Composition and dynamics of mixed flocks of birds in a remnant of Submontane Atlantic Rain Forest in southern Brazil

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Abstract. Mixed flocks are associations of two or more species that are formed and maintained through mutual behavioral responses, with advantages such as maximizing foraging and protecting against predation. This study aimed to evaluate the composition, temporal dynamics, and presence of core species in mixed flocks of birds in a remnant of the Submontane Atlantic Rain Forest in the Parque Nacional Aparados da Serra, southern Santa Catarina state, Brazil. Data collection took place from October 2016 to September 2017 through monthly campaigns, consisting of three consecutive observation days, with sampling sessions of six hours per day, resulting in a total effort of 216 h of observations. For each contact with the flocks, we recorded the species and number of individuals, stratum of occurrence, substrates of search, and agonistic interactions. We recorded 152 mixed flocks, with a total of 76 species belonging to 24 families, and five orders, with Thraupidae, Tyrannidae, Furnariidae, and Rhynchocyclidae being the richest. The flocks had an average of 4.5 ± 2.7 species and 8.7 ± 5.8 individuals, with richness and the number of individuals being positively correlated ($R^2 = 0.8$). Mixed flocks occurred throughout the year. There was a great variation in the number of contacts from October to February (from 5 to 20 contacts). Meanwhile from March to September, the coldest period of the year in the region, the number of contacts did not vary (from 9 to 14 contacts). However, there was no difference in the number of contacts between these months ($z = 0.37$; $p = 0.691$). *Basileuterus culicivorus* and *Habia rubica* were the core species because, in addition to their high participation (46.7 and 32.9%, respectively), they showed frequent and conspicuous movement and vocalization. Thus, a high capacity to enlist a greater number of individuals from different species for the flocks was demonstrated.

Keywords. Passeriformes; Heterospecific associations; Core species; Ombrophilous Dense Forest; PARNA Aparados da Serra.

INTRODUCTION

Individuals of multiple bird species can associate by forming mixed flocks, maintained by mutual behavioral responses (Moynihan, 1962; Machado, 1999). The evolution of this behavior is related to the advantages of maximizing foraging and protection against predation (Moynihan, 1962; Powell, 1985; Alves & Cavalcanti, 1996; Machado & Rodrigues, 2000). Although mixed flocks occur frequently in tropical forests (Powell, 1985; Develey, 2001; Mangini & Areta, 2018), their composition, structure, and temporal dynamics remain poorly understood.

The composition, size, and frequency of occurrence (FO) of mixed flocks is influenced by multiple factors, including the drop in the participation of species during reproductive periods, variations in the availability of food resources, and presence of migratory species (Alves & Cavalcanti, 1996; Machado, 1999; Develey & Peres, 2000). These factors are generally associated with climatic variation (Machado, 1999; Develey & Peres, 2000; Maldonado-Coelho & Marini, 2003; Mangini & Areta, 2018). In addition, other factors, such as habitat loss and fragmentation, edge effects, and successional vegetation stage, can also influence the composition and dynamics of mixed flocks in forest environments (Aleixo, 2001; Marini & Garcia, 2005).

Species associated with mixed flocks present different patterns of interaction and can be categorized into core and assistant species (Powell, 1985). Core species have a high frequency of participation and conspicuous patterns of movement

and vocalization that stimulate the formation and cohesion of the flock (Develey, 2001). Meanwhile, the assistant species have a secondary role in the flock and can be divided into regular or occasional participants, depending on the frequency of interaction (Moynihan, 1962).

Although mixed flocks of birds occur in almost all vegetation types, they are far more common in Neotropical forests (Powell, 1985). In Brazil, mixed flocks have been studied extensively in the Atlantic Forest and Amazon biomes, where more than 40% of birds participate in these associations, including species considered endemic and/or threatened (Machado, 1999; Develey & Peres, 2000; Brandt *et al.*, 2009). Despite high environmental degradation, the frequency of mixed flocks in the Atlantic Rain Forest is still high (Aleixo, 1997; Machado, 1999; Develey & Peres, 2000; Brandt *et al.*, 2009; Batista *et al.*, 2013). This biome is considered one of the most biodiverse and threatened ecosystems on the planet (Myers *et al.*, 2000) and is among the 36 global biodiversity hotspots (Merritt *et al.*, 2019). In this way, deforestation and loss of species not only represent the loss of taxonomic diversity but also the loss of interspecific interactions in which these species are involved.

Studies on the composition and dynamics of heterospecific mixed flocks are vital for understanding the autoecology of the participating species, as they contribute to filling knowledge gaps in tropical environments.

Moreover, they are essential for defining biodiversity conservation strategies in fragmented landscapes remaining in tropical forests (Develey & Peres, 2000; Maldonado-Coelho & Marini, 2003; Batista *et al.*, 2013).

In this study, we evaluated the composition, temporal dynamics, and presence of core species in mixed flocks of birds in a remnant of the Submontane Atlantic Rain Forest in the Parque Nacional Aparados da Serra, southern Santa Catarina state, Brazil. To the best of our knowledge, there are no previous studies on mixed flocks of birds in this region, and thus, the species involved in these associations, their structure, and their temporal dynamics remain unknown.

MATERIAL AND METHODS

The present study was carried out in the Parque Nacional Aparados da Serra (29°12'18.92"S and 50°3'22.81"W), municipality of Praia Grande, south of Santa Catarina state, southern Brazil (Fig. 1). The Parque Nacional Aparados da Serra is a protected area that covers 130,606 km², extending within the municipalities of Cambará do Sul in the Rio Grande do Sul state and Praia Grande in the Santa Catarina state (IBAMA-MMA, 2004).

