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BANDOS MISTOS DE AVES EM GRADIENTE FLORESTA-SAVANA NO SUDOESTE DO BRASIL

TESE DE DOUTORADO

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Santa Maria, RS, Brasil

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BANDOS MISTOS DE AVES EM GRADIENTE FLORESTA-SAVANA NO SUDOESTE DO BRASIL

Franchesco Della Flora

Tese apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Bioecologia de Vertebrados, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do grau de **Doutor em Ciências Biológicas.**

Orientador: Prof. Dr. Nilton Carlos Cáceres

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Centro de Ciências Naturais e Exatas
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A Comissão Examinadora, abaixo assinada,
aprova a Tese de Doutorado

BANDOS MISTOS DE AVES EM GRADIENTE FLORESTA-
SAVANA NO SUDOESTE DO BRASIL

elaborada por
Franchesco Della Flora

como requisito parcial para obtenção do grau de
Doutor em Ciências Biológicas

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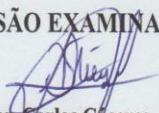
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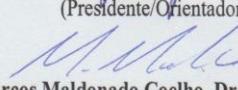
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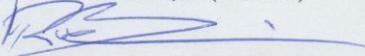
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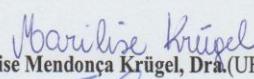
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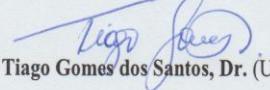
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Santa Maria, 28 de fevereiro de 2014.

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Ei, pintassilgo
Oi, pintaroxo
Melro, uirapuru
Ai, chega-e-vira
Engole-vento
Saíra, inhambu
Foge asa-branca
Vai, patativa
Tordo, tuju, tuim
Xô, tié-sangue
Xô, tié-fogo
Xô, rouxinolsem fim
Some, coleiro
Anda, trigueiro
Te esconde colibri
Voa, macuco
Voa, viúva
Utiariti
Bico calado
Toma cuidado
Que o homem vem aí
O homem vem aí
O homem vem aí

(Passaredo, Chico Buarque)

RESUMO
Tese de Doutorado
Programa de Pós-Graduação em
Biodiversideade Animal
Universidade Federal de Santa Maria

BANDOS MISTOS DE AVES EM GRADIENTE FLORESTA-SAVANA NO SUDOESTE DO BRASIL
AUTOR: FRANCHESCO DELLA FLORA
ORIENTADOR:NILTON CARLOS CÁCERES
Data e Local da Defesa: Santa Maria, 28 de fevereiro de 2014.

Bandos mistos de aves são subconjuntos da comunidade onde espécies interagem positivamente para obter benefícios para evitar predadores e aumentar a eficiência de forrageamento. Estas interações podem ser mais ou menos reforçadas dependendo das espécies envolvidas, por fatores espaciais e ambientais que podem afetar a distribuição de espécies, e de acordo com os atributos e a filogenia das espécies envolvidas. Nesta tese, verifiquei a riqueza e composição dos bandos mistos de aves, bem como a partição da diversidade Beta e sua relação com o espaço (processos neutros) e filtros ambientais (processos baseados em nicho), e quais processos ecológicos conduzem a estrutura funcional e filogenética de bandos mistos em uma escala regional, no sudoeste do Brasil. A riqueza média por bando não mostrou variação entre os quatro tipos de vegetação, mas a composição foi significativamente diferente. *Basileuterus culicivorus* (líder), *Casiornis rufus*, *Myiarchus tyrannulus* e *Turdus leucomelas* (seguidores) foram as espécies mais frequentes na maioria das fitofisionomias. De acordo com a composição de espécies e gradientes em cada tipo de vegetação, classifiquei os bandos em quatro grupos principais: (1) pequenas espécies insetívoras de bandos heterogêneos; (2) espécies de dieta generalista de dossel; (3) espécies de savanas abertas; e (4) espécies de grande porte. Todos os tipos de vegetação presentes agregação mais do que por acaso. Associações de pares de espécies apresentaram muito mais agregação do que o acaso: Cerradão apresentou maior número de agregações que florestas Estacional Semidecidual e Ripária. Além disso, associações de pares de espécies líder-líder e líder-seguidor foram menos agregadas do que seguidores-seguidores, mas não houve diferença significativa para Cerradão. O espaço geográfico foi o componente mais importante na estruturação dos bandos mistos de aves tanto para tipos de bandos (sub-bosque, heterogêneos e dossel) quanto para tipos de vegetação (Ceradão, Floresta Ripária e Estacional

Semidecídua). O componente de substituição espacial dos bandos de sub-bosque, heterogêneos, de floresteas Ripária e Semideciduais foi relacionado positivamente com a distância geográfica, enquanto a dissimilaridade de bandos heterogêneos foi positivamente relacionada com gradiente de temperatura e precipitação. No entanto, os bandos de sub-bosque apresentaram relação negativa com classes de distância superior a 400 km sugerindo uma similaridade de espécies de acordo com os tipos de floresta, e apoiando a teoria de nicho. Os padrões observados de beta diversidade de bandos mistos de aves sugerem ambos os processos neutros e baseados em nichos impulsionadas pela capacidade de dispersão e filtragem determinista das espécies em diferentes gradientes espaciais e ambientais. Bandos mistos podem ser estruturados de maneiras diferentes de acordo com sua diversidade filogenética e funcional. As características morfológicas das espécies participantes foram filogeneticamente conservadas enquanto as comportamentais foram mais instáveis ao longo da filogenia, ou mesmo convergentes. Filtros ambientais são, provavelmente, os mais importantes na organização dos bandos mistos na maioria dos ambientes florestais, enquanto que a facilitação é mais influente em savanas.

Palavras-chave: Cerrado, diversidade filogenética, diversidade funcional, espaço geográfico, facilitação, filtros ambientais, Floresta Atlântica, Pantanal, Regras de montagem.

ABSTRACT
PhD Thesis
Post-GraduationinAnimal Biodiversity
Universidade Federal de Santa Maria

MIXED-AVIAN FLOCKS IN FOREST-SAVANNA GRADIENTIN SOUTHWESTERN BRAZIL
AUTHOR: FRANCHESCO DELLA FLORA
ADVISOR: NILTON CARLOS CÁCERES

Mixed flocks of birds are subsets of the community in which species interact positively to obtain benefits in predator avoidance and increase foraging efficiency. These interactions may be more or less strengthened depending on the species involved, by spatial and environmental factors that may affect the distribution of species, and according to traits and phylogeny. In this thesis, I verified the richness and composition of avian mixed flocks, as well the partition of Beta diversity and it relation with space (neutral-based processes) and environmental filters (niche-based processes), and which ecological processes drive the functional and phylogenetic structure of mixed flocks in a regional scale in southwestern Brazil. The mean richness per flock showed no variation among the four vegetation types, but the composition was significantly different. *Basileuterus culicivorus* (leader), *Casiornis rufus*, *Myiarchus tyrannulus* and *Turdus leucomelas* (followers) were the most frequent species in most of phytophysiognomies. According to species compositions and gradients in each vegetation type, we classified the mixed flock species in four main groups: (1) small insectivorous species of heterogeneous flocks; (2) diet generalist species of canopy flocks; (3) open savanna species; and (4) large size species. All types of vegetation present aggregation more than by chance. Non-random pairwise associations presented much more aggregation than segregated: Closed woodland savanna (*cerradão*) present more number of aggregations than Semideciduous and Riparian forest. Furthermore, leader-leader and leader-follower pairwise associations were less aggregated than followers associations over all habitats, but there was no significant difference to Closed woodland savanna. The spatial turnover was the most important component in the structuring of avian mixed flocks both flock and forest types in multiple-sites. The spatial turnover dissimilarity of understory, heterogeneous, riparian forest and semideciduous flocks was related positively with geographical distance, while dissimilarity of heterogeneous flocks was positively with temperature and precipitation gradient. However, understory flocks showed negative relation with distance classes higher

than 400 km suggesting a species similarity according to forest types, and supporting the Niche theory. The observed patterns of beta diversity of avian mixed flocks suggest both neutral and niche-based processes driven by dispersal ability and deterministic filtering of the species across spatial and environmental gradients. Mixed flocks can be structured in different ways according to it phylogenetic and functional diversity. The morphological traits of the participating species were phylogenetically conserved while behavioral were more labile along the phylogeny, or even convergent. Habitat filtering are probably the most important in the organization of mixed flocks in most forest environments, while facilitation is more influential on savannas.

SUMÁRIO

INTRODUÇÃO GERAL

As comunidades modificam-se na medida em que ocorre variação dos fatores abióticos ao longo de um gradiente espacial (GASTON, 2000). Tais fatores influenciam as formações vegetais em dado local e consequentemente sua fauna. No caso das aves, existe uma procura por locais onde existam maior oferta de recursos, abrigo e locais para reprodução (CODY, 1985). Porém, modificações espaço-ambientais de uma dada região podem influenciar também em mudanças da assembleia de aves (LEE & ROTENBERRY, 2005) e consequentemente nas suas interações (HUTTO 1987).

Como medidas de diversidade, a diversidade alfa e beta se destacam como sendo as mais tradicionais em estudos de diferentes assembléias (KREBS, 1999). Essas medidas levam em conta principalmente a quantidade de espécies, o número de indivíduos e a presença ou ausência de uma dada espécie na assembléia. Porém, outras medidas de diversidade, como a filogenética (CLARKE &WARWICK , 1998; WEBB, 2000) e a funcional (DÍAZ & CABIDO, 2001; PETCHEY & GASTON, 2002; 2006), tem se mostrado mais sensível para detectar respostas das assembléias às mudanças ambientais do que as medidas tradicionais.

A diversidade beta pode ser particionada através de dois padrões de estruturação de comunidades, que são o aninhamento e a substituição de espécies. O aninhamento ocorre quando há presença de espécies de forma assimétrica na comunidade, onde espécies generalistas ocorrem tanto em áreas de maior e menor diversidade de habitats e espécies especialistas ocorrem somente em áreas com maior diversidade de habitats. Já a substituição acontece quando há troca de espécies entre duas localidades, o que pode ocorrer por interações interespecíficas, restrições espaciais e por seleção de espécies pelo meio ambiente (BASELGA, 2010).

A diversidade filogenética é uma medida da diversidade de uma assembleia que incorpora as relações filogenéticas das espécies (MAGURRAN, 2004). A premissa principal dessa medida é que a diversidade é maior em uma comunidade em que as espécies são filogeneticamente mais distintas. A percepção dominante em ecologia evolutiva é que espécies coexistindo devem diferir significativamente e que a maior parte da variação entre espécies aparentadas é uma resposta adaptativa à competição no passado, quando os traços não diferiam(HARVEY & RAMBAUT, 2000). De modo geral, esse modelo evolutivo prediz que a divergência nos traços ecológicos deve ser ampla, ou seja, uma maior diversidade funcional na comunidade. Porém, estudos demonstraram que muitas linhagens apresentam um

conservadorismo das características ecológicas dominantes (HARVEY & RAMBAUT, 2000; ACKERLY, 2003), isto é, esses atributos tendem a se manter ao longo dessas linhagens evolutivas.

A melhor medida da relação filogenética de duas espécies é a idade do evento de especiação sofrido pelo mais recente ancestral em comum. Essa informação pode ser estimada pela diferença nos pares de base de um gene neutro entre duas espécies (HARVEY & PAGEL, 1991). Medidas de diversidade filogenética podem ser usadas para analisar os processos ecológicos que organizam a comunidade (WEBB ET AL. 2002). Ela resulta não só de processos ecológicos presentes, como a competição entre as espécies (HUTCHINSON, 1959; LEIBOLD, 1998) e os filtros ambientais (WEIHER & KEDDY, 1995; CHASE 2003), mas também de processos evolutivos históricos e contínuos (TOFTS & SILVERTOWN, 2000; ACKERLY, 2003).

Estudos sobre bandos mistos são ausentes em metacomunidades de aves. Já os que se aproximam de gradientes ecológicos em regiões ecotonais carecem de réplicas espaciais. Além disso, dados sobre a ecologia e conservação de comunidades animais em biomas que estão sofrendo elevada modificação da paisagem são de elevada importância. Isto poderá promover estudos mais específicos e identificar padrões negativos que possam estar afetando a composição e a estrutura dos bandos mistos.

Esse processo de associação mutualístico embora bastante estudado em comunidades em nível local pode apresentar padrões distintos e complexos em metacomunidades quando levado em conta o grau de parentesco entre as espécies e a relação da filogenia com atributos ecomorfológicos das espécies participantes dos bandos.

Nesta tese, apresento quatro artigos a respeito da estrutura de bandos mistos de aves em metacomunidade avaliando a riqueza, a composição, as associações entre espécies, o efeito do espaço e de filtros ambientais, e a estrutura funcional e filogenética ao longo de diferentes gradientes ambientais presentes na região sudoeste do Brasil. Inicialmente mostro padrões de riqueza e composição e as relações de coocorrência das espécies participantes nos bandos ao longo de diferentes ecorregiões testando se existe dependência entre pares de espécies nucleadoras e seguidoras nos bandos. Em seguida, abordo a partição da diversidade beta através de gradientes espaciais identificando a porcentagem de substituição e aninhamento das espécies e o efeito do espaço e do clima em diferentes tipos de savana e floresta. No último artigo, verifico quais regras de montagem são responsáveis pela estrutura funcional e filogenética de bandos mistos, além de descrever gradientes filogenéticos em diferentes escalas ambientais.

1 ARTIGO 1 - RICHNESS AND COMPOSITION OF AVIAN MIXED FLOCKS IN SAVANNAS AND FORESTS OF SOUTHWESTERN BRAZIL[1]

Franchesco Della-Flora, Nilton Carlos Cáceres

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[1] Esse artigo segue as normas da revista Journal of Field Ornithology.

1.1 Abstract

We verified the richness and composition of avian mixed flocks in two types of forests and savannas in a regional scale in central South America and identified the frequency of occurrence and the ecological rule of main species in the structure and formation of mixed flocks. The mean richness per flock showed no variation among the four vegetation types, but the composition was significantly different. Golden-crowned Warbler *Basileuterus culicivorus* (leader), Rufous Casiornis *Casiornis rufus*, Brown-crested Flycatcher *Myiarchus tyrannulus* and Pale-breasted Thrush *Turdus leucomelas* (followers) were the most frequent species in most of phytophysiognomies. Golden-crowned Warbler, Sayaca Tanager *Thraupis sayaca*, Flavescent Warbler *Myiothlypis flaveola* and Red-crested Finch *Coryphospingus cucullatus* were the most common leader species in semideciduous forest, riparian forest, woodland savanna and open woodland, respectively. According to species compositions and gradients in each vegetation type, we classified the mixed flock species in four main groups: (1) small insectivorous species of heterogeneous flocks led often by Golden-crowned Warbler; (2) diet generalist species of canopy flocks led by large and small tanagers (Sayaca Tanager, Blue Dacnis *Dacnis cayana* and Guira Tanager *Hemithraupis guira*); (3) open savanna species led by Red-crested Finch and as main followers Rufous Casiornis, Brown-crested Flycatcher; and (4) large size species led by Jays (*Cyanocorax cyanomelas* and *C. chrysops*) and Red-rumped Cacique (*Cacicus haemorrhous*).

Key-words: Cerradão, cerrado, chaco, dry forest, follower species, nuclear species, riparian forest.

Mixed-species flocks of foraging birds have been documented in terrestrial habitats all over the world (Greenberg 2000; Sridhar et al. 2009). They are thought to be originated in

response to either improved feeding efficiency or better protection from predators (Morse 1977) based on mutualism and commensalism among species (Hino 1998). Interspecific avian flocks tend to range in size and specific composition (Kotagama and Goodale 2004; Pomara et al. 2007), as well as in time (Powell 1979; Terborgh 1990; Poulsen 1996; Kotagama and Goodale 2004; Amaral and Ragusa-Netto 2008; Farley et al. 2008; but see Arbeláez-Cortés et al. 2011 for absence of variation) and space (Morse 1970; Hutto et al. 1987; Maldonado-Coelho and Marini 2000; Lee and Jablonski 2006; Pomara et al. 2007).

Mixed flocks are found in a wide variety of ecosystems, from forests to open areas like savannas and deserts (Cody 1971; Greig-Smith 1978; Munn and Terborgh 1979; Greenberg 2000; Tubelis 2007). In Neotropical region most of the studies are restricted to rainforests (Davis 1946; Powell 1979; Munn and Terborgh 1979; Gradwohl and Greenberg 1980; Munn 1985; Stotz 1993; Thiollay 1999; Machado 1999; Greenberg 2000; Develey and Peres 2000; Develey and Stouffer 2001; Ghizoni-Jr and Azevedo 2006; Brandt et al. 2009) and a few studies for seasonal forests (Aleixo 1997; Maldonado-Coelho and Marini 2000, 2003). Savannas and forests from open ecoregions such as Cerrado, Pantanal and Chaco remain poorly studied (Kratter et al. 1993; Tubelis 2007; Amaral and Ragusa-Netto 2008), and comparisons of richness and composition of species associations among different habitats are still scarce in literature (see Morse 1970 for temperate forest; and Hutto et al. 1987; Gram 1998; Goodale et al. 2009; Arbeláez-Cortés et al. 2011 for tropical forest).

In this study, we show patterns of richness and composition of avian mixed flocks for four habitat types, two forests and two savannas, in southwestern Brazil. Furthermore, we feature the main gradients of species turnover according to the habitat and natural history of flock participants.

1.2 Methods

1.2.1 Study area

This study was carried out in central South America, southwest Brazil (18 to 23º S, 54 to 57º W), including three states: Mato Grosso do Sul (southern half), São Paulo (southwest) and Paraná (northwest) (Figure 1). It was developed a multisite design (Goodale et al. 2009) with 29 independent sample areas. The vegetation can be replaced between savanna like vegetation and forest in all range of the study area, but mainly at center and west (Figure 1). Generically, we divided the study area in the following main phytophysiognomies, which correspond to: semideciduous forests − SDF (e.g., seasonal forests of east, northwest and

submountain forests of the Maracaju and Bodoquena plateaus), riparian forests – RPF (e.g., gallery, "ciliar" and flooded forests from Paraguay and Parana basins), closed-canopy woodland savannas or just woodland savanna – CWS (e.g., "cerradão") and open woodland savannas or just open woodland – OWS (e.g., chaco savanna, in southwestern, and "cerrado *stricto sensu*", mainly in northeast) (Oliveira-Filho and Ratter 2002).

1.2.2 Flock sampling

Our multisite design consists in continuous and fragmented vegetation (> 100 ha), forests along rivers, and small patches of flooded forest, being sampled for four days per locality. Sampling always occurred during the dry season (May-August) from 2009 to 2011. Mixed flocks were observed in the morning (07:00-11:00) and in the afternoon (16:00-17:00), 12 to 15 hours in each area depending of climate conditions, totaling 406 h of field observation. In each site natural or anthropic trial transects were carried out from 500 to 2000 m in length, depending of the area size, in the patch interior as well as in edges and in continuous areas.
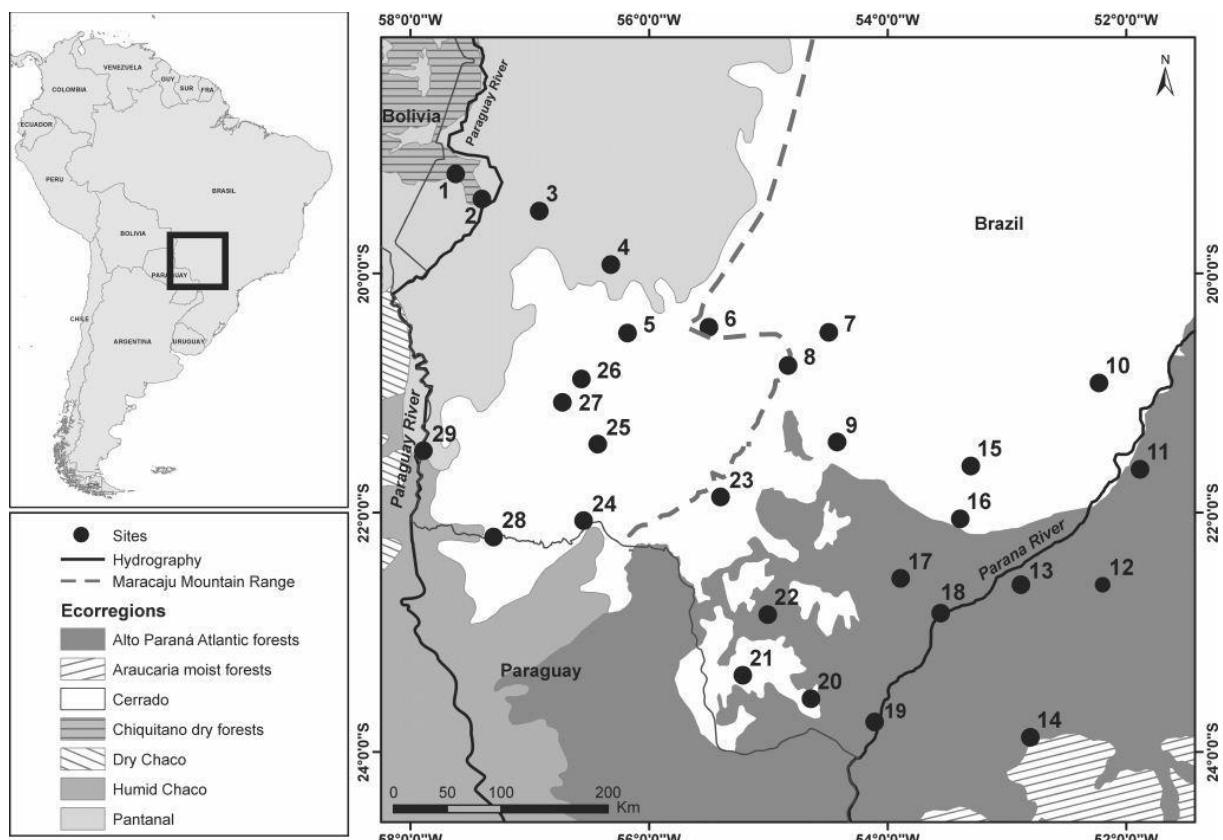
Figure 1. Map with sampled areas distributed among different ecoregions of central South America. Numbers represent the areas sampled and can contain more than one vegetation type: 1 – Corumbá (SDF), 2 – Albuquerque (SDF, RPF, CWS), 3 – Abobral (RPF), 4 – Caiman (SDF, RPF, CWS, OWS), 5 – Miranda (SDF, CWS), 6 – Aquidauna (SDF, RPF, CWS), 7 – Campo Grande (RPF, CWS, OWS), 8 – Sidrolândia (RPF, CWS),

9 – Nova Alvorada do Sul (SDF, RPF, CWS), 10 – Três Lagoas (RPF, CWS, OWS), 11 – Presidente Epitácio (SDF, RPF), 12 – Teodoro Sampaio (SDF, RPF), 13 – Diamante do Norte (SDF, RPF), 14 – Tuneiras do Oeste (SDF, CWS), 15 – Nova Casa Verde (RPF, CWS, OWS), 16 – Nova Andradina (RPF, CWS, OWS), 17 – Novo Horizonte do Sul (SDF), 18 – Naviraí (RPF), 19 – Eldorado (SDF, RPF), 20 – Iguatemi (ATL, CEF, GAL, CES), 21 – Coronel Sapucaia (RPF, CWF), 22 – Laguna Caraapã (SDF, RPF), 23 – Maracaju (SDF, RPF, CWS, OWS), 24 – Bela Vista (CWS, OWS), 25 – Jardim (RPF, OWS), 26 – Bonito (SDF, RPF, CWS, OWS), 27 – Bonito 2 (SDF, RPF, CWS), 28 – Caracol (RPF, OWS), 29 – Porto Murtinho (SDF, RPF, OWS). SDF – semideciduous forest, RPF – riparian forest, CWS –woodland savana, OWS – open woodland.

Mixed flocks were considered grouping of species with one or more individuals of two or more species that were moving together, with a minimum of five minutes staying together in a specific direction (Stotz 1993). The species were classified according to the behavior of "nuclear" and "follower" species (Moynihan 1962; Gram 1998; Hino 1998; Goodale and Kotagama 2005) and by percentage of frequency of occurrence (FO, number of times a species was recorded in different flocks divided by the total number of flocks observed) to more representative species according to the three categories proposed by Goodale and Beauchamp (2010): (a) nuclear, (b) regular, and (c) occasional species, the last two being classified as "followers". However, we maintained the four mostly used categories in mixed flock species (Powell 1985): common, regular, occasional, and rare, respectively, from the most abundant to the rarer (Table 1). Only those species participating in above 5% of flocks were included in the analyses, the others were considered rare.

1.2.3 Data analysis

Differences on flock richness and composition (matrix of presence/absence species per flocks containing only flocks with more than three species) among the four vegetation types were tested by ANOVA and NPMANOVA, respectively. Ecological gradients of change in interspecific species participants regarding to the frequency of occurrence (FO) were analyzed by a correspondence analysis (CA), which the differences among species and vegetation types were tested by contigency table, and the composition of species for each vegetation type was analyzed by principal coordinate analyses (PCoA), using Jaccard's similarity index.

1.3 Results

A total of 398 interspecific flocks were sampled in 3406 occurrences of 192 participant species. The main avian groups in the flocks were flycatchers (Tyrannidae: 41 species), tanagers (Thraupidae: 31 species), ovenbirds and woodcreepers (Furnariidae: 26 species), antbirds (Thamnophilidae: 16 species) and woodpeckers (Picidae: 13 species). The commonest species in all samples were Golden-crowned Warbler *Basileuterus culicivorus*, Rufous Casiornis *Casiornis rufus* and Brown-crested Flycatcher *Myiarchus tyrannulus* (Appendix 1). Semideciduous and riparian forests exhibited higher species richness, in contrast to woodland savanna types. However, there was no difference concerning the species richness of flocks among the different vegetation types ($F_{3,387} = 0.97$, $P = 0.459$, Table 1). In turn, the species composition showed significant difference among the four vegetation categories ($F_{3,294} = 5.68$, $P < 0.001$, Appendix 2).

Among the 50 most frequent species (common, regular and occasional categories), four are common, 11 regular, and 35 occasional species. Furthermore, 32 are followers in flocks and only 18 participated as nuclear species (Table 1, Appendix 1). The four vegetation types also showed similar proportion of species in such categories, although open savanna and the two forests (semideciduous and riparian) have had greater richness of common and occasional species, respectively.

The main nuclear species was Golden-crowned Warbler, and the main followers were Rufous Casiornis, Brown-crested Flycatcher and Pale-breasted Thrush *Turdus leucomelas*. However, these species were not the same in the four vegetation types (Appendix 2): (a) nuclear species (in descending order of importance) – Golden-crowned Warbler, Tropical Parula, Guira Tanager *Hemithraupis guira*, Gray-headed Tanager *Eucometis penicillata* and Blue Dacnis (semideciduous forest), Sayaca Tanager, Variable Oriole *Icterus pyrrhopterus*, Tropical Parula, Silver-beaked Tanager *Ramphocelus carbo* and Golden-crowned Warbler (riparian forest) Flavescent Warbler, Golden-crowned Warbler, Guira Tanager, Tropical Parula, Red-crested Finch *Coryphospingus cucullatus* and Blue Dacnis (woodland savanna), and Red-crested Finch, Sayaca Tanager, Masked Gnatcatcher *Polioptila dumicola*, Tropical Parula, Golden-winged Cacique *Cacicus chrysopterus* and Planalto Slaty-Antshrike *Thamnophilus pelzelni* (open savanna); (b) follower species – Squirrel Cuckoo *Piaya cayana* and Pale-breasted Thrush (semideciduous forest), Rufous-browed Peppershrike *Cyclarhis gujanensis* and Pale-breasted Thrush (riparian forest), Rufous Casiornis and Brown-crested Flycatcher (woodland savanna), and Brown-crested Flycatcher, Rufous Casiornis, Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*, Rufous-browed Peppershrike and Pearly-vented Tody-Tyrant *Hemitriccus margaritaceiventer* (open savanna).

In 8.3% (N= 33, mean = 4.0 species, range = 2 − 11 species per flock) of flocks there was no nuclear species. Mixed flocks without a leader species were found almost exclusively in the two forest types and in woodland savanna; in most of of cases, they consisted of Brown-crested Flycatcher (N = 11 flocks), Rufous Casiornis and Great Antshrike *Taraba major* (N = 10 flocks). These flocks were common in the understory, but vocalized little and foraging closely together.

Table 1. Number of sites and mixed flocks sampled, species classification according to the frequency of occurrence (number of species is given) and species richness for each frequence category (in bold the richness for nuclear species and in italic for follower species), and total species richness, mean (standard deviation) species richness and richness range (minimum and maximum) for four vegetation types (SDF – semideciduous forest, RPF – riparian forest, CWS –woodland savanna, OWS – open savanna) studied in southwestern Brazil.

