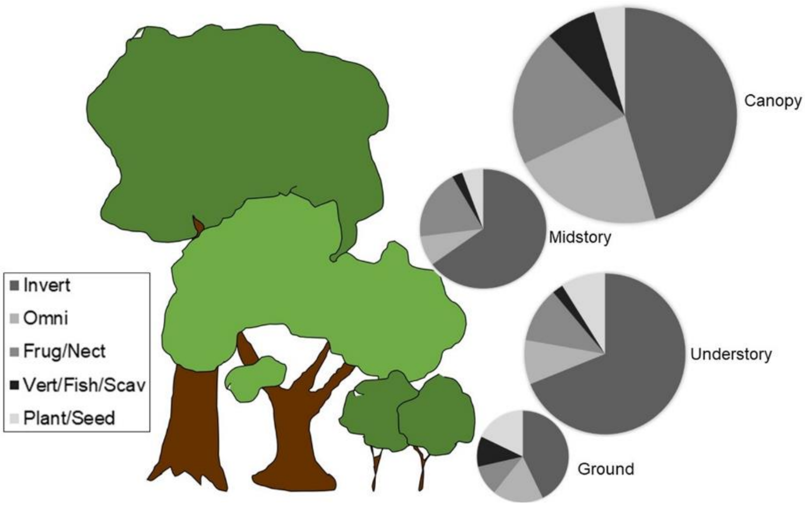

Figure 3. Round charts representing each stratum and divided according the distribution of trophic categories; the size of each chart corresponds to the proportion of number of dwelling species. (Canopy: Invert – 46%, Omni – 22%, Frug/Nec – 21%, Vert/Fish/Scav – 7%, Plant/Seed – 4%; Midstoy: Invert – 65%, Frug/Nec – 19%, Omni – 8%, Plant/Seed – 5%, Vert/Fish/Scav – 3%; Understory: Invert – 69%, Frug/Nec – 11%, Omni – 9%, Plant/Seed – 9%, Vert/Fish/Scav – 2%; Ground: Invert – 43%, Plant/Seed – 18%, Omni – 18%, Vert/Fish/Scav – 11%, Frug/Nec – 10%.

According to Paker et al. (1996), 71 species of the birds sampled in this community present low sensitivity to habitat fragmentation, 55 present medium sensitivity, and one species (*Habia rubica*) presents high sensitivity.

During quantitative surveys, a total of 115 species were recorded. The PIA values of each species ranged from 0.003 (one contact throughout the year) to 0.753 (271 contacts throughout the year) (Table 1). The cumulative PIA values for each month varied from 12 (360 contacts/30 samples, April) to 23.7 (711 contacts/30 samples, September) (Fig. 4).

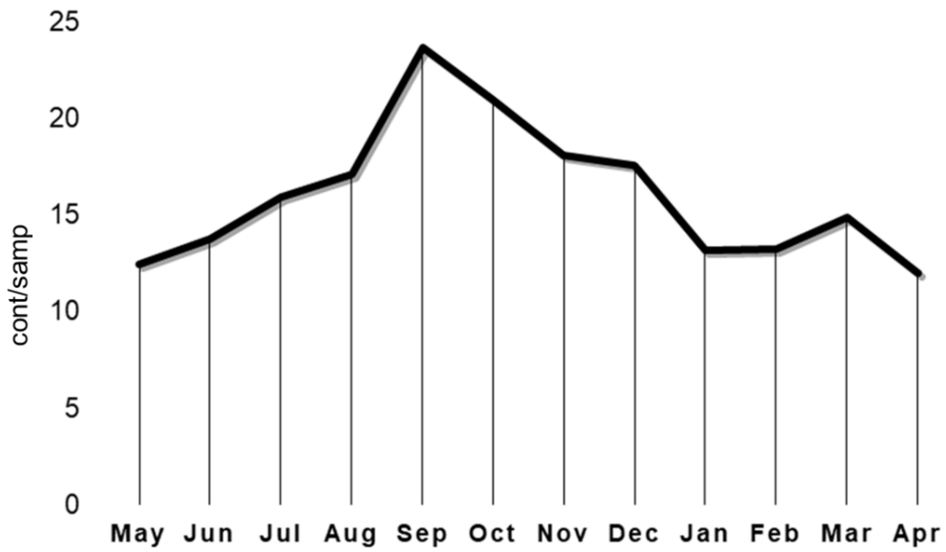

Figure 4. Annual variation of the cumulative IPA values per month (total number of contacts/30 samples).

Monthly x Biweekly acoustic censuses

During the data collection, there were bird species that were recorded only once and species that were recorded only during one of the halves of the month. When doubling the sample collection times per month there was a mean increase of 12.12 in the richness of species per month (Fig. 5).

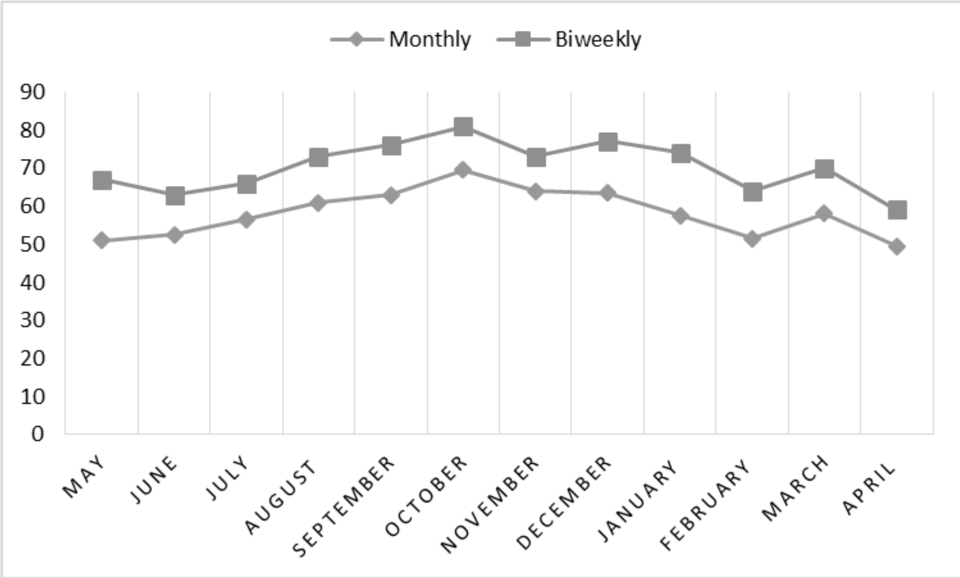

Figure 5. The number of species (y-axis) per month on monthly and biweekly surveys.

Discussion

The bird richness of a community within a forest fragment is correlated to a series of factors, among them, the patch size and thus the availability of vegetation strata (Battisti et al. 2009; Martensen et al. 2012; Barbaro et al. 2013). Over more, the presence or absence of species within a fragment provides important information regarding the environment conditions (Cueto & Casenave 1999). The species richness of the forest fragment in the Paraíso Farm represents 16.5% of all birds of São Paulo State (Willis & Oniki 2003). Of the 127 species recorded, four (*Crypturellus undulatus*, *Amazona amazonica*, *Eucometis penicillata* and *Cyanoloxia brissonii*) are threatened in São Paulo State (São Paulo 2008) and two (*Chiroxiphia caudata* and *Habia rubica*) are bioindicators because of their sensitivity to forest fragmentation (Parker et al. 1996; Piratelli et al. 2008; Alexandrino 2016).

The representation of trophic categories in this fragment followed a pattern usually observed in other tropical forest studies in which most species recorded in bird surveys are insectivores (Sick 1997). The presence and abundance of species of certain foraging habits and strata may indicate the conservation status of a forest patch (Gray et al. 2007). In a study regarding the effectiveness of protected areas for bird conservation, Duckworth and Altwegg (2018) found that the abundance and richness of species increased with the proportion of protected area, however, this relationship varied among species and could be explained by differences among feeding guilds. For instance, understory insectivores, especially ant followers, are likely to disappear in more fragmented areas (Sekercioglu et al. 2002; Willis & Oniki 1978; Korfanta et al. 2012). Although not abundant, we recorded the ant-follower *Pyriglena leucoptera*, indicating that the studied fragment presents sufficient forested area for their foraging habits and the presence of army ant species (Kumar & O'Donnell 2007). For instance, forest fragmentation may cause army ants to avoid these habitats due to low prey densities (Kumar & O'Donnell 2007) or might be directly affected since the disappearance of ant colonies in fragments below a minimum size was reported (Britton et al. 1996; Partridge et al. 1996).

The presence of large frugivores also reflect environmental quality, such as *C. undulatus*, indicating the availability of food items throughout the year (Anjos 2006), and *Penelope superciliaris*, which is usually threatened by local hunting, however, the latter presented low PIA values, likely because of this reason. Although considered as presenting a medium sensitivity to habitat fragmentation by Parker et al. (1996), because of foraging habits and occupation area, *C. undulatus* is considered as presenting a high sensitivity by other authors (see Anjos 2006; Alexandrino 2016) and the same applies for other species such as *C. caudata*, *A. aestiva*, *A. galeata*, *C. robustus*, *C. brissonii*, *M. severa* and *P. superciliaris* (Alexandrino et al. 2016). Some leaf insectivores are highly dependent on specific microhabitats that are usually found within large fragments

(Hansbauer et al. 2010). Although the studied fragment is small (77ha), it is probably well preserved, since we recorded microhabitat dependent species, such as *Synallaxis ruficapilla* (Anjos et al. 2004) with high FO rates and PIA values. High rates of forest degradation should favor omnivores and insectivores that are less specialized (Carrara et al. 2015). Species such as *Pitangus sulphuratus*, *Tyrannus melancholicus*, and *Tangara sayaca* are some examples, and present high plasticity to adaptation in anthropic environments, and tend to establish where original vegetation was suppressed. However, some omnivores, such as *Baryphtengus ruficapillus*, are forest dependents because of specific foraging habits (Sick 1997), and also sensitive to fragmentation (Ribon et al. 2003).

The low frequency of occurrence of some species could be explained by (1) bird species of less conspicuous vocalizations since sampling was only carried out by point counts; (2) migrant species such as *Turdus subalaris* and *Progne chalybea*, only registered in one of the visits, and *Tersina viridis*, considered as an “errant” species with cryptic habits (Sick 1997); and (3) low population densities in the area. Nevertheless, the high rate of species with a low frequency of occurrence is common for tropical environments (Begon et al. 1996; Macedo 2002; Telles & Dias 2010).

The data collection carried out biweekly presented an increase in bird richness for every month. Furthermore, some species would not be registered if we had sampled the community once per month. Thus, it is recommended sampling point counts more times a month to increase the chances to record migrant or less conspicuous species on a given community.

In conclusion, this was the first study and sampling of the forest fragment in the Paraíso Farm, and the bird community presents threatened, sensitive, and specialist species that reflect that this semi-deciduous forest is a suitable environment to support those species. Thus, this study provides data for management strategies and the area must be considered as a priority to conservation.

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CAPÍTULO 2

THE INFLUENCE OF FREQUENCY RANGE OF BIRD VOCALIZATIONS AND FORAGING STRATA IN THE OCCURRENCE IN POINT COUNTS

Ana Luiza Camargo Catalano

Manoel Martins Dias Filho

The influence of frequency range of bird vocalizations and foraging strata in the occurrence in point counts

Abstract. Species cohabiting the same habitat face similar environmental selection pressures, and traits of morphology, behaviour, and acoustic signals may converge. Vocalizations transmit important information for conspecifics and acoustic interference should be avoided for the communication succeed. Because richness, abundance and thus competition should be greater among small birds inhabiting closed areas, we tested how an avian assemblage occurs across 15 min point counts regarding three vocal variables (FFMIN, FDMAX, and FDOM) and foraging strata. We chose species with a frequency of occurrence higher than 25% and we collected 10 recordings, of 10 different individuals, of each species to determine mean values of the vocal variables (totaling 35 species and 350 analyzed recordings). We used dendrograms of multivariate cluster analysis to assess the vocal proximity of the 35 species and network plot with nodes connected by edges to represent the co-occurrence of species. We found that the most abundant species did not present more co-occurrence connections, and that species with significant co-occurrence presented more dispersed spectral vocal characters and occupying strata. We suggest that this distribution across point counts works as a strategy to minimize acoustic interference and avoid vocal overlap.