The altitude of the study area ranges between 200 and 350 m above sea level (IBAMA-MMA, 2004). The
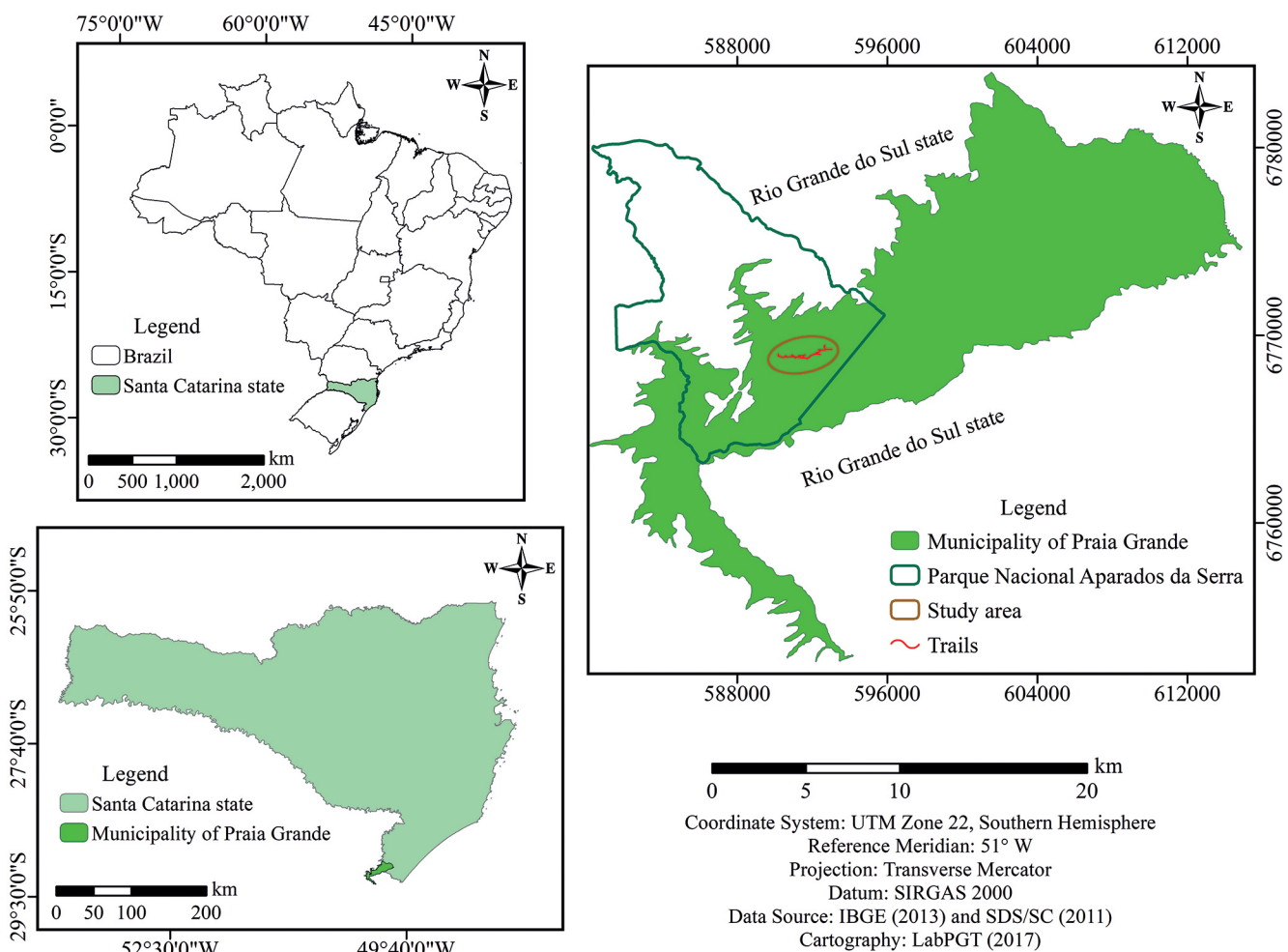

Figure 1. Location of the study area in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil.

Köppen climate classification is Cfa (humid subtropical, without a dry season, and hot summers), with a mean annual temperature of 19.0°C. However, the study area is also influenced by the Köppen climate Cfb (humid subtropical, without a dry season, and temperate summers), with an annual average temperature of 16.0°C (Alvares *et al.,* 2014). The mean temperature in the coldest periods (June-August) ranges close to 7.2°C and the annual rainfall ranges from 1,220 to 1,660 mm, with an annual total of 102-150 rainy days (EPAGRI, 2001).

The study area was covered by a Submontane Atlantic Rain Forest (IBAMA-MMA, 2004; IBGE, 2012) (Fig. 2A). The vegetation was in the secondary successional stage of regeneration, predominantly in the early and medium stages, where the canopy varies from 6-15 m in height from the ground (Fig. 2B). The understory is denser along the forest border, where Melastomataceae, Rubiaceae, Poaceae, and several pteridophytes predominate (Fig. 2D), and less dense inside the forest (Fig. 2C), where numerous lianas and epiphytes, especially bromeliads of the genus *Vriesea* persist (Fig. 2E).

Data on the detection of mixed flocks were collected between October 2016 and September 2017 in 12 monthly campaigns over three consecutive days. Sampling was carried out along a main trail of three kilometers, containing perpendicular trails ranging from 200 to 300 m (Fig. 3), covering inland environments and edges of the Submontane Forest. The group formed by the main and secondary trails was divided into three sectors (Fig. 3). Each sector was sampled in one day during sampling sessions of six hours each; 60% in the morning, starting after sunrise, and the remainder in the afternoon, ending before dusk (Machado, 1999 adapted), totaling 216 h of data collection (36 d).

Mixed flocks were detected through visual observations, aided by binoculars (8 × 42), contact calls, and aural records. Mixed flocks were defined as the association of two or more individuals of at least two distinct species following each other along the same route for a minimum period of five minutes while looking for food (Stotz, 1993). Due to difficulties in access and movement in the area, because of the slope of the terrain and the dense understory, some groups were followed in the direction of displacement only when they moved close to the trails, as suggested by Machado (1999).

Per the recommendations from Machado (1999), when in contact with a mixed flock, we recorded the time and contact time (start and end time, with a maximum observation time of 15 min), species observed, number of individuals of each species, type of record (visual or aural), and stratum of occurrence (understory or canopy) occupied by each species. When possible, search substrates (soil, litter, trunks, branches, leaves, flowers, and air), types of food items consumed (arthropods, fruits, seeds, buds, leaves, nectar, and flowers), and agonistic interactions (physical aggression and flight chase) were recorded, as suggested by Fitzpatrick (1980). Taxonomic nomenclature followed the proposition adopted by the Brazilian Committee of Ornithological Records (Pacheco *et al.,* 2021).

The FO of a species in mixed flocks was defined as the proportion of flocks in which it was present among the total registered flocks. The species were then classified into the following categories: regular (FO ≥ 25%), common (10 ≤ FO ≤ 24.9%), unusual (3.0 ≤ FO ≤ 9.9%), and rare species (FO ≤ 2.9%) (Machado, 1999).

The relationship between species richness and the number of individuals in mixed flocks was assessed using simple linear regression. To analyze the temporal variation in the frequency of mixed flocks per campaign (number of contacts), size of the flocks (number of individuals), and richness of the flocks throughout the year, the Rayleigh test (Z) was used, with a significance level of 0.05, calculated using the Oriana software, version 4.3 (Kovach, 2011).