Vegetation	SDF	RPF	CWS	OWS	All
Sites	17	17	14	12	29
Mixed flocks	151	92	92	63	398
Number of species per category					
Common (> 25%)	3 (**1**,*2*)	2 (**1**,*1*)	4 (**2**,*2*)	10 (**3**,*7*)	4 (**1**,*3*)
Regular (15 – 25%)	12 (**4**,*8*)	17 (**4**,*13*)	14 (**4**,*10*)	10 (**3**,*7*)	11 (**5**,*6*)
Occasional (5 – 15%)	37 (**11**,*26*)	37 (**14**,*23*)	23 (**8**,*15*)	27 (**8**,*19*)	35 (**12**,*23*)
Rare (< 5%)	103	81	64	47	142
Richness	142	137	105	94	192
Mean (SD)	8.6 (5.6)	8.6 (6.1)	7.8 (6.1)	9.5 (5.8)	8.5 (6.1)
Range	2 – 31	2 – 31	2 – 28	2 – 25	2 – 31

In a general overview, the species frequencies were significantly related to each phytophysiognomy (χ^2_{171} = 1576, P < 0.001; Fig. 2). The first axis of the correspondent analysis (41.58%) was related to a savanna-forest gradient with species represented by Masked Gnatcatcher (Pod), Red-crested Finch (Lac), Rusty-backed Antwren *Formicivora rufa* (For) and Golden-winged Cacique (Cac) in one extreme of the diagram (open savanna), to species more closely to semideciduous forest, such as Black-goggled Tanager *Trichothraupis melanops* (Lam), Sepia-capped Flycatcher *Leptopogon amaurocephalus* (Leam), Saffron-billed Sparrow *Arremon flavirostris* (Arf), Surucua Trogon *Trogon surrucura* (Trs) and Golden-crowned Warbler (Bac) to the opposite extreme. The second axis

(23.06%) showed a species turnover from dry (woodland savanna) to humid vegetation (riparian forest). The species Flavescent Warbler (Myfl), Guira Tanager (Heg), Purplish Jay *Cyanocorax cyanomelas* (Cycy) and Rufous Casiornis (Car) were more representative in woodland savanna. On the other hand, Variable Oriole (Icp), White-wedged Piculet *Picumnus albosquamatus* (Pia), Great Antshrike (Tam), Rufous-bellied Thrush *Turdus rufiventris* (Tur) and Great Kiskadee *Pitangus sulphuratus* (Pis) were more associated to riparian forest. Moreover, the main canopy species, such as Blue Dacnis (Dac), Chestnut-vented Conebill *Conirostrum speciosum* (Cos), Tropical Parula (Sep) and Purple-throated Euphonia *Euphonia chlorotica* (Euc) were found in all vegetation types (Fig. 2).
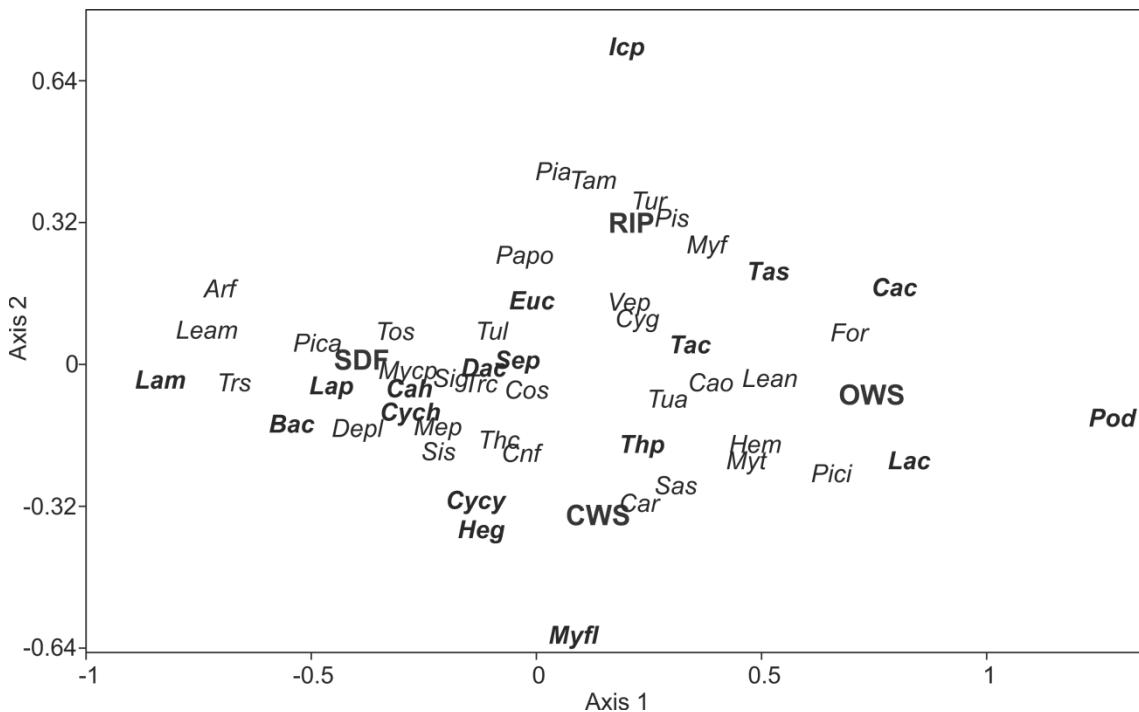
Fig. 2. Correspondence analysis for the 50 more common species of different vegetation types in southwestern Brazil. The species name codes are in Appendix 1 and in the text. Bold and italic codes represent, respectively, leader and follower species. Phytophysiognomies are in caps acronyms: SDF – semideciduous forest, RPF – riparian forest, CWS – closed-canopy woodland savanna (*cerradão*), OWS – open-canopy woodland savanna (chaco and cerrado *stricto sensu*).

1.3.1 Semideciduous forest

The first axis (9.54%) of PCoA ordinated the species from Atlantic forest, to the east, to Chiquitano forest, to the west (Fig. 3). However, only some species related to the Atlantic forest (Spot-backed Antshrike *Hypoedaleus guttatus* (Hyg), Black-goggled Tanager (Lam)

and Ochre-breasted Foliage-gleaner *Anabacerthia lichtensteini* (Anl)) and the Chiquitano forest (Bolivian Slaty-Antshrike *Thamnophilus sticturus* (Ths)) were found in more than 5% of flocks, whereas the most common flock participants showed a species composition similar to woodland savanna (Fig. 5). The second axis (7.83%) showed a species gradient from canopy species (e.g., small size: Blue Dacnis (Dac), Chestnut-vented Conebill (Cos), Gray Elaenia *Myiopagis caniceps* (Mycp); and medium size: Tityrids (Papo, Tii and Tic)) to understory species (e.g., Antshrikes (Tam, Thc and Ths), Creamy-bellied Thrush *Turdus amaurochalinus* (Tua), Black-goggled Tanager (Lam), and Fuscous and Euler's Flycatchers (Cnf and Lae)). In the center of two axes are the species more common and which are more associated with other species (e.g., Golden-crowned Warbler, Squirrel Cuckoo, Tropical Parula).
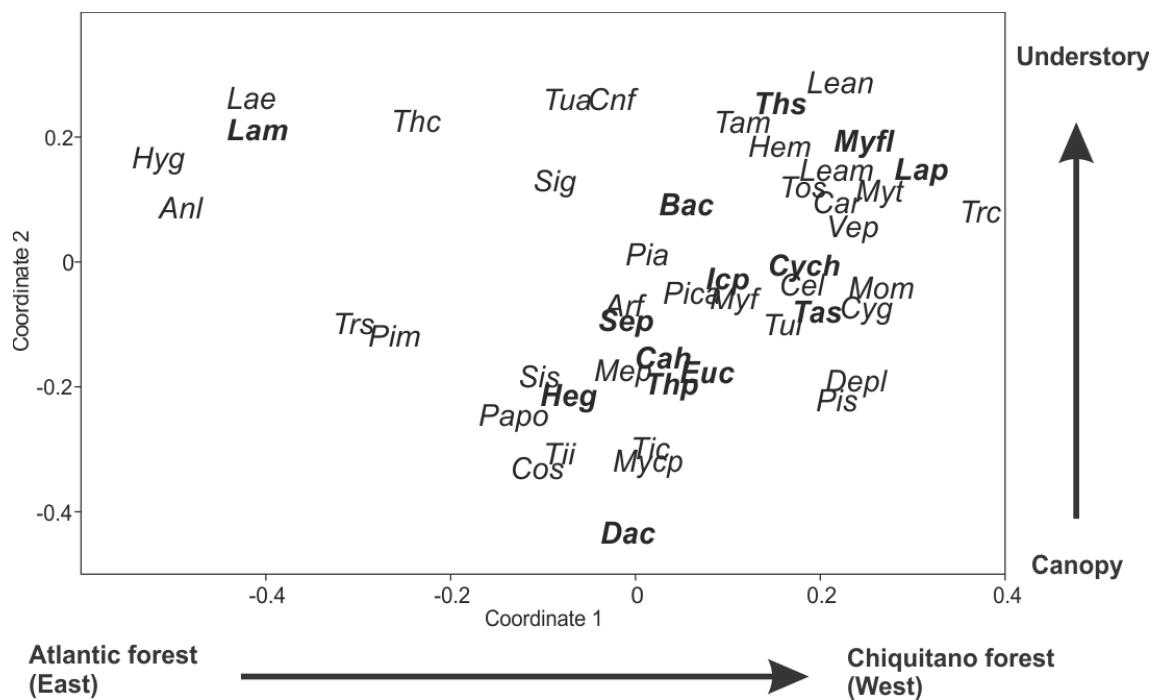
Fig. 3. Principal coordinates analysis of mixed flock species composition in semideciduous forests in southwestern Brazil. The Coordinate 1 showed a species turnover over east-western forests, and the Coordinate 2 a replacement between understory and canopy species. Leader and follower species are in bold-italic and italic codes, respectively. The species name acronyms are in Appendix 1 and in the text.

1.3.2 Riparian forest

The first coordinate (10.75%) of PCoA showed a species turnover between more dependent forest and forest-savanna species (Fig. 4). Forest (e.g., Olivaceous Woodcreeper *Sittasomus griseicapillus* (Sig), Sepia-capped Flycatcher (Leam)) were found in an extreme of gradient and are less related to riparian forest species, while in other part of axis there was a higher presence of open savanna (e.g., Barred Antshrike *Thamnophilus doliatus* (Thd), Saffron Finch *Sicalis flaveola* (Sif)) and riparian forest species (e.g., Silver-beaked Tanager (Rac), Great Kiskadee (Pis)) were more associated to edge of riparian forest flocks. The second axis (9.41%) segregated species of gallery forests (e.g., Rufous-browed Peppershrike (Cyg), Blue Dacnis (Dac), White-wedged Piculet (Pia)) from flooded forest (e.g., Variable Oriole (Icp), Silver-beaked Tanager (Rac), Yellow-billed Cardinal (Pac)) (Fig. 4). Some species participated in flocks along of two gradients and are ploted in the middle of the gradient (e.g., Sayaca Tanager (Tas), Brown-crested Flycatcher (Myt)).
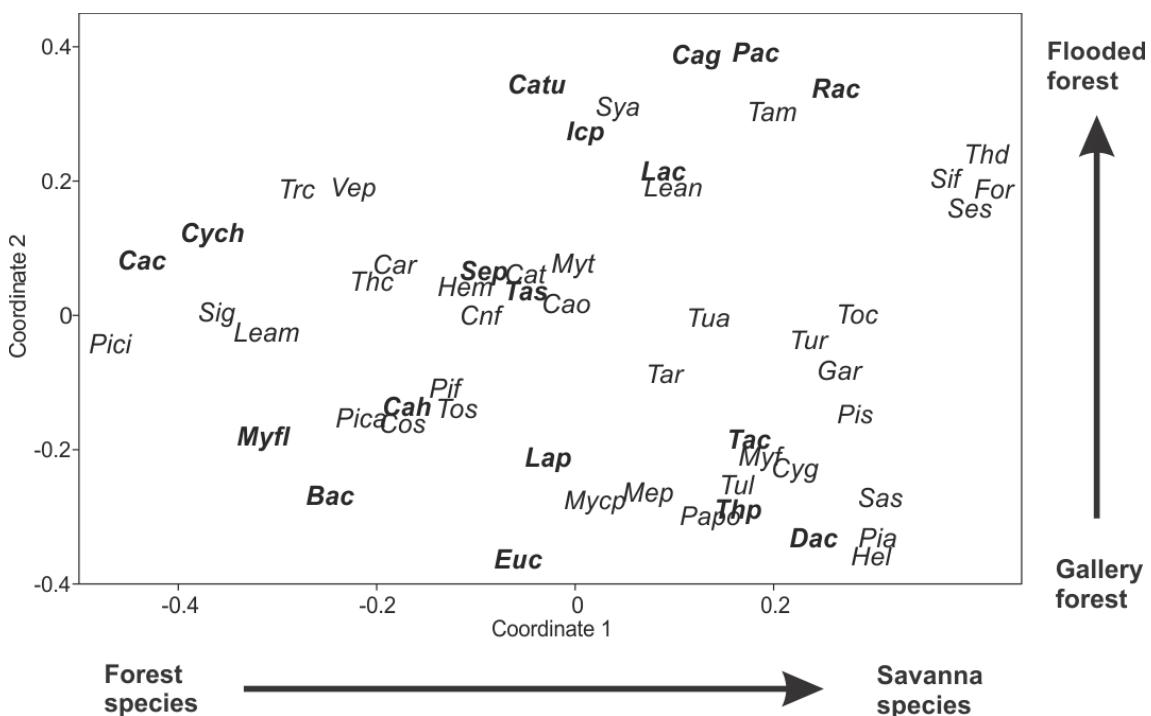
Fig. 4. Principal coordinates analysis of mixed flock species composition in riparian forests, southwestern Brazil. The Coordinate 1 showed a replacement between forest and savanna species, and the Coordinate 2 a substitution gradient from gallery forest (along small rivers) to flooded forest (Pantanal wetlands). Leader and follower species are in bold-italic and italic codes, respectively. The species name acronyms are in Appendix 1 and in the text.

1.3.4 Closed woodland savanna

The PCoA 1 axis (13.11%) explained associations from species typically found in riparian forest (e.g., Tanagers (Tas and Tac), Great Kiskadee (Pis)), to species of semideciduous forests (e.g., Woodcreepers (Depl, Sig and Lean), Yellow-olive Flycatcher *Tolmomyias sulphurescens* (Tos), Purple-throated Euphonia (Euc)) (Fig. 5). The second axis (9.91%) separated species of different body sizes and forest stratum. Small species of understory were associated with the four most common species (Rufous Casiornis (Car), Golden-crowned Warbler (Bac), Flavescent Warbler (Myfl) and Brown-crested Flycatcher (Myt)), while less frequent species, such as large-size (Plush-crested Jay *Cyanocorax chrysops* (Cych), Red-rumped Cacique *Cacicus haemorrhous* (Cah)) and canopy birds (small size: Chestnut-vented Conebill (Cos), Gray Elaenia (Mycp) and Purple-throated Euphonia (Euc); medium size: Boat-billed Flycatcher *Megarynchus pitangua* (Mep), and Tanagers (Tas, Tac)), formed other groups.
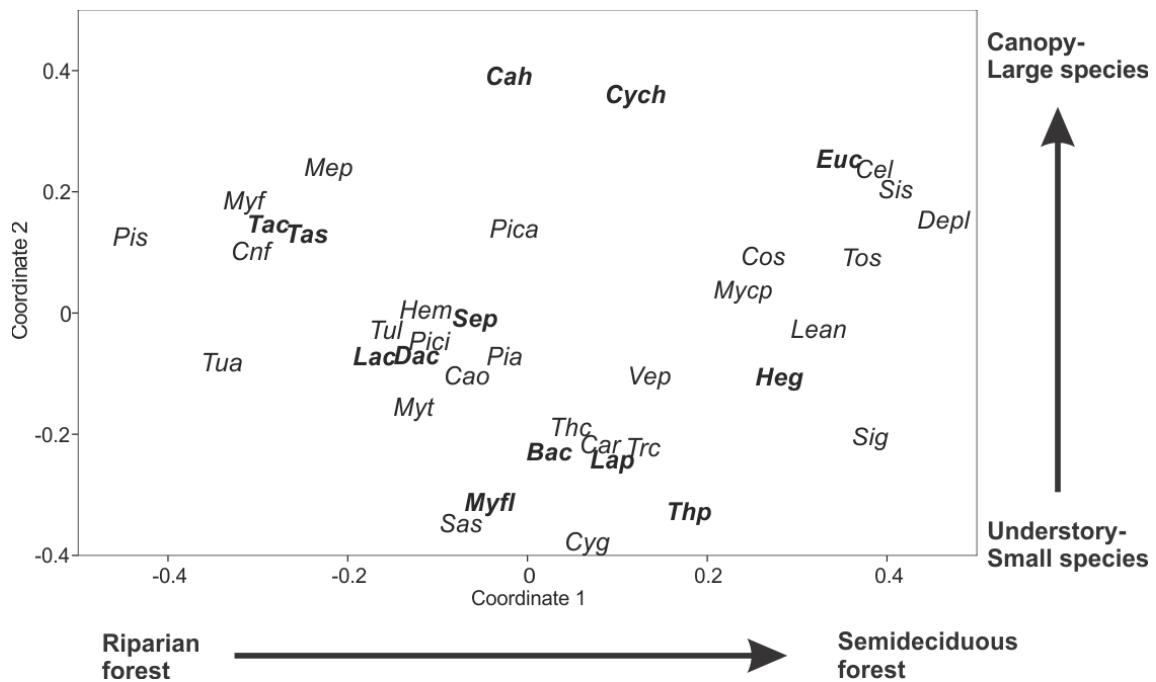
Fig. 5. Principal coordinates analysis of mixed flock species composition in closed-canopy woodland savanna, southwestern Brazil. The Coordinate 1 showed a species substitution along riparian-semideciduous forests (edaphic gradient), and the Coordinate 2 a replacement between understory-small species and canopy-large species. Leader and follower species are in bold-italic and italic codes, respectively. The species name acronyms are in Appendix 1 and in the text.

1.3.4 Open woodland savanna

The first coordinate of PCoA (15.84%) presented a gradient of the species replacement between Chaco and Cerrado savannas (Fig. 6). The main group was characterized for species more frequent over sananna gradient (Red-crested Finch (Lac), Brown-crested Flycatcher (Myt) and Rufous Casiornis (Car)). Other four smaller and less richness groups were aggrouped according to adjacent vegetation types or ecoregions (Cerrado or Chaco). Two groups were more closed to Chaco, the first represented by dry forest species (e.g., Olivaceous Woodcreeper (Sig), Golden-winged Cacique (Cac)) and the second by species associated to flooded forests of Paraguay basin (e.g., Sayaca Tanager (Tas)). The other groups were more related to Cerrado ecoregion, one of them was attended by species of gallery forest (e.g., Thrushes (Tua and Tul), Tanagers (Dac, Tac, Heg)), and other was led by two closed woodland savanna species, Planalto Slaty-Antshrike (Thp) and Flavescent Warbler (Myfl). Te second PCoA coordinate (9.50%) separated a group of grassland-savanna species from other five groups of axis 1, which were more associated to forests.
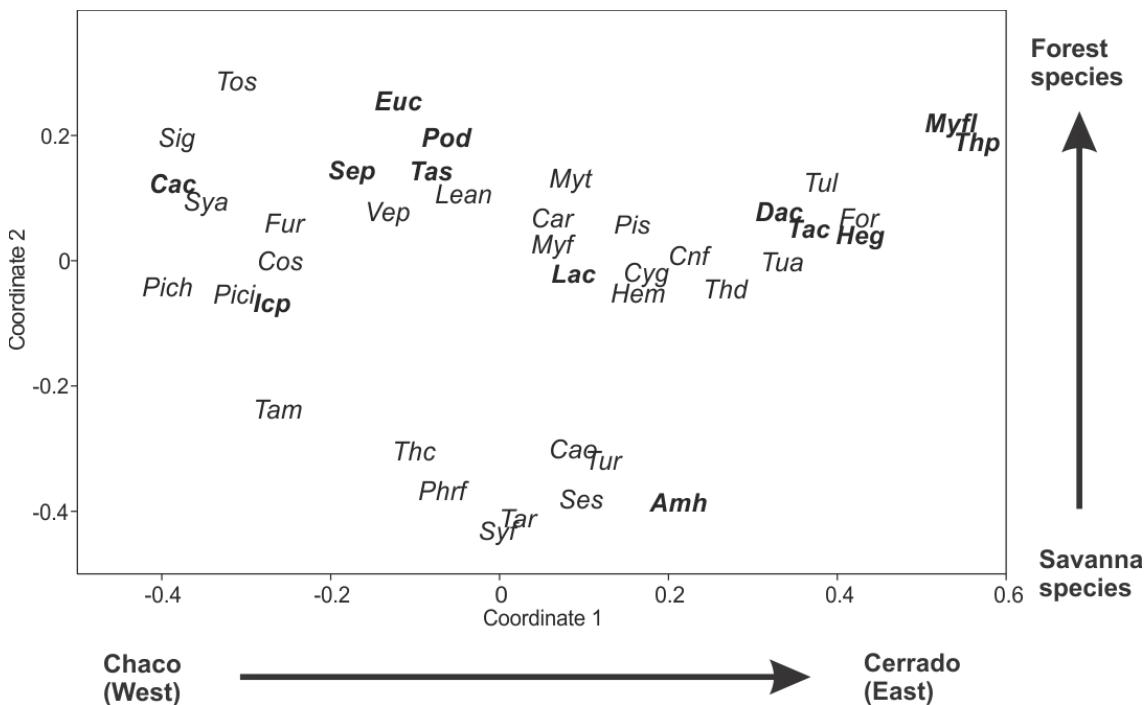

Fig. 6. Principal coordinates analysis of mixed flock species composition in open-canopy woodland savannas, southwestern Brazil. The Coordinate 1 showed a species turnover over east-western savannas, and the

Coordinate 2 a replacement between savanna and forest species. Leader and follower species are in bold-italic and italic codes, respectively. The species name acronyms are in Appendix 1 and in the text.

1.4 Discussion

The mean species richness was very similar among the four vegetation types we have studied but it is different of other Netropical localities. Only one study in southern Atlantic forest showed a mean richness similar to our results (Brandt et al. 2009). In general, all the Cerrado (Riparian forest: Marini 1992; Open woodland savannas: Alves and Cavalcanti 1996; Tubelis 2004; Tubelis et al. 2006; Amaral and Ragusa-Netto 2008) and most of the Atlantic (Rainforest: Davis 1946; Machado 1999; Develey and Peres 2000; Ghizoni-Jr and Azevedo 2006; Semideciduous forest: Maldonado-coelho and Marini 2000) mixed flocks present a richness per flock less than the present study. On the other hand, Amazonian (Munn and Terborgh 1979; Munn 1985; Stotz 1993; Develey and Stouffer 2001) and some Atlantic (Rainforest: Stotz 1993; Semideciduous forest: Aleixo 1997; Araucaria forest: Ghizoni-jr 2009) mixed flocks have a higher mean of species participants (> 10 species/flock).

Avian mixed flocks in southwestern Brazil present a species composition that combines different vegetation types, whereas the 10 more frequent species are generalist to live in several phytophysiognomies and forest strata. These species can be also part of heterogeneous flocks (Maldonado-Coelho and Marini 2003), which use understory and canopy of forest to forage and that can change their substrate foraging height when associated to mixed flocks (Machado and Rodrigues 2000). Understory species (e.g., Thrushes *Turdus*, Spinetails *Synallaxis*, Antshrikes *Thamnophilus*) were less common than midstory and canopy ones and participated togheter with these species in heterogeneous flocks. Understory flock species are more structured in Amazon (e.g., Antshrikes *Thamnomanes*) than in Cerrado and Atlantic forest (Powell 1985; Aleixo 1997; Tubelis et al. 2006). One of causes of this is a low vegetation sctructure of neotropical forests and woodland savannas allowing higher association between understory and canopy species when compared to separated Amazon canopy and understory flocks, where forest height is the highest (Munn 1985).

Some species, as the nuclear Golden-crowned Warbler (included ssp. *hypoleucus*) and Tropical Parula, are well know in literature as core species of dry forests (deciduous and semideciduous) and rainforests in South (Powell 1985; Aleixo 1997; Machado 1999; Maldonado-Coelho and Marini 2000, 2003; Ghizoni-Jr and Azevedo 2006; Brandt et al. 2009;

Ghizoni-jr 2009) and Central America (Powell 1979). However, other as the follower Rufous Casiornis, Brown-crested Flycatcher and Pale-breasted Thrush are considered rare or uncommon in mixed flocks of Cerrado (Tubelis 2007) and absent or rare in Atlantic forest ones. These five more common species were particularly found together in flocks of woodland savanna, which are relatively abundant in this vegetation type (Piratelli and Blake 2006; Cavarzere et al. 2011).

Species with different body sizes, such as the large nuclear Jays and Caciques, or large (Sayaca Tanager, Silver-beaked Tanager) and small (Guira Tanager, Blue Dacnis) tanagers, were also important in flock cohesion with other body size similar species. Jays and Caciques, for example, formed flocks from five to more than 20 individuals (e.g., Red-rumped Cacique), associated with Aracaris (Chestnut-eared Aracari *Pteroglossus castanotis*) and large Woodpeckers (Pale-crested Woodpecker *Celeus lugubris*) and Woodcreepers (Great Rufous Woodcreeper *Xiphocolaptes major* and *Dendrocolaptes* spp.), but always were solitary and vocalized very little within mixed flocks composed or guided by small species. On the other hand, other large species, as Trogons (*Trogon* spp.) and the Squirrel Cuckoo, participated as followers together with large and small species both in canopy and understory flocks, similar to that reported by Machado (1999) in Atlantic forest.

Generally, the commonest species in interspecific flocks were much more similar along the semideciduous forest, riparian forest and woodland savanna, although the composition of occasional species and the frequency of occurrence were different. Some Atlantic species, Black-goggled Tanager and Surucua Trogon *Trogon surrucura*, participated in flocks beyond the boundaries of their ecological features (humid forests, clearily defined forest stratification) and distribution, as in woodland savanna as in the Atlantic forest of São Paulo state. The inverse also happened to some Cerrado biome birds, Planalto Slaty-Antshrike and Flavescent Warbler, which are found from open savanna to interior of semideciduous forest (northeastern Atlantic forest of our study area). This ability of some species to use other habitats than those usual may suggest that they come together in mixed flocks to enlarge its range of food items during the dry season (Tubelis et al. 2006) or to reduce predation risk mainly to cross open habitats such as savannas (Dolby and Grubb Jr 2000).

There are also species confined in one or a few forest or savanna types. Such species are very important in flock dynamic and maintenance mainly in more restrictive environments such as the riparian forests (wetter) and open woodland savannas (drier). In the flooded forest, the familiar Silver-beaked Tanager (3-5 individuals) and the gregarious Yellow-billed Cardinal *Paroaria capitata* were very important in cohesion of flocks in interior and edge

forest, respectively. There are also those species that behave as sentinel mimicking other species, for example Variable Oriole (Fraga 1987) and Plush-crested Jay (Belton 1985). Other as Fawn-breasted Wren *Cantorchilus guarayanus*, behaves vocalizing in pairs (possibly in couples) all the time similarly to Golden-crowned Warbler, but which do not co-occur together. Moreover, the nuclear behavior by Fawn-breasted Wren in understory can also attract not just birds, but also squirrels to the flocks (Della-Flora et al. 2013). In western open savannas (chaco savanna), due to very proximity to Pantanal ecoregion, the flock species were similar to those found in riparian forest of Paraguay basin (flooded forest) aggregating a high richness of Icteridae in mixed flocks (one *Psarocolius*, three *Cacicus* and two *Icterus* species). Furthermore, Masked Gnatcatcher, Red-crested Finch and Pearly-vented Tody-Tyrant were very common in savannas of both Chaco and Cerrado ecoregions.

In general, there were four groups of flock species commonly encountered in most of habitats.

The first and the largest group is constituted by Squirrel Cuckoo, Trogons and small birds, basically insectivore passerines and small woodpeckers (*Veniliornis* and *Picumnus*), found from the ground to middle-story strata and from woodland savanna to semideciduous and riparian forests. Golden-crowned Warbler was the main nuclear species and Pale-breasted Thrush, Squirrel Cuckoo and Sepia-capped Flycatcher, the followers. Some species, such as Black-goggled Tanager, Sepia-capped Flycatcher, Olivaceous Woodcreeper, Yellow-olive Flycatcher, as well as the previously mentioned Golden-crowned Warbler and Tropical Parula, are listed as being important in the formation of mixed flocks in other studies in the Atlantic forest (Aleixo 1997; Machado 1999; Maldonado-Coelho and Marini 2003). Neverthless, Atlantic nuclear species as the understory Red-crowned Ant-Tanager *Habia hubica*, or the middle-story Buff-fronted Foliage-gleaner *Philydor rufum* and Rufous-winged Antwren *Herpsilochmus rufimarginatus*, which are very important in flock cohesion (Aleixo 1997; Maldonado-Coelho and Marini 2003), was not observed or were rare, respectively, in our study.

The second group is composed by small and medium sized species, canopy exclusives and with different diets and habitats. Sometimes this group can be divided by its body size in two sets: one represented by species associated to riparian forests as large Tanagers and Flycatchers, Tityras, Becards and Vireonids, such as Sayaca Tanager (nuclear), Rufous-browed Peppershrike (follower); and another group represented by small Tanagers, Parulas, Euphonias and Tyrannids, such as Tropical Parula (nuclear), Chestnut-vented Conebill and Gray Elaenia (followers), found in semideciduous forest and woodland savanna. These small

species, however, were associated to gallery forests and open savannas in other regions of Cerrado (Tubelis 2004, 2007; Tubelis et al. 2006). This absence of preference for a vegetation type could be explained by the ability of small species to adapt to different environments with different food resources (Tubelis et al. 2006).

The third flock group is formed by savanna species found in edge and interior of closed and open woodland savannas, respectively. Red-crested Finch was the main leader species, and Brown-crested Flycatcher, Rufous Casiornis, Pearly-vented Tody-Tyrant and Narrow-billed Woodcreeper, the main followers. Red-crested Finch and Saffron Finch, for example, are one of the most common core species in Bolivian and Paraguayan-Chaco savannas (Kratter et al. 1993; Smith et al. 2006). On the other hand, nuclear species of open savannas (cerrado *strictu senso* and *campo*-cerrado), White-banded Tanager *Neothraupis fasciata*, Suiriri Flycatcher *Suiriri suiriri* and White-rumped Tanager *Cypsnagra hirundinacea* (Alves and Cavalcanti 1996; Ragusa-Netto 2000; Amaral and Ragusa-Netto 2008) were rare in our observations probably because the end of their species or subspecies (*Suiriri s. affinis*) distributions in our study area (Ridgely and Tudor 1989, 1994)

The last and smallest group consists of large species of different taxonomic order and families (Aracaris, large Woodpeckers and Woodcreepers, Jays, Caciques and Oropendolas), but rarer to be seen in our trials likely due to their large territories. These species were observed in all strata of forest, in edge or interior; in most of times, the species responsible for flock cohesion were Jays (*Cyanocorax* spp.), Red-rumped Cacique and Crested Oropendola *Psarocolius decumanus*. Furthermore, these flocks were often found in the west region of our study area (less endangered by human activities like the Pantanal and Chacoan-like areas; Machado et al. 2004) than the east (Atlantic forest) or north (open Cerrado savannas). Perhaps this can be a response to the habitat fragmentation caused in last decades (Maldonado-Coelho and Marini 2000, 2004; Marini 2001), or biogeographically are regions where some species become rarer or absents (e.g. Crimson-crested Woodpecker *Campephilus melanoleucos*, Pale-crested Woodpecker, Great Rufous Woodcreeper, Purplish Jay, Crested Oropendola) allowing other larger species replace them.

1.5 Closing remarks

Our results show that there is no difference in the number of species per flock among the four vegetation types, although the species composition is significant different. Therefore, the vegetation structure (forest height and canopy openness) influences very little the mean

richness in flocks when compared to the species composition. On the other hand, as we have seen geographical gradients on the species composition of mixed flocks, ecoregions basically delimited by biomes (like Chaco, Atlantic Forest and Cerrado) are the main responsible by the differences observed on the species composition, more than ecological factors like local habitat (is a species is from canopy or understory).

The commonest species (50 species) in flocks are found in almost all savannas and forests, while only a small percentage is dependent of a particular type of vegetation. Although the most common species in the flocks are found in most habitats sampled, they tend to vary in body size and habitat use; these are thought to influence their behavior and association with other species. Thus, we can classify the mixed flocks in four groups according to species traits, which comprise (1) small insectivorous species of heterogeneous flocks led often by Golden-crowned Warbler, (2) small and medium species of canopy flocks led by Sayaca Tanager, Blue Dacnis and Guira Tanager, (3) open savanna species led by Red-crested Finch and as main followers Brown-crested Flycatcher and Rufous Casiornis, and (4) large size species led mainly by Jays and Red-rumped Cacique. However, other studies are needed to better understand the functioning of mixed flocks, given that some flocks had no leader species.

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1.7 Appendix

Appendix 1. Families and subfamilies, species and codes, vegetation type (Veg), foraging height (FH) and number of mixed flock participations (MFs) from 192 avian species along diferrent vegetation types in central South America. Leader and Follower species show bold and italic codes, respectively. Numbers represent forest and savannah physiognomies: 1 – semideciduos forest (1a – Atlantic forest, 1b – Chiquitano and non-Atlantic forests), 2 – riparian forest (2a – gallery and *ciliar* forests, 2b – flooded forest), 3 – closed woodland savanna (*cerradão*), 4 – open woodland savanna (4a –chaco savannah, 4b – cerrado *stricto sensu*).