Keywords. Acoustic communication, Neotropical, Passerine, Passeriformes, Acoustic interference.

Introduction

Studies regarding the structure and evolution of a given community are usually focused on ecological and morphological traits (Emerson & Gillespie 2008), however, these attributes may apply to the acoustic signals of a bird assemblage (Groning & Hochkirch 2008; Cardoso & Price 2010). Vocalizations convey important information for recognition of conspecifics, mate choice decisions, and competition (Bradbury & Vehrencamp 1998; Catchpole & Slater 2008). The delivery of these information relies on sound transmission efficacy, which is directly related to acoustic interference (Endler 1992; Duellman & Pyres 2013). Biotic background noise, such as heterospecific songs, is one of the main sources of interference that can affect detectability and discriminability of conspecific sounds (Wollerman & Wiley 2002; Luther & Gentry 2013). Therefore, different community structures will provide distinct acoustic compositions, having the species to adapt to different background sounds to optimize sound transmission (Slabbekoorn & Peet 2003). For example, because fragmented areas are more sensitive to the establishment of generalist species (Marvier et al. 2004; Devictor et al. 2008; Carrara et al. 2015), similar sounds from birds occupying more heterogeneous patches of a fragment could mask vocalizations of forest-dependent birds, the same applies for the interaction between native and introduced species (Pijanowski et al. 2011; Azar & Bell 2016).

Cohabiting species face similar environmental selection pressures and some traits, including vocal characters, may be driven to converge into those favored within a certain habitat (Haavie et al. 1985; Badyeav & Leaf 1997). For instance, low frequency sounds travel best through dense vegetation, forest-dwelling birds perform lower-pitched songs compared to species from open habitats (Morton 1975; Badyeav & Leaf 1997). Alternatively, competition between species that occupy the same niche may result in the dispersion of vocal traits, since signals should evolve to contrast with the background noise of the environment (Brumm & Slabbekoorn 2005; Price 2008).

Regardless of convergence and divergence in signals' evolution, there will be species facing vocal ambiguity in almost every habitat, and, to avoid both signal masking and vocal overlap, and thus a consequent waste of time and energy on vocalizations, species must coordinate their time of vocal activity (Planqué & Slabbekoorn 2008). However, few studies documented this phenomenon on a community level (but see Luther 2009; Cardoso & Price 2010), and most studies tested these occurrences on single species or small groups of closely related species (e. g. de Kort et al. 2002; Haavie et al. 2004; Ey & Fischer 2009) and have focused on oscine passerines (Slabbekoorn & Smith 2002). In addition, birds singing from different heights of the forest should also work as a strategy to avoid the clustering of similar sounds, since sound propagation at the forest floor differs from that in the canopy and previous studies have documented less dispersed sounds in different forest strata (Marten et al. 1977; Ellinger & Hodl 2003; Luther 2009).

Acoustic competition should be more intense among specific bird taxa, habitats, and times of the day. Because small bird species, which are mostly concentrated in the order Passeriformes, tend to have a higher abundance when compared to larger species (Greenwood et al. 1996), and richness (Olson et al. 2009), acoustic competition should be greater among this group. Furthermore, since the efficacy of visual communication depends on light conditions and lack of obstacles, habitats with dense vegetation, and thus low light intensities, provides ultimate competition for the acoustic space, where birds rely on songs and calls to get the message across (Ryan & Brenowitz 1985; Slabbekoorn 2004). Additionally, most species are believed to have a peak of singing at dawn (Staicer et al. 1996; Catchpole & Slater 2008), thus, one should expect intense vocal competition during the first morning hours (as demonstrated by Belinsky et al. 2012).

The aim of this study was to combine ecological attributes of passerine species (foraging strata), with acoustic characteristics (frequency range) to assess the time of singing in a semideciduous forest. Since great acoustic competition should be expected from this scenario, we predicted that birds singing in the same time interval would present more dispersed vocalisations and would occupy different strata, or that birds that sing in the same frequency range and occupy the same stratum would not be singing in the same time interval. The temporal over dispersion of signals could indicate that species singing similar songs are partitioning the acoustic space by choosing different times of the morning perform to sing, and thus avoiding acoustic interference and competition.

Material and Methods

Study area and acoustic censuses

The study was conducted in a stationary semi deciduous forest within the Paraíso Farm which is situated in the municipality of São Carlos, in São Paulo state, Brazil (25º59'08.8"S, 47º50'09.2"W). The farm occupies an area of 195 hectares in total, with 77 hectares belonging to the forest fragment. The fragment is mainly surrounded by sugar cane and corn plantations and pasture areas (Fig. 1). We established 15 points alongside three trails (five points on each), aiming to cover as much as possible of the available area of the fragment. All points had a separation distance of at least 200 m. The data collection occurred twice a month from May 2017 to April 2018 and the audio recordings were made during the morning period (05:30-09:30 AM). Since we wanted to compare the vocal activity, we visit one trail per day during the same period, totalling 72 visits and 360 samples. We used point count samples of 15 minute interval and registered the active vocal species.

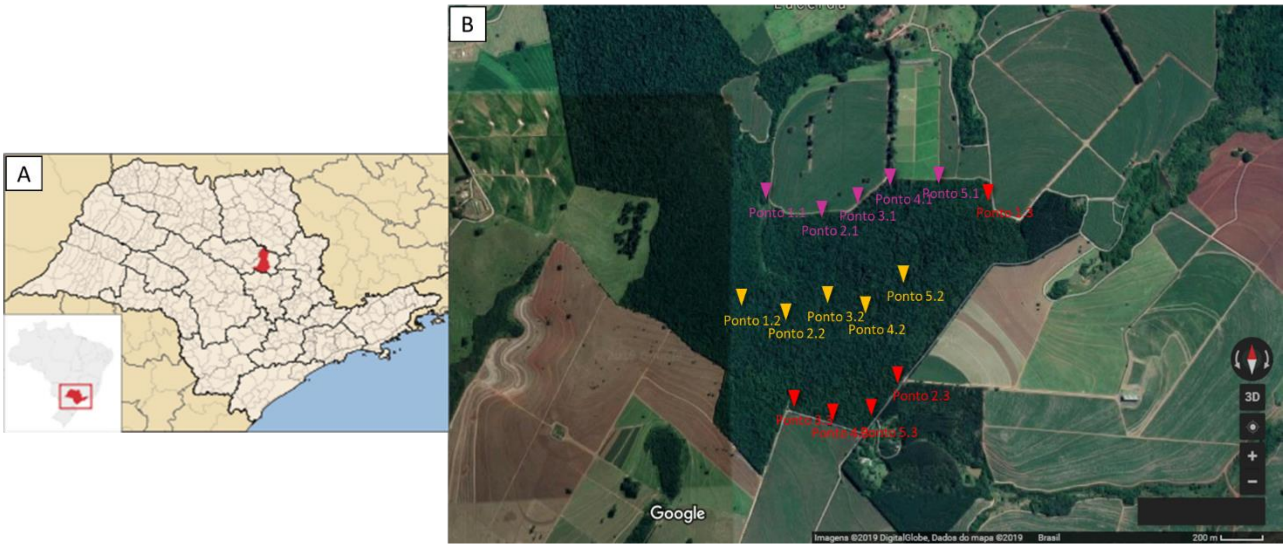


Figure 1. (A) Brazil, São Paulo state, and the municipality of São Carlos. (B) Paraíso Farm area and forest fragment, each point represents a survey site and each color represents a different trail.

Acoustic community

We considered for the analysis the passerine species that presented an index of Frequency of Occurrence (FO = number of visits that a species was registered/total number of visits) higher than 25% throughout the year, in order to avoid occasional species, and we excluded species that were usually recorded performing short calls, instead of longer vocalizations or songs (n = 35). In order to establish the vocal range of each species, we collected 10 audio recordings (total of 350 audio recordings), of distinct individuals from different locations, from the site WikiAves (<www.wikiaves.com.br>, last accessed on 10/10/2019) (see Appendix 1 for recordings' authorship). We selected only clear recordings with a high signal-to-noise ratio for analysis. We also used audio that we recorded during the fieldwork where we used a Sennheiser ME66 directional microphone and a Marantz PDM661 digital recorder, all recordings were made with a 48 kHz sampling rate and a 24-bit resolution. The foraging stratum of each species was defined according to Wilman et al. (2014): terrestrial, understory, midstory, and canopy, and classification was made using one or two of these categories.

Song analysis

To analyze the sound recordings we used the Raven Pro 1.5.0 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA) and we chose the following spectral parameters: 1) the dominant frequency (FDOM), defined as the spectrogram region with most energy concentration; 2) the minimum fundamental frequency (FFMIN); 3) the maximum dominant frequency (FDMAX) (Fig. 2). The numeric values of the maximum and minimum variables were measured with the cursor placement on the sonogram view, and the FDOM values were obtained by selecting the song portion and the desired measurement ("Peak Frequency" on Raven). These vocal variables were measured for the 10 individuals of each species and the meanings were considered for the analysis.

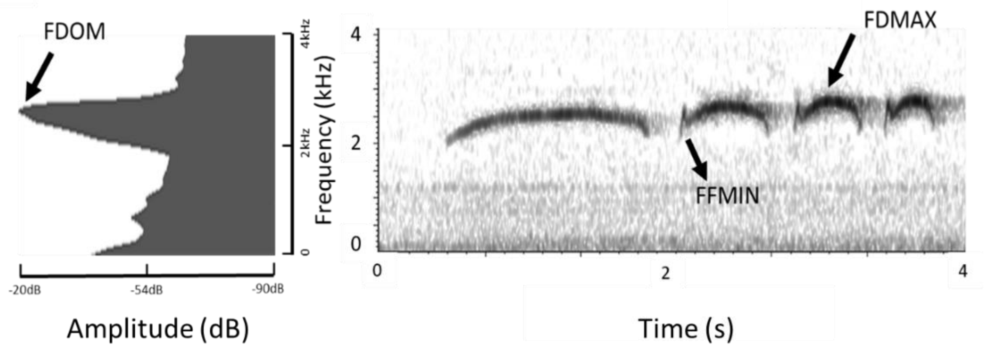


Figure 2. Sonogram of the song of tufted antshrike *Mackenziaena severa*, with the vocal variables: the dominant frequency (FDOM), the minimum fundamental frequency (FFMIN), and the maximum dominant frequency (FDMAX).

Data analysis

We run the multivariate cluster analysis to produce a dendrogram showing the distance between species (Zar 1999), considering acoustic parameters that describe their respective vocalizations. We selected the unweighted pair-group average (UPGMA) algorithm to organize the clusters in the dendrogram accordingly to the average distance between all pairs of species, based on Euclidean distance index (Manly 2008). A total of 1000 bootstrap replicates was simulated to verify the percentage of replicates each node connecting pairs or cluster of species still the same. Finally, the cophenetic correlation coefficient measured how reliably the dendrogram preserved the pairwise distances between the original unmodeled data (Jackson et al. 1989).

We elaborated a network plot with nodes (species) connected by edges (Hammer 2020) that indicate the co-occurrence relationship between species. We applied the correlation model to define edges using the similarity cutoff of 50%, i.e., only species with more than 50% of similarity, in terms of co-occurrence in point samples, were connected by edges. In the network graph, the diameter of nodes (species) is proportional to the number of connections (edges), and the thickness of edges between species is proportional to the similarity (co-occurrence patterns) between them. We used the Fruchterman-Reingold algorithm to organize the nodes starting from a random position, and then connecting species and groups of species according to the correlation similarity (Fruchterman & Reingold 1991).

We measured the frequency of occurrence and (FO) and Punctual Index of Abundance (PIA) for each species to use for the analysis only frequently registered species and use PIA values to discuss the network plot and co-occurrence of species.

We used PAST Program (Hammer et al. 2001), version 4.0 released in January 2020, to run statistical analysis and elaborate graphics.