To determine which of the recorded species acted as core species, the performance of each species in the formation and maintenance of the cohesion of the flocks was evaluated. In this case, the requirements proposed by Powell (1985) and Machado (1999) were considered: (1) neutral color patterns (*e.g.,* olive, yellow, brown, black, and without spots) – these are considered less aggressive plumes which potentially facilitate interspecific association; (2) movement – species that move during foraging cause local disturbances that attract other individuals to the flock; (3) vocalization – species that vocalize strongly during foraging reinforce the attraction and keep individuals cohesive to the flock; (4) FO in flocks – core species participate with a high frequency in mixed flocks; (5) size of the intraspecific group within the flock – quantitative data that measures the natural tendency to gregariousness of the core species (s) in the flocks; and (6) the size of the interspecific group – the total number of individuals in the mixed flock. Species were selected if they met at least four of the six requirements listed above. Next, we used a Student's t-test, with a significance level of 0.05, calculated using the PAST 3.25 software (Hammer *et al.,* 2001), to assess whether mixed flocks are richer in the number of species due to the presence of the core species when they are aggregated or solitary among the mixed flocks. Data are presented as mean ± standard deviation (SD).

RESULTS

We recorded 152 mixed flocks, with 76 participating species belonging to five orders and 24 families. Passeriformes (n = 68 species) had the highest richness, mostly represented by the families Thraupidae (n = 15), Tyrannidae (n = 8), Furnariidae (n = 6), and Rhynchocyclidae (n = 6). Cuculiformes and Apodiformes were recorded in only one species each, Trogoniformes in two, and Piciformes in four (Table 1).

The mixed flocks comprised a mean 4.5 ± 2.7 species, with a minimum of 2 and a maximum of 14 species, while the mean number of individuals was 8.7 ± 5.8, ranging between 2 and 31. Flocks with a greater number of individuals had greater species richness ($R^2 = 0.83\%$; $p < 0.05$; $df = 151$; Fig. 4). Regarding the FO, only three species were classified as regular: *Basileuterus culicivorus*

(FO = 46.7%), *Habia rubica* (FO = 32.9%), and *Sittasomus griseicapillus* (FO = 25.7%), representing 3.9% of the total richness. Common species (n = 10 spp.) accounted for 13.1% of the species richness, whereas unusual species (n = 20 spp.) accounted for 26.3%. The remaining 43 species (56.5% of total richness) were rare (Table 1).

Six events of agonistic behavior between species were observed. Of these, three intraspecific species, including
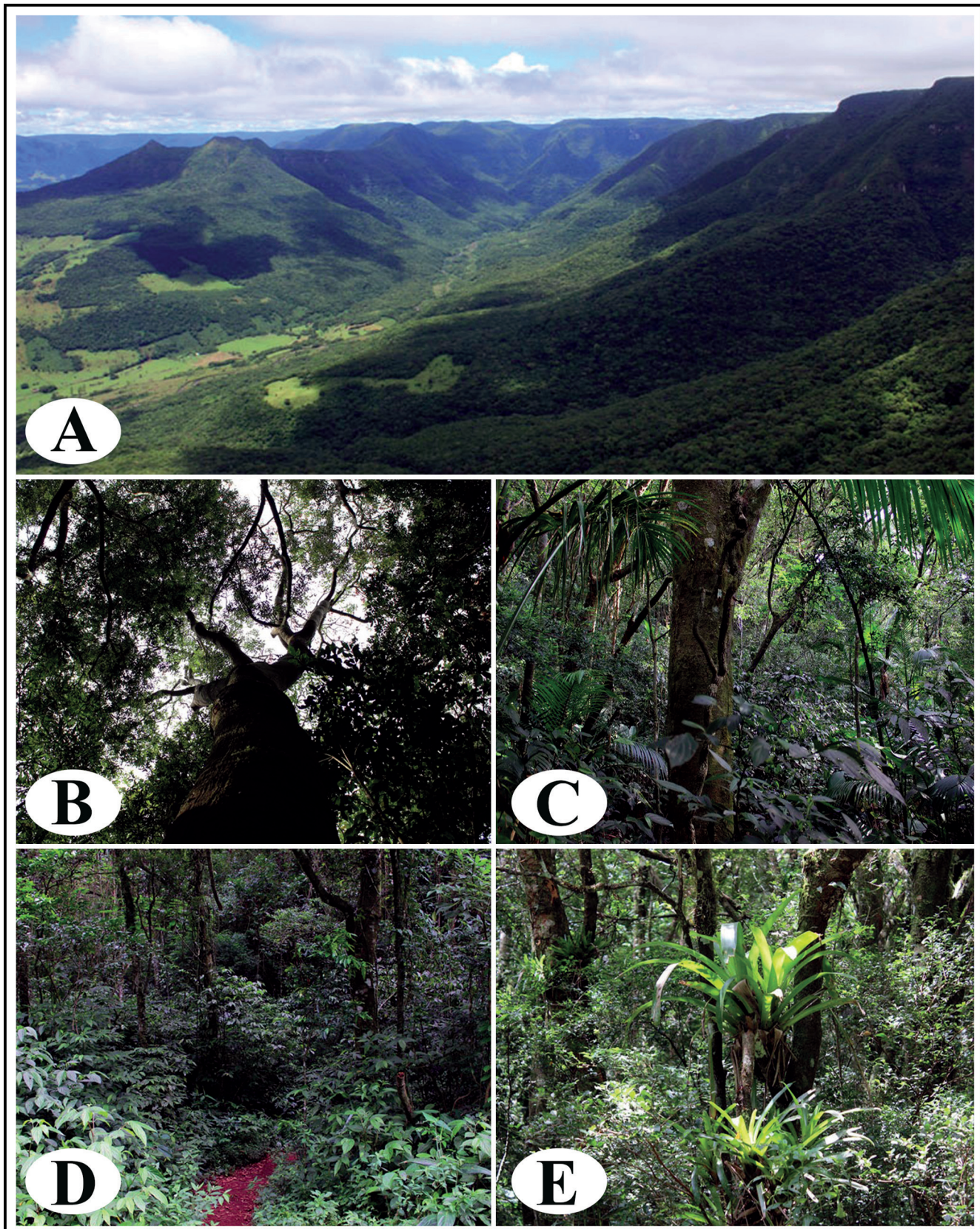