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Parulidae	*Basileuterus culicivorus*	Golden-crowned Warbler	**Bac**	1,2a,3,4b	M	134
Tyrannidae	*Casiornis rufus*	Rufous Casiornis	*Car*	All	M	117
Tyrannidae	*Myiarchus tyrannulus*	Brown-crested Flycatcher	*Myt*	All	M	116
Turdidae	*Turdus leucomelas*	Pale-breasted Thrush	*Tul*	All	U	102
Vireonidae	*Cyclarhis gujanensis*	Rufous-browed Peppershrike	*Cyg*	All	M	95
Parulidae	*Setophaga pitiayumi*	Tropical Parula	**Sep**	All	C	88
Cuculidae	*Piaya cayana*	Squirrel Cuckoo	*Pica*	1,2,3,4a	M	76
Tyrannidae	*Hemitriccus margaritaceiventer*	Pearly-vented Tody-Tyrant	*Hem*	All	U	74
Thraupidae	*Thraupis sayaca*	Sayaca Tanager	**Tas**	All	C	73
Thraupidae	*Coryphospingus cucullatus*	Red-crested Finch	**Lac**	All	U	72
Picidae	*Veniliornis passerinus*	Little Woodpecker	*Vep*	All	M	70
Turdidae	*Turdus amaurochalinus*	Creamy-bellied Thrush	*Tua*	All	U	69
Dendrocolaptinae	*Lepidocolaptes angustirostris*	Narrow-billed Woodcreeper	*Lean*	All	M	69
Parulidae	*Myiothlypis flaveola*	Flavescent Warbler	**Myfl**	1,2a,3,4b	U	68
Thraupidae	*Hemithraupis guira*	Guira Tanager	*Heg*	All	C	61
Tyrannidae	*Myiarchus ferox*	Short-crested Flycatcher	*Myf*	All	M	57

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Thraupidae	*Dacnis cayana*	Blue Dacnis	*Dac*	1,2a,3,4b	C	57
Trogonidae	*Trogon curucui*	Blue-crowned Trogon	*Trc*	All	C	56
Tyrannidae	*Pitangus sulphuratus*	Great Kiskadee	*Pis*	All	M	55
Thraupidae	*Conirostrum speciosum*	Chestnut-vented Conebill	*Cos*	All	C	54
Dendrocolaptinae	*Sittasomus griseicapillus*	Olivaceous Woodcreeper	*Sig*	All	M	53
Tyrannidae	*Tolmomyias sulphurescens*	Yellow-olive Flycatcher	*Tos*	All	M	53
Tyrannidae	*Megarynchus pitangua*	Boat-billed Flycatcher	*Mep*	All	C	48
Fringillidae	*Euphonia chlorotica*	Purple-throated Euphonia	**Euc**	All	C	46
Icteridae	*Icterus pyrrhopterus*	Variable Oriole	**Icp**	All	M	45
Thamnophilidae	*Taraba major*	Great Antshrike	*Tam*	All	U	45
Thamnophilidae	*Thamnophilus pelzelni*	Planalto Slaty-Antshrike	**Thp**	1a,3,4,7	M	46
Thamnophilidae	*Thamnophilus caerulescens*	Variable Antshrike	*Thc*	1,2a,3,4a	M	44
Tyrannidae	*Leptopogon amaurocephalus*	Sepia-capped Flycatcher	*Leam*	1,2,3	M	44
Thraupidae	*Eucometis penicillata*	Gray-headed Tanager	**Lap**	1,2,3,4a	M	44
Tyrannidae	*Cnemotriccus fuscatus*	Fuscous Flycatcher	*Cnf*	All	U	41
Tyrannidae	*Myiopagis caniceps*	Gray Elaenia	*Mycp*	1,2,3,4b	C	41
Dendrocolaptinae	*Dendrocolaptes platyrostris*	Planalto Woodcreeper	*Depl*	1,2,3,4a	U	37
Icteridae	*Cacicus haemorrhous*	Red-rumped Cacique	**Cah**	1,2,3,4b	M	36
Picidae	*Picumnus albosquamatus*	White-wedged Piculet	*Pia*	1,2,3,4b	U	35
Tyrannidae	*Sirystes sibilator*	Sibilant Sirystes	*Sis*	All	C	34
Corvidae	*Cyanocorax chrysops*	Plush-crested Jay	**Cych**	All	M	31

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Trogonidae	*Trogon surrucura*	Surucua Trogon	*Trs*	1a,2a,3,4b	C	30
Picidae	*Picumnus cirratus*	White-barred Piculet	*Pic*	1,2,3,4a	U	30
Thraupidae	*Tangara cayana*	Burnished-buff Tanager	**Tac**	1a,2,3,4	C	27
Tyrannidae	*Camptostoma obsoletum*	Southern Beardless-Tyrannulet	*Cao*	1a,2,3,4	C	26
Turdidae	*Turdus rufiventris*	Rufous-bellied Thrush	*Tur*	All	U	26
Incertae sedis	*Saltator similis*	Green-winged Saltator	*Sas*	1a,2a,3,4b	M	25
Emberezidae	*Arremon flavirostris*	Saffron-billed Sparrow	*Arf*	1,2a,3	U	25
Thamnophilidae	*Formicivora rufa*	Rusty-backed Antwren	*For*	1a,2,3,4b	U	24
Polioptilidae	*Polioptila dumicola*	Masked Gnatcatcher	**Pod**	2,3,4	C	24
Icteridae	*Cacicus chrysopterus*	Golden-winged Cacique	**Cac**	1,2b,3,4a	M	23
Tityridae	*Pachyramphus polychopterus*	White-winged Becard	*Pap*	1a,2b,3	C	21
Corvidae	*Cyanocorax cyanomelas*	Purplish Jay	**Cycy**	1,2,3,4a	M	21
Thraupidae	*Trichothraupis melanops*	Black-goggled Tanager	**Trm**	1a,3,4a	U	20
Picidae	*Celeus lugubris*	Pale-crested Woodpecker	*Cel*	1,2b,3,4	U	19
Thamnophilidae	*Thamnophilus doliatus*	Barred Antshrike	*Thd*	1b,2,3,4	U	19
Thamnophilidae	*Herpsilochmus longirostris*	Large-billed Antwren	*Hel*	1,2a,3	M	18
Thraupidae	*Ramphocelus carbo*	Silver-beaked Tanager	**Rac**	1b,2,3	M	18
Furnariinae	*Furnarius rufus*	Rufous Hornero	*Fur*	2b,3,4	U	17
Troglodytidae	*Cantorchilus guarayanus*	Fawn-breasted Wren	**Cag**	1b,2b,4	U	17
Thraupidae	*Tachyphonus rufus*	White-lined Tanager	*Tar*	1b,2,3,4	U	17

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Galbulidae	*Galbula ruficauda*	Rufous-tailed Jacamar	*Gar*	1a,2, 3	U	16
Tityridae	*Tityra inquisitor*	Black-crowned Tityra	*Tii*	1,2a,3,4a	C	16
Thraupidae	*Nemosia pileata*	Hooded Tanager	*Nep*	All	C	16
Furnariinae	*Synallaxis albilora*	White-lored Spinetail	*Sya*	1b,2b,4	U	15
Tityridae	*Pachyramphus viridis*	Green-backed Becard	*Pavi*	1,2,3,4a	C	15
Thraupidae	*Pipraeida melanonota*	Fawn-breasted Tanager	*Pim*	1,2a,3	M	15
Tityridae	*Pachyramphus validus*	Crested Becard	*Pav*	1,2a,3	C	14
Momotidae	*Momotus momota*	Amazonian Motmot	*Mom*	1,2,3	M	14
Furnariinae	*Synallaxis frontalis*	Sooty-fronted Spinetail	*Syf*	1a,2a,3,4	U	14
Tyrannidae	*Serpophaga subcristata*	White-crested Tyrannulet	*Ses*	2,4	U	14
Furnariinae	*Phacellodomus rufifrons*	Rufous-fronted Thornbird	***Phrf***	2,3,4	U	13
Pipridae	*Pipra fasciicauda*	Band-tailed Manakin	*Pif*	1a,2,3	U	13
Thraupidae	*Paroaria capitata*	Yellow-billed Cardinal	**Pac**	2b	C	13
Picidae	*Piculus chrysochloros*	Golden-green Woodpecker	*Pich*	1b,2b,3,4	M	12
Tyrannidae	*Lathrotriccus euleri*	Euler's Flycatcher	*Lae*	1	U	12
Tityridae	*Tityra cayana*	Black-tailed Tityra	*Tic*	1a,2a,3	C	12
Picidae	*Colaptes melanochloros*	Green-barred Woodpecker	*Com*	1,2a,3,4b	M	11
Troglodytidae	*Troglodytes aedon*	House Wren	**Trm**	1,2a,3,4b	U	11
Thraupidae	*Sicalis flaveola*	Saffron Finch	**Sif**	2,4	U	11
Dendrocolaptinae	*Campylorhamphus trochilirostris*	Red-billed Scythebill	*Cat*	2	M	10
Furnariinae	*Xenops rutilans*	Streaked Xenops	*Xer*	1b,2a,3	M	10

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Thamnophilidae	*Thamnophilus sticturus*	Bolivian Slaty-Antshrike	**Ths**	1b	U	10
Tyrannidae	*Inezia inornata*	Plain Tyrannulet	*Ini*	1b,2b,3,4	C	10
Troglodytidae	*Campylorhynchus turdinus*	Thrush-like Wren	**Catu**	2,3,4a	C	10
Dendrocolaptinae	*Xiphocolaptes major*	Great Rufous Woodcreeper	*Xim*	1b,2b,4b	U	9
Thamnophilidae	*Hypoedaleus guttatus*	Spot-backed Antshrike	*Hyg*	1a	M	9
Emberezidae	*Ammodramus humeralis*	Grassland Sparrow	*Amh*	2a,3,4	U	9
Icteridae	*Psarocolius decumanus*	Crested Oropendola	**Psd**	1a,2b,3,4b	M	9
Furnariinae	*Anabacerthia lichtensteini*	Ochre-breasted Foliage-gleaner	*Anl*	1a	M	8
Furnariinae	*Philydor rufum*	Buff-fronted Foliage-gleaner	*Phr*	1,3	M	8
Thamnophilidae	*Herpsilochmus rufimarginatus*	Rufous-winged Antwren	*Her*	1a	M	8
Tyrannidae	*Phyllomyias reiseri*	Reiser's Tyrannulet	*Phre*	1	C	8
Tyrannidae	*Myiozetetes cayannensis*	Rusty-margined Flycatcher	*Myca*	1a,2a,3,4b	C	8
Mimidae	*Mimus saturninus*	Chalk-browed Mockingbird	**Mis**	1a,2,4b	M	8
Thraupidae	*Tersina viridis*	Swallow Tanager	**Tev**	1a,2,3	C	7
Thamnophilidae	*Pyriglena leucoptera*	White-shouldered Fire-eye	*Pyl*	1a	U	7
Thamnophilidae	*Herpsilochmus atricapillus*	Black-capped Antwren	*Hea*	1,2a,3	M	7
Tyrannidae	*Capsiempis flaveola*	Yellow Tyrannulet	*Caf*	1,2	U	7
Icteridae	*Cacicus solitarius*	Solitary Black Cacique	*Cas*	2b,4	M	7
Picidae	*Melanerpes flavifrons*	Yellow-fronted Woodpecker		1a	C	6
Tyrannidae	*Todirostrum cinereum*	Common Tody-Flycatcher		2	U	6

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Tyrannidae	*Elaenia flavogaster*	Yellow-bellied Elaenia		1a,2a,3,4b	M	6
Pipridae	*Antilophia galeata*	Helmeted Manakin		1a,2a	U	6
Thraupidae	*Thraupis palmarum*	Palm Tanager		1a,2a	C	6
Euphoniinae	*Euphonia violacea*	Violaceous Euphonia		1a	C	6
Bucconidae	*Nystalus maculatus*	Spot-backed Puffbird		1b,3	M	5
Dendrocolaptinae	*Dendrocolaptes picumnus*	Black-banded Woodcreeper		1b,2b,3	U	5
Furnariinae	*Synallaxis ruficapilla*	Rufous-capped Spinetail		1a	U	5
Thamnophilidae	*Dysithamnus mentalis*	Plain Antvireo		1a	U	5
Tyrannidae	*Myiornis auricularis*	Eared Pygmy-Tyrant		1a	U	5
Tyrannidae	*Elaenia spectabilis*	Large Elaenia		1a,2a,3,4b	M	5
Thraupidae	*Coereba flaveola*	Bananaquit		2a,3,4b	C	5
Thraupidae	*Sporophila angolensis*	Chestnut-bellied Seed-Finch		2b,4b	U	5
Icteridae	*Icterus croconotus*	Orange-backed Troupial		1a,2b,4b	M	5
Picidae	*Picumnus temminckii*	Ochre-collared Piculet		1a	U	4
Picidae	*Veniliornis spilogaster*	White-spotted Woodpecker		1a	M	4
Furnariinae	*Clibanornis rectirostris*	Chestnut-capped Foliage-gleaner		1b,2a	M	4
Tyrannidae	*Poecilotriccus latirostris*	Rusty-fronted Tody-Flycatcher		2b,4b	U	4
Tyrannidae	*Poecilotriccus plumbeiceps*	Ochre-faced Tody-Flycatcher		1a	U	4
Tyrannidae	*Platyrinchus mystaceus*	White-throated Spadebill		1a,2a	U	4
Tyrannidae	*Suiriri suiriri*	Suiriri Flycatcher		3,4b	C	4
Tyrannidae	*Elaenia parvirostris*	Small-billed Elaenia		2a,3,4b	U	4

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Tyrannidae	*Myiozetetes similis*	Social Flycatcher		1a,2a,4b	C	4
Incertae sedis	*Saltator coerulescens*	Grayish Saltator		2,4a	U	4
Parulidae	*Geothlypis aequinoctialis*	Masked Yellowthroat		2a	U	4
Ramphastidae	*Pteroglossus castanotis*	Chestnut-eared Aracari		1a,2a,3	M	3
Picidae	*Campephilus melanoleucos*	Crimson-crested Woodpecker		1b,3,4a	M	3
Dendrocolaptinae	*Xiphorhynchus guttatus*	Buff-throated Woodcreeper		1b	U	3
Furnariinae	*Synallaxis scutata*	Ochre-cheeked Spinetail		1	U	3
Furnariinae	*Phacellodomus ruber*	Greater Thornbird		2b	U	3
Conopophagidae	*Conopophaga lineata*	Rufous Gnateater		1a	U	3
Tyrannidae	*Phaeomyias murina*	Mouse-colored Tyrannulet		3,4b	M	3
Tyrannidae	*Colonia colonus*	Long-tailed Tyrant		1a,3	C	3
Tyrannidae	*Myiophobus fasciatus*	Bran-colored Flycatcher		2a,3	U	3
Tyrannidae	*Contopus cinereus*	Tropical Pewee		1a,3	C	3
Tyrannidae	*Machetornis rixosa*	Cattle Tyrant		2a,4a	M	3
Pipridae	*Chiroxiphia caudata*	Swallow-tailed Manakin		1a	U	3
Passerellidae	*Zonotrichia capensis*	Rufous-collared Sparrow		2b,4a	U	3
Thraupidae	*Volatinia jacarina*	Blue-black Grassquit		2b,4b	U	3
Thraupidae	*Sporophila caerulescens*	Double-collared Seedeater		1b,2a	U	3
Trogonidae	*Trogon rufus*	Black-throated Trogon		1a	M	2
Picidae	*Celeus flavescens*	Blond-crested Woodpecker		1a	M	2
Picidae	*Dryocopus lineatus*	Lineated Woodpecker		1b,3	M	2

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Dendrocolaptinae	*Lepidocolaptes falcinellus*	Scalloped Woodcreeper		1a	M	2
Furnariinae	*Furnarius leucopus*	Wing-banded Hornero		2b	U	2
Furnariinae	*Synallaxis spixi*	Spix's Spinetail		1a	U	2
Furnariinae	*Synallaxis hypospodia*	Cinereous-breasted Spinetail		2a	U	2
Thamnophilidae	*Formicivora melanogaster*	Black-bellied Antwren		2b	U	2
Tyrannidae	*Corythopis delalandi*	Southern Antpipit		1a	U	2
Tyrannidae	*Phylloscartes paulista*	São Paulo Tyrannulet		1a	M	2
Tyrannidae	*Euscarthmus meloryphus*	Tawny-crowned Pygmy-Tyrant		4a	U	2
Tyrannidae	*Tyrannus melancholicus*	Tropical Kingbird		1a	C	2
Tyrannidae	*Myiarchus swainsoni*	Swainson's Flycatcher		1b	M	2
Tityridae	*Schiffornis virescens*	Greenish Schiffornis		1a	U	2
Incertae sedis	*Phibalura flavirostris*	Swallow-tailed Cotinga		1a	C	2
Corvidae	*Cyanocorax cristatellus*	Curl-crested Jay		4b	M	2
Troglodytidae	*Cantorchilus leucotis*	Buff-breasted Wren		2b	U	2
Thraupidae	*Thlypopsis sordida*	Orange-headed Tanager		1a,2b	U	2
Incertae sedis	*Saltator atricollis*	Black-throated Saltator		4b	U	2
Thraupidae	*Poospiza melanoleuca*	Black-capped Warbling-Finch		4a	U	2
Thraupidae	*Sporophila frontalis*	Buffy-fronted Seedeater		2b	U	2
Parulidae	*Myiothlypis leucoblephara*	White-browed Warbler		2b	U	2
Parulidae	*Myiothlypis leucophrys*	White-striped Warbler		2a	U	2

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Icteridae	*Gnorimopsar chopi*	Chopi Blackbird		2a	C	2
Euphoniinae	*Chlorophonia cyanea*	Blue-naped Chlorophonia		1a	C	2
Fringillinae	*Sporagra magellanica*	Hooded Siskin		4a	M	2
Columbidae	*Columbina squammata*	Scaled Dove		4a	U	1
Momotidae	*Baryphthengus ruficapillus*	Rufous-capped Motmot		4b	U	1
Bucconidae	*Nystalus chacuru*	White-eared Puffbird		2b	U	1
Bucconidae	*Nonnula rubecula*	Rusty-breasted Nunlet		1b	U	1
Ramphastidae	*Selenidera maculirostris*	Spot-billed Toucanet		1a	M	1
Picidae	*Veniliornis mixtus*	Checkered Woodpecker		4a	U	1
Dendrocolaptinae	*Xiphorhynchus fuscus*	Lesser Woodcreeper		2a	U	1
Furnariinae	*Cranioleuca vulpina*	Rusty-backed Spinetail		2b	M	1
Furnariinae	*Synallaxis cinerascens*	Gray-bellied Spinetail		1a	U	1
Formicariidae	*Chamaeza campanisona*	Short-tailed Antthrush		2a	U	1
Thamnophilidae	*Mackenziaena severa*	Tufted Antshrike		1a	U	1
Thamnophilidae	*Cercomacra melanaria*	Mato Grosso Antbird		2b	U	1
Thamnophilidae	*Drymophila malura*	Dusky-tailed Antbird		1a	U	1
Tyrannidae	*Phyllomyias burmeisteri*	Rough-legged Tyrannulet		2a	C	1
Tyrannidae	*Myiodynastes maculatus*	Streaked Flycatcher		1a	C	1
Tyrannidae	*Legatus leucophaius*	Piratic Flycatcher		1a	C	1
Tityridae	*Xenopsaris albinucha*	White-naped Xenopsaris		4a	C	1
Oxyruncidae	*Oxyruncus cristatus*	Sharpbill		1a	U	1

Family - Subfamily	Species	Common name	Code[a]	Veg[b]	FH[c]	MF
Cotingidae	*Procnias nudicollis*	Bare-throated Bellbird	1a		C	1
Pipridae	*Ilicura militaris*	Pin-tailed Manakin	1a		U	1
Vireonidae	*Vireo olivaceus*	Red-eyed Vireo	1a		C	1
Donacobiidae	*Donacobius atricapilla*	Black-capped Donacobius	2b		U	1
Thraupidae	*Tachyphonus coronatus*	Ruby-crowned Tanager	3		U	1
Thraupidae	*Cypsnagra hirundinacea*	White-rumped Tanager	4b		U	1
Thraupidae	*Neothraupis fasciata*	White-banded Tanager	4b		U	1
Incertae sedis	*Saltator maximus*	Buff-throated Saltator	2b		U	1
Thraupidae	*Sporophila pileata*	Pearly-bellied Seedeater	4b		U	1
Euphoniinae	*Euphonia pectoralis*	Chestnut-bellied Euphonia	2b		C	1
Cardinalidae	*Amaurospiza moesta*	Blackish-blue Seedeater	2b		U	1

Appendix 2. Frequency of occurrence (FO) of mixed flock species associated to four vegetation types in central of South America. Number of flocks by vegetation: semideciduous forest ($N = 149$), riparian forest ($N = 94$), closed ($N = 93$) and open woodland savanna ($N = 62$). In bold the ten more frequent species in 398 mixed flocks.

Semideciduous forest		Riparian forest		Closed woodland savanna		Open woodland savanna	
Species	FO	Species	FO	Species	FO	Species	FO
Golden-crowned Warbler	56.3	**Rufous-browed Peppershrike**	26.1	**Rufous Casiornis**	42.4	**Brown-crested Flycatcher**	57.1
Squirrel Cuckoo	30.4	**Sayaca Tanager**	26.1	**Brown-crested Flycatcher**	39.1	**Red-crested Finch**	55.6
Pale-breasted Thrush	30.4	**Pale-breasted Thrush**	25.0	**Flavescent Warbler**	39.1	**Rufous Casiornis**	44.4
Tropical Parula	24.5	Variable Oriole	25.0	**Golden-crowned Warbler**	34.8	Narrow-billed Woodcreeper	36.5
Sepia-capped Flycatcher	23.8	Great Kiskadee	23.9	**Pearly-vented Tody-Tyrant**	25.0	**Rufous-browed Peppershrike**	36.5
Rufous Casiornis	23.2	Short-crested Flycatcher	22.8	**Pale-breasted Thrush**	22.8	**Pearly-vented Tody-Tyrant**	34.9
Rufous-browed Peppershrike	21.2	**Brown-crested Flycatcher**	21.7	Guira Tanager	22.8	**Sayaca Tanager**	34.9
Yellow-olive Flycatcher	20.5	**Tropical Parula**	20.6	**Tropical Parula**	21.7	Creamy-bellied Thrush	28.6
Olivaceous Woodcreeper	19.8	Little Woodpecker	19.6	**Red-crested Finch**	20.6	Little Woodpecker	25.4
Guira Tanager	17.9	White-wedged Piculet	17.4	Creamy-bellied Thrush	18.5	Masked Gnatcatcher	25.4

Semideciduous forest		Riparian forest		Closed woodland savanna		Open woodland savanna	
Species	FO	Species	FO	Species	FO	Species	FO
Gray-headed Tanager	16.6	Silver-beaked Tanager	17.4	Blue-crowned Trogon	17.4	Rufous Hornero	19.0
Brown-crested Flycatcher	15.9	Narrow-billed Woodcreeper	16.3	**Rufous-browed Peppershrike**	17.4	Short-crested Flycatcher	19.0
Blue Dacnis	15.9	Great Antshrike	16.3	Narrow-billed Woodcreeper	16.3	**Pale-breasted Thrush**	19.0
Little Woodpecker	15.2	**Pearly-vented Tody-Tyrant**	16.3	Chestnut-vented Conebill	16.3	**Tropical Parula**	19.0
Planalto Woodcreeper	15.2	**Rufous Casiornis**	16.3	**Blue Dacnis**	16.3	Golden-winged Cacique	19.0
Blue-crowned Trogon	14.6	**Golden-crowned Warbler**	16.3	**Squirrel Cuckoo**	15.2	White-barred Piculet	17.5
Gray Elaenia	14.6	**Squirrel Cuckoo**	15.2	Variable Antshrike	15.2	Planalto Slaty-Antshrike	17.5
Boat-billed Flycatcher	14.6	Blue-crowned Trogon	15.2	Boat-billed Flycatcher	15.2	Olivaceous Woodcreeper	15.9
Chestnut-vented Conebill	13.9	Creamy-bellied Thrush	15.2	Fuscous Flycatcher	14.1	Rusty-backed Antwren	15.9
Surucua Trogon	13.2	**Blue Dacnis**	14.1	Little Woodpecker	13.0	Great Kiskadee	15.9
Creamy-bellied Thrush	13.2	Yellow-billed Cardinal	14.1	Planalto Slaty-Antshrike	13.0	Golden-green Woodpecker	14.3
Variable Antshrike	12.6	Rufous-tailed Jacamar	13.0	Short-crested Flycatcher	13.0	Rufous-fronted Thornbird	14.3
Saffron-billed Sparrow	12.6	Chestnut-vented Conebill	13.0	**Sayaca Tanager**	13.0	White-crested Tyrannulet	14.3
Purple-throated Euphonia	12.6	Purple-throated Euphonia	13.0	Green-winged Saltator	12.0	Sooty-fronted Spinetail	12.7
Great Antshrike	11.3	**Red-crested Finch**	12.0	Gray-headed Tanager	10.9	Great Antshrike	12.7
Sibilant Sirystes	11.3	Rufous-bellied Thrush	10.9	Red-rumped Cacique	10.9	Guira Tanager	12.7
Black-goggled Tanager	11.3	Barred Antshrike	9.8	White-barred Piculet	9.8	White-lored Spinetail	11.1
Flavescent Warbler	11.3	Yellow-olive Flycatcher	9.8	Gray Elaenia	9.8	Barred Antshrike	11.1
Red-rumped Cacique	11.3	Boat-billed Flycatcher	9.8	Southern Beardless-Tyrannulet	9.8	Chestnut-vented Conebill	11.1
Plush-crested Jay	10.6	Large-billed Antwren	8.7	Great Kiskadee	9.8	Burnished-buff Tanager	11.1
Narrow-billed Woodcreeper	9.9	Fuscous Flycatcher	8.7	Sibilant Sirystes	9.8	**Flavescent Warbler**	11.1
Fuscous Flycatcher	9.9	Southern Beardless-Tyrannulet	8.7	Plush-crested Jay	8.7	Variable Oriole	11.1
Planalto Slaty-Antshrike	9.3	Fawn-breasted Wren	8.7	Purple-throated Euphonia	8.7	Yellow-olive Flycatcher	9.5
Pearly-vented Tody-Tyrant	9.3	Thrush-like Wren	8.7	White-wedged Piculet	7.6	Grassland Sparrow	9.5
Sayaca Tanager	9.3	Gray-headed Tanager	8.7	Olivaceous Woodcreeper	7.6	Variable Antshrike	7.9
Great Kiskadee	8.6	**Flavescent Warbler**	8.7	Planalto Woodcreeper	7.6	Fuscous Flycatcher	7.9
Variable Oriole	8.6	Red-rumped Cacique	8.7	Yellow-olive Flycatcher	7.6	Southern Beardless-Tyrannulet	7.9
Short-crested Flycatcher	7.9	Red-billed Scythebill	7.6	Purplish Jay	6.5	Rufous-bellied Thrush	7.9
Black-crowned Tityra	7.3	White-lored Spinetail	7.6	Burnished-buff Tanager	6.5	**Blue Dacnis**	7.9
White-wedged Piculet	6.6	Variable Antshrike	7.6	Pale-crested Woodpecker	5.4	White-lined Tanager	7.9
Amazonian Motmot	6.0	Planalto Slaty-Antshrike	7.6	Great Antshrike	5.4	Blue-crowned Trogon	6.3
Pale-crested Woodpecker	6.0	Gray Elaenia	7.6			Planalto Woodcreeper	6.3
Spot-backed	6.0	White-winged Becard	7.6			Plain Tyrannulet	6.3

Semideciduous forest		Riparian forest		Closed woodland savanna		Open woodland savanna	
Species	FO	Species	FO	Species	FO	Species	FO
Antshrike							
Black-tailed Tityra	6.0	Burnished-buff Tanager	7.6			Sibilant Sirystes	6.3
Purplish Jay	6.0	Saffron Finch	7.6			Green-winged Saltator	6.3
Fawn-breasted Tanager	6.0	Olivaceous Woodcreeper	6.5			Saffron Finch	6.3
Ochre-breasted Foliage-gleaner	5.3	Rusty-backed Antwren	6.5				
Bolivian Slaty-Antshrike	5.3	Common Tody-Flycatcher	6.5				
Rufous-winged Antwren	5.3	Green-winged Saltator	6.5				
Euler's Flycatcher	5.3	White-barred Piculet	5.4				
White-winged Becard	5.3	White-crested Tyrannulet	5.4				
Red-crested Finch	5.3	Band-tailed Manakin	5.4				
		Plush-crested Jay	5.4				
		Guira Tanager	5.4				
		White-lined Tanager	5.4				
		Golden-winged Cacique	5.4				