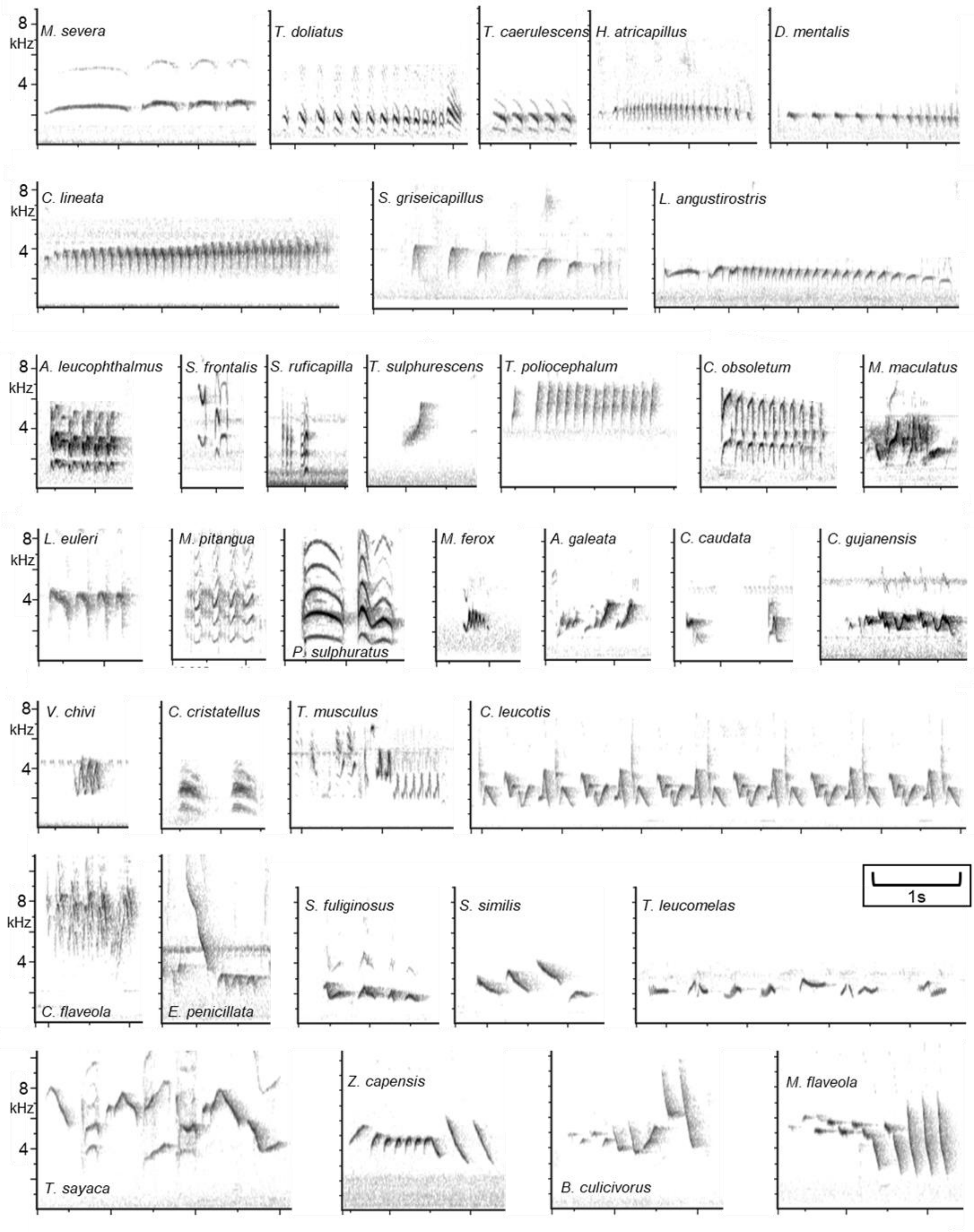
Results

Acoustic community

Throughout one year of fieldwork, 38 passerine species were recorded with a Frequency of Occurrence higher than 25%, however, three of them were mainly or only recorded performing short calls, totaling 35 species. The community was mostly represented by Tyrannidae (n = 6) followed by Thamnophilidae (n = 5) and Thraupidae (n = 5). The canopy was the most occupied stratum, with 17 dwelling species, the terrestrial the least, with five, and the other two strata (understory and midstory) were equally representative (16 species each) (see Table 1). The mean values of FFMIN ranged from 0.353 kHz (*Thamnophilus doliatus*) to 3.742 kHz (*Coereba flaveola*); FDMAX from 2.030 kHz (*Thamnophilus caerulescens*) to 12.056 kHz (*Eucometis penicillata*); and FDOM from 1.681 kHz (*T. caerulescens*) to 7.907 kHz (*C. flaveola*) (Table 1, Fig. 3).

Table 1. List of species of the fragment that presented a frequency of occurrence > 25% with the means of the vocal variables Minimum fundamental frequency (FFMIN), Maximum dominant frequency (FDMAX) and Dominant Frequency (FDOM); and foraging strata: T = terrestrial, U = understory, M = midstory and C = canopy according to Wilman et al. (2014).

Species	**FFMIN (kHz)**	**FDMAX (kHz)**	**FDOM (kHz)**	**STRAT**
Mackenziaena severa (Lichtenstein, 1823)	1.875	3.016	2.744	U
Thamnophilus doliatus (Linnaeus, 1764)	0.353	2.489	1.772	U/M
Thamnophilus caerulescens Vieillot, 1816	0.515	2.030	1.681	U/M
Herpsilochmus atricapillus Pelzeln, 1868	1.065	2.638	2.142	C
Dysithamnus mentalis (Temminck, 1823)	0.944	2.247	2.001	U/M
Conopophaga lineata (Wied, 1831)	2.258	4.596	3.481	U
Sittasomus griseicapillus (Vieillot, 1818)	1.753	5.377	4.361	M
Lepidocolaptes angustirostris (Vieillot, 1818)	1.261	2.878	2.573	U/M
Automolus leucophthalmus (Wied, 1821)	0.796	3.714	3.323	U
Synallaxis frontalis Pelzeln, 1859	1.368	7.027	4.756	U
Synallaxis ruficapilla Vieillot, 1819	0.546	4.018	3.623	U
Tolmomyias sulphurescens (Spix, 1825)	3.159	5.261	4.790	C
Todirostrum poliocephalum (Wied, 1831)	3.510	6.961	5.752	M/C
Camptostoma obsoletum (Temminck, 1824)	1.295	7.880	4.553	C
Myiodynastes maculatus (Statius Muller, 1776)	0.871	4.932	3.067	M/C
Lathrotriccus euleri (Cabanis, 1868)	1.645	4.478	3.859	M
Megarynchus pitangua (Linnaeus, 1766)	0.991	5.225	3.882	C
Pitangus sulphuratus (Linnaeus, 1766)	0.750	4.060	3.501	T/C
Myiarchus ferox (Gmelin, 1789)	1.796	3.192	2.872	M/C
Antilophia galeata (Lichtenstein, 1823)	1.525	3.749	3.040	M/C
Chiroxiphia caudata (Shaw & Nodder, 1793)	0.916	3.064	2.465	U/M
Cyclarhis gujanensis (Gmelin, 1789)	1.348	3.127	2.628	M/C
Vireo chivi (Vieillot, 1817)	2.178	4.798	3.342	C
Cyanocorax cristatellus (Temminck, 1823)	0.764	4.411	2.665	M/C
Troglodytes musculus Naumann, 1823	1.163	7.064	4.026	T/U
Cantorchilus leucotis (Lafresnaye, 1845)	0.874	4.276	3.167	U
Turdus leucomelas Vieillot, 1818	1.454	3.293	2.464	T/C
Coereba flaveoa (Linnaeus, 1758)	3.742	11.143	7.907	C
Saltator fuliginosus (Daudin, 1800)	1.284	2.911	2.207	C
Saltator similis d'Orbigny & Lafresnaye, 1837	1.403	4.243	3.326	M/C
Tangara sayaca (Linnaeus, 1766)	2.037	8.549	5.643	C
Eucometis penicillata (Spix, 1825)	1.352	12.056	5.019	U/M
Zonotrichia capensis (Statius Muller, 1776)	2.703	6.966	4.370	T/U
Basileuterus culicivorus (Deppe, 1830)	3.136	8.656	4.796	U/M
Myiothlypis flaveola Baird, 1865	2.017	7.055	5.104	T/U



8
kHz
4
M. severa
T. doliatus
T. caerulescens
H. atricapillus
D. mentalis
C. lineata
S. griseicapillus
L. angustirostris
A. leucophthalmus
S. frontalis
S. ruficapilla
T. sulphurescens
T. poliocephalum
C. obsoletum
M. maculatus
L. euleri
M. pitangua
P. sulphuratus
M. ferox
A. galeata
C. caudata
C. gujanensis
V. chivi
C. cristatellus
T. musculus
C. leucotis
1s
C. flaveola
E. penicillata
S. fuliginosus
S. similis
T. leucomelas
T. sayaca
Z. capensis
B. culicivorus
M. flaveola

Figure 3. Overview of the songs of the 35 bird species used for the analyses. Each species is represented by a spectrogram of a typical song recording.

Species grouping according to vocal parameters

According to the vocal variables, we generated a dendrogram that clustered species regarding the three vocal variables (Cophenetic Correlation Coefficient = 0.8789, Fig. 4). Species with higher mean values for FDMAX and FDOM appeared on an extreme of the dendrogram (*C. flaveola* and *E. penicillata*), contrasting with *M. ferox* and *M. severa* which presented lower overall FDOM. Considering and adding strata information, it is expected that birds closer in the dendrogram and occupying the same height of the forest are the strongest competitors (e. g. *S. frontalis* and *M. flaveola* since both occupy the understory; *D. mentalis*, *T. doliatus* and *T. caerulescens*, since all three species present similar songs and occupy both understory and midstory strata).

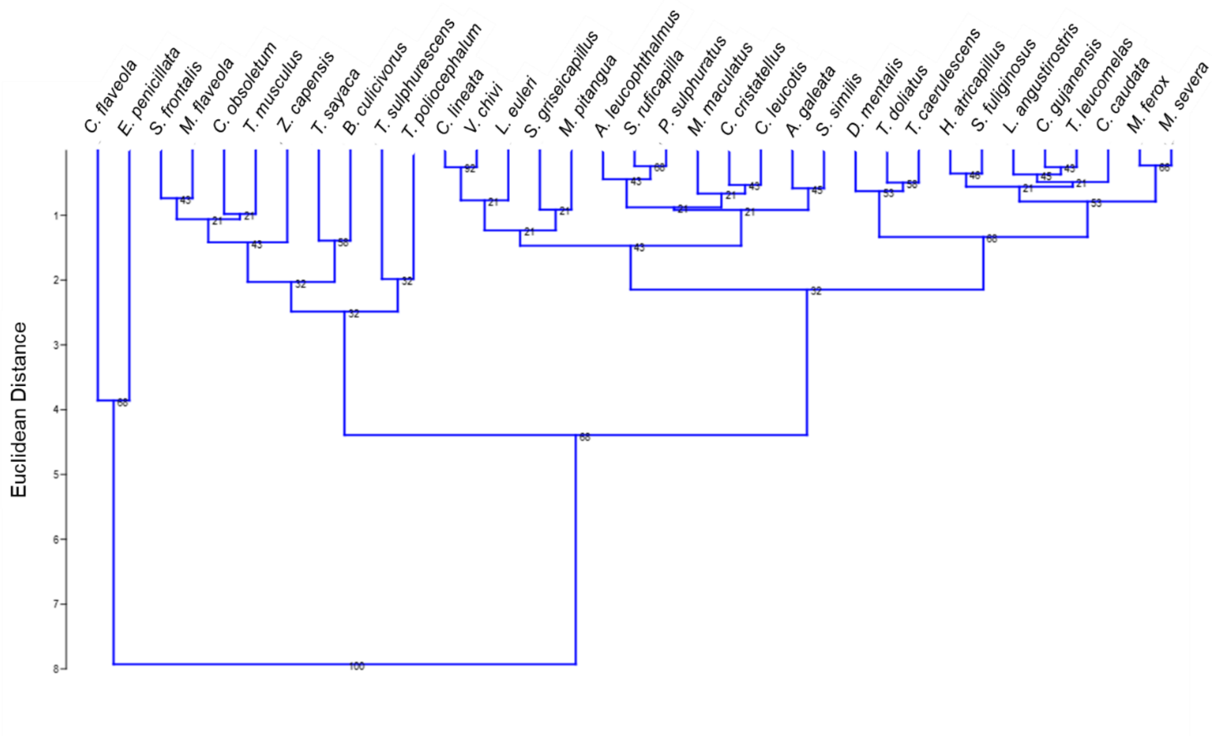


Figure 4. Dendrogram from the multivariate cluster analysis showing the distance between species based on three vocal parameters (Cophenetic Correlation Coefficient = 0.8789).

