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Soundscapes: Species Richness and Community Composition of Neotropical Atlantic Forest Avifauna

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Abstract

As tropical forests become increasingly vulnerable to land use changes, fragmentation, and climate shifts, efforts to minimise species loss are essential. Prevalent in most environments and having complex vocalisations, birds are key indicators of ecosystem health and a good model for acoustic monitoring. In Brazil, the Caparaó National Park (CNP) is a preserved remnant of the Atlantic Forest with great avian endemism. Despite having >600 species, limited research has utilised bioacoustics for species assessment. This study employed bioacoustics to examine soundscapes and community composition at two CNP locations—one with ombrophilous montane forest (OMF) and another with semi-deciduous seasonal forest (SSF). Four SongMeters were deployed, recording bird choruses from 08:00 to 11:00 a.m. for two months. Soundscape profiles and species composition were characterised using Raven Pro. Acoustic indices assessed correlations with avian species richness, and sites were compared using the Mann–Whitney U test. Ninety-eight species were detected, and species richness was greater within SSF. While acoustic indices had little impact on richness, they identified differing soundscapes: more ambient noise in OMF, and gunshots detected in SSF. The results indicate that bioacoustics can aid monitoring strategies. Given the presence of rare species and illegal activities, more studies are needed to support the conservation of birds in this critical environment.

Keywords: bioacoustics; avian species richness; Atlantic Forest; conservation monitoring

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1. Introduction

The study of bioacoustics offers valuable insights into ecological and anthropogenic drivers shaping the presence and behaviour of vocal species [1]. Bioacoustics methods have been increasingly used to assess biodiversity, given that soundscapes can reflect ecological changes, such as habitat degradation or recovery, making them valuable indicators for conservation strategies [2].

Bird species have been particularly used as a key indicator of environmental health and are an informative bioacoustic indicator given their vocal complexity and sensitivity to environmental change [3,4]. Analysing avian vocalisations can also expand knowledge in bird ethology, ecology, and evolution [5,6], and as birds are present in most environments, their vocalisation activity often describes differences within spatiotemporal soundscapes [5]. Research has demonstrated that birds modify their vocalisations to avoid overlapping with other species and to counteract the effects of environmental noise [7,8]. In urban environments, for example, many species have been shown to shift the minimum frequency of their songs upward or increase vocal amplitude in response to persistent low-frequency noise such as traffic [9]. More broadly, besides adjusting signal characteristics, birds may alter temporal activity patterns or even relocate to new territories to avoid masking effects (i.e., such as mining or industrial noise) [7–9]. These adaptations serve to reduce acoustic interference and preserve communication efficiency in anthropogenically modified soundscapes [8–10].

As bird calls are information-rich, the development of algorithms to measure acoustic community diversity has led to the use of acoustic indices as tools to quantify soundscape diversity [5,11]. However, studies have had mixed success: while some find a correlation between diversity, richness, and acoustic complexity (herein heterogeneity), others report that sound sources may confound these measures [11,12]. These findings highlight the importance of context-specific validation of acoustic indices for biodiversity monitoring [5,11,12].

The Brazilian Atlantic Forest is among the most biodiverse and endangered systems globally, retaining less than 15% of its original extent [13]. Future extinctions are predicted for numerous species, and extant avifauna inhabiting the biome are considered most threatened within the Neotropical bird assemblage [14,15]. One of the country's largest remnants of pristine Atlantic Forest is located at the Parque Nacional do Caparaó (Caparaó National Park, herein CNP), in the Southeast region of Brazil. The park contains between 1% and 8% of all living species on Earth (>1400 faunal species and >20,000 floral species) [16]. Regionally, CNP acts as a critical refuge for endemic and threatened bird species within southeastern Brazil's Atlantic Forest and functions as an ecological corridor connecting forest fragments across the states of Minas Gerais and Espírito Santo [17,18]. Its altitudinal gradient, ranging from lowland forests to high-altitude grasslands, supports a high turnover of species between habitats, contributing to the exceptional biodiversity of southeastern Brazil [16–19]. An annotated list of avifauna documented 98 endemic and 33 threatened bird species in the park, out of 348 total recorded species [18]. Notable examples of highly threatened Atlantic Forest endemics include the red-billed curassow (*Crax blumenbachii*) and the red-browed amazon (*Amazona rhodocorytha*)—both found in Espírito Santo and Minas Gerais [15]. Currently, one-third of the region's wildlife faces the risk of extinction, highlighting the importance of assessing biodiversity status [16,18–20].

Birds serve as effective indicators for monitoring changes in biodiversity because of their widespread distribution across different environments and higher detection rates compared to other taxonomic groups [4]. Research on avian species in the region could provide essential insights into the biodiversity condition of locations such as the CNP. However, the dense vegetation, complex topography, and high levels of endemism characteristic of the Atlantic Forest present logistical challenges for conventional bird surveys, which typically rely on both visual and auditory cues [21,22]. Passive acoustic monitoring (PAM) provides a powerful, non-invasive alternative, allows continuous data collection over time and space, enhances detection of vocally active or elusive species, and minimises observer bias [21–24]. These advantages are particularly valuable in high-altitude and closed-canopy ecosystems, such as the CNP, where sight-based surveys are challenging, and acoustic communication is ecologically important [21,22,24].

Despite CNP's high endemism and hosting more than 600 bird species, the area remains largely unexplored, especially in bioacoustics monitoring [20,25]. Only one study has investigated soundscape interactions (biophony–biophony), exploring the link between acoustic niches and bird vocal activity patterns. Still, it did not find a clear connection between acoustic and temporal partitioning of songs [25].

Therefore, this study employed passive acoustic monitoring to evaluate soundscapes, avian species richness, and community composition in two high-altitude ecosystems within CNP: ombrophilous montane forest (OMP) and semi-deciduous seasonal forest (SSF). Due to differences in ecosystems and geomorphology, we hypothesised that bird–soundscape interactions and species richness would vary between ecosystems, and that acoustic indices would help explain these patterns.

2. Materials and Methods

This study was completed with the ethical approval of the University of Salford, UK (STR1718-14). Licence to conduct research at the Caparaó National Park was granted by the Brazilian Ministry of Environment/SISBIO (ICMBio/SISBIO No. 49062).

2.1. Study Site

The study was conducted at Caparaó National Park (CNP), located on the border between the Brazilian states of Minas Gerais (MG) and Espírito Santo (ES) (20.422186° S, 41.853447° W; Figure 1). The CNP covers 318.53 km^2, with 79% of its area within ES. Established in 1961 as an Environmental Conservation Unit, it aims to protect the Caparaó mountain range and preserve biodiversity, fully encompassing the Atlantic Forest Biome [16]. The region features a mosaic of vegetation types, such as inselbergs, high-altitude grasslands, and two forest types: dense ombrophilous montane and semi-deciduous seasonal forest [16,26]. The regional climate exhibits a tropical highland pattern (Cwb, Köppen classification), characterised by dry winters (April–October) and wet summers (November–March). It receives 1200 mm of rainfall annually, with average temperatures ranging from 19 to 22 °C [16,27].