FO < 5%: *Semideciduous forest* (Great Rufous Woodcreeper, White-shouldered Fire-eye, Large-billed Antwren, Rufous-bellied Thrush, Burnished-buff Tanager, Yellow-fronted Woodpecker, Buff-fronted Foliage-gleaner, Streaked Xenops, Crested Becard, Green-backed Becard, Fawn-breasted Wren, Violaceous Euphonia, Rufous-capped Spinetail, Plain Antvireo , Black-capped Antwren, Eared Pygmy-Tyrant, House Wren, Hooded Tanager, Golden-winged Cacique, White-barred Piculet, Ochre-collared Piculet, Rusty-backed Antwren, Ochre-faced Tody-Flycatcher, Southern Beardless-Tyrannulet, Band-tailed Manakin, White-lined Tanager, Green-winged Saltator, Crested Oropendola, Rufous-tailed Jacamar, White-spotted Woodpecker, Green-barred Woodpecker, Buff-throated Woodcreeper, Ochre-cheeked Spinetail, Rufous Gnateater, Reiser's Tyrannulet, Yellow Tyrannulet, Swallow-tailed Manakin, Palm Tanager, Black-throated Trogon, Scalloped Woodcreeper, Black-banded Woodcreeper, Sooty-fronted Spinetail, Chestnut-capped Foliage-gleaner, Southern Antpipit, São Paulo Tyrannulet, White-throated Spadebill, Yellow-bellied Elaenia, Plain Tyrannulet, Long-tailed Tyrant, Rusty-margined Flycatcher, Tropical Kingbird, Swainson's Flycatcher, Greenish Schiffornis, Swallow-tailed Cotinga, Helmeted Manakin, Swallow Tanager, Double-collared Seedeater, Orange-backed Troupial, Blue-naped Chlorophonia, Spot-backed Puffbird, Chestnut-eared Aracari, Spot-billed Toucanet, Golden-green Woodpecker, Blond-crested Woodpecker. Lineated Woodpecker, Crimson-crested Woodpecker, Red-billed Scythebill, Spix's Spinetail, Gray-bellied Spinetail, White-lored Spinetail, Tufted Antshrike, Barred Antshrike, Black-bellied Antwren, Dusky-tailed Antbird, Rusty-fronted Tody-Flycatcher, Large Elaenia, Social Flycatcher, Tropical Pewee, Streaked Flycatcher, Piratic Flycatcher, Sharpbill, Bare-throated Bellbird, Pin-tailed Manakin, Red-eyed Vireo, Chalk-browed Mockingbird, Silver-beaked Tanager, Ruby-crowned Tanager, Orange-headed Tanager, Chestnut-bellied Euphonia, Hooded Siskin); *Riparian forest* (Rufous Hornero, Yellow Tyrannulet, Sibilant Sirystes, Crested Becard, Helmeted Manakin, Purplish Jay, Masked Gnatcatcher, Chalk-browed Mockingbird, Hooded Tanager, Swallow Tanager, Saffron-billed Sparrow, Solitary Black Cacique, Amazonian Motmot, Green-barred Woodpecker, Planalto Woodcreeper, Rufous-fronted Thornbird, Sepia-capped Flycatcher, Plain Tyrannulet, Green-backed Becard, Palm Tanager, Blue-black Grassquit, Chestnut-bellied Seed-Finch, Masked Yellowthroat, Pale-crested Woodpecker, Wing-banded Hornero, Sooty-fronted Spinetail, Greater Thornbird, Chestnut-capped Foliage-gleaner, Rusty-fronted Tody-Flycatcher, White-throated Spadebill, Euler's Flycatcher, Reiser's Tyrannulet, Yellow-bellied Elaenia, Social Flycatcher, Cattle Tyrant, Buff-breasted Wren, Bananaquit, Fawn-breasted Tanager, Grayish Saltator, Buffy-fronted Seedeater, White-browed Warbler, White-striped Warbler, Crested Oropendola, Orange-backed Troupial, Chopi Blackbird, Surucua Trogon, White-eared Puffbird, Rusty-breasted Nunlet, Chestnut-eared Aracari, White-spotted Woodpecker, Golden-green Woodpecker, Blond-crested Woodpecker, Lesser Woodcreeper, Great Rufous Woodcreeper, Black-banded Woodcreeper, Rusty-backed Spinetail, Spix's Spinetail, Cinereous-breasted Spinetail, Streaked Xenops, Short-tailed Antthrush, Bolivian Slaty-Antshrike, Black-bellied Antwren, Mato Grosso Antbird, Black-capped Antwren, Rough-legged Tyrannulet, Small-billed Elaenia, Large Elaenia, Bran-colored Flycatcher, Rusty-margined Flycatcher, Black-crowned Tityra, Black-tailed Tityra, Black-capped Donacobius, House Wren, Orange-headed Tanager, Black-goggled Tanager , Buff-throated Saltator, Black-throated Saltator, Rufous-collared Sparrow, Grassland Sparrow, Double-collared Seedeater, Blackish-blue Seedeater); *Closed woodland savanna* (Spot-backed Puffbird, Rusty-backed Antwren, Sepia-capped Flycatcher, Crested Becard, White-winged Becard, Band-tailed Manakin, House Wren, Rufous-bellied Thrush, Masked Gnatcatcher, Hooded Tanager, Fawn-breasted Tanager, Green-barred Woodpecker, Streaked Xenops, Large-billed Antwren, Reiser's Tyrannulet, Rusty-margined Flycatcher, Green-backed Becard, Black-crowned Tityra, White-lined Tanager, Surucua Trogon, Amazonian Motmot, Sooty-fronted Spinetail, Buff-fronted Foliage-gleaner, Barred Antshrike, Euler's Flycatcher, Bran-colored Flycatcher, Tropical Pewee, Black-tailed Tityra, Bananaquit, Black-goggled Tanager, Saffron-billed Sparrow, Grassland Sparrow, Crested Oropendola, Variable Oriole, Rufous-capped Motmot, Rufous-tailed Jacamar, Chestnut-eared Aracari, Golden-green Woodpecker, Lineated Woodpecker, Crimson-crested Woodpecker, Black-banded Woodcreeper, Rufous Hornero, Cinereous-breasted Spinetail, Greater Thornbird, Rufous-fronted Thornbird, Bolivian Slaty-Antshrike, Black-capped Antwren, Rusty-fronted Tody-Flycatcher, Mouse-colored Tyrannulet, Suiriri Flycatcher, Small-billed Elaenia, Yellow-bellied Elaenia, Large Elaenia, Plain

Tyrannulet, Long-tailed Tyrant, Curl-crested Jay, Thrush-like Wren Thrush-like Wren, Silver-beaked Tanager, Grayish Saltator, Swallow Tanager, Pearly-bellied Seedeater, Masked Yellowthroat, Golden-winged Cacique, Hooded Siskin); *Open woodland savanna* (Pale-crested Woodpecker, Suiriri Flycatcher, Gray Elaenia, Boat-billed Flycatcher, Green-backed Becard, Fawn-breasted Wren, Chalk-browed Mockingbird, Hooded Tanager, Solitary Black Cacique, Squirrel Cuckoo, Surucua Trogon, White-wedged Piculet, Green-barred Woodpecker, Red-billed Scythebill, Mouse-colored Tyrannulet, Small-billed Elaenia, Large Elaenia, Tawny-crowned Pygmy-Tyrant, Rusty-margined Flycatcher, White-winged Becard, Purplish Jay, Plush-crested Jay, Rufous-collared Sparrow , Black-capped Warbling-Finch, Chestnut-bellied Seed-Finch, Golden-crowned Warbler, Scaled Dove, Checkered Woodpecker, Crimson-crested Woodpecker, Black-banded Woodcreeper, Yellow-bellied Elaenia, Social Flycatcher, Cattle Tyrant, Black-crowned Tityra, White-naped Xenopsaris, Curl-crested Jay, House Wren, Thrush-like Wren, Bananaquit, Gray-headed Tanager, White-rumped Tanager, White-banded Tanager, Black-throated Saltator, Grayish Saltator, Crested Oropendola, Red-rumped Cacique, Orange-backed Troupial).

2 ARTIGO 2 - PAIRWISE ASSOCIATION OF AVIAN MIXED FLOCKS IN SAVANNA-FOREST ENVIRONMENTS[2]

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[2] Esse artigo segue as normas da revista Journal of Avian Biology

2.1 Abstract

Mixed flocks are positive interactions where the species can benefit by increasing feeding efficiency or predator avoidance. Leader and follower species behave and show frequency of occurrence different within of flocks. Leaders are more gregarious and alerts, whereas the followers participate alone or in pairs and are more dependent to live in interspecific flocks. In this study, we verify coexistence patterns of association in mixed flocks and their pairwise relations (mutualism or commensalism) between leaders and followers in several types of savanna and forest in central South America. All types of vegetation present aggregation more than by chance. Non-random pairwise associations presented much more aggregation than segregated: Closed woodland savanna (*cerradão*) present more number of aggregations than Semideciduous and Riparian forest. Furthermore, leader-leader and leader-follower pairwise associations were less aggregated than followers associations over all habitats, but there was no significant difference to Closed woodland savanna.

Key-words: Atlantic forest, Cerrado, Chaco, commensalism, dry forest, mutualism, Neotropical savannas, Pantanal, riparian forest.

2.2 Introduction

Avian mixed flocks are commonly known through of mutual and commensal relationships among two or more individuals of different species (Hino 1998). Two types of flock participants are recognized. Those that join to other species ("followers", but see other subcategories in Goodale and Beauchamp 2010) and are therefore likely to be the recipients of benefits of flock participation, and those that are joined in flocks ("leaders", "core" or "nuclear" species) (Sridhar et al. 2009).

Studies of mixed-species bird flocks have found that nuclear species, those important to flock coherence and maintenance (Moynihan 1962), are either intraspecifically gregarious (Powell 1985) or are 'sentinel' species highly sensitive to predators (Alves and Cavalcanti 1996; Ragusa-Netto 2000), or both (Goodale and Kotagama 2005a). They can provide direct foraging benefits such as flushing insects (Kotagama and Goodale 2004) and better protection through "many-eyes" (Pulliam 1973) or encounter effects (Inman and Krebs 1987) for flock followers. On the other hand, there are evidences that some nuclear species are not dependent of other species to maximize or increase protection against potential predators. It is found when there is food increasing for nuclear species (Berner and Grubb 1985) or when they live in small family groups (Hutto 1994; Hino 1998). Furthermore, the relationships of dependence between species would be stronger between follower species than core species (Graves and Gotelli 1993; Hutto 1994). In other words, it may exist as mutualistic or commensalistic relationships among species (Hino 1998), and co-occurrence patterns between them would be stronger for species more often found in mixed flocks but which are not the main leaders (Graves and Gotelli 1993).

Co-occurrence patterns in pairs of species have been evaluated in the last years with aim to determine whether the communities are more or less structured – aggregated, segregated or random – by null models (Gotelli and Graves 1996). Some studies tested for non-randomic mixed flock structure or its species pair coexistence (Jones 1977; Eguchi et al. 1993; Graves and Gotelli 1993; Hutto 1994; Latta and Wunderle 1996; Bohórquez 2003; Péron and Crochet 2009; Arbeláez-Cortés et al. 2011; Sridhar et al. 2012; Martínez and Gomez 2013). However, only two of them evaluated pairwise relationships between species with use of null models (Sridhar et al. 2012; Martínez and Gomez 2013).

In tropical open woodland savannas the avoidance of predators is a determinant factor to promote more associations (Alves and Cavalcanti 1996; Ragusa-Netto 2002). On the other hand, in tropical forests the food storage can influence higher flock participation (Develey and

Peres 2000). However, little is known about pairwise species associations between leader and follower species in those environments (Sridhar et al. 2009) and no study tested if aggregated species pairs would be higher in savannas than forests or *vice-versa*. Here, we identify co-occurrence patterns between pairs of species by null models and testing mutual/commensal relationships among species from different forest and savanna types and among leader and follower species in a regional scale.

2.3 Methods

2.3.1 Study area

This study was carried out in central South America, southwest Brazil (18 to 23º S, 54 to 57º W), including three states: Mato Grosso do Sul (southern half), São Paulo (southwest) and Paraná (northwest) (Figure 1). It was developed a multisite design (Goodale et al. 2009) with 29 independent sample areas. The vegetation predominates between savannas and forests, as in west as in east (Figure 1). Generically, we divided the study area in the following main phytophysiognomy, which correspond to: Semideciduous forests (e.g., Alto Paraná Atlantic Forest, Chiquitano Forest, and sub-mountain forests of the Maracaju and Bodoquena plateaus in mid-west); Riparian forests (e.g., gallery, *ciliar* and flooded forests from Paraguay and Parana basins); Closed woodland savannas (e.g., *cerradão*); and Open woodland savannas (e.g., chaco savanna, in southwestern, and cerrado *sensu stricto*, mainly in northeast) (Oliveira-Filho and Ratter 2002).

2.3.2 Flock sampling

Our multisite design consists in continuous and fragmented vegetation (> 100 ha), forests along rivers and small patches of flooded forest, being sampled for four days per locality. Sampling always occurred during the dry season (May-August) from 2009 to 2011. Mixed flocks were observed in the morning (07:00-11:00h) and in the afternoon (16:00-17:00h), 12 to 15 hours in each area depending of climate conditions, totaling 406 h of field observation. In each site natural or anthropic trial transects were carried out from 500 to 2000 m, depending of the area size, in vegetation interior as well as in edges of patches and continuous areas. Each flock was followed by no more than 30 min or until all species were counted.
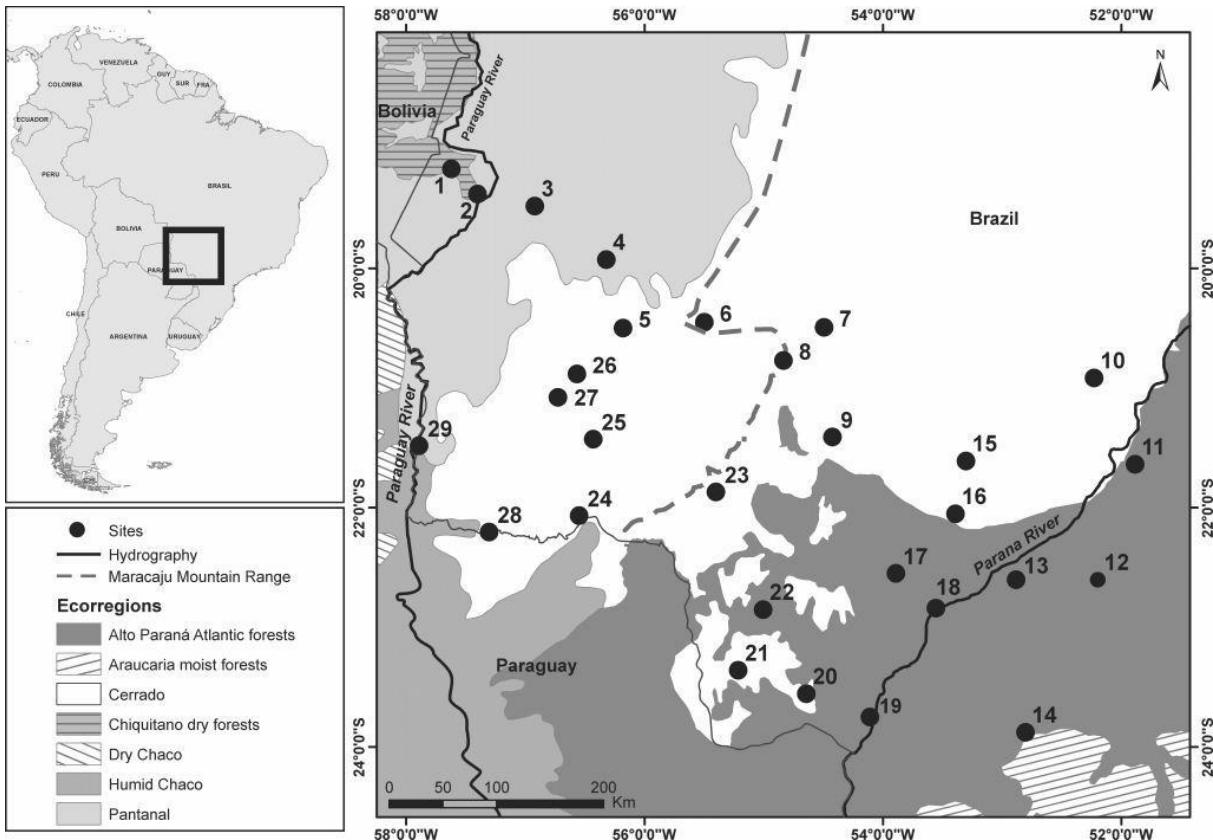
Figure 1. Map with sampled areas distributed among different eco-regions of central South America. Numbers represent the areas sampled and can contain more than one vegetation type (SDF – Semideciduous forest, RPF – Riparian forest, CWS – Closed woodland savana, OWS – Open woodland savana): 1 – Corumbá (SDF), 2 – Albuquerque (SDF, RPF, CWS), 3 – Abobral (RPF), 4 – Caiman (SDF, RPF, CWS, OWS), 5 – Miranda (SDF, CWS), 6 – Aquidauna (SDF, RPF, CWS), 7 – Campo Grande (RPF, CWS, OWS), 8 – Sidrolândia (RPF, CWS), 9 – Nova Alvorada do Sul (SDF, RPF, CWS), 10 – Três Lagoas (RPF, CWS, OWS), 11 – Presidente Epitácio (SDF, RPF), 12 – Teodoro Sampaio (SDF, RPF), 13 – Diamante do Norte (SDF, RPF), 14 – Tuneiras do Oeste (SDF, CWS), 15 – Nova Casa Verde (RPF, CWS, OWS), 16 – Nova Andradina (RPF, CWS, OWS), 17 – Novo Horizonte do Sul (SDF), 18 – Naviraí (RPF), 19 – Eldorado (SDF, RPF), 20 – Iguatemi (ATL, CEF, GAL, CES), 21 – Coronel Sapucaia (RPF, CWF), 22 – Laguna Caraapã (SDF, RPF), 23 – Maracaju (SDF, RPF, CWS, OWS), 24 – Bela Vista (CWS, OWS), 25 – Jardim (RPF, OWS), 26 – Bonito (SDF, RPF, CWS, OWS), 27 – Bonito 2 (SDF, RPF, CWS), 28 – Caracol (RPF, OWS), 29 – Porto Murtinho (SDF, RPF, OWS).

Mixed flocks were considered grouping of species with one or more individuals of two or more species that were moving together, with a minimum of five minutes staying together in a specific direction (Stotz 1993). The species were classified according to the behavior of "nuclear" and "follower" species (Goodale and Kotagama 2005b). Although Moynihan (1962) have considered core species being capable of influencing the formation and cohesion of flocks by long time, as the Amazonian antshrikes *Thamnomanes* (Munn and Terborgh

1979; Develey and Stouffer 2001), many nuclear species in non-Amazonic ecoregions are gregarious or sentinels in their cohesion into the flocks, but they do not promote the maintenance of those associations (Alves and Cavalcanti 1996; Poulsen 1996; Aleixo 1997; Ragusa-Netto 2000). Thereby, in this study, the sentinel, familiar or gregarious genus and species considering plausible nuclear species according to our observations and literature search were: *Melanerpes* – Picidae (Brandt et al. 2009); *Thamnophilus sticturus* and *Th. pelzelni* (*Th. punctatus*) – Thamnophilidae (Gradwohl and Greenberg 1980); *Cyanocorax* – Corvidae (Arbeláez-Cortés et al. 2011); *Polioptila* – Polioptilidae (Gram 1998); *Canthorchilus* (*Thryothorus*) and *Campylorhynchus* – Troglodytidae (Short 1961; Della-Flora et al. 2013); *Basileuterus*, *Myiothlypis* (*Basileuterus*) and *Setophaga* (*Parula*) – Parulidae (Aleixo 1997; Maldonado-Coelho and Marini 2003); *Icterus*, *Psarocolius* and *Cacicus* – Icteridae (Machado 1999; Amaral and Ragusa-Netto 2008); *Dacnis*, *Hemithraupis*, *Lanio* (*Coryphospingus*, *Trichothraupis*, *Eucometis*), *Ramphocelus* and *Tangara* (*Thraupis*) – Thraupidae (Machado 1999; Maldonado-Coelho and Marini 2003; Tubelis 2004; Tubelis 2007). The other species were all categorized as followers. Some species (e.g., *Conirostrum speciosum* and *Cyclarhis gujanensis*) are categorized as nuclear as follower by different authors and we keep them as followers from our field observations.

2.3.3 Data analysis

In order to analyze co-occurrence patterns in flocks, we calculated a standardized effect size (SES) for each matrix of mixed flocks *vs.* species. The SES was used to measure standard deviations in which observed values were above or below the mean values of simulated flocks. SES values equal zero represent our null hypothesis, and negative and positive values mean aggregated and segregated mixed-bird communities (Gotelli and McCabe 2002). Pairs of species present in the flocks were tested for non-random patterns of co-occurrence (Diamond 1975; Gotelli 2000; Ulrich and Gotelli 2007), considering each flock as part of an independent territory (Graves and Gotelli 1993). The co-occurrence pattern in pairs of species was measured by the C-score index (Stone and Roberts 1990). We chose the Equiprobable-Fixed null model (Gotelli 2000) based on the behavior and structure of mixed flocks (Graves and Gotelli 1993; Sridhar et al. 2012), where all species are equally likely to occur in any flock and the number of species per flocks is fixed with no constraints on the column total.

We employed four frequentist and Bayes approaches of randomization (Gotelli and Ulrich 2010). The confidence limit criterion (CL) is the simplest and most liberal of the four

methods. In CL, an observed co-occurrence metric for each pair of species is associated to the confidence limits of a randomized distribution. Species pairs with scores outside the 95% confidence limits is considered significantly segregated or aggregated (depending on whether the observed C-score is greater or smaller than the mean of the simulated C-scores for a given species pair). Another test is the Sequential Bonferroni correction or Benjamini and Yekutieli criterion (BY), which is used as a correction for large matrices in CL significance level adjusts, and represents sequential Bonferroni correction of the probability benchmark (Benjamini and Yekutieli 2001; Gotelli and Ulrich 2010). Two other methods are more conservative Bayesian approaches, Empirical Bayes mean based or Bayes M criterion (BM) and the Empirical Bayes CL based or Bayes CL criterion (BC). In all methods, instead of a comparison between observed and expected scores of each species pair, the observed frequency distribution of scores is compared with the frequency distribution of scores generated by a null model. The first step is the implementation of these methods including calculation of the observed C-score for each species pair, rescaling these C-scores to a range from 0 to 1, and grouping them into 22 classes of evenly spaced bins (Gotelli and Ulrich 2010). Then, 5000 null matrices are assembled and the mean and confidence limits of the expected number of species pairs within each bin is calculated from these null matrices. Species pairs within each bin are ordered according to their observed C-scores and pairs that fall above the mean (BM) or confidence interval (BC) for the expected number of species are considered significant.

The scores of the CL method of each pair of species were classified in three categories according to their behavior in flocks: nuclear – nuclear species (NN), nuclear – follower species (NF) and follower – follower species (FF). Then, we used ANOVA to test for: (i) differences in CL scores among pairwise categories in the entire studied region and in each vegetation type separately, and (ii) for differences in species pair scores among all vegetation types. The software Pairs (Ulrich 2008) was used to calculate SES scores and to perform pairwise analyses. The other analyses were performed in R (R Development Core Team 2013).

2.4 Results

Values of SES were different of expected by chance in all physiognomies, and in all cases they tended to aggregation (Table 1). In module, the SES scores were higher in Semideciduous forest than Riparian forest and the two savannas.

The Closed woodland savanna (CWS) was the only one that did not show significant pairwise segregations among species (Table 1). However, the pairwise segregation among species was lower (0.04-0.17%) than the aggregation among species. The proportion of aggregation value was similar among the four vegetation types (7-10%, Table 1), but differed accordingly to all species-pair CL scores ($F_{3, 7166}$ = 9.63, P < 0.001), with CWS significantly more aggregated than Semideciduous (SDF) and Riparian (RPF) forests, and SDF less aggregated than Open woodland savanna (OWS) (Figure 2).

In the CL method, nuclear species in mixed flocks had lower scores than those flocks formed by follower species only, indicating that associations among followers are more aggregated than those ones with leaders ($F_{2, 6103}$ = 29.17, P < 0.001, Figure 3 and Table 2). The same pattern occurred in Semideciduous forests ($F_{2, 2104}$ = 14.15, P < 0.001; Figure 4a), Riparian forests ($F_{2, 1950}$ = 6.19, P = 0.002; Figure 4b) and Open woodland savannas ($F_{2, 907}$ = 7.96, P < 0.001; Figure 4d). On the other hand, the Closed woodland savannas presented no difference among three species pairs categories ($F_{2, 1133}$ = 2.48, P = 0.083, Figure 4c).
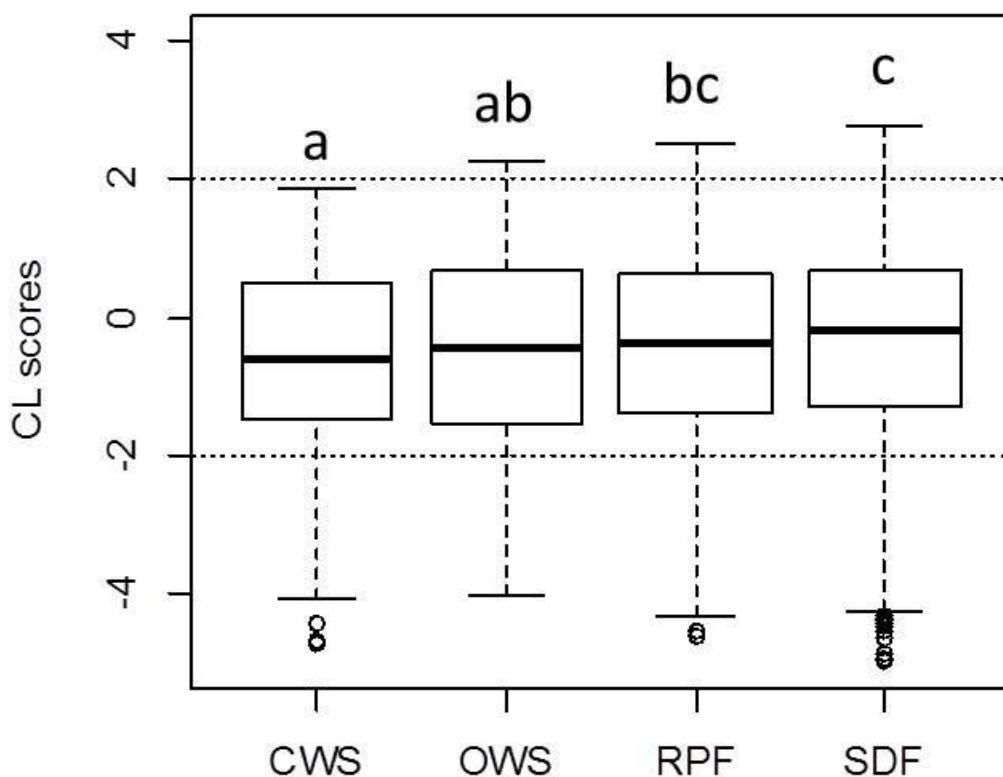
Figure 2. Box plot showing 25th, 50th and 75th percentiles (horizontal bars) and 1.5 interquartile ranges (error bars) of the scores of Confidence Limit Criterion (CL) method for seven physiognomies of central South America. Dashed lines denote limits of CL scores higher than 2.0, segregation, and lower than - 2.0, aggregation, at the 5% significance level for the C-score. Letters above the box indicate significant difference among vegetation types in an ANOVA (Tukey's test: P < 0.05). SDF – Semideciduous forest, RPF – Riparian forest, CWS – Closed woodland savanna, OWS – Open woodland savanna.

Table 1. Richness (Spp), number of mixed flocks (MF), number of species pairs (SP), Standardized effect size (SES), Probability (observed minor equal expected values), number of segregated/aggregated pairs for four frequentist (CL and BY) and Bayes (BM and BC) methods, arithmetic average of all methods (Mean-SP), and percentage of ratio between Mean-SP and total species pairs (SP) for forest and savanna types in central South America.

Vegetation	Spp	MF	SP	SES	CL	BY	BM	BC	Mean-SP	% (Mean-SP/SP)
Semideciduous forest	71	133	2485	-22.16*	16/330	1/123	0/176	0/145	4.25/193.5	0.17/7.78
Riparian forest	68	89	2278	-20.84*	4/323	0/106	0/129	0/109	1.0/166.75	0.04/7.32
Closed woodland savanna	52	90	1326	-19.75*	0/203	0/65	0/92	0/74	0.0/108.5	0.0/8.18
Open woodland savanna	47	63	1081	-16.31*	3/172	0/58	0/99	0/79	0.75/102	0.07/9.43

* $P (O \leq E) < 0.05$

Table 2. Number of species pairs (SP), number of segregated/aggregated pairs for CL methods, and percentage of ratio between richness (Spp) and number of species pairs in central South America.

Pairwise interactions	SP	CL	% (CL/SP)
All	6106	23/877	0.37/14.36
Nuclear-nuclear	764	4/94	0.52/12.30
Nuclear-follower	3217	12/443	0.37/13.77
Follower-follower	2125	7/340	0.32/16.00
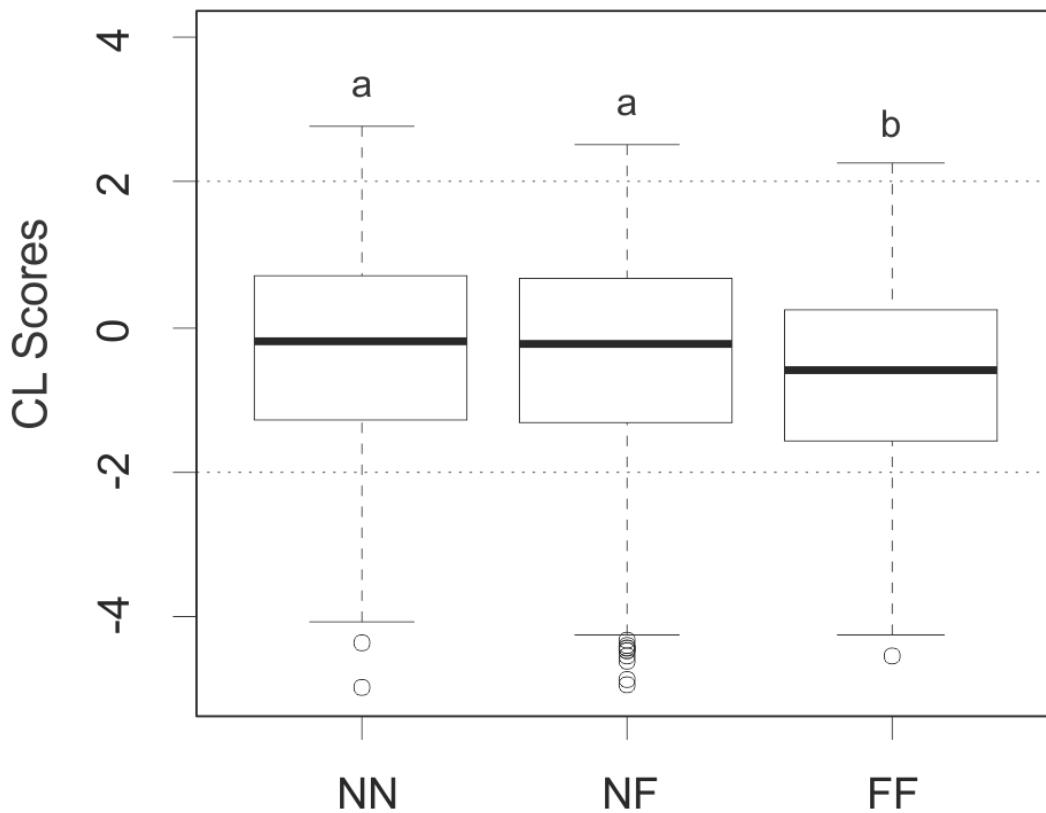
Figure 3. Box plot showing 25th, 50th and 75th percentiles (horizontal bars) and 1.5 interquartile ranges (error bars) of the scores of Confidence Limit Criterion (CL) method for six species pair categories for all physiognomies from central South America. Dashed lines denote limits of CL scores higher than 2.0, segregation, and lower than - 2.0, aggregation, at the 5% significance level for the C-score. Letters above the box indicate significant difference among species pairs categories in an ANOVA (Tukey's test: $P < 0.05$). NN – Nuclear species pairs, NF – Nuclear-Follower species pairs, FF – Follower species pairs.
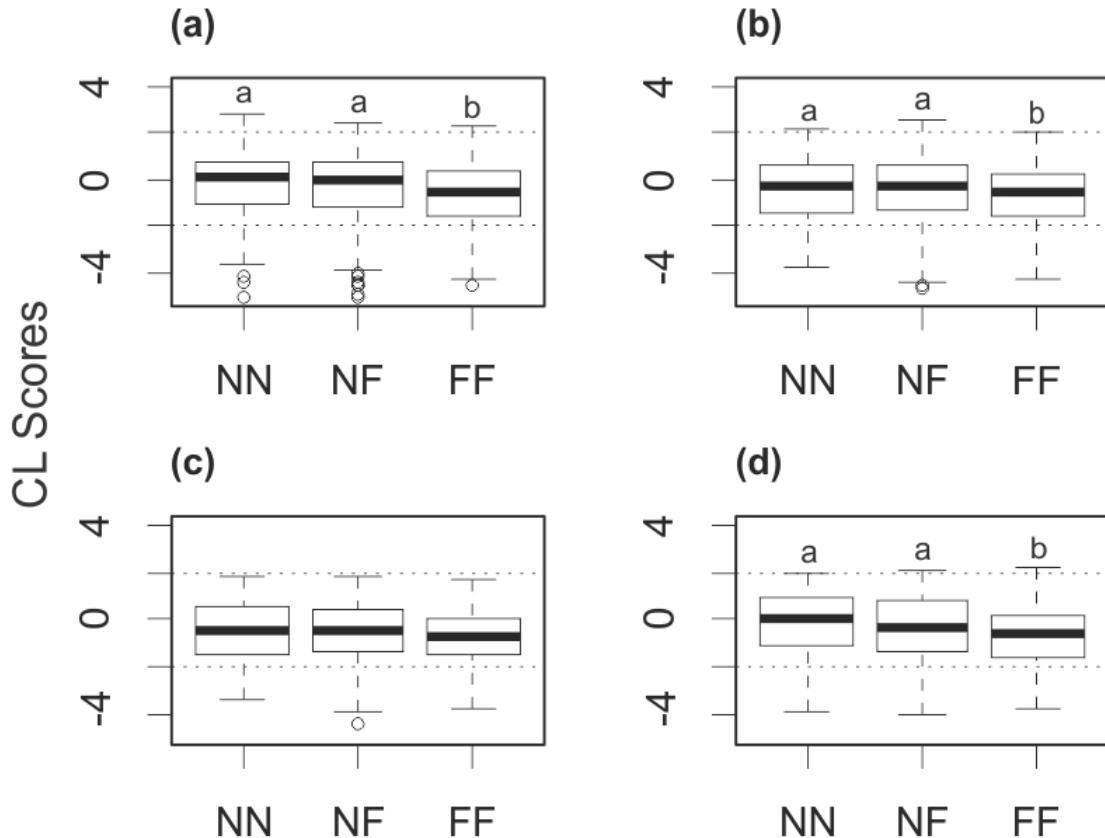
Figure 4. Box plot showing 25th, 50th and 75th percentiles (horizontal bars) and 1.5 interquartile ranges (error bars) of the scores of Confidence Limit Criterion (CL) method for three species pair categories. Dashed lines denote limits of CL scores higher than 2.0, segregation, and lower than - 2.0, aggregation, at the 5% significance level for the C-score. Letters above the box indicate significant difference among species pairs categories in an ANOVA (Tukey's test: $P < 0.05$). (a) Semideciduous forest, (b) Riparian forests, (c) Closed woodland savanna ("*cerradão*"), (d) Open woodland savanna (cerrado "*sensu stricto*" and chaco savanna). NN – Nuclear species pairs, NF – Nuclear-Follower species pairs, FF – Follower species pairs.

