Simultaneous acoustic monitoring uncovers evidence of biodiversity loss and overlooked temporal variation in a threatened Amazonian bird community

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Abstract

1. Birds are frequently used as indicator taxon in ecology, but traditional surveys are prone to error and largely inadequate in the dense, speciose tropical forests where they are most needed. Passive acoustic monitoring (PAM) has the potential to address many of these pitfalls, providing unique advantages for both long-term monitoring and rapid biodiversity assessment. Here, we evaluate the effectiveness of PAM for characterizing spatiotemporal variation in avian species richness, diversity, vocal activity, and community composition in the Amazon basin global biodiversity hotspot.

2. We employed an array of ten autonomous recording units (ARUs) spanning edge, degraded, and interior forest at a reserve on the deforestation frontier of Madre de Dios, Peru, a region featuring some of the richest, most complex avian assemblages on Earth. Recordings from 21 dawn-hours across three days at seven sites were manually annotated by a single observer.

3. ARUs and manual annotation performed well as an inventory method, especially for midstory and understory species. Sites in edge and degraded habitats featured significantly lower avian species richness, Shannon diversity, and vocal activity levels than in the forest interior, patterns that replicate the findings of prior high-effort avian censuses in the region. We observed significant temporal variation between days; at all featured sites, vocal activity was highest on January 20th and lowest on January 31st.

4. We demonstrated that novel annotation-generated metrics can work as effective proxies for abundance data and per-capita song rate, correlating with diversity indices and efficiently

characterizing habitats at a level of detail unobtainable with human observers. Generalist species were significantly overrepresented in the soundscapes of interior forest, relative to their contributed share of species richness, and interior specialists were underrepresented, suggesting that the entire 191ha site is degraded. The between-days temporal variation that we documented, almost certainly overlooked without simultaneous monitoring, may obfuscate or distort the results of traditional surveys.

5. **Synthesis & Applications.** We propose that PAM should become a cornerstone of biodiversity research. The standardization advantages demonstrated in this study, permanent storage, multi-taxa applications, and potential of automated identification make bioacoustics an ideal methodological avenue for guiding management and policy under rapid global change.

Keywords: avian biodiversity, bioacoustics, deforestation and degradation, edge effects, fragmentation, passive acoustic monitoring, Peruvian Amazon, spatiotemporal variation.

1 Introduction

The tropics account for an overwhelming share of Earth's biodiversity, featuring more than 75% of all species and over 90% of terrestrial birds (Barlow *et al.* 2018). Of particular importance is the Amazon basin, the largest intact tropical system on the planet (Allan *et al.* 2017) and the epicenter of global biodiversity (Jenkins *et al.* 2013). Like most of the tropics, the Amazon is undergoing major ecological change (Edelman 2014), primarily from the region's rapidly expanding anthropogenic land use footprint (Laurence *et al.* 2014), as well as the increasing impacts of climate change (Lovejoy 2013). Despite their importance, however, the tropics are largely neglected in biodiversity, and ecosystem function literature (Wilson *et al.* 2016), and assumptions derived from studies in temperate regions have been erroneously used to characterize tropical systems where they do not apply (Clarke *et al.* 2017). If we are to meet the international community's sustainable development goals, more biodiversity research focused specifically on tropical systems is necessary (United Nations 2015).

Land use change in Amazonia, primarily the result of agriculture, mining, and expanding road networks, is the most significant threat to biodiversity in the basin (Laurance *et al.* 2014) and likely an underestimated driver of climate change (Mahowald *et al.* 2017), compounding the importance of its study. In Madre de Dios, Peru, these pressures have driven accelerated rates of deforestation, fragmentation, and degradation over recent decades, making the region a global deforestation hotspot (Nicolau *et al.* 2019, Sánchez-Cuervo *et al.* 2020), and inducing ecosystem decay and biodiversity loss in remaining habitat patches (Canaday & Rivadeneyra 2001,