According to the obtained PIA values, the most abundant species were *B. culicivorus* (0.75), *T. leucomelas* (0.70), *S. ruficapilla* (0.63), *C. lineata* (0.55), *T. caerulescens* (0.54) and *M. flaveola* (0.50). The lowest values were from *L. angustirostris* (0.07), *S. frontalis* (0.08) *E. penicillata* (0.08), *C. cristatellus* (0.08), and *T. sayaca* (0.09) (although the lowest values were still from species with FO > 25%) (Fig. 5).

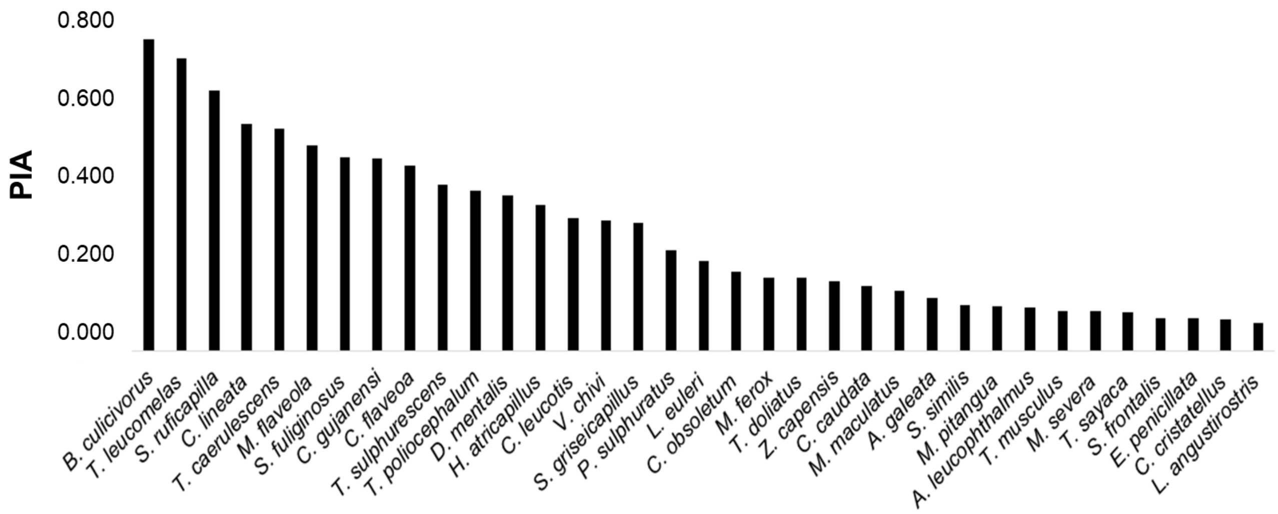


Figure 5. Punctual index of abundance (PIA) in descending order of the 35 bird species that presented a Frequency of Occurrence (FO) higher than 25%.

The network plot demonstrated the co-occurrence of species across the sample points. The species that presented more number of networks (significant co-occurrence with other species) were: *M. ferox*, *P. sulphuratus*, *S. fuliginosus*, *D. mentalis*, and *S. griseicapillus* (Fig. 6). No pair of species that presented similar vocal characters and occupy the same forest stratum was found to be significantly co-occurring. Hence, species singing in the same 15 minute period presented more varied frequency ranged songs and were more distributed among different strata.

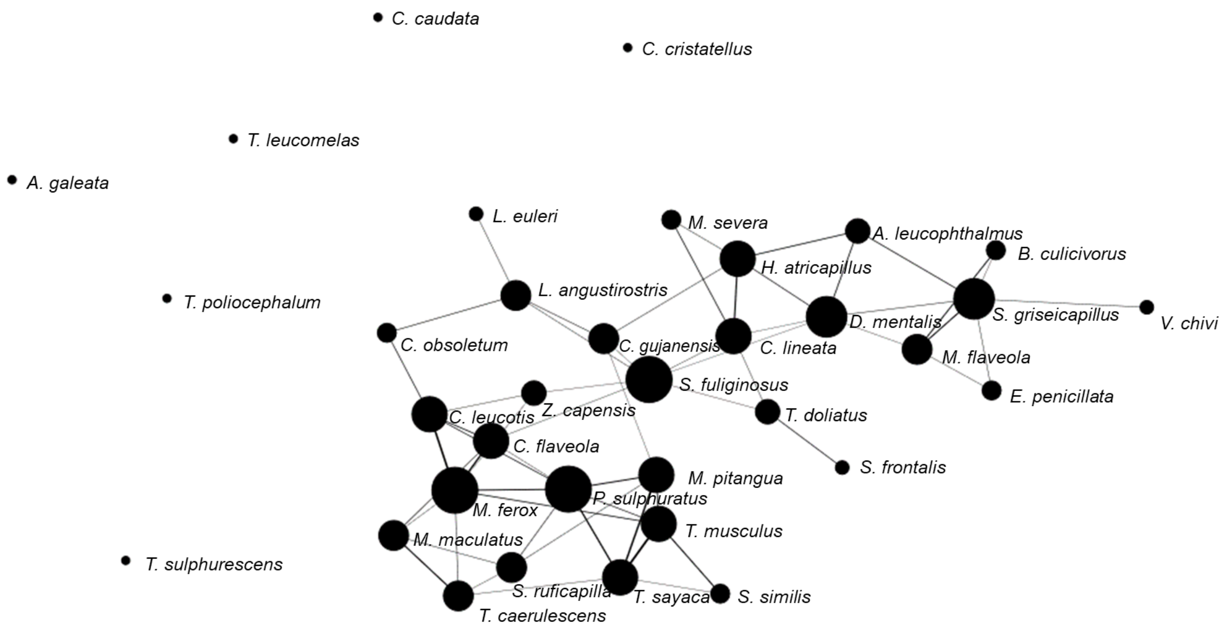


Figure 6. Network plot with nodes (species) connected by edges (Hammer 2020) that indicate the co-occurrence relationship between species.

Discussion

The focus of this study was to investigate whether avian vocalizations and foraging strata were more dispersed in the same 15-minute interval. The Euclidean distances regarding spectral parameters of the song of the 35 birds' species that presented a FO > 25%, showed that the birds from this community presented dispersed songs concerning frequency range among species singing in the 15-minute sample point. Of the 35 species, 17 are forest-dwelling exclusives and four are generalist species that usually occupy forest edges (Stotz et al. 1996). Because avian communities are a mixture of native and non-native species, and the latter can mask vocalizations of native birds (Azar & Bell 2016), we believe that the same may apply in the blend of sounds of forest exclusive and generalists' species. On a similar approach, Medeiros et al. (2016) found evidence that the introduction of new sounds from the invasive species *Lithobates catesbeianus* can cause native species to modify their vocalizations.

Different sizes and conservation status of fragments should present different communities (Devictor et al. 2008; Carrara et al. 2015) and a varied combination of acoustic signals acting as a selecting pressure on vocalizations (Pijanowski et al. 2011). For instance, Belinsky et al. (2012) found that *Spizella arborea* suffered more acoustic masking when occupying forest edges, thus one should expect more vocal competition for the species in smaller fragments. The vocal analysis and strata classification of species in this study suggest that the forest-dwelling species *B. culicivorus* may be competing for acoustic space with generalist species *T. musculus* and *Z. capensis* since they occupy similar frequency range and strata (understory). According to Laiolo (2012), the distribution of competing species determines how the structure of the environment acts regarding selecting pressures, and although *B. culicivorus* presented the highest PIA, and *Z. capensis* and *T. musculus* presented more co-occurrence networks with lower PIA, the three species did not present a connexion in the analysis. Thus, these factors may influence the non-randomization of the distribution of species across point counts.

The diverse vocal frequency and strata occupancy among co-occurring species suggest that birds singing in the same frequency range are partitioning the acoustic space by choosing different times of the morning to sing. Because species inhabiting the same community face similar environmental selection pressures, acoustic signals may converge into those favored within each habitat regarding different vegetation densities (Haavie et al. 1985; Badyeav & Leaf 1997). Additionally, passerine birds tend to have higher abundance and richness compared to larger species (Greenwood et al. 1996; Oslon et al. 2009), and acoustic competition should be greater among these birds. Thus, birds avoiding to vocalize when other species of the same frequency range are singing may be a strategy to avoid signal masking and vocal overlap (Wiley 1994; Planqué & Slabbekoorn 2008) since acoustic interference occurs mostly among species with similar songs at similar places and times, rather than across the entire bird avian community (Luther 2009). For instance, species singing in similar dominant frequencies can divide acoustic space by selecting different times to sing (Luther 2008).

The partition of acoustic space was also reported in other animal taxa, and appears to be fundamental for local co-existence of species (Sinsch et al. 2012): Boquimpani-Freitas et al. (2007) observed a temporal partitioning in acoustic dynamics and Lima et al. (2018) found spectral variance to reduce acoustic interference in anuran communities; Ruppé et al. (2015) reported call partitioning in fishes during the day and night periods; Schneider et al. (2008) observed the usage of different portions of spectral and temporal niches by four sympatric primate species that improved sound transmission; Sueur (2002) suggested that the specific features of vocalizations and preference for specific heights of calling sites of a cicada community lead to a partitioning of the acoustic environment and might thus decrease the risk of heterospecific mating.

The strata occupancy dispersion in co-occurring species is likely to be linked with competition and sound emission. Because the acoustic space has multiple axes, the spatial location of signallers (Check et al. 2003), combined with song characteristics and the timing of singing (Sueur 2002; Luther 2008) will influence the distribution of co-occurring species. Sound propagation varies across different heights (Marten et al. 1977; Ellinger & Hodl 2003; Sabatini & Ruiz-Miranda 2010), and the stratum from which birds are singing may be adapted to optimize transmission (Lemon et al. 1981; Nemeth et al 2001; Dent et al. 2009), thus the acoustic interference among co-occurrence species singing in similar frequency range may be attenuated by occupying different strata. The pattern of distribution of species across 15-minute point counts observed in this study corroborates to other authors' findings. Luther (2009) and Sueur (2002) found that species vocalizing at the same time of the morning were more dispersed in acoustic space than species singing at different times and strata.

In conclusion, the co-occurrence of birds that present distinct frequency range vocalizations and strata occupancy shows a non-randomized pattern of distribution. This result highlights the importance of acoustic censuses and analysis to assess community structure and dynamics and possible non-direct implications of forest fragmentation for forest-dependent species.

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Appendix 1. Recordings' authorship of the 35 studied species.

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CAPÍTULO 3

ACOUSTIC INTERSPECIFIC INTERACTION OF A SYMPATRIC PAIR OF PARULIDAE BIRDS IN A SEMI-DECIDUOUS FOREST

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Acoustic interspecific interaction of a sympatric pair of Parulidae birds in a semi-deciduous forest

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Abstract. Different habitats and avifaunal compositions drive signal evolution to optimize transmission. We investigate how two closely related species, *Basileuterus culicivorus* and *Myiothlypis flaveola*, which sing in similar frequency bands, coordinate song emission. We first compared vocal parameters of both species to other nine species to set the vocal proximity regarding allopatry and sympatry; then we checked the monthly occurrence of the two species in 15 survey points throughout the year and, finally, we measured interval duration and song bouts per minute when singing together and separated. PCA confirmed a significant overlap of vocal variables in the two species and regarding other sympatric or allopatric pairs. We found that *M. flaveola* presented a preference to sing in sample points where *B. culicivorus* was vocalising, but the latter performed less song phrases per minute and varied the inter song interval when vocalizing together. The first finding could be explained as an interspecific vocal interaction and the second as an adaption to avoid vocal overlap, as well as the interspecific emission of songs shortly after to fill silence windows. This result shows the acoustic dynamics between species with similar songs and enhances the importance of the prevalence and co-occurrence on an interspecific level.