2.5 Discussion

The composition of avian mixed flocks in all vegetation types are more aggregated than by chance, differently of other studies that took in account only one forest formation (Graves and Gotelli 1993; Bohórquez 2003). Our results agree that mixed flocks are more positive associations than negative ones (competition), and that there should be more than one process of assembly rule performing, such as the facilitation and habitat filtering (Sridhar et al. 2012; Della-Flora and Cáceres unpublished data).

In generally, both savannas and forests showed more aggregation in their flocks. It is also seen through the four pairwise methods, although in Closed woodland savanna had the highest scores of aggregated species pairs. The pattern followed almost equal for all methods, depending on how conservative (less odd of significant species pairs) or liberal (more odds) is the method used (Gotelli and Ulrich 2010).

Although similar in vegetation structure Closed woodland savanna showed higher aggregation than Semideciduous forest. An explanation would be the less richness of species in savannas participant in mixed flocks and the lower height of the trees, favoring therefore a greater association between understory and canopy species in Closed savannas.

In contrast, Open woodland savannas were not significant different to Riparian forest indicating that the patterns of association among species are more similar between them. There are relates in literature that some mixed flocks in Open woodland savannas (e.g., cerrado *stricto sensu*) originate from Riparian forest (e.g., Gallery forest) next to them (Tubelis et al. 2006).

The contrast among the four habitats is important to understand how pairwise interactions of mixed flock modify along gradient of vegetation. Although the follower species kept commons in most of the study area (Della-Flora and Cáceres, unpublished data) and their pairwise interactions varied few compared with the leaders, nuclear species are possibly those that respond much more to these variations among so different environments: the nuclear species because are more gregarious (Powell 1985), but not all are often observed in flocks.

Generally, the followers follow nuclear species because of their anti-predator alarm within of intraspecific groups (Sridhar et al. 2009). However, we found that this behavior cannot be confirmed in Closed woodland savanna, where there was no significant difference among the three pairwise associations.

Although our study showed a few non-random values for species pairs, they tend to associate more aggregately than segregate. Of the total of possible pair comparisons, approximately 14% are formed by dependent aggregated species pairs, slightly higher (Bohórquez 2003; Arbeláez-Cortés et al. 2011), lesser (Hutto 1994) or similar (Latta and Wunderle 1996) than some Neotropical forests. The nuclear species tend to associate with each other less than the other species of flocks when compared to species which are not participating as nuclear species. This corroborates that nuclear species, in general, are not so dependent of other species and that their presence in flocks would be secondary (Graves and

Gotelli 1993). Furthermore, intraspecific group size may not be a good predictor of joining frequency (Sridhar et al. 2009).

There is also strong evidence that species less frequent (e.g., FF pairs) in mixed flocks are those more associated among themselves, an evidence that in majority of environments the benefits by increasing foraging efficiency is more important than predator avoidance (Beauchamp 2005). On the other hand, rare and occasional flocking species would join flocks to advantage from collective vigilance (Thiollay 2003).

2.6 Closing remarks

Our data firstly present flocks in several environments aggregated more than by chance inferring that competition would not be a good assembly rule to be applied in mixed flocking interactions. Second, much more species pairs associate aggregately than segregated even when we use BY or BC methods which are more restrictive. These two patterns would be expected mainly in Closed woodland savanna because of their less vertical stratum, and more presence of follower species in the flocks.

Furthermore, there are more mutualistic (FF and NN) interactions among species than commensal (NF): nuclear species are much more independent than followers and follower species participated more together than following nuclear species.

Note that our conclusions are based on an only type of classification proposed in the literature for mixed flocks (leaders and followers). Not analyzed here, for example, the propensity of the species participating in flocks or classify species by their functional similarities (e.g., foraging behavior, diet or body size). Therefore, studies that will unite behavioral and morphological information of the species along different environments can offer more insight for understanding how mixed flocks are structured and what are the factors that explain higher aggregation of mixed flocks and their interactions between species pairs.

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3 ARTIGO 3 - MIXED FLOCKS OF BIRDS IN NEOTROPICAL SEASONAL FORESTS: RELATIONSHIP BETWEEN THE PARTITION OF BETA DIVERSITY AND SPATIAL AND ENVIRONMENTAL GRADIENTS[3]

Franchesco Della-Flora, Nilton C. Cáceres

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[3] Esse artigo segue as normas da revista Ecography.

3.1 Abstract

We investigated the Beta diversity of a metacommunity of avian mixed flocks in the center of South America and if it is structured for spatial turnover or for nestedness over space-environmental gradients. We tested the effect of space (neutral processes) and environmental filters (niche-based processes) on the dissimilarity components of beta diversity for three types of mixed flocks (understory, heterogeneous and canopy) and seasonal forests (semideciduous forest, riparian forest and woodland savanna) in southwestern Brazil. The spatial turnover was the most important component in the structuring of avian mixed flocks both flock and forest types in multiple-sites. The spatial turnover dissimilarity of understory, heterogeneous, riparian forest and semideciduous flocks was related positively with geographical distance, while dissimilarity of heterogeneous flocks was positively with temperature and precipitation gradient. However, understory flocks showed negative relation with distance classes higher than 400 km suggesting a species similarity according to forest types, and supporting the Niche theory. The canopy and woodland savanna species dissimilarities did not show relation with space or climate gradients and likely must be influenced by other not tested environmental variables. The observed patterns of beta diversity of avian mixed flocks suggest both neutral and niche-based processes driven by dispersal ability and deterministic filtering of the species across spatial and environmental gradients.

Key-words: Nestedness, Cerrado, Distance decay, Atlantic Forest, Environmental filtering, Pantanal, Beta diversity, Spatial turnover, Neutral theory, Niche theory.

3.2 Introduction

Some macro-ecological factors such as environmental filters (climate) and space (geographical distance) can interact in different ways with the metacommunity structure. In this way, the understanding of beta-diversity of a metacommunity can clarify how does change of species that interact with each other over space and environmental gradients. It is important to note that the beta-diversity, in addition to representing the variation of species composition between sites, can be partitioned in order to identify not only the replacement of the species (*turnover*), but also the nestedness resulting of dissimilarity (*nestedness*; loss of rare species in poorer assemblies with maintenance of most common species) along environmental gradients (Williams 1996, Baselga 2010, 2012, 2013, Podani and Schmera 2011, Legendre 2014).

Through the partition of beta diversity in two components, spatial turnover and nestedness (Baselga 2010), it becomes easier to identify patterns of organization of assemblies that may be being influenced by environmental filters, the Niche theory (Hutchinson 1957), or by limitation of dispersion, the Neutral theory (Hubbell 2001). Filters would be responsible for the change of the structure of assemblies due to adaptations of different species to local conditions (Whittaker and Niering 1975). On the other hand, the mechanisms that generate differences between patterns of species composition would be linked to the dispersal ability of individuals (McGill et al. 2006). Traditionally, the Niche theory was used to explain the compositional changes between localities due to the specificities of each species as far as resources for their survival (Graves and Rahbek 2005). In this sense, the generalist species could be widely distributed in space, while the specialists would have to be better competitors for a particular resource. However, changes in the structure of the metacommunity, when the environmental requirements are similar, may be a response of drift of populations (demographic stochasticity) (Hubbell 2001). In addition, the spatial distance measured in different scales can influence the similarity between the assemblies differently than environmental distance (Soininen et al. 2007).

The variations of composition in bird assemblies are observed along ecological gradients, both for the entire regional avifauna (Wiens and Rotenberry 1981, Foster 1983, Estades 1997, Lennon et al. 2001, Caceres et al. 2014) as for the subset of birds which form mixed flocks associations (Goodale et al. 2009) through positive relations (mutual and commensal) among its participants (Hino 1998, Sridhar et al. 2012).

Mixed flocks are found in a variety of habitats, from humid and seasonal forests, to open areas like deserts and savannas (Cody 1971, Munn and Terborgh 1979, Tubelis 2007, Sridhar et al. 2009). However, comparisons of the compositional variation among assemblies of mixed flocks are still fledgling in the literature (Moynihan 1979, Maldonado-Coelho and Marini 2004, for stratification of flocks; and Moynihan 1962, Powell 1985, Gram 1998, Goodale et al. 2009, for different forest formations), while there are few studies detailing how the mixed flocks are structured over spatial and environmental gradients (Goodale et al. 2009).

According to forest stratum in that species participating in flocks, they can be classified in understory, heterogeneous and canopy flocks (Maldonado-Coelho and Marini 2003). Such associations feature changes in composition between seasons as well as the size of forest area occupied. During the rainy season and in small forest fragments, for example, there is less species richness and size of mixed flocks, while during the dry season and in large forest fragments there is greater number of species involved. In addition, the number of species in canopy and understory flocks tend to be smaller, and nuclear species tend to disappear, in small forested areas (Maldonado-Coelho and Marini 2003, 2004). Therefore, for studies of compositional changes of mixed flocks at scales larger than the local must be given attention to sampling in continuous areas or larger fragments, and mainly during the dry season or outside of the reproductive period of birds, when the participation of species in flocks decreases significantly (Davis 1946, Powell 1979, Machado 1999, Develey and Peres 2000, Maldonado-Coelho and Marini 2004).

In the tropics species diversity in wet forests generally is higher than that of deciduous forests due to greater evapotranspiration and primary productivity in those ecosystems (Hawkins et al. 2003a, b). As a result of this change, the mixed flocks would tend to introduce more species in less seasonal forests (and therefore wetter) than in seasonal forests (Powell 1985, Goodale et al. 2009). However, the central region of South America, where the two largest rainforests (Amazon and Atlantic Forest) are separated by the corridor of open environments Chaco-Caatinga-Cerrado (Ab'Saber 1977), seasonal forests tend to differ regarding the structure and floristic composition. Three main types of forest are found within the forest-savanna mosaics according to edaphic conditions and the water regime in the soil (Oliveira-Filho and Ratter 2002): riparian forests, seasonal forests (mainly semideciduous) and closed woodland savannas (*cerradão*). As a result of forest dependence by more than half of avian species in the Cerrado biome (Silva 1995, Marini 2001) originated mainly from Amazonian and Atlantic forests (Silva 1996), the riparian forests generally have a higher

richness of bird species than semideciduous forests and wooded savannas (Valadão 2012), whereas the forested savannas are less rich than semideciduous forests (Rodrigues and Faria 2007, Cavarzere et al. 2011).

Based on heterogeneous flocks and more humid forests (riparian and semideciduous forest) are richer in species that the flocks of canopy and understory vegetation and woodland savanna, respectively, we predict that the spatial replacement component of beta-diversity is strongest where there is greater species richness. In this way, the exchange of species throughout the space and the environment would be more likely to occur in metacommunities with greater species diversity distributed through the gradient (Baselga 2010). Translating for mixed flocks, species with greater regularity in ecological gradient would replace other (closed phylogenetically) on cohesion of the flocks. Such a process is plausible to occur more in heterogeneous flocks and in riparian and semideciduous forests, where the number of flock-specialist species, environmentally or spatially restricted, is greater than in understory and canopy flocks and woodland savannas (Maldonado-Coelho and Marini 2003, 2004, Rodrigues and Faria 2007, Valadão 2012). Besides the natural spatial replacement of species participants in mixed flocks, is expected also a process of loss of species in the understory and canopy flocks according as the forest becomes more deciduous (woodland savanna), and a continuation of the main species of woodland savannas towards the poorest localities in species.

From the assumptions above, we investigated the beta-diversity patterns of avifauna metacommunity associated to mixed flocks and how they are structured by turnover or nestedness under the influence of spatial and environmental gradients. To this end, we verified the effect of space (neutral processes) and of temperature and precipitation (niche-based processes) on the pairwise-components of partition of beta-diversity for three types of mixed flocks (understory, heterogeneous and canopy) and three distinct forests (riparian forest, semideciduous forest and woodland savanna) in order to test if avifauna dissimilarities increases with spatial or environmental distances (similarly to distance decay of similarity).

3.3 Material and Methods

3.3.1 Area of study

Twenty-eight localities sampled are located next to center of South American continent, southwest Brazil portion, in Mato Grosso do Sul, São Paulo and Paraná States (18-23° S, 54-57° W, from 90 to 600 m a.s.l.; Figure 1, Supplementary Material 1). The study area

comprises the southern portion of the Pantanal and Cerrado ecoregions, southeast Alto Paraná Atlantic Forest, and zones of influence of the Chaco, to far west, and Chiquitano dry forest, to northwest (Figure 1). The region is rich in transitional areas of seasonal forests along slops of Urucum, Bodoquena and Maracaju plateaus (semidecidous forests) and savannas (dense and open woodlands) (Oliveira-Filho et al. 2006). In addition, the region is bounded by two major rivers, the Paraná River to east, and the Paraguay River to west. Both flood plains feature basins, and the plain of the River Paraguay too extensive to the point of being classified as an ecoregion, the Pantanal. Rivers belonging to the two basins have three types of riparian forests predominate as according its size (Oliveira-Filho and Ratter 2002): gallery forests, in the vicinity of small water courses (up to 350 m a.s.l), "ciliar" forests, in larger rivers between plateaus (150-350 m a.s.l.), and alluvial forests (90-150 m a.s.l) in the seasonally flooded plains of the Paraná and Paraguay rivers.
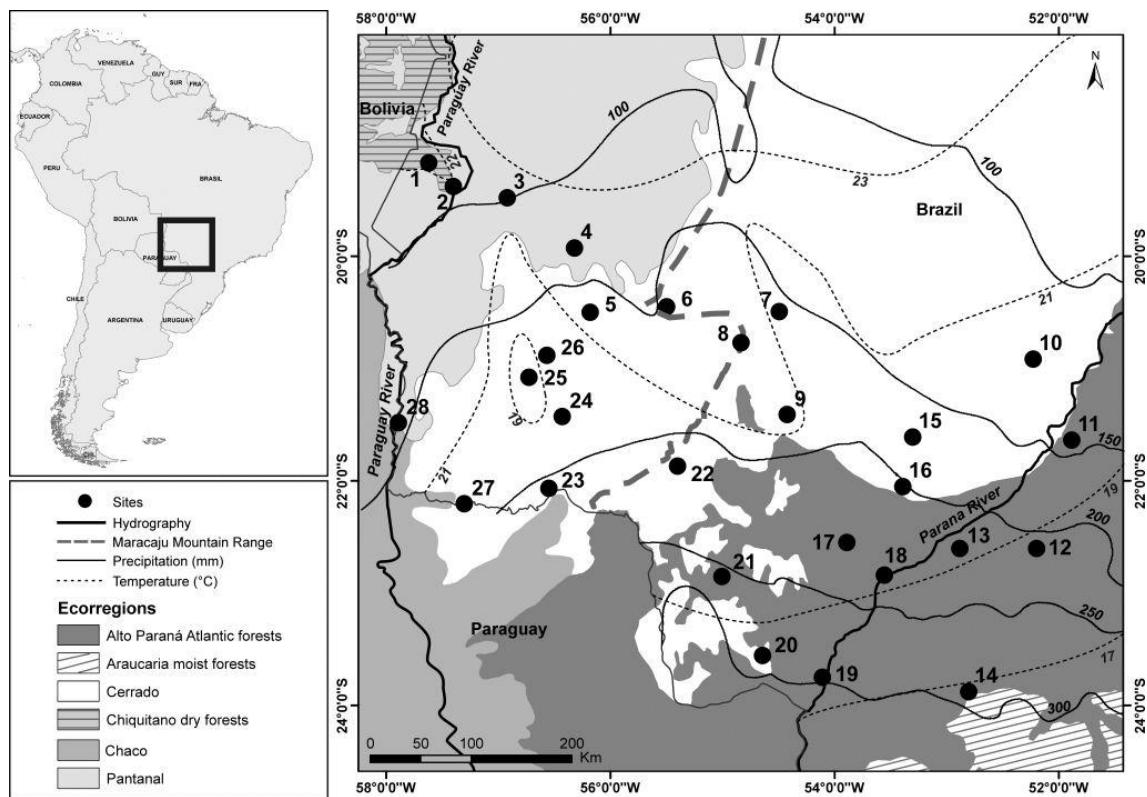
Figure 1. Map with localities sampled in southwest Brazil according to South American ecoregions. Lines with up and down numbers represent, respectively, a gradient of the averages of precipitation and temperature of the driest months (May, June and July). More details in Supplementary Material 1.

3.3.2 Sampling design

We sampled three types of mixed flocks (understory, heterogeneous and canopy) and forest formations (riparian, semideciduous and woodland) along spatial and environmental gradients. Mixed flocks types were classified according to the vertical structure of foraging and made by only one author (FDF): understory flocks (from ground to the third part of forest height, approximately 5-8 m from the ground), heterogeneous flocks (understory, canopy and intermediate forest stratum) and canopy flocks (highest treetops) (Maldonado-Coelho and Marini 2003).

We sampled the interior of continuous areas and forest fragments (over 500 ha) for four days by locality, sampling different vegetation types always in each sampling day and sometimes within the same shift of observation. Sampling occurred during the dry season (May to August) in order to standardize the sampling along the areas and inhibit the effect of reproductive period that would affect directly the richness and species composition of flock participants. The observations were carried out in the mornings (07:00-11:00h), which offers higher activity of mixed flocks (Munn and Terborgh 1979). Altogether were 395h field observation between 2009 and 2011, approximately 14 hours sampling in each locality and 220 mixed flocks sampled. The flocks were followed for a minimum of five and a maximum of 30 minutes with the purpose of not account possible flocks exclusively related to presence of a food source, such as a tree with many fruits or presence of army ants. Species with less than three registers in all metacommunity were not included in analysis.

3.3.3 Analysis of data

A matrix of presence and absence of species by sites was established for metacommunity. Initially, we checked differences between the three types of mixed flock and forest in order to compare the species composition *a priori* by permutational multivariate analysis of variance using distance matrices – PERMANOVA – through the Sørensen index. We also ordered localities by Principal Coordinates analysis (PCoA) in order to identify gradients of dissimilarity. In case of difference in composition among forests and mixed flocks, we created new matrices of presence/absence and carried out for each category analysis of beta-diversity and of its two components: spatial turnover and nestedness (Baselga et al. 2007, Baselga 2010). Sites sampled that did not contemplate at least 30% than richer site, were not used in multiple-site and pairwise dissimilarity analysis.

Multiple-site dissimilarities proposed by Baselga et al. (2007) are independent of the species richness of each site. The Beta-diversity multiple-site was calculated through Sørensen dissimilarity (β_{SOR}):

$$\frac{[\sum_{i<j}\min(bij,bji)]+[\sum_{i<i}\max(bij,bji)]}{2[\sum_i Si-ST]+[\sum_{i<j}\min(bij,bji)]+[\sum_{i<i}\max(bij,bji)]} \; ;$$

the spatial turnover component was measured by Simpson dissimilarity for multiple-sites (β_{SIM}):

$$\frac{[\sum_{i<j}\min(bij,bji)]}{[\sum_i Si-ST]+[\sum_{i<j}\min(bij,bji)]} \; ;$$

and the nestedness resulting of dissimilarity was obtained through the fraction derived of Sørensen dissimilarity (β_{NES}) (Baselga 2010) or $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$:

$$\frac{[\sum_{i<i}\max(bij,bji)]+[\sum_{i<j}\min(bij,bji)]}{2[\sum_i Si-ST]+[\sum_{i<j}\min(bij,bji)]+[\sum_{i<i}\max(bij,bji)]} \times \frac{[\sum_i Si-ST]}{[\sum_i Si-ST]+[\sum_{i<j}\min(bij,bji)]} \; ;$$

where *Si* is the total number of species in the site *i*, *ST* is the total number of species in all the sites considered together and *bji* is the number of species unique to the site *i* and *j*, respectively, when compared to pairs.

In addition, we calculate the distance matrices of the two components of beta-diversity based on the presence of species calculated between pairs of localities. Similarly to β_{SIM} and β_{NES}, the two pairwise-components of β_{sor} are the spatial replacement, corresponding to the dissimilarity of Simpson (β_{sim}), and the nestedness resulting of dissimilarity, represented by the subtraction of the dissimilarity of Sørensen for Simpson, $\beta_{nes} = \beta_{sor} - \beta_{sim}$ (Baselga 2010), i.e.,

$$\frac{b+c}{2a+b+c} - \frac{\min(b,c)}{a+\min(b,c)} = \frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)} \; ,$$

where *a* is the number of species that exist in both sites *i* and *j*, while *b* and *c* is the number of species which is unique in *i* and *j*, respectively.. Distance matrices of the two components of dissimilarity generated, β_{sim} and β_{nes}, were related to the matrices of seasonality of temperature and precipitation (Hijmans et al. 2005), and with the matrices of geographical distance between localities, both calculated by Euclidean distance and one another through of Mantel test using Pearson correlation. Partial Mantel test was performed s in order to remove the effect of space on the environmental variables when these were significant. We also used Mantel correlogram to access for spatial correlation in different classes of distances in cases of absence of correlation between spatial and environmental distances (Tuomisto et al. 2003).

Partition analyses of beta-diversity were carried out by functions "beta.multi" and "beta.part", the first measures to multiple-sites and the second for distances between communities (Baselga 2010), through the package 'Betapart' (Baselga and Orme 2012). The PERMANOVA, Principal Coordinates Analysis (PCoA) and the correlations of Mantel and partial Mantel and Mantel correlogram were performed using the functions "adonis",

"cmdscale", "mantel", "mantel.partial" and "mantel.correlog", respectively, through the package 'vegan' (Oksanen et al. 2013). All analyses were performed in R (R Development Core Team 2013).

3.4 Results

The avian mixed flock metacommunity presented richness of 160 species, but only 86 occurred in more than two sites and were used to analysis (Figure 2a). Heterogeneous and riparian and semideciduous forest flocks were richer than the other flock and forest types, respectively (Table 1). For both mixed flocks and forests, there were significant differences in species composition (mixed flocks: $F_{(2,38)} = 4.703$, $R^2 = 0.153$, $P < 0.001$; forests: $F_{(2,38)} = 3.864$, $R^2 = 0.126$, $P = 0.001$; mixed flocks * forests: $F_{(4,38)} = 3.864$, $R^2 = 0.101$, $P = 0.013$). In understory and canopy flocks there were significant differences between riparian and semideciduous forests (understory: $P = 0.049$, canopy: $P = 0.017$), whereas in heterogeneous flocks differed only between riparian forests and woodland savannas ($P = 0.015$).

Table 1. Multiple-site dissimilarity values for beta-diversity (β_{SOR}), spatial turnover (β_{SIM}), nestedness (β_{NES}), and total (S_T), mean (S_M), maximum ($_{max}$) and minimum ($_{min}$) richness, for all metacommunity, for mixed flock (understory, heterogeneous and canopy) and for forest (riparian forest, semideciduous forest and woodland savanna) sites. Localities sampled are in parentheses beside name of each category. Only to metacommunity that all mixed flocks and their species sampled were used in the analysis (see Supplementary material 1 for more details).

	β_{SOR}	β_{SIM}	β_{NES}	S_T	S_M ($_{min-max}$)
Metacommunity (28)	0.90	0.86	0.04	86	33.2 (16-56)
Understory (11)	0.90	0.87	0.03	59	13.2 (11-29)
Heterogeneous (25)	0.89	0.85	0.04	86	31.3 (15-48)
Canopy (11)	0.86	0.84	0.02	57	14.5 (8-20)
Semideciduous Forest (16)	0.87	0.81	0.06	79	28.5 (17-50)
Riparian Forest (11)	0.85	0.80	0.05	81	27.7 (16-47)
Woodland savanna (13)	0.83	0.75	0.08	67	21.7 (11-36)

In multiple-site dissimilarities, the overall beta diversity (β_{SOR}) and its spatial turnover component (β_{SIM}) for the three flock types and for the three forest physiognomies were very

similar to metacommunity and presented high values. However, the values of nestedness (β_{NES}) approached zero, indicating that species replacement is responsible for most of the beta diversity patterns (Table 1). The metacommunity showed a gradient northwest – southeast with sites and species related to Pantanal wetland (riparian forests) in an extreme and Atlantic forest (semideciduous forests) in other, and woodland savannas in center (Figure 2b).

The role of the both strata and forest information for understanding mixed flocks patterns in south-western South American seasonal forests is showing by ordination of avifauna flock participant data (Figure 3). The most of understory and canopy mixed flock sites were concentrated on opposite sides of the ordination diagram, whereas the heterogeneous flock sites were more scattered over wider space. In forest formations, most of the semideciduous forest and woodland savanna sites were distributed, respectively, to one edge and center of the diagram, whereas the riparian forest sites showed more heterogeneity and forming a clear gradient of species replacement among sites.
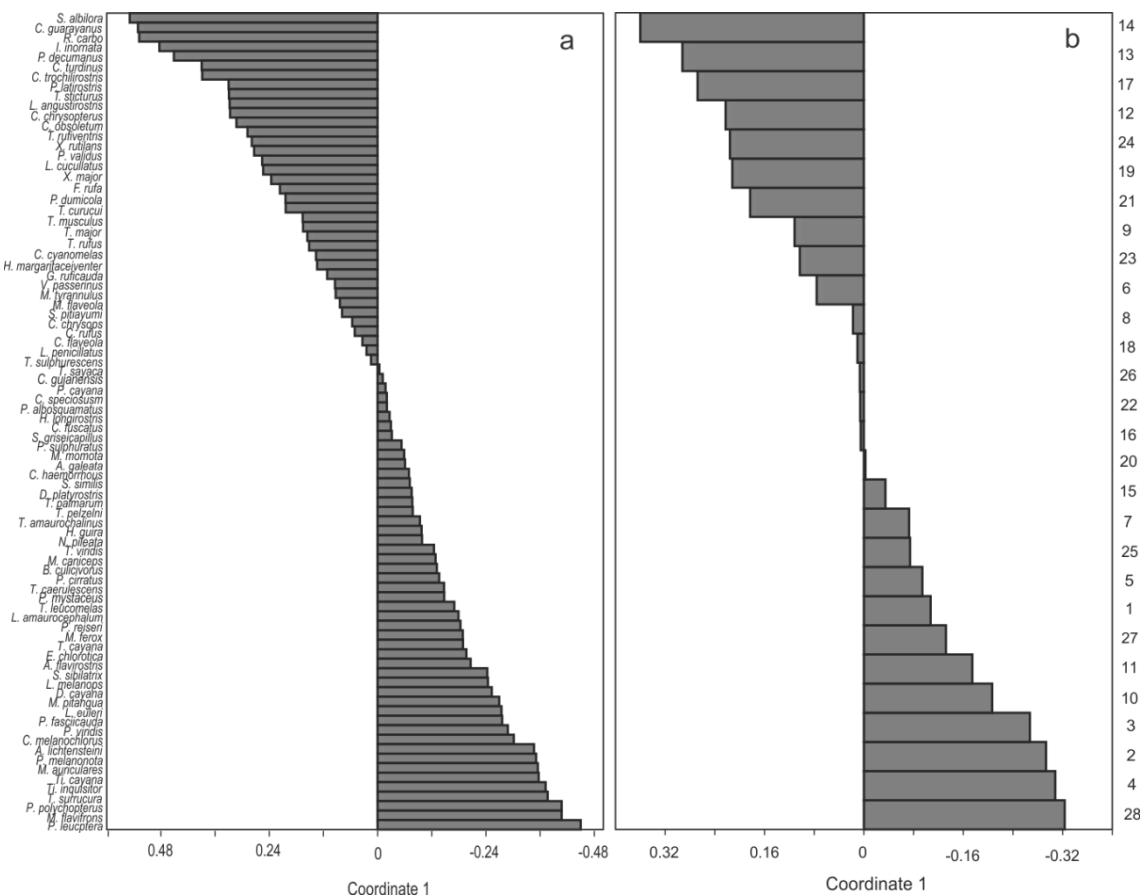
Figure 2. Histograms showing the first coordinate of overall metacommunity. Eigenvalues of (a) 28 sites and (b) 86 species.
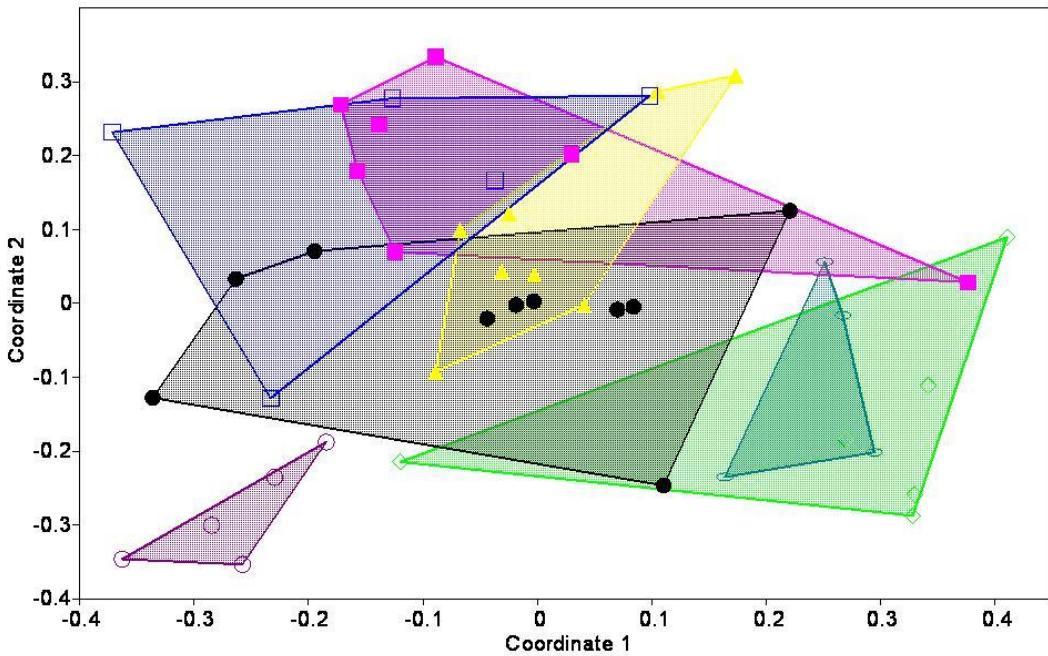
Figure 3. Avifauna relationships among different types of mixed flocks and forests in south-western South America sites: similar sites are more close together, and dissimilar sites are far apart. The principal coordinate analysis is based on avifauna similarities (Sørensen Index). Symbols and colors depicted sites from mixed flocks and forests (from left to right): open squares (riparian forests – understory flocks), full squares (riparian forests – heterogeneous flocks), circle (semideciduous forests – understory flocks), dots (semideciduous forests – heterogeneous flocks), diamonds (semideciduous forests – canopy flocks), full triangles (woodland savannas – heterogeneous flocks) and ovals (woodland savannas – canopy flocks).