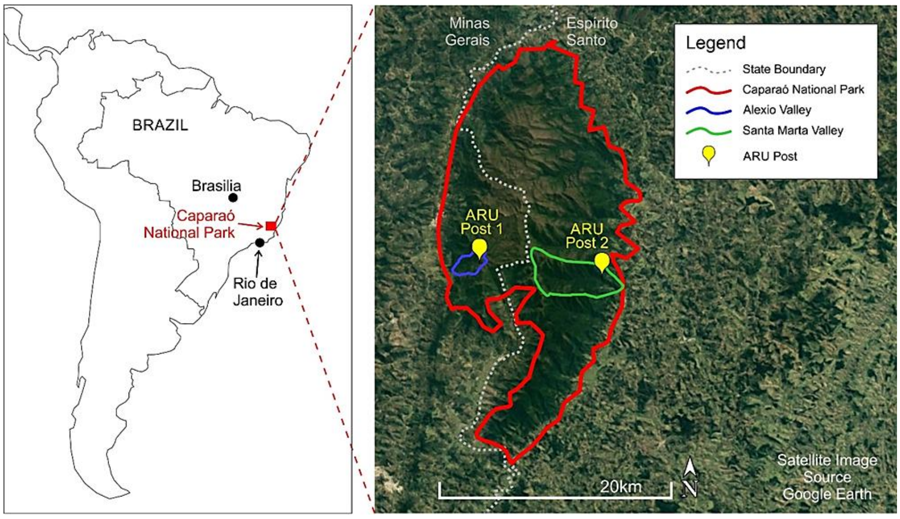

Figure 1. Location of the two study sites—Aleixo Valley and Santa Marta Valley—within the Caparao National Park. Bird vocalisations were recorded at each location using autonomous recording units (ARUs) indicated by the yellow markers. Polygons outlining each valley are indicative and based on imagery from previous research; precise area measurements are not available [28].

Data collection occurred between January and February 2017, aligning with the wet season when increased food availability boosts bird activity and coincides with the breeding period for many local species, resulting in higher vocal activity, which improves species detection. The two-month timeframe was selected to minimise inter-annual meteorological variability and logistical difficulties, while maintaining consistent effort across sites. We recognise that species with non-seasonal or out-of-season vocal activity may be under-detected.

Two locations within CNP were selected for sampling: Aleixo Valley (herein AV), on the western side at 1687 m above sea level, predominantly featuring semi-deciduous seasonal forest, and Santa Marta Valley (herein SMV), on the eastern side at 1348 m above sea level, characterised by dense ombrophilous forest (Figure 1).

2.2. Sampling Methods

Field recordings were obtained using four autonomous recording units (ARU) (SongMeter SM3; Wildlife Acoustics Inc., Maynard, MA, USA). Two ARUs were installed in each location, 1.8 m above the ground, oriented north and south on a fixed post at AV (−20.479444° S, −41.840277° W) and similarly at SMV (−20.490555° S, −41.739444° W). Additional external omnidirectional microphones (External Acoustic Microphone for SM3, Wildlife Acoustics Inc., USA) were positioned facing east and west beside the ARUs to record sounds from all four cardinal directions simultaneously. Daily soundscapes were captured from 8:00 a.m. to 11:00 a.m. in one-hour intervals, at 16 bits per second and 44.1 kHz sampling rate. Recordings were synchronised with Garmin GPS equipment to allow spatial triangulation of sound sources and ensure consistent sampling coverage. Based on previous tropical forest studies, e.g., [22], the effective detection radius of the SongMeter SM3 units with external microphones is approximately 50–100 m. However, this can vary with vegetation density and habitat structure. While the differing forest types—semi-deciduous seasonal at AV and dense ombrophilous at SMV—may influence sound propagation and species composition, the standardised ARU setup, detection range radius and synchronised recording times across both sites helped to minimise bias related to area and habitat differences.

2.3. Data Processing and Analysis

Recordings were analysed using spectrograms with Raven Pro [29]. Avian species were identified by their vocalisations to measure richness and species occurrence. Only identifiable vocalisations were included to minimise observer bias. Species identification was supported by existing acoustic data [25], input from local ornithologists, and references to online repositories (WikiAves, Xeno-Canto). Multiple calls within a 10 s window were treated as a single individual unless overlapping by distinct callers; conservative rules avoided double-counting. Species richness and composition were determined by compiling a species list and occurrences from 48 one-hour recordings (24 per site).

For the acoustic index analysis, 12 samples were randomly selected per site, and the first 10 min of each recording were processed using the R packages Soundecology, Seewave, and tuneR [30]. The following acoustic indices were calculated: the Bioacoustic Index (BI) was analysed from 0.5 to 12.0 kHz with a limit of −50 decibels [21,31], while the Acoustic Complexity Index (ACI) was analysed from 0 to 12.0 kHz with a cluster size of 10 s [32]; the Acoustic Evenness Index (AEI) was analysed at a frequency range of 0 to 12.0 kHz with a limit of −50 decibels using 1000 steps [33]. The Normalised Difference Soundscape Index (NDSI) was analysed using the ratio of power spectral density values for biophony (0.5 to 12.0 kHz) and anthrophony (0 to 0.5 kHz) [34]. The Acoustic Entropy Index (H) was analysed at the 0 to 12.0 kHz frequency range [35], and the Acoustic Diversity Index (ADI) was analysed at a frequency of 0 to 12.0 kHz with a limit of −50 decibels using 1000 steps [31]. Results are visually represented using Z-normalised values calculated by subtracting the mean and dividing by the standard deviation for each index across all recordings ($Z = (x - \mu)/\sigma$), allowing for standardised comparison of indices with different scales and units.

All data analysis was completed using R (version 4.4, 2025) and a significance level of $p < 0.05$ was applied. Descriptive statistics were calculated for all relevant metrics, and the results are summarised as counts, percentages, means, and medians with relevant dispersion. Normality of data was assessed using the Shapiro–Wilk test (abundance and residuals of diversity-index comparisons).

Species diversity was calculated as the number of unique species recorded at each location. Total abundance was determined by counting all individual records at each site. Species richness was estimated using the Shannon diversity index (H') with the R package vegan, which calculates H' from the observed abundance distribution [36]. To compare Shannon diversity between sites, we employed Hutcheson's *t*-test [37], using the entropart package in R [38]. We reported H' for each site along with Hutcheson's *t*-test results to assess whether within-site diversity significantly differs across locations. To assess compositional differences in species membership, we applied Fisher's exact test to a 2 × 2 contingency table that contrasted the counts of unique species (present at one location only) versus shared species (present at both locations) across the two locations.

Differences in acoustic indices between locations and abundance between locations were tested using the Mann–Whitney U test. Correlations between acoustic indices and avian species richness at each site were evaluated using Spearman's rank correlation coefficient (rs). Raw data used in the analysis is available online [39].