Laurance *et al.* 2002, Haddad *et al.* 2015, Stouffer 2020), but the full impacts of these changes remain unknown. *Várzea* floodplain forest, the focus of this study, is particularly vulnerable to these dynamics due to its limited distribution, easy access from river-based transport, and high concentration of endemic bird species, many of which are restricted to particular successional stages in this forest type (Foster *et al.* 1994, Robinson & Terborgh 1997). Even in intact Amazonian systems, long-term studies have recently uncovered baseline shifts and population declines in avian communities, perhaps due to climate change (Blake & Loiselle 2015, Stouffer *et al.* 2020). However, such assessments are complicated by the difficulty of tropical field surveys, leading to flawed baseline species occurrence data (Boakes *et al.* 2010, Lees *et al.* 2014, Robinson *et al.* 2018) and overlooked biodiversity losses in Amazonia (Socolar *et al.* 2019), which interfere with conservation efforts in the region.

Birds, which are generally accessible, identifiable, and better understood than other Neotropical groups, are presently the most cost-effective study taxa for monitoring Amazonian biodiversity (Gardner *et al.* 2008, Lees *et al.* 2014). Birds are ubiquitous and can be highly responsive to habitat conditions, making them excellent proxies for understanding ecosystem health and global change (Remsen 1994, Blackburn & Gaston 1998, Bibby 1999). Despite these advantages, the Amazon's avifauna remains poorly documented and subject to significant knowledge gaps (Barlow *et al.* 2011, Lees *et al.* 2014). While high-quality, standardized, scalable data on birds and other taxonomic groups is necessary for guiding conservation priorities in the tropics, such data are difficult to generate with traditional survey methods. Overwhelming avian species richness, including many rare and similar species, challenging logistics, and poor viewing conditions typical of dark, densely vegetated rainforest interiors (Fig. 1) contribute to the unreliability of avian surveys in Amazonia, where upwards of 95% of birds are heard but never seen by a field observer (Robinson *et al.* 2018). Amazonian soundscapes include thousands of vocalization types, inducing high rates of false-negative and false-positive identification errors (Remsen 1994), and it can take months for skilled observers to reach a comfort level attainable in just one to two weeks of field experience in temperate systems (Parker 1991). Additionally, neotropical soundscapes are subject to high levels of spatiotemporal heterogeneity, with species singing in narrow time windows (Parker 1991, Hart *et al.* 2015), at seasonally variable rates (Blake 1992), and as a function of fine-grain floristic, geographic, and spatial variables, which are still poorly understood (Menger *et al.* 2017). As a result, studies relying on point counts and other non-simultaneous survey methods in Amazonia may require substantial sample sizes, which are often infeasible to obtain (Esquivel & Peris 2008, Rodriguez *et al.* 2014).

Figure 1: Site 07, typical *várzea* habitat in the reserve.

Autonomous Recordings Units (ARUs) effectively address many of the shortfalls of traditional point counts in tropical systems. Simultaneous and continuous monitoring of many locations has the capacity to completely eliminate temporal bias in surveys (Venier *et al.* 2012, Tegeler *et al.* 2012), data collection is independent of observer skill level, and permanent records can be reviewed, distributed, and verified by experts at will, enabling independent verification, reducing identification errors (Rempel *et al.* 2005, Rempel *et al.* 2019), and serving as ecological time capsules (Sugai & Llusia 2019). ARUs can generate significantly greater data volume than traditional methods without increasing field time or cost (Hobson *et al.* 2002, Acevedo & Villanueva-Rivera 2006, Tegeler *et al.* 2012), and bioacoustic data contains vocalizations of non-target taxa and other soundscape elements, opening the door for more holistic research (Newson *et al.* 2017), while studies focused exclusively on birds can come at the expense of developing knowledge of other groups (Gardner *et al.* 2008). Human presence in the field during survey periods, which can bias results, is unnecessary (Jorge *et al.* 2018), and habitat structure influences bioacoustic surveys less than point counts (Darras *et al.* 2018). Perhaps most importantly, acoustic data introduces the possibility of automated detection and identification, which would have a transformative impact on biodiversity monitoring (Kahl *et al.* 2020). ARUs provide equivalent or superior data to point counts, especially in tropical forests like the Amazon, where the number of experienced observers is limited, access is difficult, the vast majority of species are best detected aurally, and sites are highly heterogenous over space and time (Haselmayer & Quinn 2000, Acevedo & Villanueva-Rivera 2006, Cellis-Murillo *et al.* 2012, Shonfield & Bayne 2017, Darras *et al.* 2018, Darras *et al.* 2019, Pillay *et al.* 2019, Blake 2021).