Keywords. Acoustic space; vocal overlap; warblers; vocal divergence.

Introduction

Communication signals among birds express important information that enables specific recognition, mate choice decisions, and hierarchy settle on territorial disputes (Catchpole and Slater 1995; Bradbury and Vehrencamp 1998). To optimize sound transmission, species must aim to adapt and perform their songs on different ecological conditions, such as vegetation and the avifaunal community (Ryan and Brenowitz 1985; Cardoso and Price 2010). Different habitats imply a variety of vegetation types and densities that can cause acoustic effects on frequency and amplitude of vocalizations, and thus, on sound transmission (Morton 1975; Ryan and Brenowitz 1985). Habitat fragmentation also acts as a selective force for the acoustic community, since it can lead to variations on species richness and abundance (e. g. local absences and establishment of ecotonal species) depending on the edge-to-interior ratios (Odum 1958; Helzer and Jelinski 1999; Baker et al. 2002). Hence, different levels of habitat degradation provide a varied combination of background sounds that will also affect song evolution (Kirschel et al. 2009).

Acoustic interference from background noise can reduce the efficacy of sound transmission and, therefore, the ability of the receiver to process the signal information (Wiley 1994). Signal masking can lead to interspecific communication, and thus possible hybridization, and to unnecessary energy spent if an individual is emitting a signal that will not be delivered (Endler 1992). Biotic sounds are one of the main sources of background noise and, because of that, the evolution of signals may favor sounds that fit the available frequency portions on the acoustic space (Seddon 2005; Azar and Bell 2016). However, even with song evolution and divergence, there are still species singing in similar frequency bands in the same bird assemblage. Because of that, these species face ecological competition, driving the use of different portions of the acoustic space to avoid vocal overlap, and thus signal masking (Miller 1982; Brumm and Slabberkoorn 2005).

The acoustic space can be partitioned, when birds either choose times and places to sing to avoid interference (e. g. Luther 2009), or birds could coordinate their singing bouts at the same period of time to fit into silence windows (e. g. Ficken et al. 1974; Popp et al. 1985). And, besides getting the message across, the type of signal, timing and the ability to coordinate and avoid overlapping, carry information about the quality, status and motivation of the sender (Vehrencamp 2000). Furthermore, species may sing less to avoid singing when other species using the same frequency range are active, and may suffer some degree of fitness costs (Planqué and Slabberkoorn 2008).

Because closely related species have more chance of interbreeding, the phylogenetic composition of a bird community can shape the song structure within populations (Kroodsma and Canady 1985). Considering sympatric species as co-habiting closely related, and allopatric as closely related but isolated populations (Mayr 1963), patterns of song evolution can be outlined in both cases: the species recognition hypothesis proposes that differences in song structure among species have evolved to reduce hybridization, and, thus, a shift in species-specific vocal characters should be expected in sympatry (Miller 1982). This prediction was tested in a few studies and confirmed (e. g. Haavie et al 2004; Seddon 2005) although refuted by others (Irwin 2000). On an evolutionary approach, mating signals will diverge in sympatry because selection favours traits that increase assortative mating and works against signals that would lead to unfit hybrids (Liou and Price 1994; Seddon 2005).

The species *Basileuterus culicivorus* (Deppe, 1830) and *Myiothlypis flaveola* Baird 1865 are two passerine birds from the Parulidae family. Both species formerly belonged to the same genus (*Basileuterus*) along other *Myiothlypis*, but molecular evidence suggested that *Myiothlypis* should be separated in a different genus (Lovette et al. 2010). Although both species occupy the understory to forage, *M. flaveola* is also commonly registered in terrestrial strata, while *B. culicivorus* tends to occupy the midstory (Wilman et al. 2014). Nonetheless, the two species are closely related genetically and a sympatric pair. Because both species are usually found occupying the same avifaunal community and the same habitat, and personal observations revealed one species singing immediately after another, we aimed to investigate the vocal dynamics between these two species. For that, we asked the following questions: (1) how close are the vocal variables between these two species regarding other sympatric and allopatric species of both genera? (2) Are both species portioning acoustic space and thus coordinating to sing at different times of the day? (3) Is there a variation on the vocal behavior of both species when singing together and separated? Since both species are closely related and sing in a similar frequency range, we predict a shift on vocal behavior when singing together, and, although contradicting previous works, we also expect that these two sympatric species sing more similar songs than others occurring in allopatry. With those raised question we aimed to investigate the vocal evolution among a complex of species and to understand the vocal interaction among the ones occurring in sympatry.

Material and Methods

Study site and field data

The study was conducted in a stationary semi-deciduous forest within the Paraíso Farm which is situated in the municipality of São Carlos, in São Paulo state, Brazil (25º59’08.8”S, 47º50’09.2”W). The farm occupies an area of 195 ha in total, with 77 ha belonging to the forest fragment. The fragment is mainly surrounded by sugar cane and corn plantations and pasture areas. We established 15 points alongside three trails (five points on each) aiming to cover as much as possible of the available area of the fragment. All points had a separation distance of at least 200 m (Fig. 1).

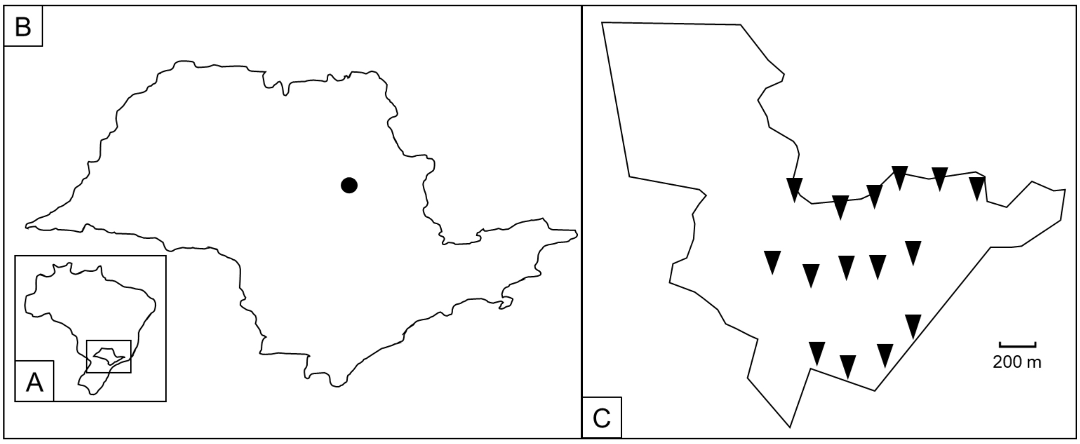

Figure 1. Maps of (A) Brazil, (B) São Paulo State, and the city of São Carlos and (C) the studied forest fragment area with the 15 sample points highlighted.

The data collection occurred twice a month from May 2017 to April 2018 and the audio recordings were made during the morning period (6:00-10:00). Since we wanted to compare the vocal activity, we visit one trail per day during the same period, totaling 72 days of field monitoring and 90 hours of song recordings. We collected audio samples of 15 min interval for each survey point while annotating the active vocal species and the number of individuals on a spreadsheet. To obtain the best quality examples of both species' songs, we used a Sennheiser ME66 directional microphone and a Marantz PDM661 digital recorder, all recordings were made with a 48 kHz sampling rate and a 24-bit resolution.

Vocal features of species occurring in sympatry x in allopatry

To test the species recognition hypothesis, that sympatric species have a higher level of song divergence than allopatric species, we chose other nine species to sample and compare vocal features. Out of the nine species, three were sympatric from the genus *Myiothlypis* (*Myiothlypis leucoblephara* (Vielliot, 1817); *Myiothlypis rivularis* (Wied, 1821); *Myiothlypis leucophrys* (Pelzeln, 1868)), three were allopatric from the same genus (*Myiothlypis fulvicauda* (Spix, 1825); *Myiothlypis bivittata* (d'Orbigny & Lafresnaye, 1837); *Myiothlypis nigrocristata* (Lafresnaye, 1840)) and three were allopatric from the genus *Basileuterus* (*Basileuterus rufifrons* (Swainson, 1838); *Basileuterus tristriatus* (Tschudi, 1844); *Basileuterus trifasciatus* Taczanowski, 1880). We collected 10 audio recordings of each species from the WikiAves site (<http://www.wikiaves.com> Last accessed on 10 Jun 2019) and Xeno-canto (<http:// https://www.xeno-canto.org> Last accessed on 10 Jun 2019), selecting only clear recordings with high signal-to-noise ratio for analysis. For the focus species of this study, *M. flaveola* and *B. culicivorus*, we collected recordings from WikiAves (18) and included recordings made on our fieldwork (2), to obtain mean values of vocal variables of individuals from different locations across the distribution (see Appendix 1 for authorship information).

The sound analyses and measurements were made in the Raven 1.5.0 software (Bioacoustics Research Program 2014) and the selected vocal parameters were: 1) the dominant frequency (Fdom), defined as the spectrogram region with most energy concentration; 2) the minimum fundamental frequency (Ffmin); 3) the maximum fundamental frequency (Ffmax) (minimum and maximum frequencies of the fundamental harmonic, respectively); 4) total duration of the song patch (Sdur) and 5) the number of notes (Nnot) (Fig. 2). The numeric values of the maximum and minimum variables were measured with the cursor placement on the sonogram view, and the Fdom values were obtained by selecting the song portion and the desired measurement ("Peak Frequency" on Raven).

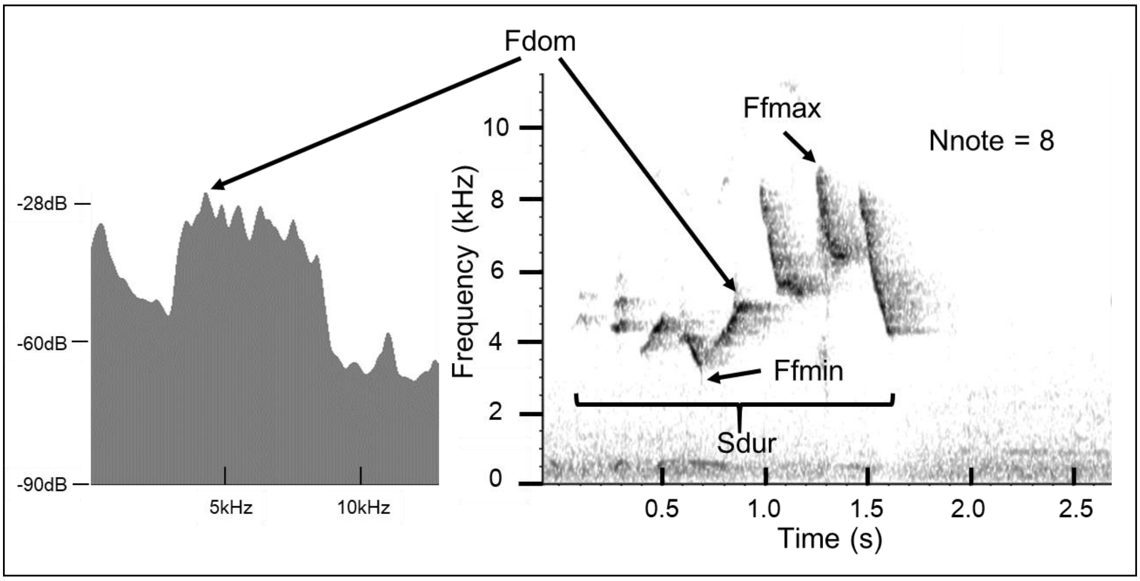

Figure 2. The sonogram and Fast Fourier transformation of the song of *B. culicivorus*, illustrating the vocal parameters measured: Ffmax, maximum fundamental frequency, Ffmin, minimum fundamental frequency, Fdom, dominant frequency, Nnote, number of notes; Sdur, song duration.