Figure 2. (A-E) Images of Atlantic Rain Forest in the lower part Sif Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil. (A) overview of Submontane Atlantic Rain Forest; (B) detail of canopy height; (C) detail of the understory within the forest; (D) detail of understory at the forest edge; (E) presence of lianas and bromeliads in the understory within the forest.
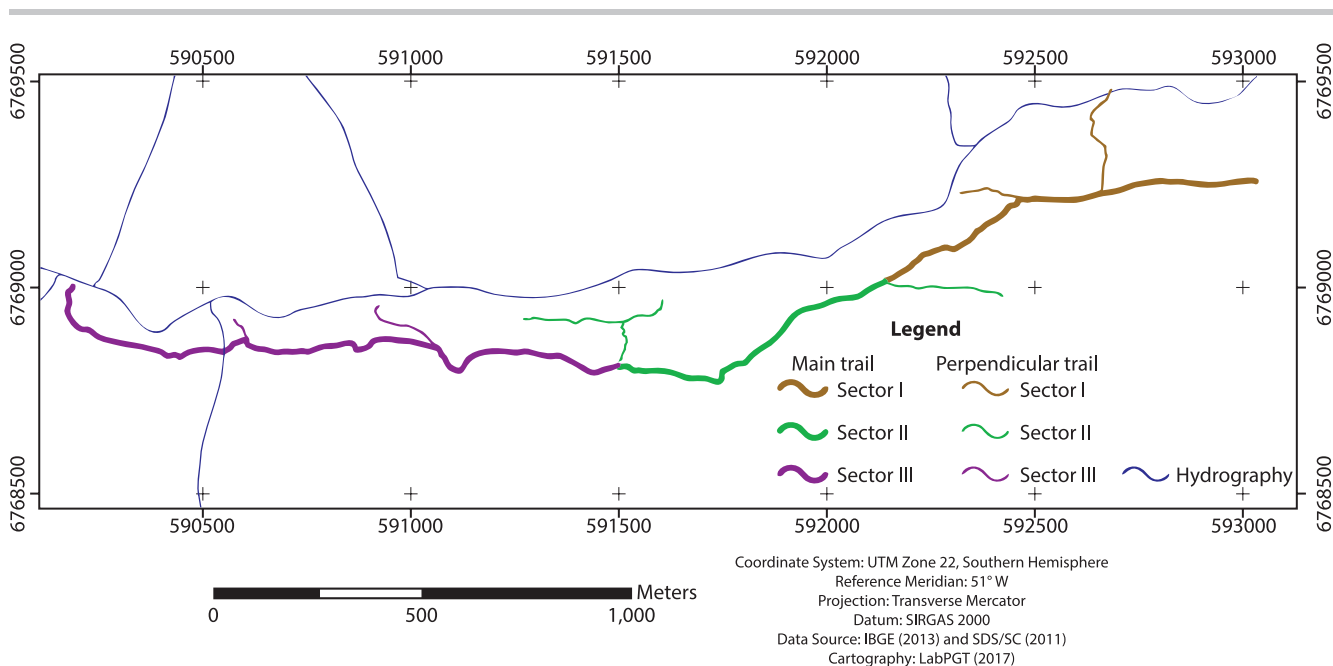
Figure 3. Distribution of the three sampling sectors (I, II, and III) in the study area, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil.
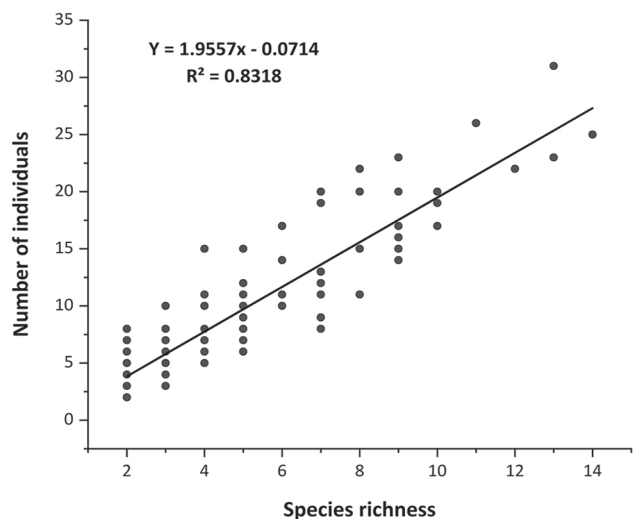

Figure 4. Simple linear regression of the relationship between species richness and the number of individuals from mixed flocks of birds, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil, between October 2016 and September 2017.

H. rubica (two events) and *Turdus subalaris* (one event), and three interspecific species, including *Lathrotriccus euleri* (two events), one against *Myiothlypis leucoblephara,* the other against *Platyrinchus mystaceus,* and finally, *Turdus albicollis* against an individual of *Turdus rufiventris,* who was not part of the flock.

Mixed flocks occurred throughout the year, with variations in their frequencies. From October to February, a greater number of flocks were detected with a wide fluctuation in the number of contacts in October (n = 17), November (n = 12), December (n = 5), January (n = 20), and February (n = 18). Between March and September, fewer flocks were detected with less variation; March (n = 9), April (n = 14), May (n = 11), June (n = 12), July (n = 14), and August and September (n = 10, each). There were no differences observed in the number of contacts

between months (z = 0.369; *p* = 0.691); therefore, no peak was observed (Fig. 5).

The average species richness in the mixed flocks (4.5 ± 2.7 species) did not differ throughout the year (z = 0.005; p = 0.995; Fig. 6), and there was no difference in the average number of individuals per flock (z = 0.572; p = 0.564; Fig. 7).

Among the 76 species participating in the mixed flocks, *B. culicivorus* and *H. rubica* had the highest frequency of participation (Table 1) and presented physical and behavioral characteristics that allowed them to be classified as core species (Table 2). *Basileuterus culicivorus* was the most frequent species in the flocks (Table 1) and generally occurred at a frequency of two to four individuals, always exhibiting intense movement and strong vocalization. These individuals were present from the understory to the canopy and used different substrates, such as thin trunks, branches, and leaves, to forage for arthropods, seeds, insects, and small larvae. In addition, individuals of this species have been observed alone on a few occasions and are most commonly seen in pairs or in small monospecific flocks. *Habia rubica,* in turn, was the second most frequent species in the mixed flocks, always occurring in the understory and represented by groups of two to eight members (Table 1). Usually, *H. rubica* forages along branches, trunks, and leaves, where it preys upon small arthropods, insects, and larvae. The mixed flocks in which *B. culicivorus* and *H. rubica* occurred (n = 95) were richer (4.9 ± 2.8 species) than in those (n = 57) where they did not occur (3.6 ± 2.2 species; t = 2.845; *p* = 0.005).

DISCUSSION

The species richness recorded in the present study (76 species) was similar to that found in the Southeast Atlantic Rain Forest by Davis (1946), Develey & Peres

Table 1. Bird species participating in mixed flocks, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil, between October 2016 and September 2017. Frequency of occurrence of species in the mixed flocks (FO, %). Categories of frequency of occurrence of species (FC): Regular (RE) FO ≥ 25.0%, Common (COM) 10.0 ≤ FO ≤ 24.99%, Unusual (U) 3.0 ≤ FO ≤ 9.99%, and Rare (RA) FO ≤ 2.99%. Foraging stratum (FS): Understory (Und) and Canopy (Can).