Here, we used ARUs to explore spatiotemporal variation in avian species richness, Shannon diversity, vocal activity, and community composition between sites at a threatened Amazonian reserve. Situated 15 km east of the rapidly growing frontier town of Puerto Maldonado and adjacent to an unmarked road, Inkaterra Reserva Amazónica (ITRA), our study site, faces intense land use pressure (Fig. 2). Likely inducing compositional changes and biodiversity loss across the reserve (Canaday and Rivadeneyra 2001, Laurance *et al.* 2002, Stouffer 2020), these dynamics are expected to intensify in coming years (Bird *et al.* 2012), making high-quality, baseline bioacoustic data especially valuable. Additionally, fully annotated Amazonian dawn choruses are critical for training automated soundscape identification algorithms, for which this dataset has already been used (Kahl *et al.* 2020).

We asked three overarching questions in our analyses. (1) Performance of acoustic sampling: how well do ARUs document avian community structure within the reserve, and can acoustic data serve as a proxy for abundance data, replicating the results of historic census efforts in Amazonia? (2) Temporal analysis: was there significant temporal variation between days that non-simultaneous survey methods might overlook? (3) Spatial analysis: do differences in habitat type and quality, particularly between edge and interior habitats, significantly impact avian species richness, diversity, community composition, and vocal activity? Can bioacoustic data be used to efficiently characterize habitats, without relying on manual estimates of per-capita song rate?

2 Materials & Methods

2.1 Site Selection

The data for this study was collected at Inkaterra Reserva Amazónica (ITRA) in the Madre de Dios Department of southeastern Peru (12°32'07.8" S, 69°02'58.2" W). This 191 ha private reserve is located at an elevation of ~200 m along the Madre de Dios River, directly across from the Reserva Nacional de Tambopata, in one of the most biodiverse regions on the planet (Foster *et al.* 1994) (Fig. 2). The habitat at ITRA primarily consists of *várzea* floodplain forest, the most endangered forest type in the southwestern Amazon (Phillips *et al.* 1994), interspersed with seasonally flooded *Mauritia* palm swamp forest.