3. Results

3.1. Species Occurrence and Diversity

A total of 900 vocalisations from 98 unique bird species (Table A1) were recorded during the study period. Of these, 67.8% (N = 611) were recorded at AV and 32.1% (N = 289) at SMV. Among all detected species, 43 were found in both locations, indicating a substantial overlap in community composition. However, AV exhibited a considerably higher number of unique species (N = 50; Fisher's exact test odds ratio = 10.0, $p < 0.001$) than SMV, which had only five unique species (S1). On average, each species at AV was detected approximately 6.6 times (SD = 5.4), while at SMV, each species was detected approximately 6.0 times (SD = 4.6). Nonetheless, the abundance distribution per species did not differ significantly between locations (Mann–Whitney U = 2248, $p = 0.783$).

Shannon diversity indices revealed higher diversity at AV ($H' = 6.08$) than SMV ($H' = 5.14$), yielding a highly significant difference ($t = 12.2813$, df ≈ 597.27, $p < 0.001$). The overall dataset diversity index was $H' = 6.20$, indicating that AV diversity approached that of the combined dataset.

Among all species, Itatiaia spinetail (*Asthenes moreirae*) was most frequently detected with 32 occurrences; the Southern yellowthroat (*Geothlypis velata*) was the most common species found at AV, and an unidentified species was most common at SMV. The most frequently detected bird species are presented in Table 1, along with their call frequency ranges and IUCN conservation status.

Species classified as Least Concern comprised 67% of detected species, while six of the 98 recorded species (6.4%) were listed as Near Threatened, Vulnerable, or Endangered on the IUCN Red List. These were: Bare-throated bellbird (*Procnias nudicollis*; NT), Buffy-fronted seedeater (*Sporophila frontalis*; V), Vinaceous-breasted Amazon parrot (Amazona vinacea; E), Ochre-rumped antbird (*Drymophila ochropyga*; NT), Temminck's seedeater (*Sporophila falcirostris*; V), and Yellow-browed woodpecker (*Piculus aurulentus*; NT). Notably, the vulnerable buffy-fronted seedeater was among the most detected species (N = 23 occurrences) and was present at both sites. Similarly, Temminck's seedeater, also classified as vulnerable, was recorded 12 times but only at AV. The endangered Vinaceous-breasted parrot was detected predominantly at AV (N = 8 occurrences) and only once at SMV. Twelve bird species recorded in this study were endemic to Brazil, comprising 13.5% of all species detected. Among these, *Asthenes moreirae*, *Chamaeza meruloides*, *Stephanoxis lalandi*, *Drymophila genei*, and *Thraupis ornata* were among the most frequently recorded species (Table 1). The near-threatened Ochre-rumped antbird was detected exclusively at AV in 10.4% of recordings.

Table 1. Most frequently observed (N > 10) avian species (confirmed IDs) at the CNP and the number of times they occurred, location found, their vocalisation frequency ranges (kHz), and IUCN conservation statuses (IUCN, 2022). AV= Aleixo Valley, SMV = Santa Marta Valley; V = vulnerable, LC = least concern.

Avian Species	Occurrence	Location	Call Frequency Range (kHz)	IUCN Conservation Status
Itatiaia Spinetail *Asthenes moreirae*	32	AV, SMV	1.0–20.0	LC
Mouse-coloured Tapaculo *Scytalopus speluncae*	28	AV, SMV	2.0–22.0	LC
Green-winged Saltator Saltator *similis*	24	AV, SMV	1.0–10.0	LC
Short-crested Flycatcher *Myiarchus ferox*	24	AV, SMV	4.0–6.0	LC
Buffy-fronted seedeater *Sporophila frontalis*	23	AV, SMV	1.5–10.5	V
Southern Yellowthroat *Geothlypis velata*	23	AV	3.0–11.0	LC
Cryptic Ant thrush *Chamaeza meruloides*	21	AV, SMV	1.0–2.0	LC
Golden-crowned warbler *Basileuterus culicivorus*	21	AV, SMV	3.0–9.0	LC
Maroon-bellied Parakeet *Pyrrhura frontalis*	20	AV, SMV	2.0–23.0	LC
Green-crowned Plovercrest *Stephanoxis lalandi*	17	AV, SMV	5.0–7.0	LC
White-vented Violetear *Colibri serrirostris*	17	AV	5.0–8.0	LC
Chestnut-vented Conebill *C. speciosum speciosum*	16	AV	5.0–8.0	LC
Rufous-collared Sparrow *Zonotrichia capensis*	16	AV	4.0–8.0	LC
Surucua Trogon Trogon *surrucura*	15	AV, SMV	1.0–2.5	LC
White-throated Hummingbird *Leucochloris albicollis*	15	AV, SMV	3.0–10.0	LC
Black-billed Scythebill *Campylorhamphus falcularius*	14	SMV	4.0–22.0	LC
Double-collared Seedeater *Sporophila caerulescens*	14	AV, SMV	3.0–22.0	LC
Drab-breasted bamboo tyrant *Hemitriccus diops*	14	AV	5.0–8.0	LC
Rufous-tailed Antbird *Drymophila genei*	14	AV, SMV	2.0–10.0	LC
Yellow-legged Thrush *Turdus flavipes*	14	AV, SMV	6.0–11.0	LC
Chalk-browed Mockingbird *Mimus saturninus*	13	AV, SMV	6.0–16.0	LC
Temminck's Seedeater *Sporophila falcirostris*	12	AV	5.0–11.0	V
Yellow-bellied Elaenia Elaenia *flavogaster*	12	AV, SMV	2.0–20.0	LC
Golden-chevroned Tanager *Thraupis ornata*	11	SMVV	4.0–20.0	LC
Olivaceous Elaenia Elaenia *mesoleuca*	11	AV, SMV	5.0–22.0	LC

Twenty-five species detected within this study were confirmed as Aves but were unidentifiable to genus or species level. These were confirmed as unique based on distinct vocalisations verified using spectrograms, online databases (e.g., Xeno-Canto), and expert consultation.

3.2. Avian Vocalisation Patterns and Acoustic Soundscape Dynamics

Bird species exhibited considerable variation in frequency range (kHz), with the lowest being 0.5 kHz from the pale-vented pigeon (*Patagioenas cavennensis*) and the highest at 22.0 kHz from species such as the black-billed scythebill (*Campylorhamphus falcularius*) and the maroon-bellied parakeet (*Pyrrhura frontalis*). Many species displayed a broad frequency range, such as the double-collared seedeater (*Sporophila caerulescens*), which ranged from 3.0 to 22.0 kHz, and the mouse-coloured tapaculo (*Scytalopus speluncae*), with calls spanning 2.0 to 22.0 kHz (Table 1). In contrast, some species had significantly narrower ranges, including the cryptic antthrush (*Chamaeza meruloides*), which typically calls between 1.0 and 2.0 kHz, and the white-vented violetear (*Colibri serrirostris*), whose vocalisations fell within 5.0 to 8.0 kHz (Table 1).