Taxa	Range of Number of Individuals in the Flocks	Number of Contacts	FO (%)	FC	FS
Cuculiformes Wagler, 1830					
Cuculidae Leach, 1820					
Piaya cayana (Linnaeus, 1766)	1	3	2.0	RA	Und, Can
Apodiformes Peters, 1940					
Trochilidae Vigors, 1825					
Thalurania glaucopis (Gmelin, 1788)	1	1	0.7	RA	Und
Trogoniformes A.O.U., 1886					
Trogonidae Lesson, 1828					
Trogon surrucura Vieillot, 1817	1-2	4	2.6	RA	Und, Can
Trogon chrysochloros Pelzeln, 1856	1	1	0.7	RA	Und
Piciformes Meyer & Wolf, 1810					
Picidae Leach, 1820					
Picumnus temminckii Lafresnaye, 1845	1	3	2.0	RA	Und, Can
Veniliornis spilogaster (Wagler, 1827)	1-2	8	5.3	U	Und
Celeus flavescens (Gmelin, 1788)	2	1	0.7	RA	Und
Piculus aurulentus (Temminck, 1821)	1-2	6	3.9	U	Und, Can
Passeriformes Linnaeus, 1758					
Thamnophilidae Swainson, 1824					
Rhopias gularis (Spix, 1825)	2-4	3	2.0	RA	Und
Dysithamnus mentalis (Temminck, 1823)	1-4	28	18.4	COM	Und, Can
Thamnophilus caerulescens Vieillot, 1816	1-2	4	2.6	RA	Und
Myrmoderus squamosus (Pelzeln, 1868)	1	1	0.7	RA	Und
Conopophagidae Sclater & Salvin, 1873					
Conopophaga lineata (Wied, 1831)	1	5	3.3	U	Und
Formicariidae Gray, 1840					
Chamaeza campanisona (Lichtenstein, 1823)	1	1	0.7	RA	Und
Scleruridae Swainson, 1827					
Sclerurus scansor (Ménétries, 1835)	1-2	2	1.3	RA	Und
Dendrocolaptidae Gray, 1840					
Sittasomus griseicapillus (Vieillot, 1818)	1-3	39	25.7	RE	Und, Can
Dendrocolaptes platyrostris Spix, 1825	1	4	2.6	RA	Und
Xiphorhynchus fuscus (Vieillot, 1818)	1-2	37	24.3	COM	Und
Lepidocolaptes falcinellus (Cabanis & Heine, 1859)	1-2	5	3.3	U	Und, Can
Xenopidae Bonaparte, 1854					
Xenops rutilans Temminck, 1821	1-2	6	3.9	U	Und, Can
Furnariidae Gray, 1840					
Heliobletus contaminatus Pelzeln, 1859	1-2	7	4.6	U	Und, Can
Philydor atricapillus (Wied, 1821)	1-4	29	19.1	COM	Und, Can
Anabacerthia amaurotis (Temminck, 1823)	1-3	11	7.2	U	Und, Can
Syndactyla rufosuperciliata (Lafresnaye, 1832)	1	3	2	RA	Und, Can
Dendroma rufa (Vieillot, 1818)	1-6	15	9.9	U	Und, Can
Synallaxis ruficapilla Vieillot, 1819	1-2	6	3.9	U	Und
Pipridae Rafinesque, 1815					
Chiroxiphia caudata (Shaw & Nodder, 1793)	1-4	13	8.6	U	Und, Can
Tityridae Gray, 1840					
Schiffornis virescens (Lafresnaye, 1838)	1	1	0.7	RA	Und
Pachyramphus castaneus (Jardine & Selby, 1827)	1-4	6	3.9	U	Und, Can
Pachyramphus polychopterus (Vieillot, 1818)	1-2	7	4.6	U	Und, Can
Pachyramphus validus (Lichtenstein, 1823)	1-6	6	3.9	U	Und, Can
Platyrinchidae Bonaparte, 1854					
Platyrinchus mystaceus Vieillot, 1818	1-4	17	11.2	COM	Und
Rhynchocyclidae Berlepsch, 1907					
Mionectes rufiventris Cabanis, 1846	1	2	1.3	RA	Und
Leptopogon amaurocephalus Tschudi, 1846	1-2	15	9.9	U	Und, Can
Phylloscartes ventralis (Temminck, 1824)	1-5	20	13.2	COM	Und, Can

Taxa	Range of Number of Individuals in the Flocks	Number of Contacts	FO (%)	FC	FS
Tolmomyias sulphurescens (Spix, 1825)	1	6	3.9	U	Und, Can
Poecilotriccus plumbeiceps (Lafresnaye, 1846)	3	1	0.7	RA	Und
Hemitriccus obsoletus (Miranda-Ribeiro, 1906)	1	1	0.7	RA	Und
Tyrannidae Vigors, 1825					
Tyranniscus burmeisteri (Cabanis & Heine, 1859)	1	1	0.7	RA	Und
Camptostoma obsoletum (Temminck, 1824)	1-2	3	2	RA	Can
Phyllomyias virescens (Temminck, 1824)	1	3	2	RA	Und
Attila rufus (Vieillot, 1819)	1	1	0.7	RA	Can
Myiarchus swainsoni Cabanis & Heine, 1859	1	1	0.7	RA	Can
Myiodynastes maculatus (Statius Muller, 1776)	1	1	0.7	RA	Can
Megarynchus pitangua (Linnaeus, 1766)	1	2	1.3	RA	Can
Lathrotriccus euleri (Cabanis, 1868)	1-2	7	4.6	U	Und
Vireonidae Swainson, 1837					
Cyclarhis gujanensis (Gmelin, 1789)	1	4	2.6	RA	Ca
Hylophilus poicilotis Temminck, 1822	1-3	9	5.9	U	Und, Can
Vireo chivi (Vieillot, 1817)	1-4	23	15.1	COM	Und, Can
Troglodytidae Swainson, 1831					
Troglodytes musculus Naumann, 1823	1	1	0.7	RA	Can
Turdidae Rafinesque, 1815					
Turdus rufiventris Vieillot, 1818	1-3	4	2.6	RA	Und, Can
Turdus subalaris (Seebohm, 1887)	2-5	2	1.3	RA	Und
Turdus albicollis Vieillot, 1818	1-4	22	14.5	COM	Und, Can
Fringillidae Leach, 1820					
Euphonia violacea (Linnaeus, 1758)	1-4	4	2.6	RA	Und, Can
Euphonia pectoralis (Latham, 1801)	1-2	4	2.6	RA	Und, Can
Icteridae Vigors, 1825					
Cacicus chrysopterus (Vigors, 1825)	1-3	4	2.6	RA	Und, Can
Icterus pyrrhopterus (Vieillot, 1819)	4-4	1	0.7	RA	Can
Parulidae Wetmore, Friedmann, Lincoln, Miller, Peters, van Rossem, Van Tyne & Zimmer, 1947					
Setophaga pitiayumi (Vieillot, 1817)	1-4	33	21.7	COM	Und, Can
Myiothlypis leucoblephara (Vieillot, 1817)	1-3	12	7.9	U	Und
Basileuterus culicivorus (Deppe, 1830)	1-8	71	46.7	RE	Und, Can
Cardinalidae Ridgway, 1901					
Habia rubica (Vieillot, 1817)	1-8	50	32.9	RE	Und
Thraupidae Cabanis, 1847					
Hemithraupis ruficapilla (Vieillot, 1818)	2-5	11	7.2	U	Und, Can
Tersina viridis (Illiger, 1811)	2-5	4	2.6	RA	Und, Can
Dacnis cayana (Linnaeus, 1766)	1-2	2	1.3	RA	Und, Can
Saltator similis d'Orbigny & Lafresnaye, 1837	1	3	2	RA	Und
Coereba flaveola (Linnaeus, 1758)	1	2	1.3	RA	Und, Can
Trichothraupis melanops (Vieillot, 1818)	1-8	21	13.8	COM	Und, Can
Tachyphonus coronatus (Vieillot, 1822)	1-4	23	15.1	COM	Und, Can
Haplospiza unicolor Cabanis, 1851	1-4	3	2	RA	Und
Pipraeidea melanonota (Vieillot, 1819)	1-6	3	2	RA	Can
Stephanophorus diadematus (Temminck, 1823)	1-2	2	1.3	RA	Und
Thraupis sayaca (Linnaeus, 1766)	1-4	6	3.9	U	Und, Can
Thraupis cyanoptera (Vieillot, 1817)	1-4	3	2	RA	Und
Stilpnia preciosa (Cabanis, 1850)	1-5	3	2	RA	Und, Can
Tangara seledon (Statius Muller, 1776)	3-6	2	1.3	RA	Und, Can
Tangara cyanocephala (Statius Muller, 1776)	2-2	1	0.7	RA	Und