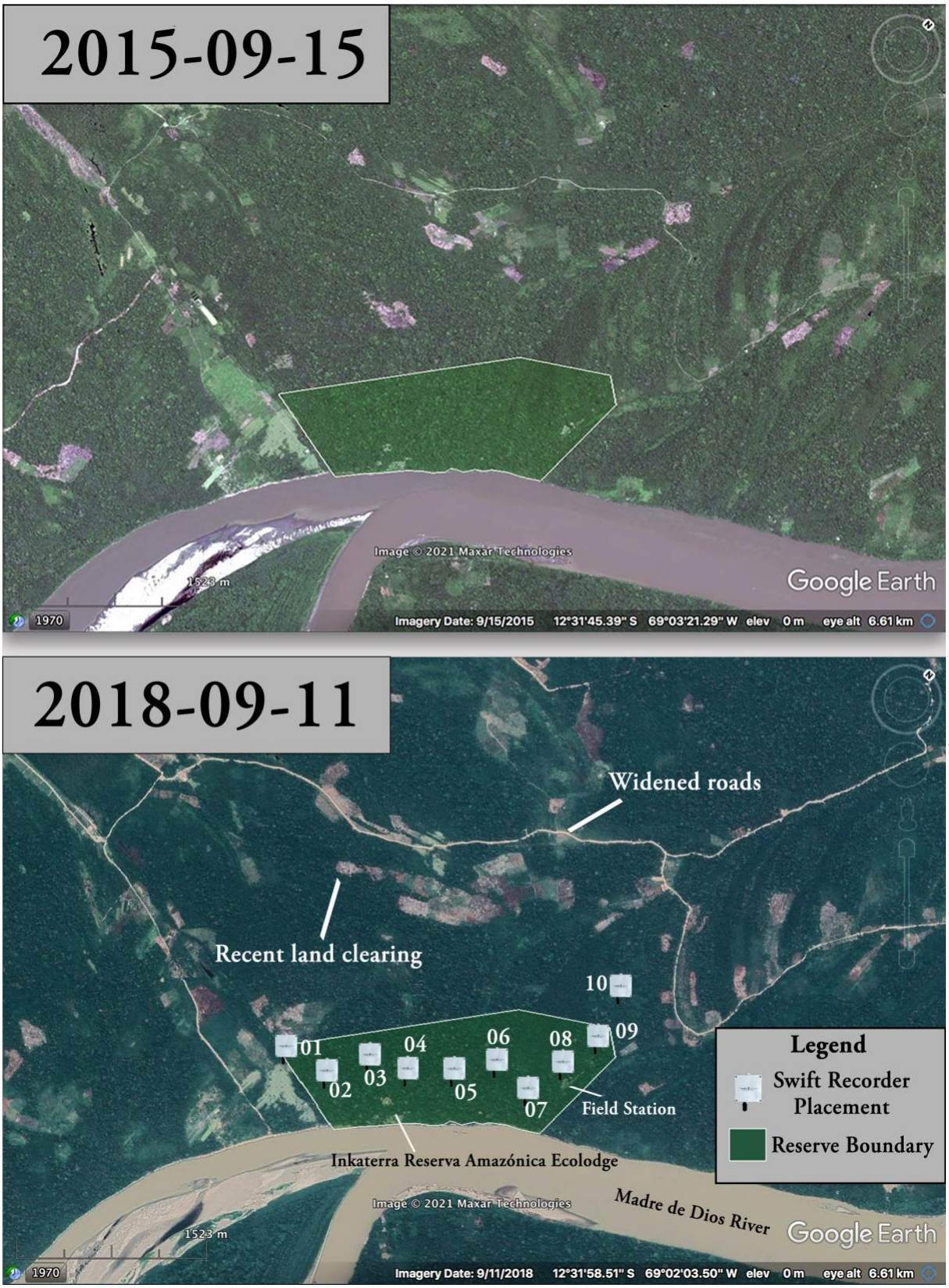

Figure 2: Swift recorder layout and progression of deforestation at the study site. Recorder placements covered a range of habitats including edge (Site 01), degraded forest (Site 10), and intact *várzea* in the reserve's interior

2.2 Data Collection

Data were collected January 14-February 2, 2019, using ten ARUs (Swift recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA). ARUs were deployed across the entire reserve, at a minimum distance of 350 m from each other and 450 m from the river, to limit overlapping detection (pseudo-replication) and background noise (Ralph *et al.* 1995). Deployment locations were chosen to represent a gradient of intactness and forest habitat type, including edge (Site 01), degraded (Site 10), mature *várzea* in the reserve's interior (Site 04 and Site 06), and mixed palm swamp-*várzea* habitat (Site 02 and Site 05) (FIG. 2). Placed at a height of 1.5 m above the ground, the 10 ARUs recorded continuously (mono, WAV format) throughout the deployment using a sampling rate of 48 kHz (16-bit resolution) and a gain setting of 35 dB. The microphone sensitivity of the Swift was -44 dBV/Pa (+/- 3 dB) and featured a flat frequency response (+/- 3 dB) in the frequency range of the vocalizations of interest. The clipping level of the analog-to-digital (ADC) converter was +/- 0.9 V.