Time of singing and monthly occurrence

To test if both species divide the acoustic space, we analyzed the audio recordings from sample points made throughout the year to check if birds were avoiding to sing in the same 15 min time interval. Since field trips occurred two times per month on each trail, we checked the occurrence of both species on the 15 points, totaling 360 samples. We gathered data into three groups: 1) *B. culicivorus* vocally active without *M. flaveola*; 2) *M. flaveola* vocally active without *B. culicivorus*; 3) *B. culicivorus* and *M. flaveola* vocally active.

Vocal activity dynamics between B. culicivorus and M. flaveola

To compare how both species performed and emitted song bouts in the presence of the other, we only used recordings made during the reproductive period (from July to December (Sick 1997)) of both species to avoid tendencies on the vocal parameters (e. g. more song patches in a month of the breeding period when compared to a non-reproductive month). We then selected sites where birds were singing continuously for at least three min. We did not use the same survey site in the same category to avoid sampling the same individual, therefore we selected 10 points of 15 min interval of each category (*B. culicivorus* vocally active without *M. flaveola*; *M. flaveola* vocally active without *B. culicivorus*; *B. culicivorus* and *M. flaveola* vocally active), totaling 30 points. We then made the following comparisons: 1) Vocal activity of *B. culicivorus* without *M. flaveola* versus vocal activity of *B. culicivorus* with *M. flaveola*; 2) Vocal activity of *M. flaveola* without *B. culicivorus* versus vocal activity of *M. flaveola* with *B. culicivorus*.

For this vocal analysis, we measured the time interval between song patches and the number of song patches per min. After obtaining the mean of the inter-song time duration of each individual we calculated the coefficient of variation, defined as the ratio of the standard deviation to the mean, to check how individuals were emitting songs and varying the timing.

Statistical analysis

To assess the variation among allopatric and sympatric species, we used Principal Component Analysis (PCA) to reduce the multivariate data set to the main two significant vocal parameters, accounted for most of the variance (Manly and Alberto 2016). Since the five selected vocal parameters are measured in different units, the procedure was carried out using a correlation matrix with the SDV algorithm, which normalized all variables using division by their standard deviations (Hammer 2019). The PCA routine plotted points (individuals) in a bidimensional coordinate system given by two principal components, aiming to visually describe differences among groups of points (11 species) with a two-axis graph. To evaluate the occurrence of both species in the survey points and the variation of the singing activity when singing together and separated, we performed Kruskal-Wallis and Mann-Whitney tests, respectively. We used PAST Program to run these analyses (Hammer et al. 2001; vers.3.25 released in April 2019).

Results

Species recognition hypothesis

The principal component analysis of five vocal parameters of the 11 species of the *Myiothlypis*/*Basileuterus* complex revealed a random grouping regarding allopatry and sympatry (Fig. 3). For instance, the species *M. nigrocristata*, an allopatric species that occurs in Colombia, Venezuela, and Peru (Curson, 2019), showed the proximity of vocal characteristics to both of the focal species of this study, however, *Myiothlypis leucoblephara*, a sympatric species, also showed a close relationship regarding the vocal parameters.

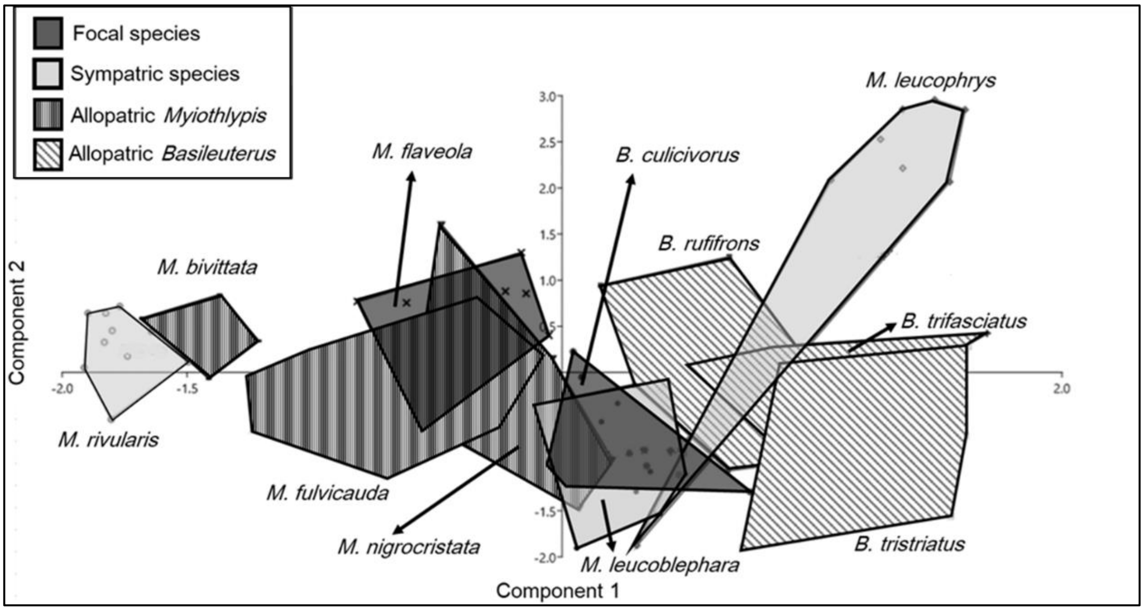

Figure 3. Principal component analysis of five vocal parameters of the 11 species: Ffmax and Fdom (81.97% and 12.81%, respectively) best explained the variation among species.

The components that best explained the variation among species in the PCA were the Ffmax and the Fdom (81.97% and 12.81%, respectively). This result expresses an overall tendency among the 11 species: even with expressive variations on maximum and dominant frequencies (4.1 kHz to 10 kHz and 3.3 kHz to 7.4 kHz, respectively), the minimum fundamental frequency did not present a parallel variation, for example, species with higher maximum frequencies did not have higher minimum frequencies (Table 1, but see Appendix 1 for individual measurements).

Table 1. Mean values and standard deviations for the five-song variables of the 11 species of allopatric and sympatric populations.

	Focal species		Sympatric species			Allopatric *Basileuterus*			Allopatric *Myiothlypis*		
	B. culici	*M. flaveo*	*M. leucob*	*M. rivula*	*M. leucop*	*B. tristr*	*B. trifas*	*B. rufifr*	*M. bivitt*	*M. fulvic*	*M. nigroc*
Variables	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD	x ± SD
Fdom (kHz)	4.8 ± 0.5	5.1 ± 0.5	4.9 ± 0.3	3.3 ± 0.3	7.4 ± 2.1	6.2 ± 0.8	6.3 ± 0.6	5.9 ± 0.6	3.8 ± 0.2	4.0 ± 0.7	4.7 ± 0.7
Ffmin (kHz)	3.4 ± 0.2	2.0 ± 0.2	3.5 ± 0.4	1.7 ± 0.1	2.1 ± 0.2	3.9 ± 0.4	3.9 ± 0.4	2.7 ± 0.1	1.7 ± 0.3	1.9 ± 0.2	2.5 ± 0.5
Ffmax (kHz)	8.7 ± 0.5	7.0 ± 0.5	8.5 ± 0.6	4.1 ± 0.3	9.8 ± 0.2	10 ± 0.8	9.5 ± 0.6	8.9 ± 0.9	4.9 ± 0.2	6.8 ± 0.8	7.5 ± 0.8
Sdur (s)	1.7 ± 0.1	1.9 ± 0.2	5.4 ± 0.8	4.2 ± 0.9	3.0 ± 1.0	3.4 ± 0.7	2.5 ± 0.5	1.5 ± 0.2	1.9 ± 0.2	4.1 ± 0.7	2.4 ± 0.9
Nnote	8.5 ± 1.2	13 ± 1.2	24 ± 2.9	15 ± 2.6	31 ± 5.8	49 ± 5.9	29 ± 3.4	13 ± 1.5	14 ± 1.8	26 ± 4.3	17 ± 4.9
n	10	10	10	10	10	10	10	10	10	10	10

Table legend: *B. culici* = *Basileuterus culicivorus*; *M. flaveo* = *Myiothlypis flaveola*; *M. leucob* = *Myiothlypis leucoblephara*; *M. rivula* = *Myiohtlypis rivularis*; *M. leucop* = *Myiothlypis leucophrys*; *B. tristr* = *Basileuterus tristriatus*; *B. trifas* = *Basileuterus trifasciatus*; *B. rufifr* = *Basileuterus rufifrons; M. bivitt* = *Myiothlypis bivittata*; *M. fulvic* = *Myiothlypis fulvicauda*; *M. nigroc* = *Myiothlypis nigrocristata.*

Nevertheless, the analysis of the five vocal variables among individuals, showed that *B. culicivorus* and *M. flaveola* have similar songs, confirming that both species present vocal characteristics to overlap and occupy the same frequency band on a given acoustic niche (Fig. 4).

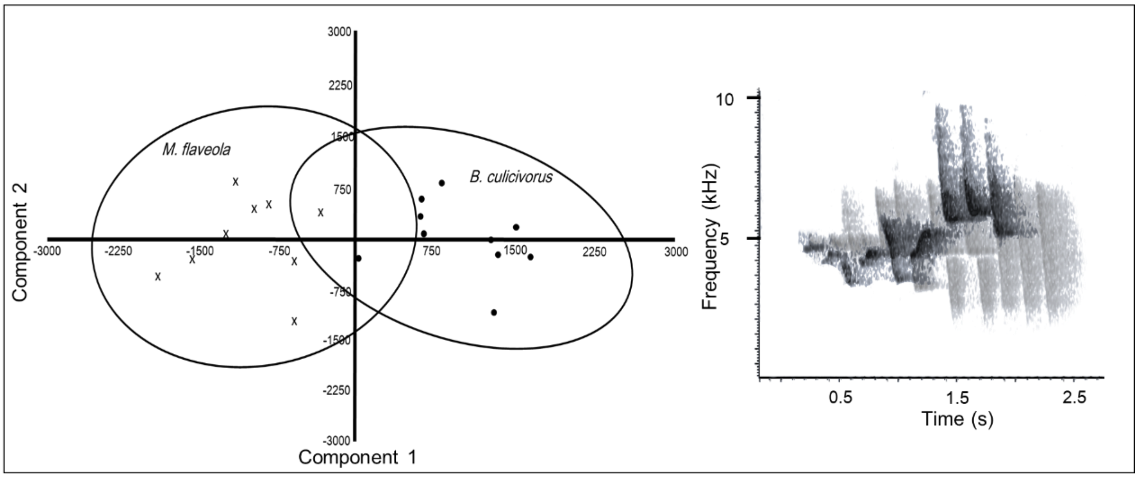

Figure 4. Principal component analysis of the five vocal parameters of *B. culicivorus* and *M. flaveola* (left); spectrograms of the two songs (darker from *B. culicivorus*, paler from *M. flaveola*) showing an overlap when singing at the same time (right).

Species occurrence

Out of the 360 samples of 15 min obtained from the survey points, *B. culicivorus* was vocally active in 240, while *M. flaveola* was active in 169 samples. Although these two groupings showed a significant higher vocal activity from *B. culicivorus*, when separating the samples into three groups, *B. culicivorus* singing without *M. flaveola*, *M. flaveola* singing without *B. culicivorus* and both singing in the same point, the variation among these groups were explained differently and not randomly: *B. culicivorus* was registered singing without *M. flaveola* in 111 samples, *M. flaveola* was registered singing without *B. culicivorus* in 40 and both species were registered singing at the same 15 min interval in 129 samples. The means and standard deviation for monthly occurrence were: 9.3 ± 2.16 times which *B. culicivorus* was registered singing without *M. flaveola*; 3.3 ± 0.94 times which *M. flaveola* was registered singing without *B. culicivorus*; and 10.8 ± 3.42 times which both were registered singing in the same 15-minute interval, showing a significant higher vocal activity from *M. flaveola* when *B. culicivorus* was singing (Kruskal-Wallis: $p < 0.001$) (Fig. 5).