(2000), and Maldonado-Coelho & Marini (2003), who reported, 77, 72, and 78 species, respectively. In contrast, considering the studies conducted in the southern Atlantic Rain Forest region, the species richness recorded in our study was higher than that found by Ghizoni-Jr. & Azevedo (2006) and Ghizoni-Jr. (2009), who recorded 64 and 56 species, respectively, but lower than that recorded by Brandt *et al.* (2009), who recorded 117 species. The highest richness of species in mixed flocks in the Atlantic Rain Forest biome was recorded by Machado (1999), in the upper region of Serra do Paranapiacaba, São Paulo state, where 120 species were recorded. However, in the study by Machado (1999), in addition to the diversity of sampled environments, the number of hours of sampling (n = 432 h) was much higher than that of the present study (n = 216 h). Therefore, the diversity detected in the present study can be considered representative as it covered all four seasons of the year and was conduct-
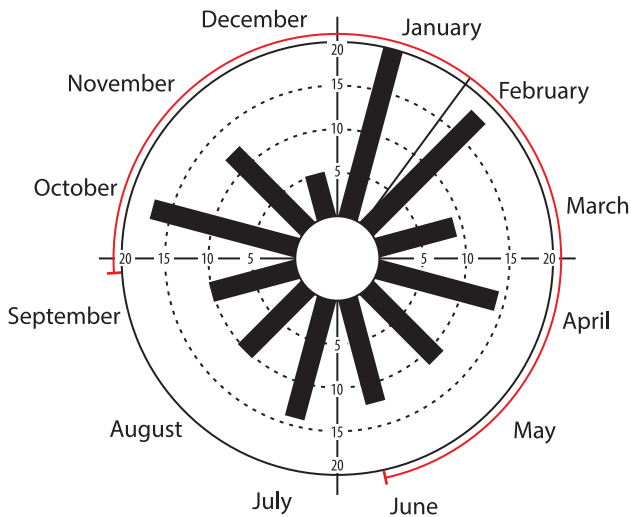
Figure 5. Variation in the number of contacts of mixed flocks of birds per month, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil, between October 2016 and September 2017.
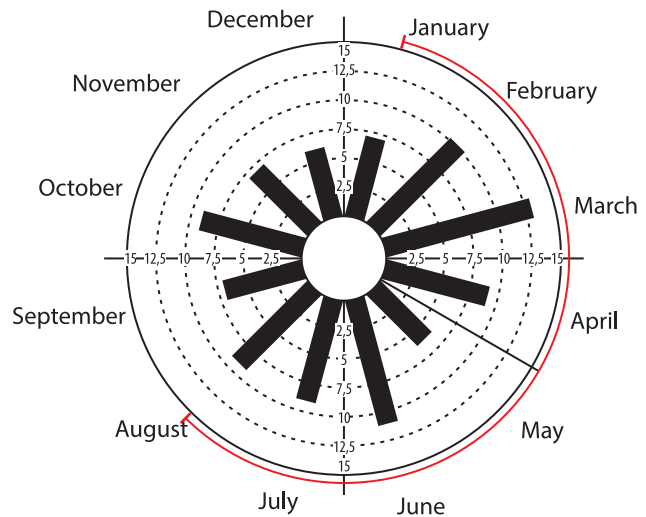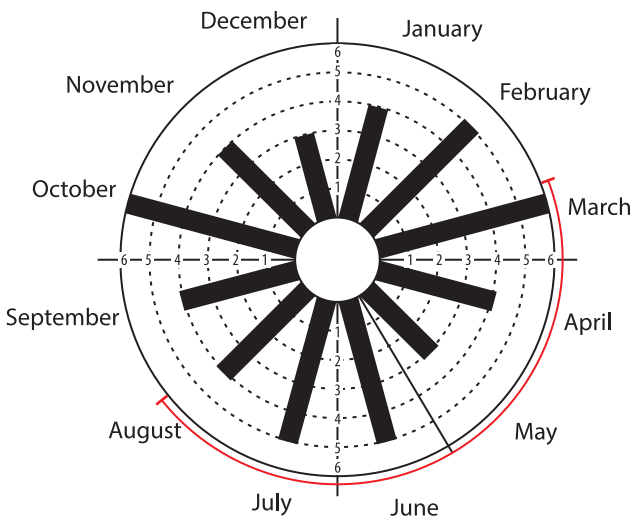

Figure 6. Monthly variation in the average richness of mixed flocks of birds, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil, between October 2016 and September 2017.

Figure 7. Monthly variation of the average size (in the number of individuals) of the mixed flocks of birds, in Parque Nacional Aparados da Serra, municipality of Praia Grande, southern Santa Catarina, Brazil, between October 2016 and September 2017.

Table 2. Physical and behavioral characteristics of the two most frequent species in mixed flocks of birds (n = 152), recorded in PARNA of Aparados da Serra, municipality of Praia Grande, southern Santa Catarina state, Brazil, between October 2016 and September 2017.