The metacommunity showed positive relationship (P < 0.001) between Simpson dissimilarity (β_{sim}) and the space (geographic distance) and environmental filters (both temperature and precipitation). On the other hand, the nestedness component (β_{nes}) was not influenced neither space nor clime, both in overall metacommunity and in types of flock and forest.

As for mixed flock and forest types, the spatial turnover component was positively associated with the geographic distance in understory and heterogeneous flocks (Figure 4a-b), and in riparian and semideciduous forests (Figure 4e-f). Furthermore, the spatial turnover presented positive correlation with precipitation and temperature of heterogeneous flocks (Figure 4c-d). Nevertheless, neither canopy flocks nor woodland savannas showed significant relations between spatial turnover component and spatial and environmental distances.

The space and the environmental filtering were related positively in understory, heterogeneous, riparian and semideciduous flocks ($P < 0.01$). The analysis by distance classes showed that the increase of Simpson dissimilarity by space disappeared in distances higher than 400 km for understory flocks (Figure 5a), but kept significant in all distance classes in heterogeneous, riparian and semideciduous forest flocks (Figure 5b-d).
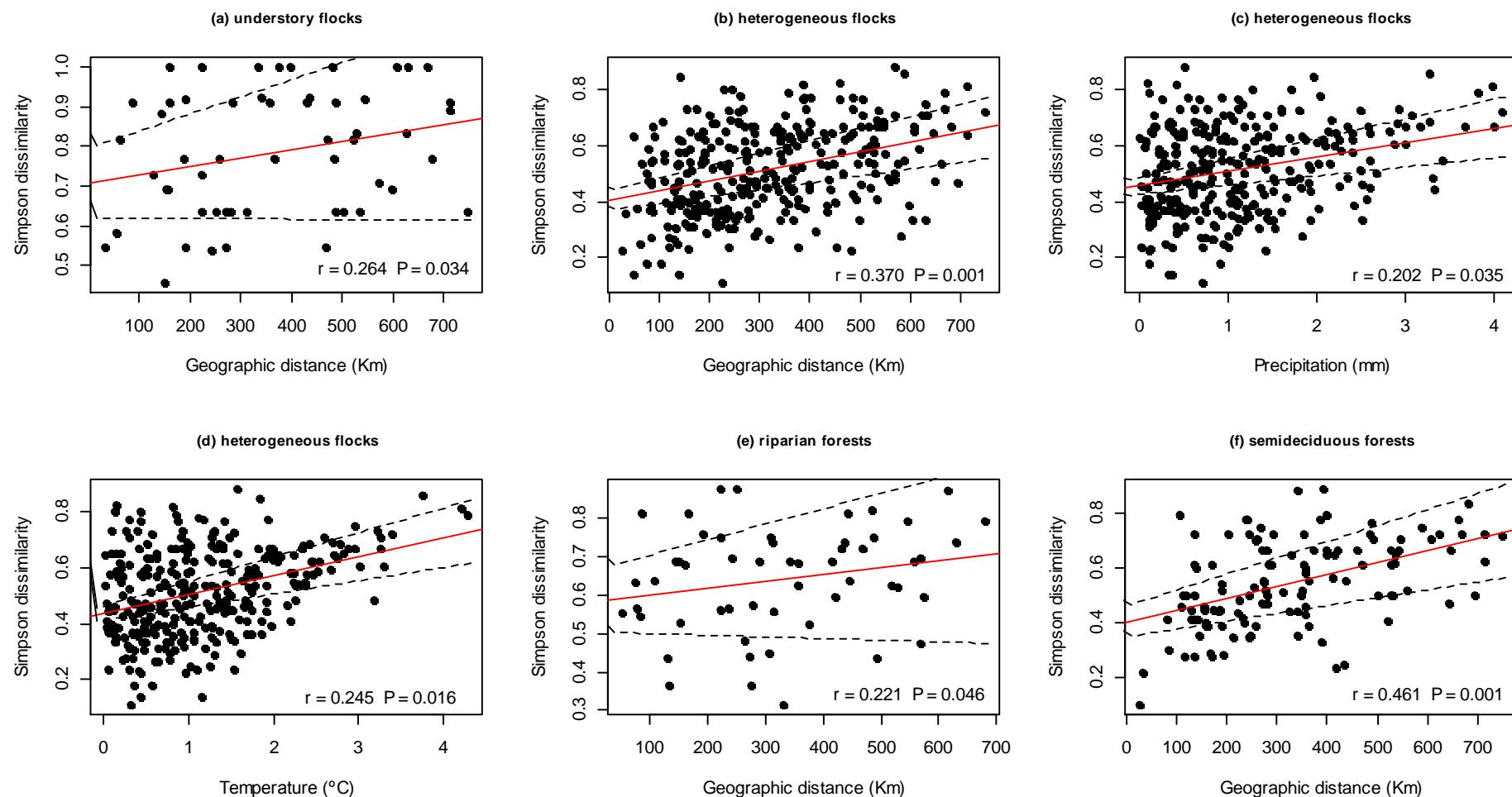
Figure 4. Significant relationships between Simpson dissimilarity (spatial turnover component) in species composition and geographical distance, precipitation and temperature for different mixed flock (a-d) and forest types (e-f). (a) understory flocks, (b-d) heterogeneous flocks, (e) riparian forest flocks, (f) semideciduous forest flocks. Dashed lines represent the 95% confidence interval.
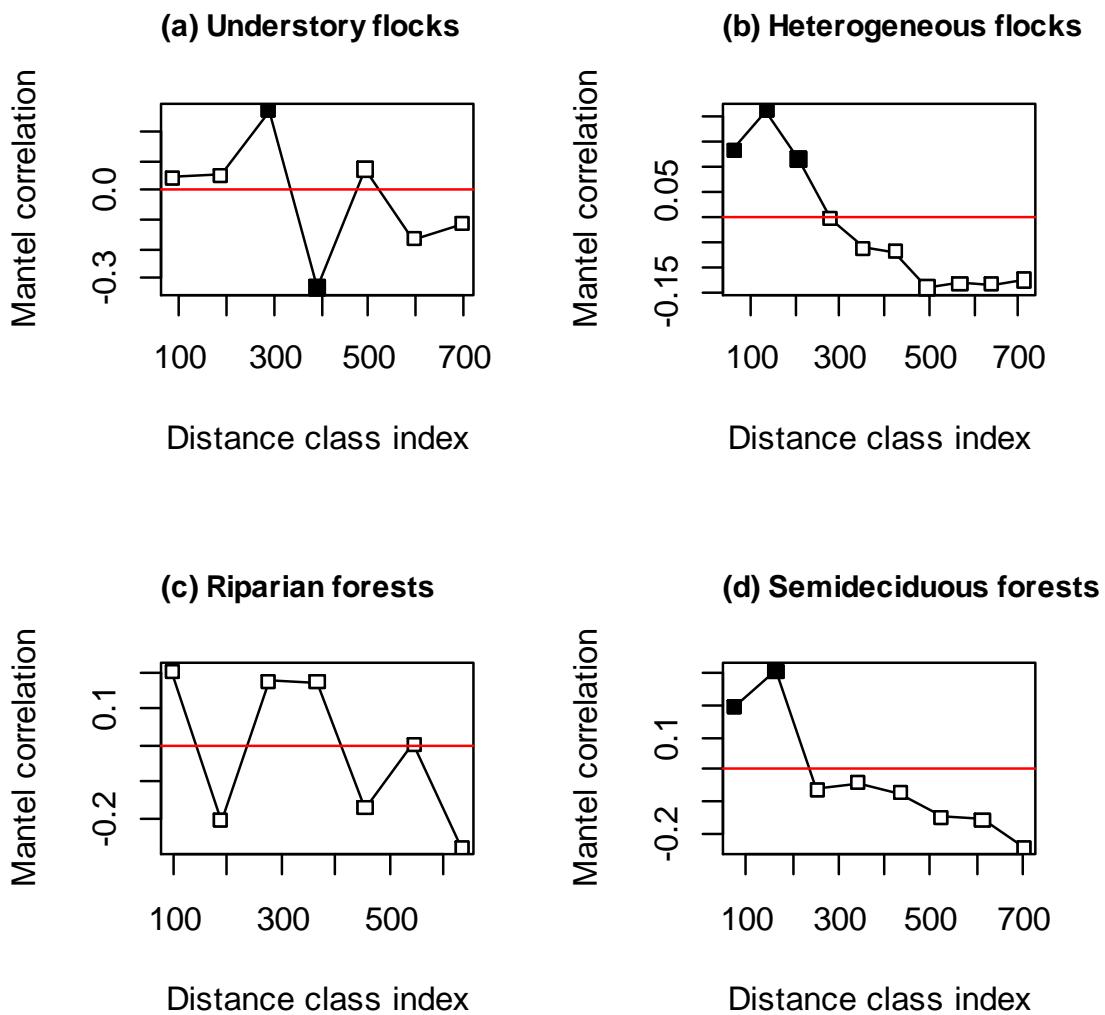
Figure 5. Mantel correlogram showing the relationships of pearson's correlations according to distance classes for: (a) understory flocks (distance class: 102 km), (b) heterogeneous flocks (distance class: 72 km), (c) riparian forest flocks (distance class: 89 km) and (d) semideciduous forest flocks (distance class: 90 km). Black points are significant associations of distance and species dissimilarity (spatial turnover) at the alpha = 0.05.

3.5 Discussion

Our results suggest that there are changes in the composition of mixed flocks not only among different types of forest and their vertical strata, but also that most of beta diversity is a product of spatial replacement of species, both in spatial and climatic gradients, showing dissimilarity increase with increasing environmental and geographical distance.

Although the geographic space is driving the species gradient in heterogeneous and understory flocks and riparian and semideciduous forests, one of the few studies that tested the relationship of geographic variation in mixed flocks into a regional scale, Goodale et al. (2009) in India and Sri Lanka, identified that the variation of composition is not related to geographical distance, but with the altitude (possibly correlated to temperature variation). Similar pattern was also found by Gram (1998) at different altitudes and forests in Mexico. Although not shown here, altitude variation is small in our study area and features at most a marginal relationship with flocks of riparian forests (P = 0.10).

Temperature and precipitation influenced in spatial turnover of heterogeneous flocks. Generally, these flocks are formed by canopy and understory species that stay more part of time together (Munn 1985). As consequence of this meeting of species, heterogeneous flocks show a higher richness than other flock types and proportionally a higher number of rare and uncommon species. Due to this contribution of rare species, heterogeneous flocks should be more vulnerable to environmental changes, such as more elevate temperature over gradient. Furthermore, regular species are also replaced for others that, in parts, it is proportioned by compositional differences in riparian and semideciduous forest flocks.

Although our results indicate an absence of relation between species dissimilarity of understory flocks and climate gradient when controlled by space, this likely tolerance of the species is not affected in relation to forest type (Figure 2). Flocks of understory riparian forests, for example, are more susceptible to sudden floods that in others forest types. In semideciduous forest and woodland savanna, nuclear species of the Parulidae family (*Basileuterus* and *Myiothlypis*) were replaced by *Cantorchilus* (Troglodytidae) and *Ramphocelus carbo* (Thraupidae) in lowland riparian forests, for example. Goodale and Kotagama (2007) found similar results for understory flocks in an altitudinal gradient in Sri Lanka, where the extremes of the gradient showed different core species. As support to Niche Theory, in distances far 400 Km there was a decrease of space effect over dissimilarity indicating a higher number of species shared besides the one distance class. This decrease of species dissimilarity with distance, which is not expected based on Neutral Theory (Hubbell

2001), can be explained according to more similarity among faunas present in both flooded forest next to Paraguay and Parana rivers, which shared some common wetland species (*R. carbo*, *Thamnophilus doliatus*, *C. haemorrhous*, *Campyloramphus trochilirostris*, *Icterus pyrrhopterus*), which are absents or rare in other two vegetation. This pattern was also observed in other study with birds and mammals (Caceres et al. 2014), which the authors identified a more similarity between Chiquitano and Atlantic forest faunas than between those forests and Cerrado woodland savannas.

At the other extreme, the canopy flocks, which are more adapted to living in the warmer portions of the forest, featured a gradual replacement, although not related to the spatial and environmental gradients. The smaller species commonly found in most eastern semideciduous forest, particularly in the Atlantic forest (e.g., *Dacnis cayana*, *Conirostrum speciosum*, *Myiopagis caniceps*, *Hemithraupis guira*), are different from those larger body size species of semideciduous forest from Maracaju, Bodoquena and Urucum plateaus in west (e.g., Icteridae – *Psarocolius decumanus*, *Cacicus* and *Icterus*). The scarcity of mixed flock species in the canopy of riparian forest and woodland savanna suggests the low height of vegetation as a whole (when compared to semideciduous forests), because the species that make up the canopy flocks in most of the gradient are found only in heterogeneous flocks of these two forest formations (Della-Flora and Cáceres, unpublished data).

The spatial turnover in riparian and semideciduous forests also increased with the geographical distance in part due to influence of woodland savanna species of Pantanal (*Synallaxis albilora*) Chaco (*Xiphocolaptes major, Inezia inornata*) and Cerrado (*Phyllomyias reiseri*, *Thamnophilus pelzelni*, *Herpsilochmus longirostris*) ecoregions in west. Specifically for semideciduous forests, there also was a replacement of congeneric species in northwest (*Lanio penicillatus*, *M. tyrannulus*, *Trogon curucui*, *Cacicus chrysopterus*, *Pachyramphus validus*, *Thamnophilus sticturus*) southeast (*Lanio melanops*, *Myiarchus ferox*, *Trogon surrucura*, *Cacicus haemorrhous*, *Pachyramphus polychopterus*, *T. pelzelni*) direction, suggesting a likely influence of these genera in the formation and cohesion of mixed flocks over gradient.

On the other hand, the flocks of woodland savannas did not show a relationship between spatial turnover and the gradients of space and climate. Somehow, there must be other factors more locals such as fragment size, proximity of other ecoregions (e.g., Atlantic forest, Chaco) or vegetation types (open savannas, wet grasslands), which allow that the species replacement prevails over species loss.

The role of space like limiting factor of dispersal ability can be observed mainly in species from understory flocks in way from riparian to semideciduous forests. Coincidentally or not, the Pantanal wetlands have an important function as geographic barrier altering substantially the understory flock composition and not allowing that Chiquitano forest sites, for example, had high richness in canopy flocks as in Atlantic forest sites. On the other hand, the temperature and precipitation affected more than space the heterogeneous flocks and likely understory flocks in distance classes more than 400 Km, suggesting that small changes in environmental filters must interfere in capacity of the species in obtain resources, and consequently in their distributions.

3.6 Conclusion

We study is very important in comprehension of how avian mixed flocks in different seasonal forests are structured and differentiate not only themselves, but also over gradients, which processes operate more strongly in the structuring of mixed flock assemblies and which patterns are more frequents.

The spatial turnover component of Beta diversity was more important than nestedness in multiple-sites over three flock and forest types. Furthermore, there is an increase of dissimilarity of spatial turnover component with the spatial distance in understory, heterogeneous, riparian and semideciduous flocks, and with environmental filters (temperature and precipitation) in heterogeneous flocks.

In general, the different ecoregions encountered in the surrounding region create geographic barriers related to higher or lower dispersal ability of species, and that the climate variables, temperature and rainfall precipitation, would be secondarily affecting the beta diversity of mixed flocks mainly in flock species more generalists in relation to forest stratum like in heterogeneous flocks.

Other factors not examined here must also be contributed for avian mixed flock assembly, mainly in flocks with less number of species (understory and canopy) or with high spatial turnover among proximal sites (woodland savannas). Future research, thus, should give emphasis on other mechanisms that can be assembling avian mixed flocks.

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6.8 Supplementary material

Supplementary material 1. Information regarding to map numbers of Figure 1 describing their respective localities, richness, mixed flock and forest types (number of mixed flocks sampled), geographical coordinates and environmental variables (temperature and precipitation).

Map number	Localities	Richness	Mixed flock	Forest	Latitude	Longitude	Temperature (°C)	Precipitation (mm)
1	Corumbá	39 (10)	U (5) H (5)	S (10)	-19.17	-57.62	21.5	41.0
2	Albuquerque	49 (13)	U (6), H (7)	R (9), W (4)	-19.38	-57.40	22.6	43.0
3	Abobral	29 (7)	U (3), H (4)	R (7)	-19.48	-56.92	22.7	45.7
4	Caiman	38 (7)	H (5), C (2)	R (4), S (3)	-19.93	-56.32	21.9	55.3
5	Miranda	30 (6)	H (3)	W (6)	-20.50	-56.18	20.9	62.3
6	Aquidauana	56 (10)	U (3), H (7)	R (3), S (3), W (2)	-20.45	-55.50	21.2	61.3
7	Campo Grande	19 (5)	H (3)	W (4)	-20.49	-54.50	20.8	60.7
8	Sidrolândia	40 (8)	H (7)	S (5), W (3)	-20.77	-54.83	21.3	60.0
9	Nova Alvorada	27 (5)	H (4)	R (2), S (3)	-21.41	-54.43	20.7	63.3
10	Três Lagoas	24 (5)	U (2), H (3)	W (5)	-20.92	-52.23	20.9	42.7
11	Caiuá	18 (4)	H (4)	S (4)	-21.64	-51.88	19.5	48.3
12	Teodoro Sampaio	49 (14)	U (3), H (8), C (3)	R (3), S (10)	-22.60	-52.20	18.6	66.0
13	Diamante do Norte	23 (6)	H (2), C (4)	R (6)	-22.60	-52.88	19.1	67.7
14	Tuneiras do Oeste	50 (20)	U (9), H (8), C (3)	S (20)	-23.88	-52.81	16.8	112.7
15	Casa Verde	35 (10)	H (7)	R (3), W (7)	-21.61	-53.31	20.6	55.3
16	Nova Andradina	28 (7)	H (4), C (2)	W (7)	-22.05	-53.39	20.0	61.7

17	Novo Horizonte	29 (7)	H (3), C (4)	S (7)	-22.55	-53.89	20.1	70.7
18	Naviraí	32 (6)	U (2), H (4)	R (6)	-22.84	-53.56	19.3	78.3
19	Eldorado	17 (5)	-	S (5)	-23.75	-54.11	17.9	109.3
20	Iguatemi	31 (4)	H (3)	R (2), W (2)	-23.55	-54.64	18.2	101.0
21	Campanário	46 (13)	U (3), H (7), C (3)	R (5), S (8)	-22.85	-55.01	19.2	85.0
22	Maracaju	34 (6)	H (4), C (2)	S (3), W (3)	-21.87	-55.40	19.6	76.3
23	Bela Vista	36 (11)	H (7), C (3)	W (11)	-22.07	-56.55	20.2	86.7
24	Jardim	16 (6)	U (3)	R (6)	-21.43	-56.43	20.2	74.0
25	Bonito	27 (5)	H (2), C (2)	S (3), W (2)	-21.08	-56.73	18.9	69.0
26	Pitangueira	44 (12)	U (3), H (9)	S (2), W (10)	-20.88	-56.57	19.5	67.3
27	Caracol	47 (4)	H (3)	R (4)	-22.21	-57.30	20.5	74.7
28	Porto Murtinho	18 (4)	H (3)	S (4)	-21.48	-57.89	21.3	59.0

4 ARTIGO 4 - FILTROS AMBIENTAIS E FACILITAÇÃO SÃO OS ORGANIZADORES DA ESTRUTURA DE BANDOS MISTOS DE AVES[4]

Franchesco Della-Flora, André Luís Luza, Nilton Carlos Cáceres

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[4] Esse artigo segue as normas da revista Oikos

4.1 Resumo

As assembleias de aves que compõem os bandos mistos apresentam certas lacunas no que diz respeito a como essas associações se organizam na comunidade. Regras de montagem podem ser aplicadas em bandos mistos a fim de testar quais seriam os processos ecológicos que atuariam em diferentes escalas espaço-ambientais. As escalas finas envolveriam relações positivas (proteção contra predadores e aumento do forrageio, facilitação) ou negativas (uso de recursos similares por espécies aparentadas, competição) entre espécies, e as escalas maiores, seriam influenciadas pelos filtros ambientais (variáveis abióticas) ou por barreiras de dispersão (espaço geográfico). Em nosso estudo, avançamos o conhecimento acerca da organização dos bandos mistos e das espécies que os compõe, avaliando a estrutura funcional e filogenética dos bandos quanto às regras que organizam esses subconjuntos da comunidade ao longo de diferentes escalas (fitofisionomia e estratificação florestal). Nós testamos para agrupamento e repulsão filogenética e funcional 192 espécies de aves em 398 bandos mistos, além de termos avaliado o sinal filogenético e a conservação filogenética dos atributos morfológicos e comportamentais das aves participantes. Maior parte dos atributos apresentou sinal filogenético, porém somente os atributos morfológicos foram conservados filogeneticamente. A frequência de ocorrência em bandos mistos foi o único atributo convergente nas espécies demonstrando que existem vários clados não relacionadas que são importantes na formação e coesão dos bandos. Nós achamos maior ação de filtros ambientais seguidos pela facilitação, porém não houve papel da competição na montagem dos bandos. Embora os dois primeiros processos ecológicos estejam atuando de maneiras distintas nas fitofisionomias e estratos verticais da vegetação, descobrimos que em ambientes savânicos há maior facilitação (maior agrupamento e sobredispersão filo-funcional) entre as espécies, ao passo que nos florestais, oeste e leste da nossa área de estudo, observamos maior efeito dos filtros ambientais em decorrência de maior agrupamento funcional, tanto nos atributos conservados quanto no convergente.

Palavras-chave: Estrutura funcional da comunidade, Estrutura filogenética da comunidade, Estratificação florestal, Fitofisionomias, Mutualismo, Passeri, Regras de montagem, Sinal filogenético, Tyranni.

4.2 Introdução

Cada vez mais se reconhece a necessidade de incorporar em estudos sobre a biodiversidade informações sobre o parentesco filogenético das espécies (Clarke e Warwick 1998, Santos et al. 2010). Investigar esses padrões dentro de comunidades pode render um rico entendimento dos processos ecológicos e evolutivos que influenciam a organização das assembleias em escalas locais e regionais (Bryant et al. 2008, Fine e Kembel 2010, Pillar e Duarte 2010, Gómez et al. 2010). Além disso, inúmeros estudos têm abordado o papel de atributos funcionais e mecanismos evolutivos sobre padrões de coexistência entre espécies (Webb et al. 2002, Cavender-Bares et al. 2004, Kraft et al. 2007, Hardy 2008, Kembel 2009, Vamosi et al. 2009). A teoria de "montagem filogenética de comunidades" sugere que processos que dirigem a organização das comunidades podem resultar em assembleias compostas de espécies que são mais intimamente aparentadas (agrupamento ou sub-dispersão filogenética) ou menos aparentadas (repulsão ou sobredispersão filogenética) do que esperado ao acaso (Cavender-Bares et al. 2004, Anderson et al. 2011).

Quando há tendência de conservação filogenética de nicho (existência de sinal filogenético) e os filtros ambientais predominam, tem-se agrupamento filogenético, enquanto que a predominância de similaridade limitante (presença de características distintas entre as espécies) devido às interações bióticas (e.g., competição) causa repulsão filogenética (Cavender-Bares et al. 2009). Outro fator importante é a capacidade de ocorrer exclusão por competição sobre espécies mais distintas e não aparentadas (Mayfield e Levine 2010), que seria o oposto do papel da similaridade limitante. Há ainda a possibilidade de ocorrer facilitação funcional, tanto entre espécies próximas (agrupamento funcional) quanto distantes filogeneticamente (repulsão funcional) (Valiente-Banuet e Verdú 2007, Satischandra et al. 2007, Sridhar et al. 2012), demonstrando que não só os filtros ambientais e a competição são importantes na montagem das comunidades (Figura 1).

Entretanto, tais padrões de organização das comunidades tendem a ser altamente dependentes da escala, e análises em escalas espaciais, taxonômicas e ambientais distintos podem gerar resultados e interpretações completamente diferentes, quando considerada a importância relativa de interações bióticas e filtros ecológicos na montagem de comunidades (Brooker et al. 2009, Fine e Kembel 2011, Gómez et al. 2010). Cabe ressaltar também que a maioria das comunidades em diferentes escalas espaciais podem ser muito mais aleatórias que filogeneticamente agrupadas ou sobredispersas (Gómez et al. 2010, Machac et al. 2011),

evidenciando, por um outro lado, que eventos estocásticos, distúrbios ou ligados a capacidade de dispersão das espécies (Hubbel 2001) podem estar promovendo um padrão aleatório da estrutura filogenética da comunidade (Figura 1).

Os atributos das espécies geralmente são mantidos entre aquelas com maior grau de parentesco (tendência ao sinal filogenético), embora diferentes atributos possam ser mais ou menos conservados ao longo da história evolutiva (Blomberg et al. 2003). Quanto à evolução dos atributos, as espécies podem apresentar três padrões distintos: um quando o sinal filogenético é maior que o esperado por movimento Browniano tendo como resultado a conservação filogenética de nicho (atributos); o segundo é o próprio movimento Browniano que prediz que as características das espécies são esperadas evoluir por seleção aleatória ou deriva genética, que por fim pode apresentar certa instabilidade dos atributos; e o terceiro seria o equivalente ao "anti-sinal" filogenético, que representaria padrões de convergência dos atributos, ou seja, quando o anti-sinal é menor que esperado pelo movimento Browniano (Blomberg et al. 2003). Desse modo, assumindo que as espécies apresentam conservação de nicho, as assembleias deveriam alterar sua estrutura filogenética (de agrupadas a sobredispersas) ao longo de gradientes espaço-ambientais (Cavender-Bares et al. 2009, Graham et al. 2009), onde os filtros ambientais agiriam nas escala maiores e a limitação da similaridade nas escalas menores (Brooker et al. 2009).
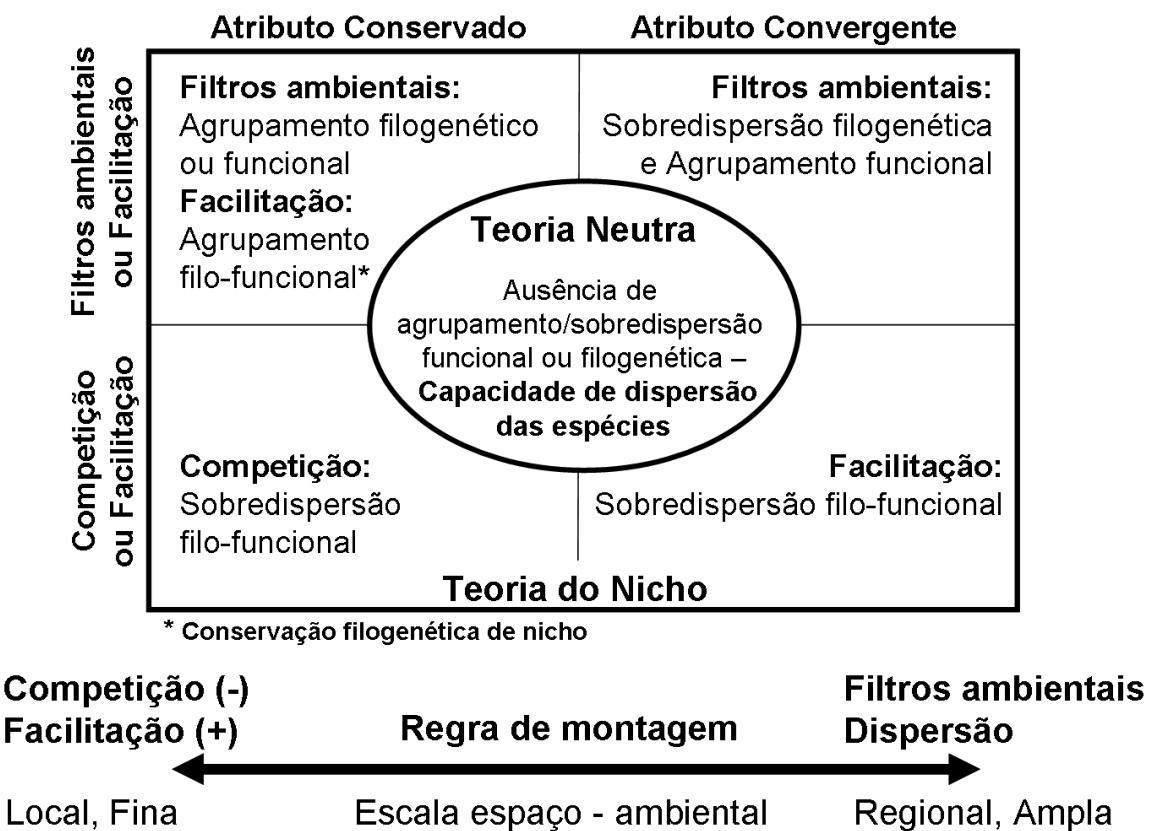
Figura 1. Resumo geral dos principais processos que estruturam as comunidades, identificando o papel das regras de montagem sobre a estrutura filogenética e funcional das assembleias, as escalas espaço-ambientais em que elas atuam e a inserção da teoria do Nicho e da teoria Neutra da Biodiversidade dentro dos processos ecológicos.

Um ponto a destacar é que a maior parte da informação contida nas principais métricas de estrutura filogenética de comunidades, NRI (*Net-Relatedness Index*) e *NTI (Nearest Taxon Index)* (Webb 2000), não são capazes de levar em conta as especificidades ambientais de cada espécie (Duarte 2011). Além disso, informações de gradientes de parentesco entre espécies de cada comunidade podem oferecer evidências se as comunidades são diferentes conforme as mudanças na estrutura do ambiente, como o espaço geográfico, vegetação, clima, ou os próprios atributos das espécies (Gómez et al. 2010, Brum et al. 2012, Gianuca et al. 2013). Dessa forma, além de saber como a filogenia é estruturada nas comunidades, podemos identificar quais são os taxa responsáveis por essa estrutura (Duarte 2011).