Consistent with spectrogram observations, SMV exhibited consistently high acoustic energy with low temporal variation, likely influenced by a nearby waterfall, which reduced frequency band differentiation. Meanwhile, at AV, the soundscape had high temporal and frequency variations, mostly intermediate to high acoustic energy levels distributed unevenly across frequency bands. Using the Bioacoustic Index (BI) as a proxy for acoustic energy, we identified high-energy bouts (top 10% BI within each site) across the recording sequence. AV exhibited more frequent and higher-magnitude high-energy events than SMV, consistent with its generally elevated acoustic activity (Figure 2). SMV showed fewer and lower-amplitude peaks, reflecting a more stable soundscape with less pronounced surges in energy. These patterns align with the higher overall BI at AV and support the interpretation of a more dynamic, energetically intense soundscape at this site.

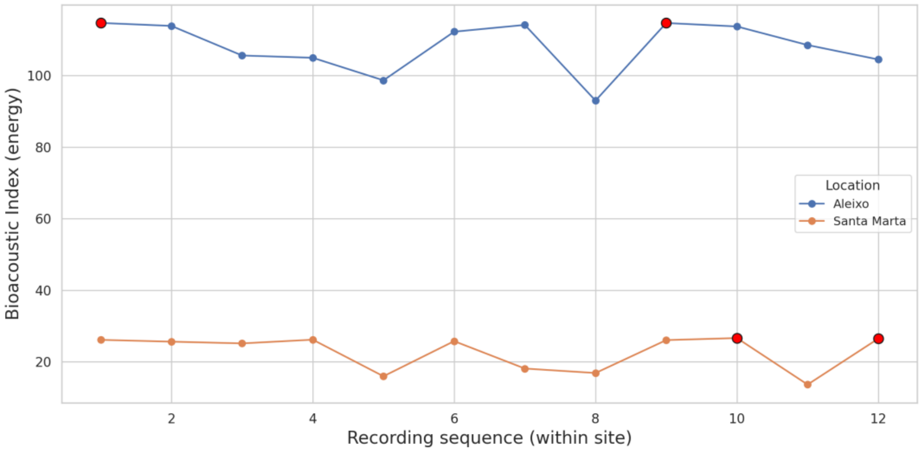

Figure 2. High energy bouts over time by site. Line plots show BI across the within-site recording sequence; red markers denote high-energy bouts (top 10% BI per site). Higher BI = higher acoustic energy.

However, both locations exhibited bouts of high acoustic energy levels, with high temporal variation from biophonic and geophonic events and low frequency variation from high wind and rainstorms. In addition, three anthropogenic sounds were detected within AV on 25/01 between 9:00 a.m. and 11:00 a.m., resembling the sound of gunshots.

Descriptive statistics for the six acoustic indices (ACI, NDSI, BI, ADI, AEI, and H) are summarised in Table 2. AV consistently showed higher acoustic complexity and bioacoustic activity, with significantly greater values for the Acoustic Complexity Index (9142.97 ± 122.58, U = 144, $p < 0.001$) and Bioacoustic Index (108.19 ± 7.08, U = 144, $p < 0.001$) compared to SMV (Figure 2). The Acoustic Evenness Index (AEI) and Acoustic Entropy (H) were also significantly higher (AEI = 0.40 ± 0.15, U = 133, $p < 0.001$; H = 0.85 ± 0.03, U = 117, $p = 0.008$) at AV (Figure 3).

Table 2. Acoustic indices calculated from samples collected using ARUs in the Caparao National Park.

	Acoustic Indices											
	ACI [a]		**NDSI** [b]		**BI** [c]		**ADI** [d]		**AEI** [e]		**H** [f]	
Site	**AV ***	**SMV**	**AV**	**SMV**	**AV ***	**SMV**	**AV**	**SMV**	**AV ***	**SMV**	**AV ***	**SMV**
Min	9142.97	4492.3	0.53	0.47	108.19	22.72	2.1	2.38	0.4	0.16	0.85	0.83
Max	122.58	11.59	0.2	0.09	7.08	4.97	0.23	0.14	0.15	0.11	0.03	0.02
Mean	9009.9	4475.31	−0.03	0.35	92.97	13.64	1.71	2.03	0.23	0.06	0.78	0.81
STD	9464.53	4508.05	0.83	0.61	114.67	26.63	2.34	2.48	0.65	0.41	0.89	0.85

[a] ACI = Acoustic Complexity Index: Measures temporal variability in acoustic signals; [b] NDSI = Normalised Difference Soundscape Index: Ratio of biophonic to anthropophonic sounds; [c] BI = Bioacoustic Index: Concentration of acoustic energy in frequency bands used by birds; [d] ADI = Acoustic Diversity Index: Diversity of acoustic signals across frequency bands; [e] AEI = Acoustic Evenness Index: Evenness of acoustic energy distribution; [f] H = Acoustic Entropy: Measure of acoustic complexity and randomness; * Indicate significant difference at $p < 0.05$.

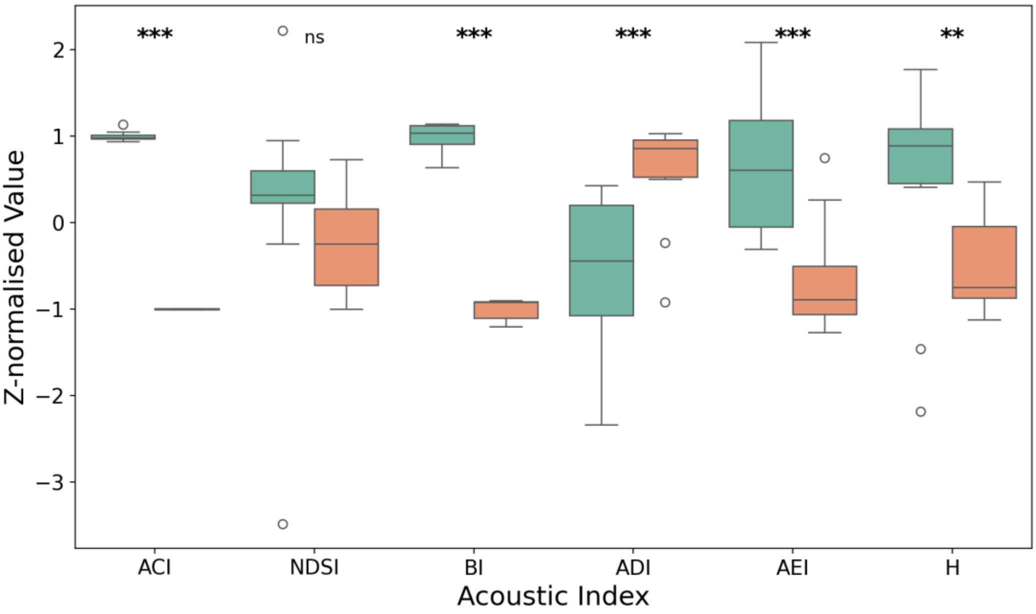

Figure 3. Differences in the six acoustic indices (Acoustic Complexity Index [ACI], Normalised Difference Soundscape Index [NDSI], Bioacoustic Index [BI], Acoustic Diversity Index [ADI], Acoustic Evenness Index [AEI], and Acoustic Entropy [H]) as measured at two different locations in the Caparao National Park. Different colours represent the locations: Green = Aleixo Valley, Pink = Santa Marta Valley. Stars indicate significant differences between locations (*** $p < 0.001$; ** $p < 0.01$, $p < 0.05$).