Physical and Behavioral Characteristics	Species	
	B. culicivorus	*H. rubica*
Neutral coloring	Yes	Yes
Vocalization	Conspicuous	Conspicuous
Movement intensity	High	High
Frequency of occurrence	Regular	Regular
Number of contacts	71	50
Number of individuals in the intraspecific groups	2.9 ± 1.5	3.6 ± 1.3
Richness of flocks without the presence of the other species	4.0 ± 2.2 (n = 47)	4.8 ± 2.7 (n = 26)
Richness of flocks without the presence of the two species	3.6 ± 2.2 (n = 57)	

ed during both the reproductive and non-reproductive periods.

Migratory species also contributed to the recorded species richness. Among these, *Vireo chivi* stands out, which, according to Machado (1997), is recognized as a regular participant in mixed flocks within the Atlantic Rain Forest. This species remains in the southern region of Brazil (Sick, 1997) for only six to seven months and participated in the flocks from October 24, 2016, to April 20, 2017 (first and last records). However, it was among the most frequent in flocks, a result supported by the findings of Machado (1997, 1999). Generally, *V. chivi* accompanies flocks in pairs through the canopy and sometimes within the medium understory where it uses various substrates such as thin trunks, branches, and leaves to forage for seeds and small fruits. Other registered migratory birds that caused seasonal displacement in the region were *T. subalaris, L. euleri, Myiarchus swainsoni, Haplospiza unicolor, Myiodynastes maculatus,* and *Pachyramphus poly-*

chopterus. These last three species were also recorded by Brandt *et al.* (2009) and are considered potential members of mixed flocks by Machado (1997). The low values found for the average richness of species in the flocks and average size of the flocks in relation to other studies carried out in Brazil can be explained by the diversity of species that is accompanied by changes along the latitudinal gradient between the Atlantic Rain Forest and Amazon biomes (Develey & Peres, 2000). In addition to biogeographic factors, the successional stages of vegetation may also influence species composition, richness, and the size of registered flocks, as mentioned by Aleixo (1997) and Maldonado-Coelho & Marini (2003).

Neotropical mixed flocks are either primarily or exclusively composed of passerines (Moynihan, 1962). They are stable flocks formed by a couple of species, mainly insectivorous and omnivorous birds (Powell, 1985), which is justified by the observations made during the present study. However, this does not mean that other orders cannot be typical followers of mixed flocks, such as Cuculiformes, Trogoniformes, and Piciformes, which were recorded here and are commonly reported in other

studies of mixed flocks in the Atlantic Rain Forest. *Piaya cayana* specimens were always observed alone, discreetly following the mixed flocks through the upper understory where they captured arthropods disturbed by the flocks. This was also observed in the middle understory of *Trogon surrucura* and *Trogon chrysochloros,* although the participation of trogonids in mixed flocks is considered rare (Machado, 1999). In the present study, these two species followed the flocks for long periods of time (more than 15 min). In contrast, *Picumnus temminckii, Veniliornis spilogaster,* and *Piculus aurulentus* benefited mainly from protection against predators, as their diets are composed of larvae and not arthropods disturbed by the flock (Machado, 1999). The participation of *Thalurania glaucopis* in mixed flocks may be related to a response to the aggregation instinct or even to the temporary protection obtained by the presence of a greater number of individuals (Moynihan, 1962).

Some of the richest families, such as Thraupidae, Tyrannidae, and Furnariidae, observed were also among the most frequent in other studies with mixed flocks of Atlantic Rain Forest birds. This is possibly because a large part of the species belonging to these families are insectivorous, small sized, and have a great capacity to adapt to forest environments (Sick, 1997), characteristics that facilitate participation in heterospecific associations (Develey & Peres, 2000; Maldonado-Coelho & Marini, 2003).

Among the "regular species," *B. culicivorus* was the species with the highest FO; a same result was also found in the Brazilian Southeast Region by Machado (1999) and in the Brazilian south region by Ghizoni-Jr. & Azevedo (2006) and Brandt *et al.* (2009). The other two regular species, *H. rubica* and *S. griseicapillus,* also occurred with a high frequency in other studies (*e.g.,* Machado, 1999; Maldonado-Coelho & Marini, 2003; Ghizoni-Jr., 2009). This fact was true for most of the registered "common species," *Xiphorhynchus fuscus, Philydor atricapillus* (Brandt *et al.,* 2009), *Setophaga pitiayumi, Phylloscartes ventralis* (Ghizoni-Jr., 2009), *Dysithamnus mentalis* (Davis, 1946; Brandt *et al.,* 2009), *Tachyphonus coronatus* (Ghizoni-Jr. & Azevedo, 2006; Brandt *et al.,* 2009), *Trichothraupis melanops* (Brandt *et al.,* 2009; Ghizoni-Jr., 2009), *T. albicollis* Brandt *et al.,* 2009), and *V. chivi* (Machado, 1997, 1999). The exception was *P. mystaceus,* which in this study alone was among the most frequent.

Previous studies on mixed flocks carried out in other regions of the Atlantic Rain Forest found that some of the species registered here as "uncommon" have a marked presence in heterospecific associations. These include *Lepidocolaptes falcinellus, Xenops rutilans, Dendroma rufa, Anabacerthia amaurotis, Heliobletus contaminatus, Leptopogon amaurocephalus, Tolmomyias sulphurescens, Hylophilus poicilotis,* and *Hemithraupis ruficapilla.* Individuals of these species were rarely seen outside the flocks and thus can be considered flock participants in this study.

The rare species group accounted for 56.5% of the total richness recorded. This result was similar to that found by Machado (1999) in the Serra de Paranapiacaba, southeast Brazil, which registered 53.3% of the species as rare. Thus, as observed in this study, these species do not contribute significantly to the cohesion and maintenance of the mixed flocks, while a large proportion of them eventually participated in the flocks. A good example of the latter includes records of *Chamaeza campanisona, Sclerurus scansor, Schiffornis virescens, Rhopias gularis,* and *Myrmoderus squamosus,* which forage in the lower understory and participate in the flocks only when they pass through their territory. The same can be mentioned for *Thamnophilus caerulescens, T. rufiventris, Phyllomyias virescens,* and *Tyranniscus burmeisteri* in the middle understory and *Troglodytes musculus* in border areas. The participation of *Celeus flavescens* and *Hemitriccus obsoletus* was purely accidental; on both occasions when these species were recorded, they were following a separate foraging route and accidentally entered the flock.

The agonistic interactions recorded between species participating in mixed flocks, as mentioned by Powell (1985), may be related to the defense and demarcation of the foraging territory of the flock. Such behaviors structurally reinforce groups, as they prioritize group members to avoid further confrontations, which is beneficial due to the increase in efficiency of use of food resources (Lagory *et al.,* 1984).