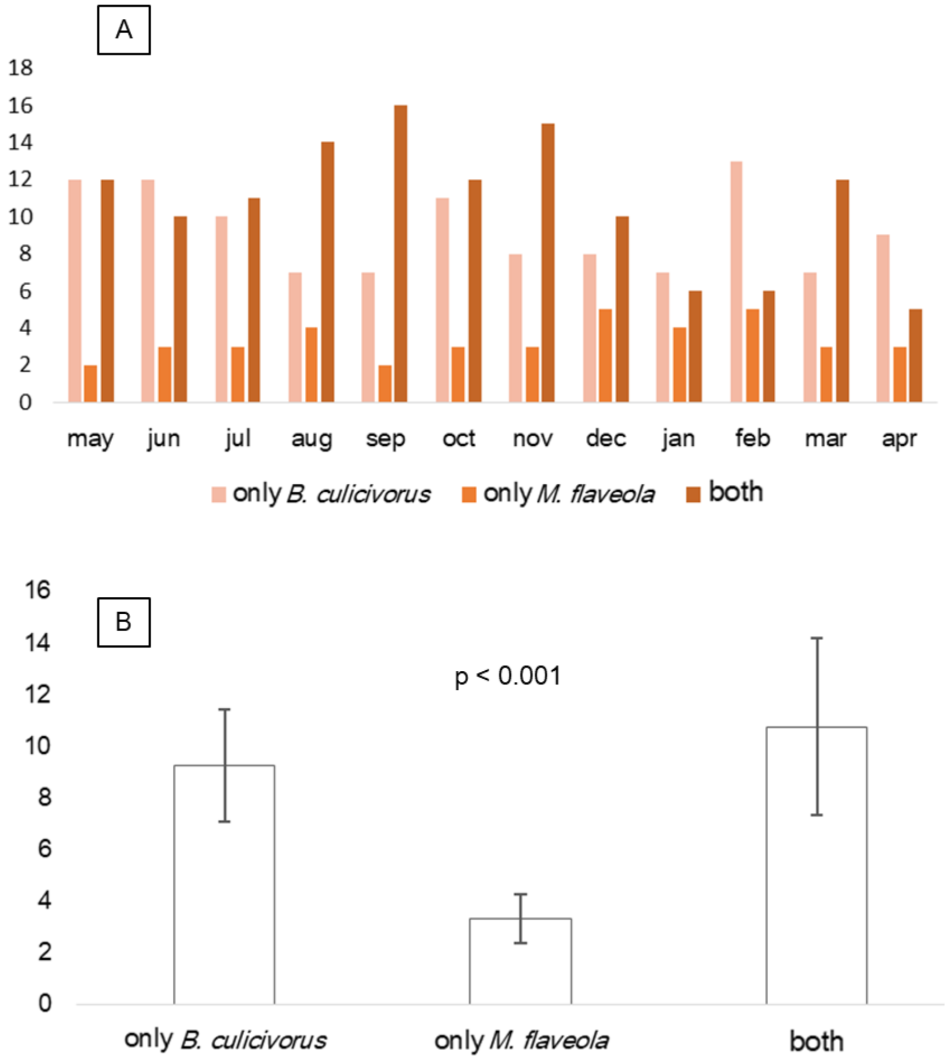

Figure 5. (A) Vocal occurrence of *B. culicivorus* and *M. flaveola* for each month of the year and (B) mean per month (Kruskal-Walis: $p < 0.001$).

Singing activity

The duration of silent intervals between song bouts varied significantly for *B. culicivorus* and *M. flaveola* when singing together (Mann-Whitney test, $p = 0.002$ and $p = 0.047$, respectively). The coefficient of variation presented a significant increase since birds remained silent for longer or either sang in short periods of time immediately after the other species. Although both species presented a higher coefficient of variation on the interval duration, only *B. culicivorus* was observed singing right after *M. flaveola*. This vocal interaction was observed 73 times throughout the survey points where both species were singing (Fig. 6). Although not statistically significant (p = 0.051 and 0.055), both species performed fewer song patches per min in this scenario.

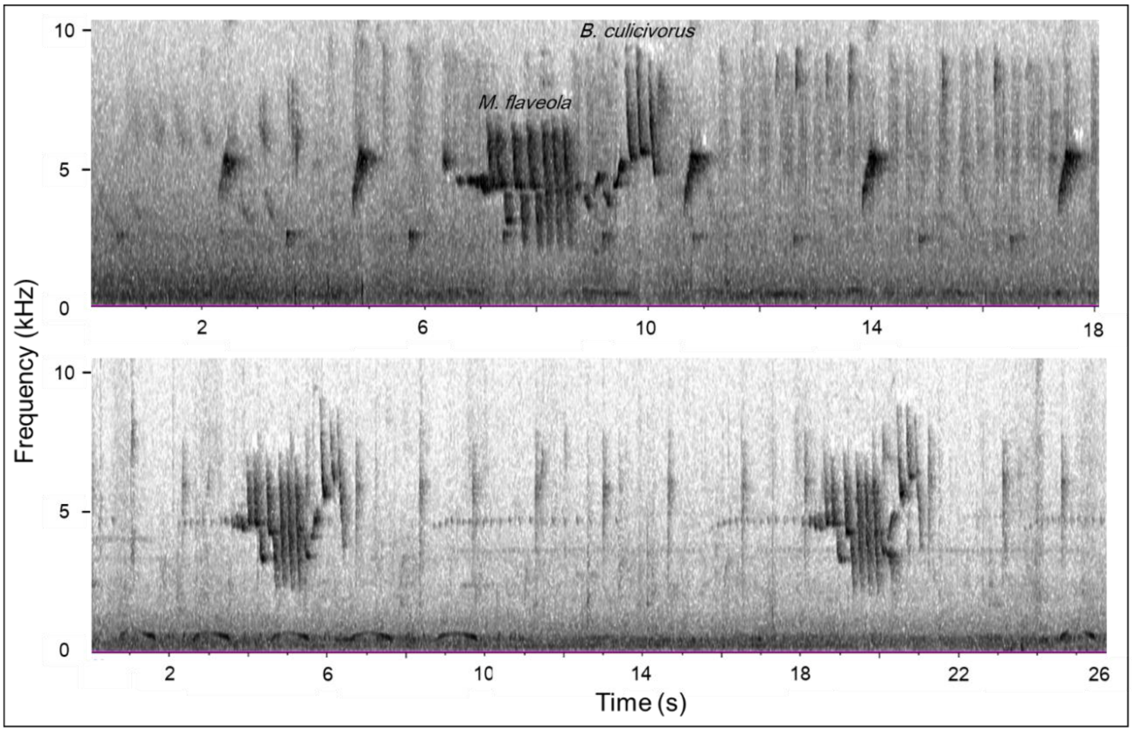

Figure 6. Two samples from distinct survey points showing *B. culicivorus* singing shortly after *M. flaveola*.

Discussion

The principal component analysis revealed that there are allopatric and sympatric species that are acoustically closely related to *B. culicivorus* and *M. flaveola*. However, regardless of the random grouping concerning allopatry and sympatry, the vocal variables of both species are similar and presented an overlap in the analysis and in the spectral band. This analysis implies that the species recognition hypothesis, which proposes that differences in song structure have evolved to reduce hybridization, is not fully supported for song evolution in this complex of species. This result contradicts other previous studies where sympatric pairs diverged more vocally than allopatric ones (Haavie et al.

2004; Seddon 2005). Therefore, other processes may have influenced song evolution more strongly in these species, such as adaptation to the signaling environment, when song evolution is driven to optimize sound transmission in different habitats, or morphological adaptation, when song evolved as a by-product of selection for changes in phenotypic traits (i. e. body size and consequently syrinx size) (Marten et al. 1977; Ryan and Brenowitz 1985; Podos 2001; Seddon 2005; Torres et al. 2019).

The focal species of this study are often reported occupying the same avifaunal community (Almeida et al. 1999; Telles and Dias 2007; Manica et al. 2010), hence we predicted that both species would adopt strategies to avoid overlapping each other's songs, and, therefore, avoid acoustic interference. One possible strategy is to coordinate different times to sing. Luther (2008) observed that two bird species with similar dominant frequencies divided the acoustic space, with one species singing early in the morning and the other later in the morning. On a different study, but a similar approach, Luther (2009) also observed that birds singing in the same stratum and in the same 30 min interval were more dispersed in the acoustic space than species singing in different strata and at different times of the morning.

Because both species occupy different strata (midstory and terrestrial for *B. culicivorus* and *M. flaveola*, respectively) (Wilman et al. 2014) and sound transmission varies from the canopy to the forest floor (Ellinger and Hodl 2003), this could be a possible explanation for the significant co-occurrence across the sample points, since the height from which birds sing may attenuate acoustic interference and may be adapted to optimize sound transmission (Nemeth et al. 2001). However, both species also share the understory stratum, and the vocal dynamic of singing after the other species to fill silence windows may be a strategy to avoid similar sounds to overlap.

The results of this study showed a significant variation in the 15-minute interval survey points where *M. flaveola* was reported singing with and without *B. culicivorus*. This variation can be explained by the low number of survey points where *M. flaveola* was registered singing without *B. culicivorus*. Since both birds are genetically closely related (Lovette 2010), this increase of vocal activity from *M. flaveola* in the presence of *B. culicivorus* could be explained as an interspecific interaction (Moller 1992; Magrath et al. 2007). Moller (1992) points out three possible explanations for heterospecific song eliciting: first, it can occur in a context of interspecific territoriality; second, the song of *B. culicivorus* could indicate the absence of predators, and thus eliciting the vocal activity of *M. flaveola*; and third, it may occur as a mistake when identifying heterospecific songs as conspecifics'. Since no territorial vocal behavior was observed from *M. flaveola* (e. g. temporal overlap *B. culicivorus* song, see Dabelsteen et al. 1997, Hall et al. 2006), the vocal activity of B. culicivorus likely works as an indicator of reduced risks of predation, thus other species, such as *M. flaveola*, consider a profitable situation to sing (Moller 1992).

The reported interaction in this study can also be observed in mixed bird flocks, in which information produced by a species can influence the organization of the bird community (Goodale et al. 2010). According to Goodale and Beauchamp (2010), leading species in mixed flocks are responsible for making critically important vocalizations, since it may attract predators, to provide information to their conspecifics, but other species might follow the emitted signal. This could be a possible explanation to *M. flaveola* not singing after *B. culicivorus*, but the opposite has often occurred since the latter is not the intended receiver but is detecting information (Peake 2005). In addition, leading species are reported to be less often silent than following species (Pagani-Núñez et al. 2018), since *B. culicivorus* performed fewer songs per minute when singing in the same 15-minute sample point.

Although apparently to be an advantage to sing when the other species is singing, *B. culicivorus* performed fewer songs per min and had a significant variation on the interval duration between song bouts in the presence of *M. flaveola*. The significant statistical variation translated the longer periods of silence followed by shorter intervals of *B. culicivorus* to sing immediately after the other species as opposed to more uniform vocal emissions when singing in the absence of *M. flaveola*. This vocal activity shift may have two possible explanations. First, it could also be a case of interspecific response because both species are closely related (Moller 1992; Magrath et al. 2007). Yet, because the activity of the species had a decrease when singing together, this explanation is unlikely to be the case. The second explanation for this acoustic dynamics is that, because both species sing in the same frequency band, *B. culicivorus* is avoiding spectral overlap and filling the available silence windows after *M. flaveola* stops singing (Ficken et al. 1974; Naguib 1999; Mennil and Ratcliffe 2004). This adaptation would prevent unnecessary energy spent (e. g. when emitting a song that is overpowered by others of similar frequency) and signaling errors (Ficken et al. 1974). Furthermore, the ability to time their songs and avoid overlapping could indicate male quality (Vehrencamp 2000).

In conclusion, this study present findings regarding the temporal niche of two closely related species. The increase of vocal activity driven by heterospecific song, as a possible indicator of the absence of predators, and the adaptation to avoid overlapping highlights the importance of the prevalence of species in the community structure on an interspecific level.