In contrast, SMV exhibited a higher Acoustic Diversity Index (2.38 ± 0.14, U = 14, $p < 0.001$), indicating greater diversity of acoustic signals across frequency bands despite lower overall activity (Figure 3). The Normalised Difference Soundscape Index (NDSI) did not differ significantly between sites ($p > 0.05$; Figure 3). These results demonstrate that AV supports a more complex and active soundscape, while SMV maintains higher acoustic diversity.

Spearman rank correlations assessed the relationship between species richness and acoustic indices, but no significant correlations were observed at AV. In contrast, at SMV, a moderately strong negative correlation emerged between species richness and NDSI (rs = -0.736, $p = 0.006$). This suggests that species richness increased as anthropophonic sound decreased in relation to biophonic sounds.

Further analysis of the Acoustic Complexity Index at both sites revealed varied contributions of specific bird species to the overall soundscape. ACI values for species at both sites spanned a broad range, with AV consistently presenting higher values (mean = 9139.45, range: 9009.9–9464.53) than SMV (mean = 4490.58, range: 4475.31–4508.05). The ACI is a quantitative measure of the variability and richness of acoustic signals produced by each species, with higher values indicating more complex and dynamic vocalisations.

At AV, all species exhibited ACI values exceeding 9000, with species such as *Asthenes moreirae* (mean ACI = 9247) and *Basileuterus culicivorus* (mean ACI = 9145) among the most acoustically complex, contributing substantially to the richness of the local soundscape (Figure 3). In contrast, SMV showed uniformly lower ACI values; still, species such as *Myiothlypis leucoblephara* (mean ACI = 9210) and *Turdus albicollis* (mean ACI = 9180) dominated the upper range, highlighting the site-specific differences in the acoustic contributions of the avifauna. Notably, the species with the highest number of recordings were not always those with the highest mean ACI, indicating that acoustic complexity is not solely a function of abundance. Overall, based on the AIC results, AV supports a greater number of species and host species that produce more complex and varied acoustic signals (Figure 4).

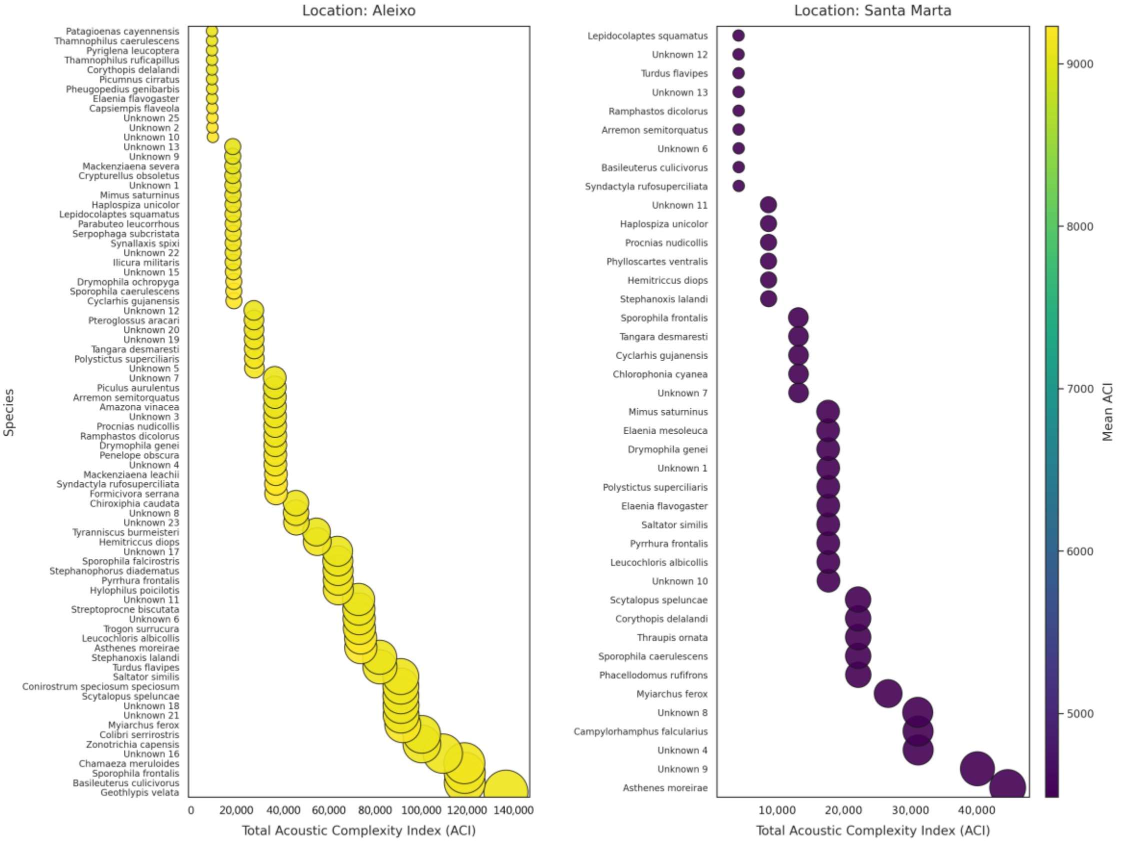

Figure 4. Contribution of each bird species to the acoustic complexity at Aleixo Valley and Santa Marta Valley. Bubbles represent different species. Bubble size indicates the number of recordings, and colour indicates the mean Acoustic Complexity Index (ACI, lighter colours represent higher AIC).

4. Discussion

This study demonstrates key differences in avian community composition, species richness, and acoustic characteristics between two forest types in Caparaó National Park, Brazil. Overall, the semi-deciduous forest in AV supported significantly higher species richness, a more diverse soundscape, and greater acoustic complexity compared to the dense ombrophilous forest in Santa Marta Valley. Furthermore, the detection of threatened and endemic species, including *Sporophila frontalis*, *Ramphastus vitellinus*, and *Amazona vinacea*, supports the conservation value of the study area.

The higher species richness observed at AV aligns with previous studies in the park [25] and supports the hypothesis that the site may offer more suitable conditions for a broader range of bird species. Still, these interpretations are made with caution given potential differences in the extent and heterogeneity of sampled environments.

Bird species richness is generally influenced by habitat complexity, with more varied environments supporting diverse bird communities [40]. In this study, contrasts were also anticipated due to differences in ecosystems, specifically with AV representing a semi-deciduous seasonal forest and SMV comprising a dense ombrophilous forest. Semi-deciduous forests are typically simpler in structure, with research from the CNP and surrounding areas indicating fewer understory species in semi-deciduous forests compared to the richer flora found in ombrophilous forests [30]. While ombrophilous forests are known to maintain high biodiversity levels [41], the lower species richness observed at SMV implies that other environmental factors might influence biodiversity more significantly than vegetation type alone. For example, local factors (elevation, proximity to water, masking noise) can reduce detectability and alter apparent richness in short timeframes [42,43].