A influência da estruturação filogenética sobre diferentes tipos de regra de montagem ainda é pouco avaliada em assembleias animais, e os poucos estudos que aplicaram abordagens filogenéticas considerando diferentes tipos de escalas ambientais/espaciais em

aves se restringem geralmente a um clado específico (e.g., Lovette e Hochachka 2006, Graham et al. 2009, Gómez et al. 2010, mas ver Gianuca et al. 2013 para toda assembleia de aves) ou enfocam de maneira indireta aspectos filogenéticos nas análises, dando mais ênfase nas relações funcionais entre as espécies (Sridhar et al. 2012).

Gómez et al. (2010), por exemplo, utilizaram a filogenia e os atributos das espécies de Thamnophilidae da Região Neotropical a fim de verificar quando em escalas locais, intermediárias e regionais quais regras de montagem melhor explicam a grande diversidade filogenética e funcional da família. Como observado em um estudo recente com bandos mistos (Sridhar et al. 2012), a escala local (composição de bandos mistos) proposta por Gómez et al. (2010) apresentou maior agregação filogenética sob os atributos conservados, ao contrário que prediz a teoria de montagem da comunidade filogenética na qual, em escalas pequenas, as espécies tenderiam a competir mais que o esperado ao acaso, causando repulsão filogenética (Cavender-Bares et al. 2009). Além disso, não há evidência que os atributos sejam mais agrupados que sobredispersos funcionalmente dentro dos bandos (Gómez et al. 2010), embora os autores tenham testado poucos bandos mistos e restritos a apenas duas localidades da Floresta Amazônica. Além do mais, partindo de que associações mistas de espécies de aves compreendem um sistema social comum em vários ambientes terrestres (Greenberg 2000), seria prudente a análise de mais amostras, distribuídas em diferentes ambientes para que se pudesse concluir que esse padrão de estrutura filogeneticamente agrupada fosse mesmo corroborado e, ainda, se ele seria regrado somente pelos filtros ambientais (Gómez et al. 2010), ou também por facilitação (Sridhar et al. 2012), onde as espécies mais aparentadas e mais similares coexistiriam nos bandos mais que o esperado para espécies não relacionadas filo-funcionalmente.

De maneira geral, grande parte das espécies participantes de bandos interespecíficos na Região Neotropical é composta por aves insetívoras de sub-bosque, principalmente por espécies Passeriformes formadas por Thamnophilidae, Furnariidae e Thraupidae (Moynihan 1962, Powell 1979, Munn e Terborgh 1979, Munn 1985, Aleixo 1997, Maldonado-Coelho e Marini 2003). Ou seja, se as características da maior parte das espécies que compõem os bandos são preservadas, agrupadas funcionalmente, então poderíamos predizer que as caraterísticas filogenéticas também seriam se houvesse facilitação das espécies mais aparentadas (Sridhar et al. 2012).

Para tanto, os bandos mistos compõem um interessante tema para estudos sobre os mecanismos de estruturação filogenética e funcional de metacomunidades. Se espécies

filogeneticamente próximas tendem a coexistir nos bandos com menor frequência do que o esperado ao acaso, pode ser que seja um reflexo da limitação de similaridade (Graves e Gotelli 1993). Por outro lado, mesmo que os atributos sejam conservados, as espécies próximas filogeneticamente podem conviver juntas se existirem associações positivas para ambos os participantes, ocorrendo dessa forma facilitação (Sridhar et al. 2012). Há indícios que a territorialidade interespecífica previne que congêneres ecologicamente similares venham a ocupar o mesmo bando, o que causa um padrão de distribuição em tabuleiro de espécies intimamente aparentadas (Graves e Gotelli 1993, Lovette e Hochachka 2006). Em contraste, existe a questão que para a própria formação de bandos mistos possa haver também um componente de conservação de nicho (Harrison e Whitehouse 2011), principalmente quando a frequência de espécies aparentadas participantes é maior que aquela entre espécies menos relacionadas filogeneticamente (Sridhar et al. 2012).

Nesse estudo apresentamos, inicialmente, como os bandos mistos de aves são estruturados filogeneticamente e funcionalmente entre diferentes tipos de fitofisionomias e estratos verticais da vegetação e, secundariamente, como os atributos das espécies formadoras dos bandos mistos são conservados ao longo dos ramos da árvore filogenética. Junto a isso, verificamos se a capacidade de dispersão, os filtros ambientais, a similaridade limitante (competição), ou a facilitação seriam responsáveis pela montagem dos bandos mistos. Para tanto, testamos se os bandos nos diferentes ambientes apresentam maior agrupamento ou repulsão nas suas estruturas filogenéticas e funcionais que o esperado ao acaso. Por último, empregamos uma análise baseada em extração de coordenadas principais da estrutura filogenética (PCPS; Duarte 2011), a fim de identificar relações entre os principais clados de aves e as diferentes categorias pertencentes às fitofisionomias e estratificação da vegetação.

4.3 Material e métodos

4.3.1 Área de estudo

O local de estudo compreende 29 localidades amostradas ao longo da região sudoeste do Brasil entre a metade sul do Mato Grosso do Sul, o noroeste do Paraná e o sudoeste de São Paulo. Os locais são representativos de várias ecorregiões da América do Sul, a destacar o Chaco, o Pantanal, a Floresta Amazônica (Floresta Chiquitana), o Cerrado e a Floresta Atlântica; além de estarem incluídos em duas grandes bacias hidrográficas, Paraná (leste) e Paraguai (oeste). Os ecossistemas predominantes são florestas semidecíduas (noroeste,

sudeste e leste), savanas florestadas (centro), savanas abertas (sudoeste e norte) e pantanais (bacias de inundação dos rios Paraguai, a oeste, e Paraná, a leste). Além disso, há a existência outros ambientes menores em escala, mas de grande importância ecológica, como as florestas de galeria ou ciliares, que margeiam pequenos e grandes rios inseridos dentro de uma matriz campestre-savânica.

A região é rica em zonas de ecótonos e enclaves encontrados em bordas de serranias e planaltos (Bodoquena a oeste, Urucum a noroeste, Maracaju no centro, Guarapuava e Ocidental a leste), onde predominam florestas estacionais decíduas e semidecíduas. O Planalto de Maracaju, por exemplo, é uma barreira geográfica importante, pois separa no sentido leste-oeste a Floresta Atlântica do Cerrado, e no sentido norte-sul, apresenta um cordão florestal de origem Atlântica, que segrega edaficamente as duas principais vegetações arbóreas do Cerrado na área de estudo: o cerradão, tipo de floresta seca ou savana arbórea com dossel fechado, a oeste, e o cerrado senso estrito, mais savânico, a leste (Oliveira-Filho e Ratter 2002). Além do Planalto de Maracaju, existem ainda grandes rios que impõem barreiras físicas e ambientais na região, tais como o Rio Paraná e o Paraguai, os quais apresentam planícies de inundação com florestas adaptadas a esse ambiente, sendo a planície do Rio Paraguai muito extensa a ponto de ser classificada como uma ecorregião a parte, o Pantanal (Veloso et al.1991).
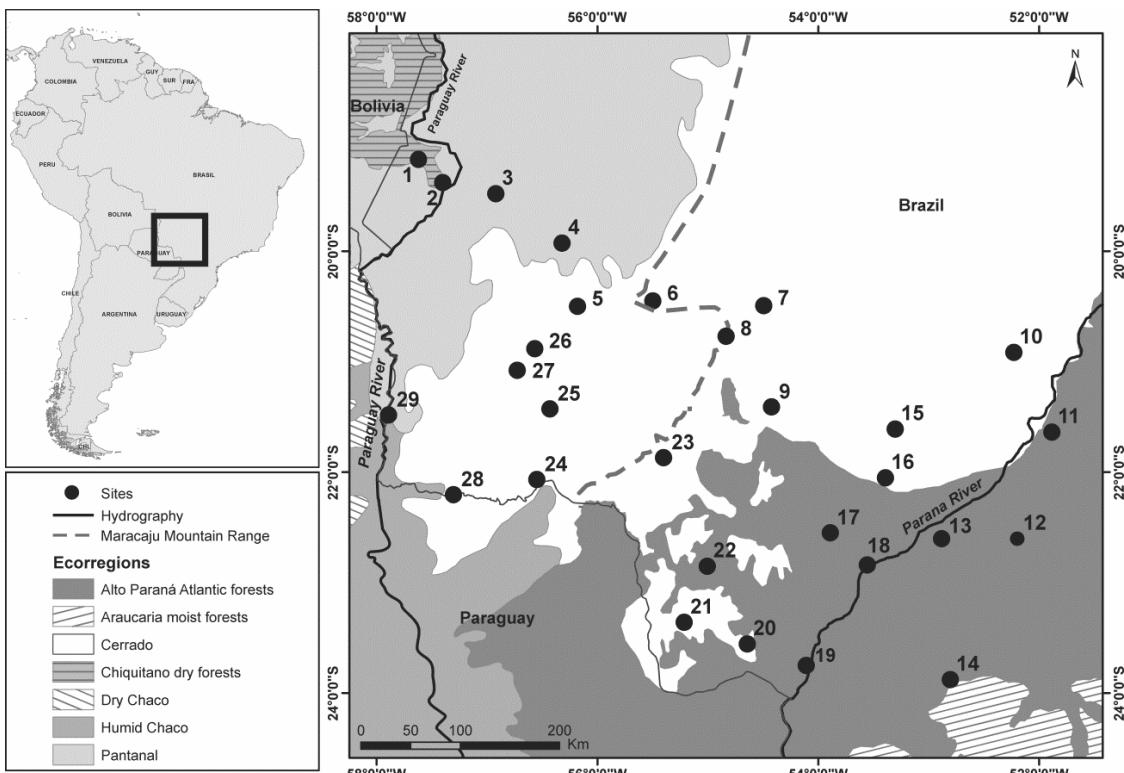
Figura 2. Mapa com as ecorregiões e ecótonos (diferentes símbolos) e as respectivas localidades amostradas de acordo com as quatro regiões geográficas: Região Noroeste (1 – Corumbá, 2 – Albuquerque); Região Centro-oeste (3 – Abobral, 4 – Caiman, 5 – Miranda, 24 – Bela Vista, 25 – Jardim, 26 – Bonito, 27 – Bonito 2, 28 – Caracol, 29 – Porto Murtinho); Região Centro-leste (6 – Aquidauna, 7 – Campo Grande, 8 – Sidrolândia, 9 – Nova Alvorada do Sul, 10 – Três Lagoas, 15 – Nova Casa Verde, 16 – Nova Andradina, 17 – Novo Horizonte do Sul, 18 – Naviraí, 19 – Eldorado, 20 – Iguatemi, 21 – Coronel Sapucaia, 22 – Laguna Caraapã, 23 – Maracaju); e Região Leste (11 – Presidente Epitácio, 12 – Teodoro Sampaio, 13 – Diamante do Norte, 14 – Tuneiras do Oeste). Ecorregiões e Ecótonos: Pantanal (triângulo invertido), Florestas estacionais do Oeste e Cerrado (círculo), Cerrado (quadrado), Floresta Atlântica e Cerrado (triângulo), Floresta Atlântica (losango).

4.3.2 Definição das escalas ambientais

Bandos mistos foram considerados como unidades amostrais dentro de cada ambiente. Assim, examinamos gradientes de estruturação filogenética e funcional de bandos mistos em duas escalas ambientais diferentes, (a) Fitofisionomia e (b) Estratificação Florestal.

As fitofisionomias foram divididas em: (a) floresta estacional (florestas das encostas dos planaltos de Urucum, Bodoquena e Maracaju, além das demais áreas de Floresta Atlântica; 149 bandos mistos), (b) floresta de galeria e ciliar (floresta localizada a beira de rios e córregos e nascentes, mas não sazonalmente inundáveis; 49 bandos), (c) floresta de inundação (floresta associada a pantanais dos rios Paraná e Paraguai, 45 bandos), (d) cerradão (formação florestal do Cerrado, possuindo dossel fechado; 92 bandos), (e) cerrado senso

estrito (formação savana-arbórea semelhante floristicamente ao cerradão, mas com dossel aberto e com presença de gramíneas; 36 bandos) e (f) chaco (formação savana-arbórea, mas com presença de espécies xerófitas típicas da ecorregião Chaco; 27 bandos) (Veloso et al.1991, Oliveira-Filho e Ratter 2002).

A estratificação da floresta foi categorizada em três grupos de acordo com o ambiente vertical onde os bandos eram encontrados. O primeiro grupo foi composto por associações de sub-bosque (144 bandos), representando bandos que utilizam desde o chão da floresta até o estrato médio (em savanas, abaixo da copa das árvores). O segundo grupo foi denominado heterogêneo (225 bandos), pois faz parte os bandos que foram observados ao longo de todo o estrato vertical da floresta, desde as espécies observadas próximas ao chão junto àquelas amostradas no dossel. O terceiro grupo foi constituído por espécies típicas ou presentes nos bandos de dossel (59 bandos), e caracterizado por bandos mistos que forrageiam tanto acima quanto abaixo da copa das árvores.

4.3.3 Coleta de dados dos bandos mistos

Áreas contínuas e fragmentos de vegetação (acima de 100 ha) foram amostrados a cada quatro dias por localidade. As amostragens ocorreram durante a estação seca (maio a agosto) de modo a padronizar as amostragens ao longo de todas as ecorregiões, regiões transicionais e geográficas. As observações dos bandos mistos foram realizadas no período da manhã (0700-1100h) e a tarde (1600-1700h) (adaptado de Davis, 1946) totalizando entre 12 e 15h dependendo das condições de cada local. Ao todo foram 406 h de observação de campo entre os anos de 2009 e 2011. Os bandos foram seguidos por no máximo 30 min, e das espécies participantes foram obtidas informações da estrutura vertical de forrageamento. Um segundo bando encontrado durante a observação de outro iniciado foi descartado ou adicionado caso houvesse aglutinação dos bandos. Em média foram observados 13,7 (7-21) bandos mistos por localidade e 8,5 (2-31) espécies por bando de um total de 398 bandos. A identificação das espécies foi realizada por guias de identificação de campo (Narosky 2006, Sigrist 2009) e por registros sonoros com a ajuda de gravador portátil.

4.3.4 Espécies e Filogenia

O *pool* de participantes dos bandos mistos totalizou 192 espécies pertencentes às ordens Passerifomes com 166 espécies (Tyranni, 98 espécies e Passeri, 68 espécies), seguido pelos Piciformes (15 espécies), Galbuliformes (quatro), Trogoniformes (três), Coraciiformes (duas), e Cuculiformes e Columbiformes com uma espécie cada, respectivamente (Material

suplementar 1).

Cem árvores com as distâncias filogenéticas entre as espécies foram geradas a partir do site birdtree.org baseado em Jetz et al. (2012) através das informações contidas em Hackett et al. (2008). A escolha da melhor árvore (Material Suplementar 1) baseou-se na confirmação de publicações com maior grau de certeza na hipótese filogenética (e.g., *bootstrapping* acima de 70%) nos níveis de família e gênero de alguns taxa conflitantes (Irestedt et al.2004, Moore et al. 2006, Barber e Rice 2007, Fuchs et al. 2007, Chaves et al.2008,Nylander et al.2008, Campagna et al. 2010, Tello et al. 2009, Lovette et al. 2010, Derryberry et al. 2011), sendo que alterações nas posições dos ramos foram realizadas no programa Mesquite (Maddison e Maddison 2007).

4.3.5 Atributos das espécies e relações funcionais

Características funcionais das espécies participantes dos bandos foram coletadas de acordo com dados observados em campo (frequência de ocorrência ponderada pela distribuição geográfica: FOP; índice do uso da estratificação florestal médio: EFM; padrão de coloração: COR) ou retirados da literatura (dieta: DIE e massa corporal; Belton 1994, Reinert et al. 1996, Marini et al. 1997, Pirateli et al. 2001, Piratelli e Pereira 2002) ou coletados em museus (comprimentos do corpo, largura, comprimento e cúlmen do bico, comprimentos do tarso e do dedo médio e a razão entre eles (dedo médio/tarso); Museu de Zoologia da USP – MUZUSP e Museo de Ciencias Naturales Bernardino Rivadavia).

Os atributos comportamentais, FOP, EFM e DIE, foram categorizados de maneiras distintas. A FOP foi medida de acordo com a frequência de ocorrência das espécies ponderada pelo número de bandos mistos amostrados dentro da distribuição da espécie, respeitando suas características ambientais (espécies estritamente florestais e campestres não foram computadas exceto nos bandos localizados na borda desses ambientes). A FOP representa a porcentagem de participação das espécies nos bandos, ou seja, uma medida comportamental do grau de dependência em viver associado junto com outras espécies. Ela é similar à frequência de ocorrência encontrada em vários trabalhos de estrutura de bandos mistos, onde as espécies são classificadas entre comuns, ocasionais e raras (Powell, 1985, Machado 1999). O EFM varia de 0, para espécies que participavam somente no chão, até 1, para espécies de dossel. Para cada bando misto observado, a espécie recebia um valor de estratificação (Machado 1999) que foi somado com os demais eventos e dividido pelo total das participações. A DIE foi classificada entre espécies insetívoras, insetívoras-granívoras,

insetívoras-frugívoras, onívoras (insetívoras-granívoras-frugívoras-nectarívoras) e frugívoras, e recebeu nessa ordem valores de 1 para espécies exclusivamente insetívoras a 5 para espécies predominantemente frugívoras.

O atributo morfológico COR foi classificado de acordo com o grau de camuflagem das espécies (plumagens neutras com o ambiente a coloridas): 1 − camufladas sem dimorfismo sexual de plumagem; 2 − camufladas com dimorfismo sexual; 3 − com dimorfismo sexual em que a fêmea é camuflada e o macho colorido; 4 − sem camuflagem aparente, mas com dimorfismo sexual; e 5 − coloridas e sem dimorfismo sexual. A cor da plumagem tende a ser importante para muitas espécies que participam dos bandos mistos (Harrison e Whitehouse 2011), tanto para espécies nucleadoras geralmente coloridas, quanto para as seguidoras mais camufladas (Moynihan 1962, Chipley 1977, Willis 1989, Aleixo 1997, Beauchamp e Goodale 2011). Os demais atributos morfológicos foram escolhidos por serem considerados bons indicadores de sobreposição do uso de recursos (Miles e Ricklefs 1984, Leyequién *et al*. 2007), e dessa forma foram agrupados em três conjuntos de atributos: (a) medidas de tamanho corporal − TAM (massa corporal e comprimento do corpo), (b) medidas de bico − BIC (largura, comprimento, cúlmen), e (c) medidas dos membros posteriores − TAR (comprimento do tarso e do dedo médio e razão entre comprimento do dedo médio/tarso). Todas as medidas morfológicas quantitativas foram log-transformadas a fim de reduzir a amplitude da variância das amostras.

A fim de gerar uma matriz de distâncias entre espécies de acordo com os atributos, ou seja, um dendograma funcional, nós realizamos análises de agrupamento para cada conjunto de atributos, três dendogramas comportamentais (FOP, EFM e DIE) e quatro morfológicos (COR, TAM, BIC e TAR), através de distância euclidiana usando o algoritmo UPGMA (Pavoine e Bonsall 2011). As distâncias funcionais das espécies foram exportadas como arquivo *nexus* e usadas para medir a estrutura funcional dos bandos mistos.

Para o teste de sinal filogenético nós reduzimos as colinearidades das variáveis morfológicas das espécies em três Análises de Componentes Principais (PCA), uma para cada conjunto de atributos: (a) medidas de tamanho corporal (massa corporal e comprimento do corpo), (b) medidas de bico (largura, comprimento, cúlmen), e (c) medidas dos membros posteriores ou tarso (comprimento do tarso e do dedo médio e razão entre comprimento do dedo médio/tarso). Utilizamos o método *scree plot* com distribuições *broken stick* (função '*screeplot*' do pacote vegan; Oksanen et al. 2013) contra os eixos dos principais componentes a fim de determinar um ponto de corte para escolha do número de eixos que seriam utilizados

para a seleção de modelos. Foi selecionado o primeiro eixo de cada conjunto de atributos: atributos corporais (PC_{corpo} 1: 93,9%); do tarso (PC_{tarso} 1: 88,53%); do bico (PC_{bico} 1: 95,31%). O PC_{corpo} 1 apresentou alto coeficiente de correlação com todas as medidas corporais. O PCA_{tarso} 1 se relacionou positivamente com todas as medidas dos atributos de tarso, com exceção da razão entre comprimento do dedo médio/tarso. Todos os atributos do bico se relacionaram positivamente com o PCA_{bico} 1. Para todas as correlações os valores de significância foram menores que 5%.

4.3.6 Estrutura filogenética e funcional dos bandos mistos

A partir da hipótese filogenética escolhida e dos dendogramas funcionais, foi gerada uma matriz de distância filogenética/funcional entre pares de espécies D**f,** utilizando a função "*cophenetic*" do pacote Picante (Kembel et al. 2010) dentro do software R (R Core Team 2013). A análise de estrutura filogenética e funcional, a fim de verificar se há agrupamento ou sobredispersão maior que o acaso entre os bandos mistos, foi realizada através das funções "*ses.mpd*" e "*ses.mntd*" também no pacote Picante (Kembel et al. 2010), que calcula a distância média entre pares de espécies (MPD - *mean pairwise distance*) e a distância média do táxon mais próximo (MNND - *mean nearest neighbor distance*) (Webb 2000)) através de índices (- NRI e - NTI, respectivamente) padronizados pelo desvio padrão das distâncias filogenéticas/funcionais (SES − *standardized effect size*) geradas a partir de modelos nulos, onde SES = (valor observado − valor esperado pelo modelo nulo) / desvio padrão do modelo nulo (Webb et al. 2008). A MPD é considerada uma medida basal das relações filogenéticas de espécies co-ocorrentes por capturar os maiores ramos de uma árvore filogenética ou dendograma funcional e, por isso, as maiores distâncias entre as espécies. Já a MNND ou MNTD é considerada uma medida terminal entre espécies devido à captura dos menores ramos de uma árvore filogenética, ou seja, das menores distâncias entre as espécies co-ocorrentes (Webb 2000). Em decorrência de espécies passeriformes serem muito similares em alguns atributos quando comparado com espécies maiores de "não-Passeriformes", somente a MPD foi usada para análises de estrutura funcional. Valores de NRI e NTI maiores que 0 indicam agrupamento filogenético/funcional, enquanto que menores indicam repulsão (Webb et al. 2002). O uso inadequado de métricas e modelos nulos para inferir como a comunidade é estruturada filogeneticamente ou funcionalmente pode recair em erros Tipo 1 e 2, além de criar viés na interpretação dos resultados (Kembel 2009). Em decorrência disso, utilizamos o modelo nulo "*independente swap*" (Gotelli 2000), que é recomendado por apresentar baixo erro Tipo 1 em NRI e NTI, além de detectar a ação de filtros ambientais nos processos de

montagem da comunidade mesmo quando baseados em vários atributos das espécies (Kembel 2009).

4.3.7 Gradientes de estrutura filogenética e gradientes ambientais

A matriz Df foi transformada em uma matriz de similaridade filogenética Sf, a qual foi utilizada para ponderar a composição de espécies em uma matriz de presença/ausência W(espécies x bandos mistos). Para tanto, foi utilizado o método de ponderação filogenética difusa (Pillar e Duarte 2010). Logo em seguida, foi gerada uma matriz P, contendo a composição de espécies ponderada pela filogenia para cada bando misto. Através da matriz P, realizamos uma Análise de Componentes Principais (PCA), baseada em Distância Euclidiana entre comunidades e entre espécies (matriz transposta) gerando Coordenadas (ou componentes) Principais de Estrutura Filogenética (PCPS) (Duarte 2011). Cada PCPS descreve um gradiente filogenético ortogonal para os bandos mistos e para espécies. As matrizes W e P foram construídas utilizando o pacote SYNCSA (Debastiani e Pillar 2012) no ambiente R (R Core Team 2013).

Os valores de NRI, NTI e dos PCPSs (selecionados com mais de 5% da variação total na composição de espécies ponderadas pela filogenia) dos bandos mistos tiveram seus escores submetidos à Análise de Variância (ANOVA) a fim de comparar a diferença dos ambientes de cada escala ambiental (Fitofisionomia e Estratificação Florestal), utilizando como unidade amostral os bandos mistos.

4.3.8 Sinal filogenético e evolução dos atributos

Os atributos comportamentais e morfológicos (PCs) foram testados para verificar se são conservados filogeneticamente ou se são instáveis nas espécies participantes dos bandos. Para isso, realizamos primeiramente um teste de aleatorização para sinal filogenético (Blomberg et al. 2003), o qual calcula a variância dos contrastes independentes de cada atributo através da filogenia e compara os valores com um modelo nulo com 1000 aleatorizações dos atributos entre as espécies. Variâncias observadas entre os primeiros e os últimos 25 quantis das 1000 modelos nulos foram identificados como sendo sinal filogenético e anti-sinal, respectivamente. Valores intermediários indicam aleatoriedade. Após, usamos a estatística K para quantificar o poder do sinal filogenético esperado para atributos evoluídos sob o movimento Browniano. Se K é maior que 1, então existe conservação filogenética do atributo e as espécies mais próximas evoluem mais que o esperado pelo movimento Browniano. Se K é menor que 1, então os atributos são instáveis e as espécies evoluem sob o

movimento Browniano. Mas, se K é igual a 0, diferenças nos atributos entre espécies são proporcionais ao comprimento dos ramos dentro da filogenia (Blomberg et al. 2003).

4.5 Resultados

Os valores de NRI e NTI representaram agrupamento filogenético apenas para bandos mistos de dossel, encontrados em ambientes savânicos como chaco e cerrado senso estrito, e florestais como em floresta de galeria encontrada adjacente a esses ambientes abertos (Figura 3). Quando verificadas diferenças entre diferentes tipos de vegetação e estratificação para os escores de NRI e NTI, houve diferenças significativas para Fitofisionomia (NRI: $F_{(5,392)} = 3,373$ e $P = 0,005$; NTI: $F = 3,620$ e $P = 0,003$) e Estratificação Florestal (NRI: $F_{(2,395)} = 7,283$ e $P < 0,001$; NTI: $F = 4,634$ e $P = 0,003$) (Figura 3). Para valores de fitofisionomia, NRI apresentou escores em média maiores na floresta de galeria que em floresta estacional, enquanto que para NTI foram bandos do chaco que apresentaram valores com maior agregação filogenética que a floresta estacional. Em relação à estratificação florestal, para ambos os índices houve diferença para bandos mistos de dossel (agrupamento filogenético) comparados aos bandos de sub-bosque e heterogêneos.

Quanto à estrutura funcional dos bandos mistos, houve forte agrupamento funcional dos atributos morfológicos em relação aos comportamentais (Figura 4). O atributo morfológico que apresentou maior agrupamento ao longo de diferentes ambientes foi o tamanho do bico das aves (BIC), o qual não foi significativo apenas n a região Noroeste, no Pantanal e Florestas do Oeste - Cerrado e em floresta de inundação, todos localizados na porção oeste da área de estudo, onde existem mais espécies de grande porte que nos demais locais onde BIC foi significativo (bicos menores). Os atributos tamanho corporal (TAM) e membros posteriores (TAR) foram agrupados em relação aos ambientes presentes nas fitofisionomias cerrado senso estrito e cerradão; além disso, na escala de estratificação, TAM foi agrupado somente no sub-bosque e TAR no dossel, ou seja, espécies de pequeno porte são encontradas mais no sub-bosque e as espécies de dossel possuem membros posteriores mais curtos. Entretanto, a coloração (COR) apresentou padrão distinto dos outros três atributos, com sobredispersão no cerrado senso estrito, resultado de maior presença de espécies com plumagem colorida. O índice de estratificação (EFM) foi o atributo comportamental com maior agrupamento funcional principalmente em florestas (cerradão, de galeria e estacional). Nesses ambientes mais florestais, as espécies que vivem no sub-bosque e dossel se associam

menos entre si quando comparado com ambientes mais savânicos. A frequência de ocorrência (FOP) apresentou espécies mais redundantes funcionalmente que ao acaso no chaco e floresta de inundação, além daquelas de dossel as quais se mantiveram comuns na maior parte dos bandos mistos. A dieta (DIE), por outro lado, foi mais sobredispersa na floresta de galeria, mas aleatória quanto à estratificação florestal, ou seja, mais espécies onívoras (maior diversidade de itens vegetais como grãos e frutos) que insetívoras em bandos mistos em florestas próximas a cursos de água.
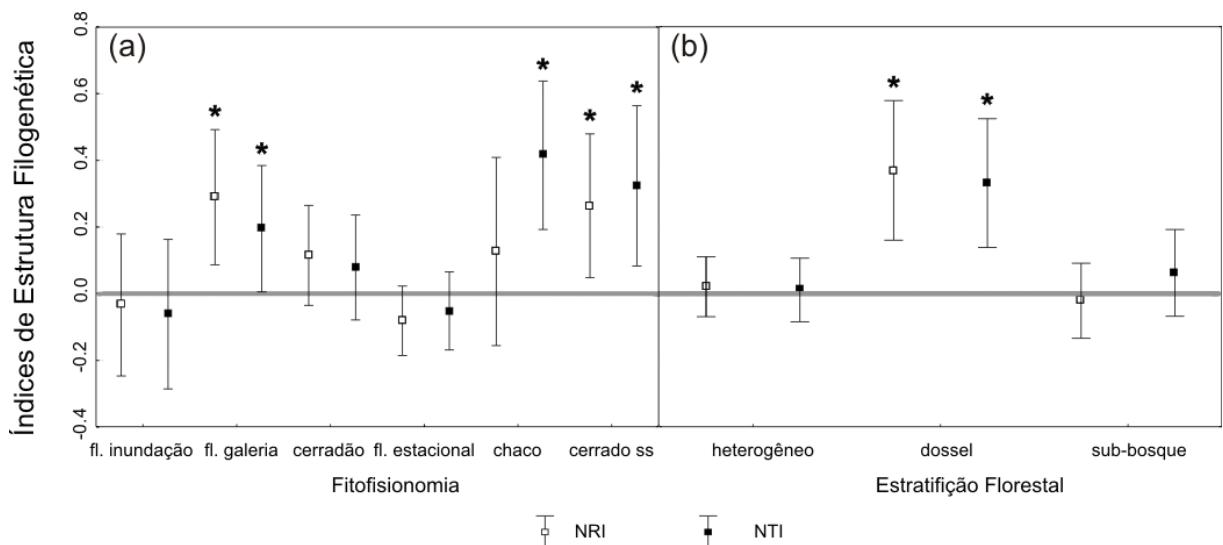
Figura 3. Estrutura filogenética dos bandos mistos indexados por NRI e NTI para Fitofisionomia (a) e Estratificação Florestal (b) representando agrupamento filogenético maior que o esperado pelo acaso (* P < 0,05) para bandos mistos de cerrado senso estrito, floresta de galeria e chaco (NTI); e dossel (NRI e NTI).
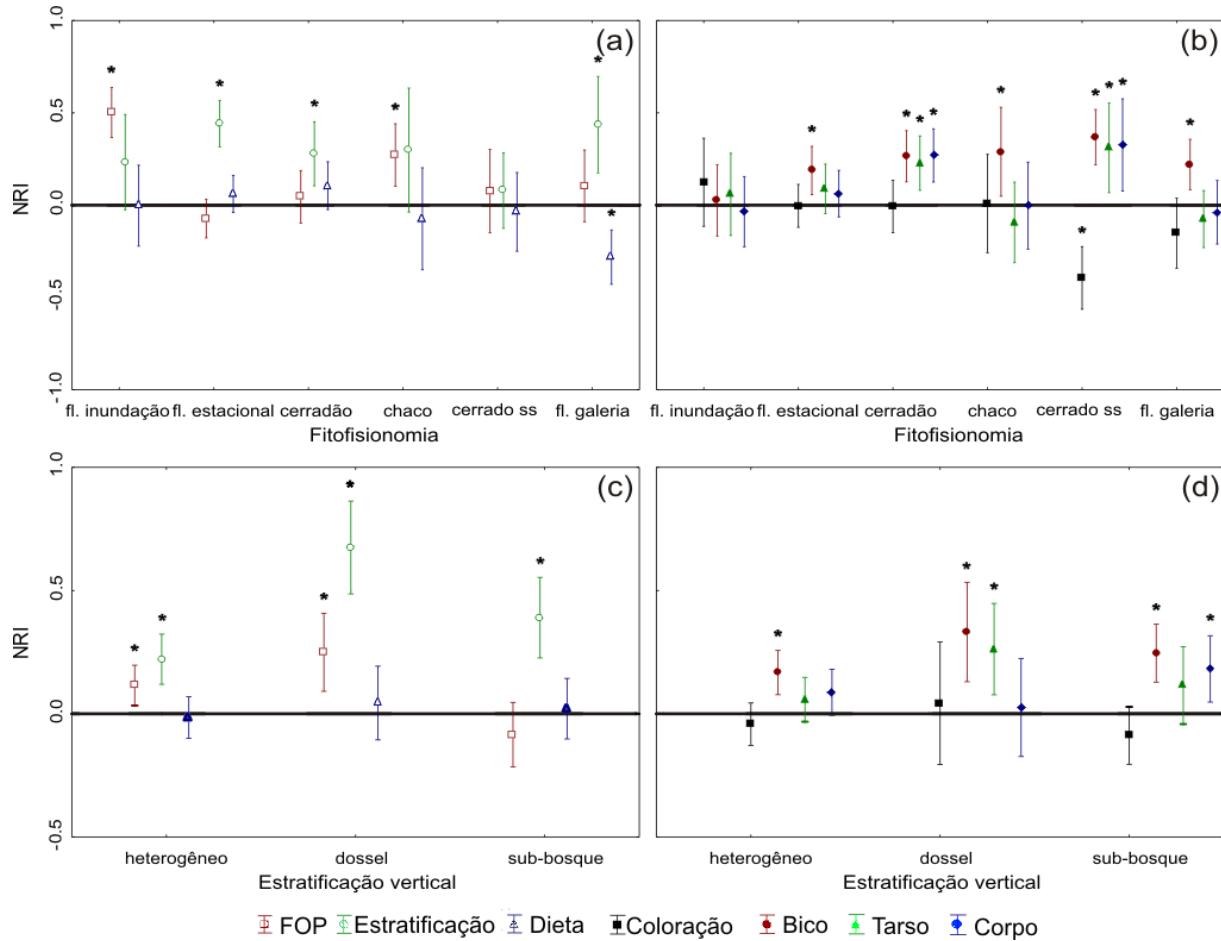
Figura 4. Estrutura funcional de sete atributos comportamentais (a,c) e morfológicos (b,d) dos bandos mistos de acordo com o índice de parentesco líquido (NRI) para Fitofisionomia (a-b) e Estratificação Florestal (c-d). Asteriscos representam significativo agrupamento ou sobredispersão funcional ($P < 0,05$) dos bandos mistos.