In areas of the Atlantic Rain Forest in the southeast, Davis (1946) and Machado (1999) found that mixed flocks occur more frequently in the sub-dry season, from April to September, and may present peaks in the coldest months of the year such as July and August. However, this was not observed in the present study, as there were no high frequencies of contact with flocks in the winter months. Concurrently, certain variations in the number of contacts appeared to be similar to the pattern found by Machado (1999) and Batista *et al.* (2013). The decrease in the number of contacts with flocks observed between November and December was also recorded by Machado (1999). This decrease may be linked to the reproductive period of the birds, where most species establish territory during this time of the year and participate with a lower frequency within mixed flocks. This justifies the various reproductive behaviors observed among birds in these months, such as cutting, nest building, and care for nestlings. Contrary to the findings of Davis (1946) and Machado (1999), the greatest number of contacts with mixed flocks was obtained in the summer months of January and February in the present study. However, during these months, the flocks were less cohesive, with many young individuals present and greater distances between members, in addition to remaining united for short periods of time. Furthermore, it was observed on many occasions that the flocks disintegrate, either by dilution when the flock fragmented (but followed the same direction) or even by division, with two or more groups following different directions. This fact was also highlighted by Machado (1999). The flocks remained stable between March and September. In the winter months of June and July, the flocks were cohesive with members remaining close to each other or being united for long periods.

As for the variation in the average species richness and average size of the flocks, the decrease observed in the months of November and December may also be related to the reproductive period of the birds. The observed increases in these variables in the summer months of January, February, and March are similar to those found by Davis (1946) and Machado (1999); however, in this study, the flocks were less frequent during this period. Machado (1999) highlighted that the low frequency of flocks in these months may be due to the greater concentration of species in the few formed flocks, resulting in an increase in both the richness and size of the flocks. In this study, unlike Davis (1946) and Machado (1999), the increase in the average species richness and average size of the flocks seemed to accompany the monthly flock frequency, mainly in the months of January and February, in which a greater contact number with flocks was registered. Concurrently, the possibility that the inverse relationship may occur in March is not ruled out, being precisely one of the months with the lowest number of contacts with flocks. However, it ranks among the months with the greatest richness and size of registered flocks.

Another pattern observed was the increase in species richness and flock size during the winter months, especially in June and July, which was a result also found by Batista *et al.* (2013) in areas of the Atlantic Rain Forest in the northeast. This increase may be related to the low availability of potential prey items in the winter months, and thus, the birds tend to participate more frequently in flocks to maximize foraging and increase protection against predation (Machado, 1999).

The dynamics of the flocks recorded in this study seem to follow the same trend observed in other studies carried out in the Atlantic Rain Forest (*e.g.,* Machado, 1999; Batista *et al.,* 2013). Nevertheless, it is important to note that the results obtained for the frequency variation in flock occurrence, species richness, and flock size did not show differences in the respective values throughout the year.

Basileuterus culicivorus and *H. rubica,* due to their high frequency of participation as well as the conspicuous pattern of movement and vocalization, were responsible for the formation of 62.5% of the total registered flocks. In the Atlantic Rain Forest biome, *B. culicivorus* has been considered a nuclear species of mixed flocks in some studies (*e.g.,* Maldonado-Coelho & Marini, 2003; Ghizoni-Jr. & Azevedo, 2006; Brandt *et al.,* 2009). This species is frequent throughout the year in the study area and exhibits conspicuous behavior and strong vocalization, which is why it was present in 46.7% of the registered flocks. In addition, flocks with the presence of *B. culicivorus* without other nuclear species had a higher average species richness compared to flocks with no nuclear species. These results reinforce the idea that in the Atlantic Forest, *B. culicivorus* plays a fundamental role in the cohesion and maintenance of mixed flocks. However, some authors (*e.g.,* Machado, 1999; Maldonado-Coelho & Marini, 2004) also cite *H. rubica* as an indispensable species for the cohesion and maintenance of mixed flocks

in the Atlantic Rain Forest, noting that its absence can result in the disintegration of the group. Maldonado-Coelho & Marini (2004) also pointed out that the presence of *H. rubica* in mixed understory flocks in fragments of the Atlantic Rain Forest keeps individuals cohesive during foraging. This was clearly observed in the present study, in which the flocks registered with the presence of *H. rubica* were always cohesive and generally remained together for longer periods of time. Moreover, some species are typical followers of *H. rubica,* such as *P. atricapillus* (Cestari, 2007), in addition to *S. griseicapillus* and *X. fuscus.* These species forage preferentially on trunks, branches, and leaves, where they capture arthropods, seeds, and small fruits, in addition to searching for epiphytic bromeliads which harbor many insects. Even so, the flocks where *H. rubica* occurred without the presence of the other core species (*B. culicivorus*) also had a higher average species richness than flocks without their presence. This shows the high capacity of this species to attract and retain individuals of different cohesive species, forming mixed flocks. It should be noted, however, that when considering studies with mixed flocks carried out in the southern region of Brazil (*e.g.,* Ghizoni-Jr. & Azevedo, 2006; Ghizoni-Jr., 2009; Brandt *et al.,* 2009), *H. rubica* demonstrated the exercise function of nuclear species only in this study.

It was observed that the mixed flocks formed during this study were dependent on the presence of *H. rubica* and *B. culicivorus.* Therefore, these species are considered vital for the cohesion and maintenance of the mixed flocks of the Submontane Atlantic Rain Forest in the southern region of Brazil. Machado (2002), in the southeast Atlantic Rain Forest, found not only one or two core species, but a set of species responsible for the cohesion and maintenance of mixed flocks, which he termed the "core-complex." Ghizoni-Jr. (2009) also found evidence of this same pattern in a Mixed Ombrophilous Forest, in the southern region of Brazil. Thus, the flocks recorded in this study without the presence of the two nuclear species may have been formed by a core-complex. However, this consideration is not conclusive, because in addition to these flocks being less rich in species, they were less cohesive and remained united for shorter periods of time.

CONCLUSIONS

The composition and richness of species in the bird assemblage within the mixed flocks were recognized by species already recorded in studies carried out in other areas of the Atlantic Rain Forest. However, the presence of migratory species, and the structure of the vegetation, may have influenced the number of recorded species, as most of the vegetation in the study area comprises plant species typical of the early and middle stages of regeneration. The low average species richness and flock size may be related not only to biogeographic factors but also to the successional stage of vegetation in the study area.

The variation in the FO, species richness, and size (in the number of individuals) of the flocks throughout

the year may be related to the reproductive period and availability of food resources that occur in the southern region of Brazil, depending on the seasonality present at these latitudes.

Basileuterus culicivorus and *H. rubica* behaved as typical nuclear species, a result that was expected due to their behavior, color pattern, and abundance in the Atlantic Rain Forest in southern Brazil. Thus, as suggested by previous studies on mixed flocks, we reinforce the importance of these two species for the cohesion and maintenance of mixed flocks in the Atlantic Rain Forest.

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