Longitudinal studies and longer periods of recording could offer more detailed information on species composition than the two months of our research allow.

Human factors, such as land use, may also contribute to the decline in species diversity [43,44]. Crops and pastures surround the CNP, and the greater distance between agricultural land and AV (~2.6 km) compared to SMV (~1.6 km) may lessen edge effects and acoustic interference. This could result in higher detection rates and a more diverse community, corroborating previous research [40,43,44]. Furthermore, incidental signs of human disturbance—such as recorded gunshots captured in our dataset and the presence of ecotourism infrastructure (e.g., trails)—indicate additional anthropogenic pressures that may influence bird community composition in different areas of CNP. While we did not include anthropogenic covariates in our models, their observed occurrence highlights the importance of acknowledging both measured and unmeasured impacts when interpreting spatial variation in bird assemblages. Indeed, past research has demonstrated that human disturbance–even when not specifically quantified–can significantly alter species composition; omitting such factors may lead to incomplete or biased ecological inferences [45].

Acoustic indices revealed further distinct site-specific patterns that contribute to understanding biodiversity variations. Elevated ACI and BIA values at AV suggest frequent, structurally complex bird vocalisations. Acoustic structural complexity, indicated by higher ACI, can result from both species composition and within-species calling dynamics such as overlapping calls and varying syllable rates [46]. The notably higher BI at AV is likely due to the presence of numerous high-amplitude species such as *Amazona vinacea* and *Sporophila falcirostris*. In contrast, significantly fewer species with high-amplitude vocalisations were recorded within SMV. These calls tend to feature sudden changes in amplitude and frequency, often coinciding with dawn and dusk chorus or weather events. Such calls rapidly alter energy and temporal complexity, resulting in significant increases in ACI and BI scores [47,48].

SMV exhibited significantly higher ADI values, suggesting a flatter, more even distribution of acoustic energy across frequency bands. This pattern is most likely driven by reduced biophony and elevated geophony from the nearby waterfall. Such persistent broadband noise raises background levels and masks low-amplitude calls, particularly those of quieter species, thereby decreasing their detectability [48–50]. In addition, masking may diminish the apparent contribution of short, high-energy calling bouts from vocal active species, artificially lowering ACI and BI values [48–50]. These results are consistent with previous findings showing that natural broadband noise sources can interfere with biophonic-based indices, especially in rugged or montane tropical environments [40,48,49]. The combination of high ADI and low H at SMV supports the conclusion that waterfall noise homogenises the acoustic environment, suppressing both entropy and variability across time and frequency [48,50].

Most bird vocalisations in this study fell within the 2–6 kHz range (~72% of all detections), with peak activity between 3 and 5.5 kHz. This frequency band overlaps with the spectral range of the waterfall noise at SMV, where persistent broadband signals may reduce effective communication distances and increase the energetic cost of signalling for species with narrowband, low-frequency songs [51,52]. Such overlaps can have fitness consequences by limiting a signaller's ability to detect competitors, predators, or mates, and by reducing the receiver's perceptual range [51,53]. In contrast, AV's quieter environment facilitated clearer transmission of biophonic signals, with species such as *Thamnophilus desmarestii* and *Simoxenops striatus*, which produce structurally rich, modulated calls in the 3.5–5.5 kHz range, contributing significantly to elevate ACI values.

These findings corroborate previous studies showing ACI and BI are sensitive to vocal complexity and amplitude in bird-dominated frequency bands [54,55], whereas ADI shows reduced sensitivity under masking conditions [5,56].

The masking effect was further demonstrated by the reduced detection of species with high-pitched or subtle calls at SMV. Although *Sprorophila frontalis* and *Zonotrichia capensis* were recorded at both sites, their narrowband calls (2.5–3.5 kHz) were likely compromised at SMV, consistent with literature on the vulnerability of such signals to acoustic masking [5,49,50]. Low-frequency geophony significantly impacts species that vocalise within similar frequency ranges or lack vocal learning capabilities [57], potentially explaining the lower species richness found at SMV. Persistent ambient noise may discourage certain birds from inhabiting acoustically unsuitable areas.

To better isolate the effects of environmental noise, a logical next step would be to compare detection rates and acoustic indices for species present at both sites, while also quantifying variations in geophony and anthropophony. Focusing on species common to both locations controls for interspecific differences in vocal structure, allowing clearer attribution of any observed patterns to noise rather than species turnover. For example, *Myiarchus cinerascens* is known to alter breeding site selection in response to geophony and anthropophony [58,59], and spectrogram data for *Geothlypis velata* indicate site-specific vocal adaptations, with calls ranging from 4 to 11 kHz at SMV versus 4–6 kHz at AV—possibly to avoid masking. As both species exhibit documented vocal flexibility in noisy environments and occur at both sites, they represent promising focal species for future investigations into how ambient noise influences vocal behaviour and habitat use within CNP.

Vocal frequency also plays a crucial role in conservation monitoring, as species that vocalise at higher frequencies (>5.5 kHz), such as many passerines, may be disproportionately underdetected at sites with strong geophonic or anthropogenic noise [60]. Overlapping frequency bands combined with the temporal clustering of calls can increase masking, reducing the likelihood of detecting low-amplitude species during concurrent choruses [60,61]. This is especially important for rare, endemic, or threatened species with subtle or higher-pitched calls. For example, the threatened species *Drymophila ochropyga* and *Piculus aurulentus*, detected only at AV, typically vocalise between 3 and 6kHz and 3–10kHz, respectively, which makes them particularly vulnerable to masking effects in noisier environments.

During this study, vocalisations of *Ramphastus vitellinus* were detected in one AV recording, despite its documented range in Brazil being limited to the northern states of Amapá, Pará, Roraima, and Amazonas [62]. However, records from the Xeno-Canto database indicate occurrences in Minas Gerais (N = 7) and Espírito Santo (N) [63,64], suggesting a broader distribution than previously recognised. Similarly, the vulnerable *Sporophila frontalis*, which lacks local documentation in both literature and IUCN assessments [65], was detected in 23 out of 48 recordings. Given that tropical moist montane forests are critical habitats for this species [66,67], and the presence of dense bamboo patches (*Guadua tagoara*) provides essential foraging and nesting resources [68], these findings emphasise the role of CNP as a significant, yet under-recognised, habitat for *Sporophila frontalis*.

The detection of rare or elusive species that might otherwise be missed during visual surveys highlights the effectiveness and potential of acoustic monitoring for identifying rare species within increasingly complex environments [69–71]. Further avian research using bioacoustics and other field methods is strongly recommended to update regional management plans, being suggested for other studies investigating highly endangered birds in different areas in Brazil (e.g., cherry-throated Tanager (*Nemosia rourei*), Alagoas Antwren (*Myrmotherula snowi*), and Blue-eyed Ground-dove (*Columbina cyanopis*)) [69].