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Appendix 1

Recordings' authorship and individual vocal variables

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
B. culicivorus_01	WA252443	Gallaci 2010	4.393	3.420	9.195	1.590
B. culicivorus_02	WA1458567	Barbosa 2014	4.996	3.407	8.156	1.776
B. culicivorus_03	WA68597	Alves 2009	4.737	2.733	9.496	1.639
B. culicivorus_04	WA1214375	Zampieri 2013	4.737	2.784	7.730	1.735
B. culicivorus_05	WA865192	Godoy 2010	4.479	3.335	8.894	1.790
B. culicivorus_06	WA584983	Kaseker 2012	5.168	3.046	8.353	2.043
B. culicivorus_07	WA308022	Melo 2011	4.651	2.941	9.079	1.599
B. culicivorus_08	WA130533	Marques 2010	3.704	3.382	8.662	1.613
B. culicivorus_09	WA3285798	Filipino 2019	5.426	2.981	8.451	1.859
B. culicivorus_10	ALC034.1	Catalano 2017	5.672	3.328	8.546	1.414

Alves, W. N. 2009. [WA68597, *Basileuterus culicivorus* (Deppe, 1830)]. Wiki Aves - A Enciclopédia das Aves do Brasil. Available at: <http://www.wikiaves.com/68597>.

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Filipino, J. C. 2019. [WA3285798, *Basileuterus culicivorus* (Deppe, 1830)]. Wiki Aves - A Enciclopédia das Aves do Brasil. Available at: <http://www.wikiaves.com/3285798>.

Gallaci, R. 2010. [WA252443, *Basileuterus culicivorus* (Deppe, 1830)]. Wiki Aves - A Enciclopédia das Aves do Brasil. Available at: <http://www.wikiaves.com/252443>.

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
B. trifasciatus_01	XC463042	Ordóñez-Delgado 2010	6.374	4.062	9.073	3.351
B. trifasciatus_02	XC259488	Moore 1997	6.546	4.258	9.466	3.122
B. trifasciatus_03	XC259486	Moore 1999	5.771	3.057	9.913	3.175
B. trifasciatus_04	XC206829	Fischer 2014a	6.891	4.455	10.187	2.551
B. trifasciatus_05	XC8648	Vellinga 2005	7.666	4.354	10.701	2.425
B. trifasciatus_06	XC6543	Anthanas 2002	6.115	3.701	9.401	2.126
B. trifasciatus_07	XC55829	Sanchez 2010	5.943	3.706	8.477	2.054
B. trifasciatus_08	XC206016	Fischer 2014b	5.857	3.963	9.335	2.376
B. trifasciatus_09	XC136043	Ordóñez-Delgado 2013a	6.632	4.389	8.844	2.408
B. trifasciatus_10	XC118557	Ordóñez-Delgado 2013b	5.599	3.832	9.597	1.873

Athanas, N. 2002. [XC6543, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/6543>.

Fischer, J. 2014a. [XC206829, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/206829>.

Fischer, J. 2014b. [XC206016. *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/206016>.

Moore, J. V. 1997. [XC259488, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/259488>.

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Ordóñez-Delgado, L. 2013b. [XC118557, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/118557>.

Sanchez, M. 2010. [XC55829, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/55829>.

Vellinga, W. P. 2005. [XC8648, *Basileuterus trifasciatus* Taczanowski, 1880]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/8648>.

Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
B. tristriatus_01	XC387713	Fischer 2017	5.685	3.752	11.673	3.373
B. tristriatus_02	XC353318	Gallardy 2016	6.375	3.815	9.269	2.806
B. tristriatus_03	XC296994	Gallardy 2015	5.512	4.356	9.532	4.266
B. tristriatus_04	XC275774	Nilsson 2002	6.374	4.262	10.701	3.181
B. tristriatus_05	XC259484	Moore 1998	6.202	4.215	10.701	3.756
B. tristriatus_06	XC250541	Krabbe 2007	6.804	4.225	10.121	3.006
B. tristriatus_07	XC343239	Ordóñez-Delgado 2016	7.149	4.225	10.449	3.665
B. tristriatus_08	XC22420	Spencer 2008	7.312	3.565	10.945	4.699
B. tristriatus_09	XC219728	Boesman 2000	4.565	4.127	9.827	3.241
B. tristriatus_10	XC112289	Brooks 2012	6.374	3.104	11.627	2.286

Boesman, P. 2000. [XC219728, *Basileuterus tristriatus* (Tschudi, 1844)]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/219728>.

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Fischer, J. 2017. [XC387713, *Basileuterus tristriatus* (Tschudi, 1844)]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/387713>.

Gallardy, R. 2015. [XC296994. *Basileuterus tristriatus* (Tschudi, 1844)]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/296994>.

Gallardy, R. 2016. [XC353318, *Basileuterus tristriatus* (Tschudi, 1844)]. Xeno-canto Foundation. Available at: < http://www.xeno-canto.org/353318>.

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
B. rufifrons_01	XC219699	Boesman 2001	6.115	2.617	7.717	1.852
B. rufifrons_02	XC335300	Webster 2015	5.340	2.672	8.565	1.436
B. rufifrons_03	XC273706	Boesman 2010	6.287	2.981	8.189	1.374
B. rufifrons_04	XC180811	van Dort 2014	6.460	2.501	8.697	1.515
B. rufifrons_05	XC101820	Minns 2012	5.340	2.719	8.877	1.651
B. rufifrons_06	XC76601	Kanapp 2011	4.910	2.501	9.960	1.352
B. rufifrons_07	XC72398	Spencer 2011	5.719	2.460	11.195	1.445
B. rufifrons_08	XC7396	Bradley 2006	6.546	2.751	8.975	1.694
B. rufifrons_09	XC433376	Vanegas 2017	6.288	2.719	8.582	1.769
B. rufifrons_10	XC428318	Fischer 2018	6.977	2.826	8.616	1.411

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. flaveola_01	WA251101	Guimarães 2010	4.996	1.992	6.346	1.870
M. flaveola_02	WA1225656	Stübing 2014	5.906	1.714	7.210	1.978
M. flaveola_03	WA1163071	Zurdo 2013	4.996	1.899	7597	1.978
M. flaveola_04	WA3359461	Filipino 2019	5.512	1.900	7.206	1.936
M. flaveola_05	WA3245706	Bernardes 2019	5.599	1.992	7.365	1.748
M. flaveola_06	WA3212754	Pires 2018	5.254	1.969	6.786	2.055
M. flaveola_07	WA3123754	Godoy 2016	4.823	2.131	5.837	2.082
M. flaveola_08	WA3089390	Gomes 2018	3.844	2.067	7.185	1.581
M. flaveola_09	WA2958124	Basseto 2018	5.426	2.620	7.534	2.311
M. flaveola_10	ALC053.3	Catalano 2017	4.687	1.891	7.487	1.939

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. rivularis_01	WA401990	Rosa 2011	3.187	1.437	4.387	3.620
M. rivularis_02	WA1034612	Cruz 2013	3.618	1.946	4.239	4.596
M. rivularis_03	WA3115240	Oliveira 2018	2.584	1.737	4.470	4.319
M. rivularis_04	WA2983521	Correia 2018	3.445	1.575	3.729	6.245
M. rivularis_05	WA2635520	Maluf 2017	3.704	1.876	3.845	4.214
M. rivularis_06	WA1687789	Langenegger 2015	3.445	1.876	3.914	2.859
M. rivularis_07	WA1657003	Marcelli 2014	2.928	1.621	3.984	4.847
M. rivularis_08	WA1227070	Melo 2014	3.531	1.621	3.868	3.322
M. rivularis_09	WA800349	Sanches 2012	3.445	1.703	4.848	4.348
M. rivularis_10	WA3326182	Souza 2018	3.281	1.765	3.958	3.847

Correia, M. 2018. [WA2983521, *Myiothlypis rivularis* (Wied, 1821)]. Wiki Aves - A Enciclopédia das Aves do Brasil. Available at: <http://www.wikiaves.com/2983521>.

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. leucoblephara_01	WA238044	Melo 2010	4.307	3.244	7.992	5.235
M. leucoblephara_02	WA174060	Silva 2009	5.426	2.872	7.736	5.797
M. leucoblephara_03	WA1463841	Jesus 2014	4.220	3.308	8.254	7.522
M. leucoblephara_04	WA2578599	Pacheco 2000	4.910	2.826	9.192	4.598
M. leucoblephara_05	WA1747388	Horikawa 2015	4.996	3.832	8.516	5.735
M. leucoblephara_06	WA1367897	Caviquiolo 2014	4.823	3.636	8.713	4.385
M. leucoblephara_07	WA776933	Andriola 2012	4.910	3.865	8.385	5.824
M. leucoblephara_08	WA733633	Silva 2012	4.969	4.109	8.849	5.044
M. leucoblephara_09	WA343253	Silva 2011	5.082	3.931	9.663	5.288
M. leucoblephara_10	WA3416777	Paula 2019	5.254	3.011	7.898	4.745

Andriola, J. V. 2012. [WA776933, *Myiothlypis leucoblephara* (Vieillot, 1817)]. Wiki Aves - A Enciclopédia das Aves do Brasil. Available at: <http://www.wikiaves.com/776933>.

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. fulvicauda_01	XC467533	de By 2018	3.101	1.807	5.767	3.409
M. fulvicauda_02	XC455136	Rengifo 2018	3.359	1.807	6.995	3.809
M. fulvicauda_03	XC445415	Ulloa 2018	5.082	1.853	7.921	3.931
M. fulvicauda_04	XC412252	Walters 2018	4.220	1.992	7.829	4.151
M. fulvicauda_05	XC371506	Rumm 2017	3.618	1.899	5.373	5.347
M. fulvicauda_06	XC355602	Livezey 2017	4.307	2.260	7.075	2.816
M. fulvicauda_07	XC353924	Gallardy 2016	5.250	1.513	7.160	4.192
M. fulvicauda_08	XC344323	Culasso 2016	3.250	1.882	7.193	4.027
M. fulvicauda_09	XC343940	Funes 2016	4.125	1.916	5.773	5.204
M. fulvicauda_10	XC342235	Krabbe 2016	3.790	2.085	7.273	4.343

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. bivittata_01	XC288818	Krabbe 2015	3.790	1.933	5.012	1.896
M. bivittata_02	XC88780	Blanchon 2015	4.220	1.760	4.725	1.783
M. bivittata_03	XC27391	Boesman 2013	3.962	1.474	4.782	1.701
M. bivittata_04	XC99606	Rupp 2011	3.962	1.853	5.119	1.974
M. bivittata_05	XC4797	Maccormick 2005	3.531	1.760	5.119	1.541
M. bivittata_06	XC395788	van Oosten 2017	3.531	1.605	4.677	1.651
M. bivittata_07	XC457391	Krabbe 2019	3.531	1.048	4.471	1.961
M. bivittata_08	XC361116	Krabbe 2017	3.445	2.047	4.979	2.388
M. bivittata_09	XC32436	Krabbe 2000	3.962	1.783	5.327	1.952
M. bivittata_10	XC1541	Mayer 1992	3.876	1.459	4.632	1.985

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Appendix 1 continued

Species	Code	Author	Fdom (kHz)	Ffmin (kHz)	Ffmax (kHz)	Sdur (s)
M. nigrocristata_01	XC461010	Rengifo 2019	4.907	2.686	8.058	2.555
M. nigrocristata_02	XC417051	Lau 2018	3.876	2.270	8.940	2.087
M. nigrocristata_03	XC390437	Fischer 2017	5.082	2.733	7.829	1.840
M. nigrocristata_04	XC374438	St-Michel 2017	4.048	2.478	6.861	2.398
M. nigrocristata_05	XC262483	Jahn 2006	5.426	3.669	7.246	1.619
M. nigrocristata_06	XC259463	Moore 1996	4.479	2.316	8.940	2.443
M. nigrocristata_07	XC259462	Moore 1998	5.426	2.872	6.856	3.301
M. nigrocristata_08	XC219674	Boesman 2000	5.857	1.899	6.254	1.564
M. nigrocristata_09	XC219673	Boesman 2008	3.937	2.084	7.411	1.837
M. nigrocristata_10	XC101577	Minns 2012	4.048	1.714	7.087	4.867

Boesman, P. 2000. [XC219674, *Myiothlypis nigrocristata* (Lafresnaye, 1840)]. Xeno-canto Foundation. Available at: <http://www.xeno-canto.org/219674>.

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