Os atributos morfológicos, exceto COR, apresentaram sinal filogenético significativo e conservação filogenética de nicho. COR também apresentou sinal filogenético significativo, porém foi um atributo instável com movimento browniano. Igualmente COR, EFM e DIE também apresentaram sinal filogenético e instabilidade. FOP, além de possuir instabilidade em sua evolução, também apresentou padrão aleatório, ou seja, uma possível convergência dentro do *pool* de espécies participantes dos bandos (Tabela 1).

Tabela 1. Análises de evolução dos atributos das espécies de aves participantes de bandos mistos indicando presença de sinal filogenético em atributos morfológicos e comportamentais, mas conservação filogenética somente nos atributos morfológicos. K é o valor correspondente ao poder do sinal filogenético esperado para

atributos evoluídos sob o movimento Browniano. PC: significa o primeiro componente principal de PCAs para três conjuntos de atributos morfológicos (corpo, tarso e bico); COR: coloração; EMF: estratificação florestal média; FOP: frequência de ocorrência padronizada; DIE: dieta. *Apresenta sinal filogenético significativo ($P < 0.05$).

Atributos	K	Evolução	Sinal filogenético
Morfológicos			
PC 1_{corpo}	8,201	Conservado	Sinal*
PC 1_{tarso}	1,313	Conservado	Sinal*
PC 1_{bico}	5,160	Conservado	Sinal*
COR	0,446	Instável	Sinal*
Comportamentais			
EMF	0,367	Instável	Sinal*
FOP	0,286	Instável	Aleatório
DIE	0,404	Instável	Sinal*

Os dois principais eixos de PCPS representando os escores das espécies (N = 102 eixos > 0,001) explicaram 46,1% e 26,9%, respectivamente, do total, e apresentaram a formação de três grupos distintos (Figura 5). O primeiro eixo separou o grupo formado pela subordem Passeri e do clado Tyrannida do grupo formado por "Não-passeriformes", mais os clados Furnariida, Thamnophilida e Tyrannida (Rynchocyclidae e Tyrannidae - Elaeniinae). Já o eixo 2 separou os Passeri (clado "*nine-primaried*": Fringillidae, Thraupidae de áreas abertas, Icteridae, Cardinalidae e Parulidae) dos demais Tyrannida (demais Tyrannidae, Pipridae, Cotingidae e Tityridae) e Passeri "basais" (Corvida, Troglodytidae, Donacobiidae, Polioptilidae, Mimidae e Turdidae) mais os outros *nine-primaried* (Passerilidae, os *Saltator* e os Thraupidae florestais).

Os primeiros dois eixos da PCPS dos bandos mistos (N = 166 PCPSs > 0,001) explicaram 88,51% da variação total em **P**, sendo o primeiro 80,92% e o segundo 7,59% de explicabilidade. Os demais PCPSs explicaram 11,5% da variação total e não foram usados nas análises. Não houve diferenças entre os seis tipos de vegetação para o PCPS 1 ($F_{(5, 392)} =$

1,238; P = 0,290), enquanto que no PCPS 2 houve forte separação entre floresta estacional e as duas savanas (chaco e cerrado senso estrito), e entre cerrado com cerradão e floresta de inundação ($F_{(5,392)}$ = 6,064; P < 0,001; Figura 5). Para a estratificação da floresta, houve distinção entre bandos heterogêneos e os de dossel e de sub-bosque no PCPS 1 ($F_{(2, 395)}$ = 56,262; P < 0,001), mas nenhuma diferença entre as categorias no PCPS 2 ($F_{(2, 395)}$ = 1,462; P = 0,233; Figura 6).
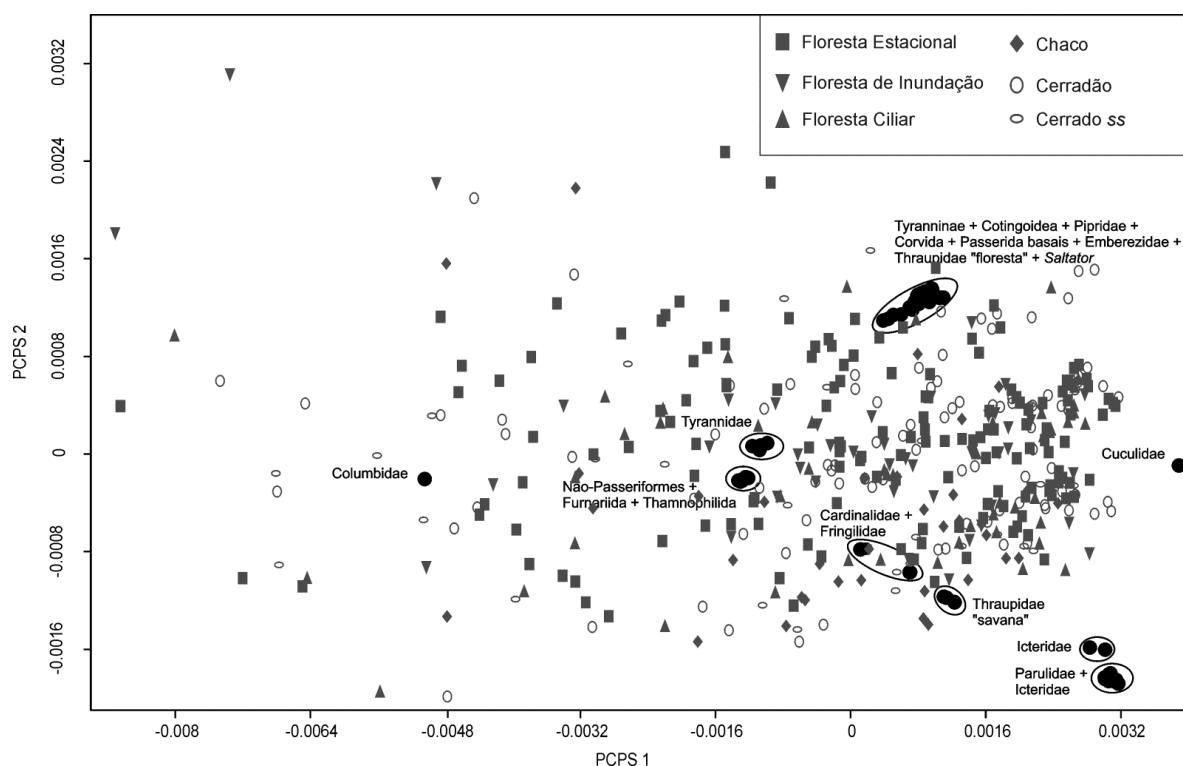
Figura 5. *Biplot* com valores das Coordenadas Principais de Estrutura Filogenética (PCPS) mostrando a ordenação das espécies de aves (círculos pretos) participantes dos bandos mistos (símbolos) representados por seis Fitofisionomias no sudoeste do Brasil. As elipses que circundam as espécies representam os principais clados de aves participantes dos bandos mistos.
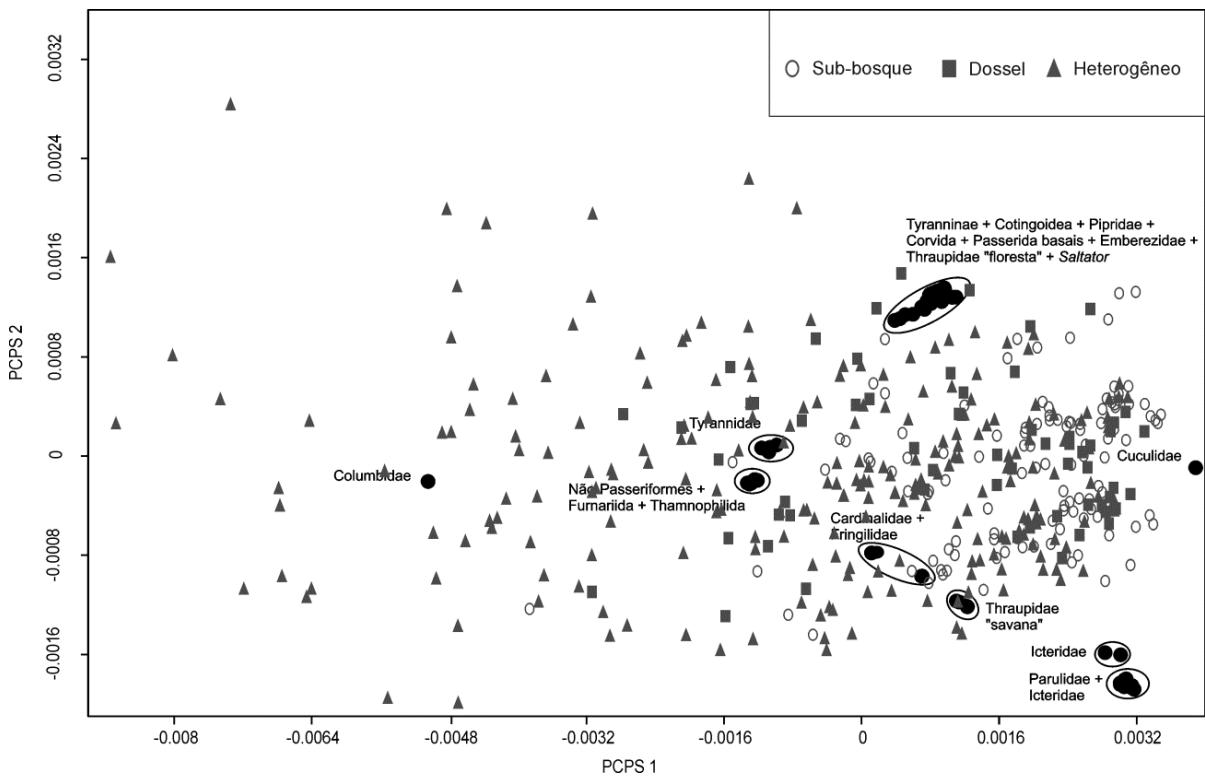
Figura 6. *Biplot* com valores das Coordenadas Principais de Estrutura Filogenética (PCPS) mostrando a ordenação das espécies de aves (círculos pretos) participantes dos bandos mistos (símbolos) representados por três níveis de Estratificação Florestal no sudoeste do Brasil. As elipses que circundam as espécies representam os principais clados de aves participantes dos bandos mistos.

4.6 Discussão

Nós encontramos mais ambientes estruturados por filtros ambientais (agrupamento filogenético ou funcional) que por facilitação (agrupamento filo-funcional) ou capacidade de dispersão (ausência de estruturação filogenética e funcional) em bandos mistos de aves. Embora nós tenhamos desenhado nossa metodologia de maneira diferente de Gómez et al. (2010) e Sridhar et al. (2012), encontramos resultados similares à ambos autores. Além disso, nem a fitofisionomia nem a estratificação apresentou bandos mistos estruturados por limitação de similaridade devido à competição (sobredispersão filogenética e funcional) na presença de atributos conservados filogeneticamente, como seria esperado em ambientes florestais onde há maior a presença de espécies próximas filogeneticamente (Graves e Gotelli 1993). Entretanto, não ficou evidente qual a regra de montagem é a mais importante na estrutura dos bandos. Três atributos morfológicos foram conservados filogeneticamente (TAM, TAR e BIC), indicando que na presença de agrupamento funcional e filogenético poderíamos prever

facilitação nos bandos encontrados nas principais vegetações relacionadas a ambientes abertos, como floresta de galeria, cerrado senso estrito e chaco, além do dossel; e na presença de agrupamento funcional apenas, a ação de filtros ambientais em florestas estacionais e em bandos redundantes quanto à morfologia no sub-bosque e estrato heterogêneo. No caso dos demais atributos, maioria comportamentais, que foram instáveis (COR, DIE, EMF e FOP), ou convergentes entre espécies não aparentadas, os filtros ambientais estariam agindo na forma de sobredispersão funcional (floresta de galeria e cerrado senso estrito), ao passo que nas espécies divergentes quanto a esses atributos, no caso de bandos mistos, haveria também facilitação (floresta de inundação).

Cabe ressaltar que para algumas fitofisionomias, chaco, floresta de galeria, floresta estacional e floresta de inundação, e os estratos sub-bosque e heterogêneo, é mais provável que os filtros ambientais e a facilitação compartilhem o papel de organização com a capacidade dispersão das espécies, principalmente devido ao baixo número de atributos com padrão aleatório de estruturação filogenética. Nesse sentido, a avaliação da distância geográfica seria pertinente principalmente devido ao efeito de ambientes ecotonais (e.g. o Pantanal), para que pudéssemos afirmar com mais clareza o papel dos filtros ambientais, da facilitação e dos processos neutros nessa escala espacial (Capítulo 2).

Embora não esteja tão claro quem são os principais regentes da estrutura filogenética e funcional dos bandos mistos, parece evidente que a facilitação predomina sobre os ambientes mais abertos e heterogêneos, enquanto que filtros ambientais agem sobre os ambientes fechados e mais complexos. Como em nossa área de estudo as florestas, principalmente as estacionais, localizam-se nos extremos noroeste (Floresta Chiquitana) e leste (Floresta Atlântica), pode ser que se tenha um papel mais forte dos filtros ambientais; enquanto que no centro, principalmente savanas (Chaco, Pantanal e Cerrado), a facilitação é responsável pela organização dos bandos. Nesse sentido, temos que, por exemplo, as espécies mais granívoras e frugívoras, junto com aquelas menos camufladas, são mais comuns onde a facilitação predomina.

A estrutura filogenética dos bandos mistos se comporta de acordo com os diferentes ambientes em que se encontram e das diferentes espécies que os compõem. Em geral, os bandos mistos tenderam a ter espécies mais insetívoras (Não-Passeriformes e Tyranni basais), que utilizam bandos heterogênios, padrões similares ao encontrado para Floresta Atlântica (Aleixo 1999, Maldonado-Coelho e Marini 2003), e se adaptam a diversos tipos de fitofisionomia (plasticidade fenotípica; West-Eberhard 1989) através de inúmeras subespécies presentes ao longo das ecorregiões amostradas (e.g., *Sittasomus g. griseicapillus*, *Basileuterus*

culicivorus hypoleucus e *Cyclarhis gujanensis cearenses* no Cerrado, e *S. g. sylviellus*, *B. c. auricapilla* e *C. g. ochrocephala* na Floresta Atlântica). O grupo formado pelas espécies pertencentes a ordens mais basais no PCPS 1 apresenta as características citadas acima, diferentemente do resto dos Passeriformes mais derivados, onde os participantes tendem a ser mais especialistas a algum tipo de ambiente e dieta (Morton 1973, Alves 1991, Piratelli e Pereira 2002, Brum et al. 2012). Nesse caminho, existem bandos mistos compostos de espécies mais especialistas em certos tipos de ambientes. Fazem parte desses bandos os Passeri e maior parte dos Tyrannida. Os primeiros são, em geral, adaptados a ambientes mais abertos (savanas do Chaco, Pantanal e Cerrado), enquanto os Tyrannida são fortemente silvícolas (Floresta Atlântica e Floresta Chiquitana). Embora exista diferença para NRI e NTI entre bandos de dossel e demais estratos da floresta, algo não observado nos dois primeiros PCPSs, é provável que essa diferença ocorra dentro dos Passeri basais e Tyrannida derivados. Nesses dois grupos, a maior parte das espécies ocorre no dossel, como por exemplo, os Cotingidae, Tityridae e Tyranninae (Tyrannida) e o grupo formado pelos gêneros *Dacnis*, *Conirostrum*, *Tangara* e *Hemithraupis* (Thraupidae). Desse modo, temos que os filtros ambientais podem estar agindo mais sobre as espécies do grupo Não-passeriformes, Furnariida e Thamnophilida que nos demais Passeriformes, que seriam regidos por facilitação, além de serem amplamente distribuídos na maior parte das localidades e comporem as principais espécies formadoras dos bandos mistos na área de estudo (Capítulo 1).

Nosso estudo aborda o quanto que diferentes escalas ambientais são estruturadas e montadas de acordo com o grau de parentesco e funcionalidade das espécies formadoras de bandos mistos. De maneira geral, os atributos morfológicos são conservados ao longo da evolução das espécies participantes, ao passo que os atributos comportamentais são lábeis ou instáveis (Scheuerlein e Ricklefs 2004), corroborando como que geralmente é observado em atributos altamente mutáveis regionalmente ao longo de diferentes populações (Blomberg et al. 2003) como o caso da participação de espécies em bandos mistos (FOP). Além do mais, nossos resultados ajudam a compreender quais mecanismos de montagem dos bandos mistos são responsáveis pelos padrões de agrupamento filogenético e funcional encontrado ao longo de diferentes níveis de estrutura das comunidades.

Deixamos claro aqui que a competição, como interação negativa, não influencia na organização tanto funcional quanto filogenética dos bandos como prediz a teoria clássica de montagem filogenética de comunidades (Cavender-Bares et al. 2009). Além disso, a facilitação e os filtros ambientais atuam em diferentes escalas ambientais e, portanto, não devem ser subestimadas pelo menos quando houver interação positiva entre espécies (Sridhar

et al. 2012) e fortes diferenças ambientais (Gianuca et al. 2013). De fato, tanto as diferentes fitofisionomias e os estratos da floresta compõem distintas condições para as espécies participantes dos bandos mistos, mas isso não quer dizer que processos neutros, como a deriva genética, seleção aleatória ou capacidade de dispersão (Hubbell 2001), não possuam porcentagem de explicação na organização das espécies participantes. Um próximo passo, portanto, será testar se variáveis espaciais e ambientais junto com a filogenia e os atributos estão jogando positiva ou negativamente no padrão de associação de bandos mistos nessas escalas ambientais.

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4.7 Material suplementar
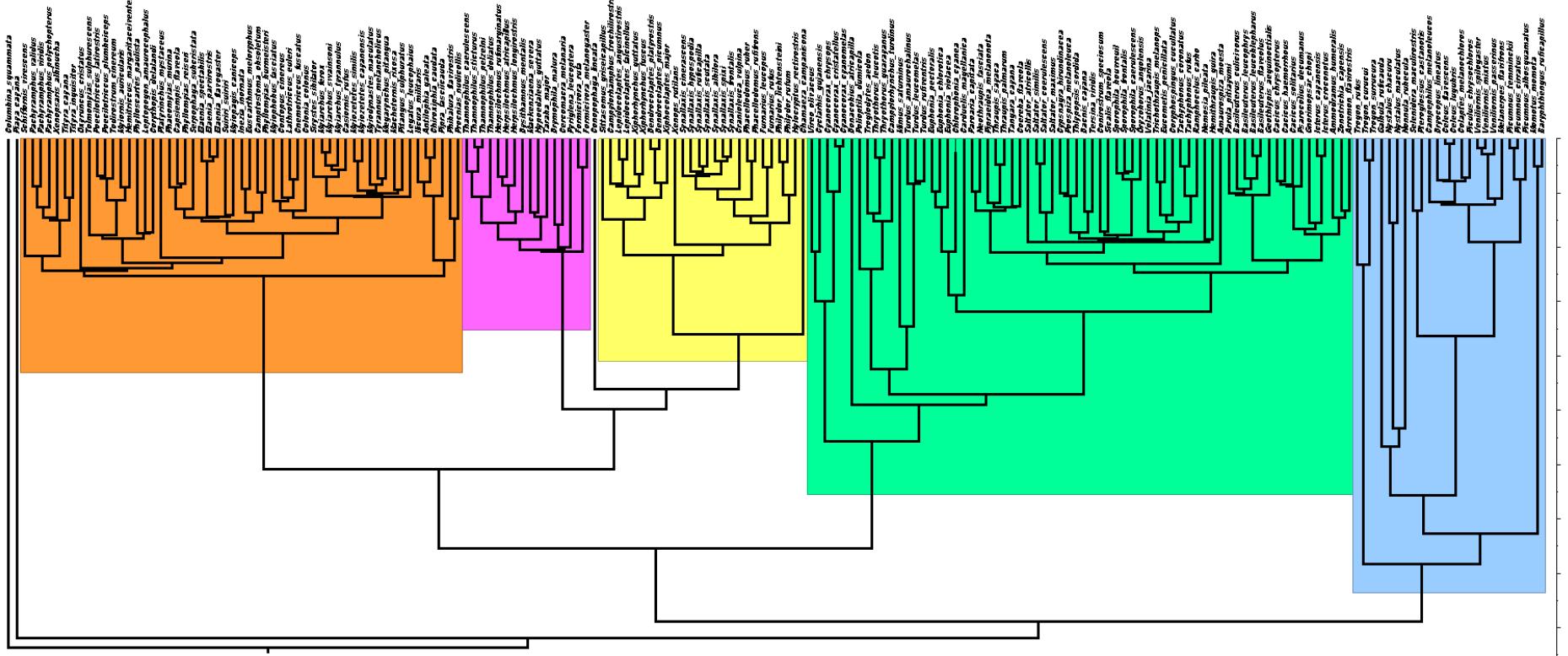
Material suplementar 1. Árvore filogenética do *pool* de espécies de aves participantes dos bandos mistos na região sudoeste do Brasil. "Não-Passeriformes" – Ordens Columbiformes, Cuculiformes (à esquerda e sem coloração), Trogoniformes, Coraciiformes, Galbuliformes e Piciformes (azul), Ordem Passeriformes – subordem Tyrannii: Tyrannida (laranja), Thamnophilida (lilás) e Furnariida (amarelo), Passeriformes – subordem Passeri (verde).

DISCUSSÃO

Os quatro artigos apresentados nesta tese abordam como que as espécies que participam de bandos mistos de aves co-ocorrem juntas, se relacionam positivamente, interagem ao longo de gradientes ambientais e se alternam de acordo com filtros do habitat ou por barreiras espaciais. A existência de grupos de espécies que co-ocorrem juntas, geralmente com mesmas características morfológicas e comportamentais fortalece a ideia que relações positivas causadas por facilitação moldam a estrutura de comunidades e podem transformar seus nichos quando na presença de outras espécies (SRIDHAR ET AL., 2012). Espécies que vivem em ambientes mais estáveis como os florestais apresentam maior agregação entre as espécies. Isso pode ser expandido também para as interações par a par, principalemte entre as espécies seguidoras dos bandos. Essas espécies dependem muito mais em viver nos bandos mistos para sobreviver que aquelas espécies que vivem em grupos familiares ou possuem sistemas de alarme bem desenvolvidos para sinalizar contra predadores (espécies nucleares). Essas espécies seguidoras foram as que apresentaram maior labilidade dos atributos ao longo da filogenia, demostrando que certros atributos como a coloração (COR) e a frequência de ocorrência (FOP) surgiram mais de uma vez na história das aves participantes. Pode-se inferir, portanto, que essas relações entre espécies podem ter aparecido a bastante tempo tendo por base que existem ordens e famílias distantes entre si por milhões de anos de evolução mas que conservam os mesmos atributos funcionais (e.g., COR e EMF são similares em Piciformes e Furnariida).

Em ambientes mais dinâmicos, que sofrem mudanças ambientais sazonalmente, ou que nunca atingem um estágio clímax, apresentam mais espécies nucleadoras, geralmente mais coloridas e com dieta menos insetívora que aquelas espécies seguidoras de bandos (SRIDHAR ET AL., 2009). Nesse sentido, observa-se que em cerrado senso estrito, chaco e florestas de inundação dos rios Paraná e Paraguai há em média menor agregação de pares de espécies quando comparado com outros tipos de floresta. Ainda nesses locais, percebe-se maior ação da facilitação que dos filtros ambientais devido a heterogeneidade desses ambientes e a capacidade de espéceis florestais participarem juntamente com as típicas de savana, algo que não ocorre com tanta frequência nas áreas florestais.

Partindo do que ocorre em escalas mais finas, pode-se compreender melhor o que ocorre na escala regional quando se avalia a diversidade beta das comunidades participantes dos bandos. Nessa escala, a maioria das áreas amostradas apresentou mais de um tipo de

vegetação, demonstrando que essa porção do Brasil e da América do Sul compreende um grande ecótono e por que não dizer, uma ecorregião a parte, formada principalmente por florestas secas (cerradão) e semi-úmidas (estacionais), as quais apresentam espécies com livre distribuição no sentido leste-oeste. Essas florestas apresentam espécies mais floresta-dependentes adaptadas ao sub-bosque e as de dossel relacionadas às savanas e florestas de galeria. Embora existam espécies comuns encontradas nesses gradientes florestais e savânicos, existem muitas espécies raras que são encontradas em poucos sítios, ou que apresentam baixa participação em bandos mistos. Essas espécies raras diminuem o poder de aninhamento das comunidades até mesmo onde não é ecótono como o Cerrado e a Floresta Atlântica, que se esperaria menor substituição de espécies. Essas ecorregiões apresentam uma grande diversidade de Passeriformes quando comparado com o Pantanal e Chaco, a oeste (STOTZ ET AL., 1996), ambientes muito secos durante o período que foi realizado as amostragens.

CONCLUSÃO

Esse estudo de bandos mistos de aves em gradiente floresta-savana abordando sua estrutura composicional, filogenética e funcional., além dos efeitos do espaço e dos filtros ambientais sobre a diversidade beta e seus componentes, substituição e aninhamento, apresenta informações que vem complementar estudos recentes sobre processos ecológicos que atuam na estrutura dos bandos mistos (GRAVES & GOTELLI, 1993; GÓMEZ ET AL., 2010; SRIDHAR ET AL., 2012). Portanto, as conclusões apresentadas a seguir vêm contribuir com a lacuna de conhecimento que existe entre a ecologia de comunidades e a ecologia comportamental dos bandos mistos. Além disso, levanta a questão do porquê que a maioria dos estudos em ecologia de comunidades não levam em conta a facilitação como regra de montagem das comunidades, tendo em vista as interações positivas como o comensalismo e o mutualismo.

Em termos de composição de espécies, os bandos mistos apresentam-se de diferentes formas ao longo dos gradientes de vegetação. A princípio, pelo menos três, senão quatro, grupos de bandos mistos são observados, e eles variam em tamanho comporal, estratificação florestal e tipo de vegetação. Essas diferenças de composição e estrutura ao longo das fitofisionomias acaba sendo observado nas relações entre espécies, as quais são mais agregadas em ambientes florestais que em ambientes savânicos. Em termos de comportamento das espécies nucleadoras e as demais seguidoras dos bandos, existem mais associações fortes de coexistência entre as espécies seguidoras que as nucleadoras entre si ou com estas. Esse resultado demonstra que o comensalismo em bandos mistos, ou seja, as espécies seguidoras seguirem as líderes em troca de proteção ou acréscimo de alimento, é menor que o mutualismo entre as espécies seguidoras, as quais não apresentam características de líderes pois não se comportam como sentinelas ou vivem em grupos familiares.

O espaço geográfico foi o componente mais importante na estruturação dos bandos mistos de aves tanto para tipos de bandos (sub-bosque, heterogêneos e dossel) quanto para tipos de vegetação (Ceradão, Floresta Ripária e Estacional Semidecídua). O componente de substituição espacial dos bandos de sub-bosque, heterogêneos, de florestas Ripária e Semideciduais foi relacionado positivamente com a distância geográfica, enquanto a dissimilaridade de bandos heterogêneos foi positivamente relacionada com gradiente de temperatura e precipitação. No entanto, os bandos de sub-bosque apresentaram relação negativa com classes de distância superior a 400 km sugerindo uma similaridade de espécies de acordo com os tipos de floresta, e apoiando a teoria de nicho. Os padrões observados de

beta diversidade de bandos mistos de aves sugerem ambos os processos neutros e baseados em nichos impulsionadas pela capacidade de dispersão e filtragem determinista das espécies em diferentes gradientes espaciais e ambientais.

Filtros ambientais e facilitação são os responsáveis pela organização dos bandos mistos de aves. Filtros atuam mais em ambientes florestais, onde os atributos morfológicos são mais conservados filogeneticamente e as espécies participantes são não-Passeriformes e Passeriformes basais (insetívoros); enquanto que a facilitação atua em ambientes savânicos onde os atributos comportamentais são mais lábeis e sem estrutura aleatória (agrupamento ou sobredispersão funcional), e as espécies formadoras dos bandos são Passeriformes derivados que vivem no dossel da floresta, são onívoros e representam os clados Tyrannida e Passeri. Nenhuma das duas escalas ambientais apresentou bandos mistos estruturados por limitação de similaridade devido à competição (sobredispersão filogenética e funcional) na presença de atributos conservados filogeneticamente.

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