This approach aids in detecting acoustic signals and gaining a better understanding of the distributions and conservation needs of these and other declining species [70,71].

The negative correlation observed between the Noise Disturbance Index and species richness at SMV—but not at AV—likely reflects greater human disturbance near the former site. Although no direct anthropogenic structures are present within the core sampling area at SMV, its proximity to agricultural landscapes and human settlements may increase noise pollution and edge effects, thereby reducing avian richness through habitat degradation and behavioural avoidance [72,73]. NDSI is widely used to detect anthropogenic acoustic disturbance [32,74], and its effects may be attributed to microhabitat structure and persistent background noise impacting detectability. This suggests that even low-level human noise may alter community composition, although we did not systematically assess anthropogenic noises in CNP. Future surveys should incorporate standardised sound level metrics (e.g., Leq, dBA) and annotated noise classification to directly evaluate anthropogenic effects on the detectability of species and acoustic indices.

Although infrequent, the detection of gunshot raises important conservation concerns. Gunshot events were recorded exclusively at AV, despite its relatively remote location and higher biodiversity. In Brazil, wildlife hunting and trade are prohibited by Federal Law (Law No. 5197/67), and CNP is designated as a fully protected area under the National System of Protected Areas (SNAC) due to its importance in conserving threatened and endemic species [16]. While the correlation between gunshot presence and species richness or acoustic indices was not statistically significant, these detections indicate ongoing illegal hunting within the park, targeting threatened or high-value species such as *Thamnophilus desmaresti* and *Zonotrichia capensis* [75]. These finding aligns with reports of reduced enforcement capacity and persistent poaching threats in Caparaó, highlighting that illegal activities, alongside land use changes, remain among the main threats to the long-term integrity of Brazilian protected areas [76]. The ability to detect the presence of such sounds within a protected and remote area supports the value of passive acoustic monitoring for biodiversity assessments and detecting illegal activities [77]. Still, the absence of detected gunshots at SMV should not be interpreted as an absence of poaching, especially given the masking effects of geophonic noise, which may conceal such impulsive sounds.

Among the 98 distinct bird species recorded, 25 could only be classified at the Aves level, based on the clarity of their calls, confirming their avian origin. This accounts for nearly one-third of all species detected in this study. These birds' call patterns were visually and aurally distinctive compared to the vocalisations of local species or those from the broader region, as seen in the previously mentioned online databases. Consequently, specialists must conduct further research to identify these birds, as some of these unidentified species might be rare and of significant conservation concern.

While our study provides valuable insights into the use of passive acoustic monitoring for assessing soundscape composition and avian communities, some limitations warrant further investigation. First, acoustic indices remain vulnerable to geophonic interference, such as the persistent waterfall noise at SMV, which complicates interpretation in acoustically complex environments. To address this challenge, future studies should explore frequency filtering techniques and supervised classification models to better differentiate overlapping biotic and abiotic sounds [78,79]. Additionally, incorporating full-spectrum analyses rather than relying solely on aggregated indices could improve the temporal and spatial resolution of vocal activity patterns, offering nuanced insights into behaviour, habitat use, and anthropogenic impacts [80].

Second, the study's temporal scope was restricted to a brief sampling period, potentially underrepresenting species with peak vocal activity outside this window. As such, our results represent a conservative snapshot of actively vocalising birds during this timeframe, and estimates should be considered preliminary due to the inability to capture seasonal variations. Long-term or seasonal deployments would enable a more comprehensive understanding of such species turnover, migratory activity and vocal phenology, thereby offering a richer depiction of ecological variability [42].

Lastly, while acoustic indices and passive acoustic monitoring represent promising tools for biodiversity assessment, their reliability depends heavily on contextual calibration [47]. In this study, index performance varied substantially across sites, underscoring the need for ground-truthing and ecological validation [5,6,81,82]. Combining PAMs with habitat quality assessments, remote sensing data, and land use information can provide a more comprehensive and multi-scale evaluation of ecosystem health and environmental threats [73,82–84]. Moreover, the adoption of automated species identification tools and deep learning models could greatly enhance detection rates and reduce analyst workload in future monitoring efforts [81].

5. Conclusions

This study demonstrates the value of passive acoustic monitoring (PAM) for evaluating soundscape composition and avian community dynamics across ecologically distinct habitats. By integrating acoustic indices with species-specific detections, we showed that PAM can effectively distinguish between vegetation types and offer insights into community structure, particularly in relation to habitat variation. Patterns of vocal activity, especially within the 2–5 kHz frequency range, revealed important ecological signals linked to species presence and habitat complexity.

At the same time, our results highlight limitations that warrant further research. Acoustic indices were sensitive to both geophonic and anthropophonic noise, which can obscure assessments of biotic activity. Additionally, the variability in index performance across sites highlights the need for localised calibration and ecological validation. Future studies should focus on refining analytical approaches—such as supervised classification, full-spectrum analyses, and deep learning techniques—to distinguish overlapping sound sources better and enhance biodiversity assessments. Integrating complementary datasets, including habitat quality metrics and remote sensing data, would further improve understanding of the ecological drivers behind acoustic patterns and support more informed environmental monitoring and conservation planning.

It is important to acknowledge that long-term acoustic monitoring projects in Caparaó National Park and the wider Brazilian Atlantic Forest remain scarce, primarily due to logistical and financial challenges. Consequently, our findings represent one of the most comprehensive acoustic surveys conducted in CNP to date, providing critical baseline data on avian acoustic communities within the park.

Ultimately, this study contributes to the growing evidence that PAM is an indispensable tool in conservation science. With continued methodological improvements and expanded temporal and spatial coverage, PAM holds great promise for long-term ecological monitoring and for informing management strategies in rapidly changing environments.

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Abbreviations

The following abbreviations are used in this manuscript:

AV	Aleixo Valley
ARU	Autonomous recording units
ACI	Acoustic Complexity Index
ADI	Acoustic Diversity Index
AEI	Acoustic Evenness Index
BI	Bioacoustic Index
CNP	Caparao National Park
E	Endangered
H	Acoustic Entropy
IUCN	International Union for Conservation of Nature
kHz	Kilohertz
LC	Least Concern
NDSI	Normalised Difference Soundscape Index
NT	Near-threatened
PAM	Passive acoustic monitoring
SMV	Santa Marta Valley
STD	Standard deviation
V	Vulnerable

Appendix A

Table A1. List of Bird Species and Unidentified Occurrences Recorded at the Aleixo Valley and Santa Marta Valley Locations at the Caparaó National Park (N = 98).

Species	Common Name	Location	Number of Recordings
Asthenes moreirae	Itatiaia spinetail	Aleixo, Santa Marta	32
Scytalopus speluncae	Mouse-coloured tapaculo	Aleixo, Santa Marta	28
Myiarchus ferox	Short-crested flycatcher	Aleixo, Santa Marta	24
Saltator similis	Green-winged saltator	Aleixo, Santa Marta	24
Geothlypis velata	Southern yellowthroat	Aleixo	23
Sporophila frontalis	Buffy-fronted seedeater	Aleixo, Santa Marta	23
Basileuterus culicivorus	Golden-crowned warbler	Aleixo, Santa Marta	21
Chamaeza meruloides	Cryptic antthrush	Aleixo, Santa Marta	21
Pyrrhura frontalis	Maroon-bellied parakeet	Aleixo, Santa Marta	20
Aves	Unknown 8	Aleixo, Santa Marta	19
Aves	Unknown 9	Aleixo, Santa Marta	19
Aves	Unknown 16	Aleixo	18
Aves	Unknown 4	Aleixo, Santa Marta	18
Colibri serrirostris	White-vented violetear	Aleixo	17
Stephanoxis lalandi	Green-crowned plovercrest	Aleixo, Santa Marta	17
Conirostrum speciosum speciosum	Chestnut-vented conebill	Aleixo	16
Zonotrichia capensis	Rufous-collared sparrow	Aleixo	16

Table A1. *Cont.*

Species	Common Name	Location	Number of Recordings
Aves	Unknown 21	Aleixo	16
Leucochloris albicollis	White-throated hummingbird	Aleixo, Santa Marta	15
Trogon surrucura	Surucua trogon	Aleixo, Santa Marta	15
Aves	Unknown 18	Aleixo	15
Campylorhamphus falcularius	Black-billed scythebill	Santa Marta	14
Drymophila genei	Rufous-tailed antbird	Aleixo, Santa Marta	14
Sporophila caerulescens	Double-collared seedeater	Aleixo, Santa Marta	14
Turdus flavipes	Yellow-legged thrush	Aleixo, Santa Marta	14
Aves	Unknown 11	Aleixo, Santa Marta	14
Mimus saturninus	Chalk-browed mockingbird	Aleixo, Santa Marta	13
Aves	Unknown 6	Aleixo, Santa Marta	13
Elaenia flavogaster	Yellow-bellied elaenia	Aleixo, Santa Marta	12
Polystictus superciliaris	Grey-backed tachuri	Aleixo, Santa Marta	12
Sporophila falcirostris	Temminck's seedeater	Aleixo	12
Aves	Unknown 1	Aleixo, Santa Marta	12
Elaenia mesoleuca	Olivaceous elaenia	Aleixo, Santa Marta	11
Hemitriccus diops	Drab-breasted bamboo tyrant	Aleixo	11
Streptoprocne biscutata	Biscutate swift	Aleixo	11
Thraupis ornata	Golden-chevroned tanager	Santa Marta	11
Corythopis delalandi	Southern antpipit	Aleixo, Santa Marta	10
Hylophilus poicilotis	Rufous-crowned greenlet	Aleixo, Santa Marta	10
Tangara desmaresti	Brassy-breasted tanager	Aleixo, Santa Marta	10
Aves	Unknown 17	Aleixo	10
Aves	Unknown 7	Aleixo, Santa Marta	10
Amazona vinacea	Vinaceous-breasted Amazon	Aleixo, Santa Marta	9
Ramphastos dicolorus	Green-billed toucan	Aleixo	9
Aves	Unknown 10	Aleixo, Santa Marta	9
Aves	Unknown 13	Aleixo, Santa Marta	9
Chiroxiphia caudata	Blue manakin	Aleixo	8
Haplospiza unicolor	Uniform finch	Aleixo, Santa Marta	8
Procnias nudicollis	Bare-throated bellbird	Aleixo, Santa Marta	8
Stephanophorus diadematus	Diademed tanager	Aleixo	8
Tyranniscus burmeisteri	Rough-legged tyrannulet	Aleixo	8
Aves	Unknown 12	Aleixo, Santa Marta	8
Aves	Unknown 3	Aleixo	8
Aves	Unknown 19	Aleixo	7
Aves	Unknown 23	Aleixo	7
Arremon semitorquatus	Half-collared sparrow	Aleixo, Santa Marta	6
Cyclarhis gujanensis	Rufous-browed peppershrike	Aleixo, Santa Marta	6
Lepidocolaptes squamatus	Scaled woodcreeper	Aleixo, Santa Marta	6
Mackenziaena severa	Tufted antshrike	Aleixo	6
Penelope obscura	Dusky-legged guan	Aleixo	6
Pteroglossus aracari	Black-necked aracari	Aleixo	6
Syndactyla rufosuperciliata	Buff-browed foliage-gleaner	Aleixo, Santa Marta	6
Drymophila ochropyga	Ochre-rumped antbird	Aleixo	5
Formicivora serrana	Serra antwren	Aleixo	5
Phacellodomus rufifrons	Rufous-fronted thornbird	Santa Marta	5
Pheugopedius genibarbis	Moustached wren	Aleixo	5
Piculus aurulentus	Yellow-browed woodpecker	Aleixo, Santa Marta	5
Pyriglena leucoptera	White-shouldered fire-eye	Aleixo	5
Aves	Unknown 15	Aleixo	5
Mackenziaena leachii	Large-tailed antshrike	Aleixo	4
Parabuteo leucorrhous	White-rumped hawk	Aleixo	4
Synallaxis spixi	Spix's spinetail	Aleixo	4
Aves	Unknown 22	Aleixo	4
Chlorophonia cyanea	Blue-naped chlorophonia	Santa Marta	3
Hemitriccus diops	drab-breasted bamboo tyrant	Santa Marta	3
Phylloscartes ventralis	Mottle-cheeked tyrannulet	Santa Marta	3
Serpophaga subcristata	White-crested tyrannulet	Aleixo	3
Aves	Unknown 2	Aleixo	3
Aves	Unknown 20	Aleixo	3
Aves	Unknown 5	Aleixo	3
Crypturellus obsoletus	Brown tinamou	Aleixo	2
Ilicura militaris	Pin-tailed manakin	Aleixo	2
Patagioenas cayennensis	Pale-vented pigeon	Aleixo	2
Thamnophilus caerulescens	Variable antshrike	Aleixo	2
Turdus albicollis	White-necked thrush	Aleixo	2
Turdus rufiventris	Rufous-bellied thrush	Aleixo, Santa Marta	2
Aves	Unknown 24	Aleixo	2

Table A1. *Cont.*

Species	Common Name	Location	Number of Recordings
Capsiempis flaveola	Yellow tyrannulet	Aleixo	1
Cyclarhis gujanensis ochrocephala	Rufous-browed peppershrike	Aleixo	1
Leptodon cayanensis	Grey-headed kite	Aleixo	1
Myiarchus swainsoni	Swainson's flycatcher	Aleixo	1
Picumnus cirratus	The white-barred piculet	Aleixo	1
Ramphastos dicolorus	Green-billed Toucan	Santa Marta	1
Ramphastos vitellinus	Channel-billed toucan	Aleixo	1
Sittasomus griseicapillus	Olivaceous woodcreeper	Aleixo	1
Thamnophilus ruficapillus	Rufous-capped antshrike	Aleixo	1
Aves	Unknown 25	Aleixo	1
Aves	Unknown 26	Aleixo	1

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