2.3 Acoustic Analysis (Annotation Process)

Twenty-one total dawn-hours, from 05:00-06:00 PET (10:00-11:00 UTC), representing 7 of the 10 sites on three days, were manually annotated by the lead author using the Raven Pro Sound Analysis Software® (version 1.5; K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA). Six of these sites were used for analyses, two in each habitat type: fringe (edge and degraded), mixed, and *várzea*, with Site 08 excluded. For some analyses, mixed and *várzea* were grouped together as interior habitats. The three days, January 16 (Day A), January 20 (Day B), and January 31 (Day C), 2019, were randomly chosen from a subset of days that featured less than 5 minutes of heavy rain during the dawn-hour. The dawn-hour was selected because it contains the highest level of vocal activity and diversity among neotropical birds (Berg *et al.* 2006), including many species that only sing in narrow time windows around first light (Parker 1991, Blake 1992). Additionally, the dawn soundscape in Amazonia features far less anthropogenic activity and insect noise than other periods, reducing interference with avian species detection (Hart *et al.* 2015, Metcalf *et al.* 2020).

Spectrograms were viewed in 60-second increments split over two rows (Hann window, 3dB bandwidth = 100 Hz, 690 FFT window size, 1024-sample DFT, 95% temporal overlap). To reduce bias introduced by improved sound identification knowledge developed throughout the project, the order in which site days were annotated was determined using a random number generator. Vocalizations were labeled for both species and a handful of broader groups with confusing or indistinguishable calls, e.g., “TRSP” as “trogon species” (*Trogonidae sp.*). Background vocalizations, audible but not clearly visible on a spectrogram, were denoted with a ‘1’ and excluded from most analysis. To account for inter-specific variation in call volume and

frequency, consistency for applying 'background' designation was approached on a species-specific basis. In cases where vocalizations from the same species were separated by fewer than 5 seconds, they were included as part of the same annotation, while annotations were split if the gap between vocalizations exceeded 5 seconds. An assortment of unlabeled sound clips, featuring both identified and unidentified species, were sent to regional experts for secondary verification. Annotations were reviewed repeatedly until unidentified vocalizations made up less than 10% of the total avian vocal activity on a given recording. Considerable effort was made to accurately label as many foreground and background vocalizations as possible, with the goal of improving the value of this dataset for training soundscape-based automated identification algorithms.

2.4 Statistical Analyses

For each site, day, and individual recording, four metrics were calculated: species richness, Shannon diversity, vocal prevalence, and Bray-Curtis dissimilarity. Species richness and Shannon diversity were included as standard measures of ecological diversity (Okansen *et al.* 2019, Metcalf *et al.* 2020). Vocal prevalence (VP), the number of 15-second blocks in a recording containing at least one foreground vocalization from a species or taxa, was used to quantify vocal activity levels or soundscape abundance. Bray-Curtis dissimilarity was calculated between days, sites, and individual site days, ranging from 0 (no difference) to 1 (completely different).

Certain taxa were excluded from most analysis for data quality reasons: parrots (*Psittacidae sp*.), because they occurred almost exclusively as calling flyovers, along with *Columbiformes* (pigeons and doves) and three congeneric tinamou species, Cinereous Tinamou (*Crypturellus cinereus*), Little Tinamou (*C. soui*), and Bartlett's Tinamou (*C. bartletti*), which had overlapping vocalizations and were inconsistently identified with confidence. Non-species taxa were excluded from calculations of species richness and Shannon diversity but included in total vocal prevalence. Species were assigned to broad habitat-preference groups: interior (primary forest) specialists, edge (secondary forest) specialists, and generalists, based on the *Birds of Peru* field guide (Schulenberg *et al.* 2010), the Cornell Lab of Ornithology's *Birds of the World* (Billerman *et al.* 2020), and personal field experience (Supporting Information).

The scientific questions posed in the introduction were addressed as follows:

1: Performance of acoustic sampling. The list of species identified during this study was compared with data submitted from the reserve to the citizen science database eBird during the Dec-Feb season, over 13 years through 2020 (Sullivan *et al.* 2009). Because the relative utility of ARUs vs field observers varies across groups, species were placed in one of 10 guilds to facilitate more detailed comparisons: soaring raptors, hummingbirds, parrots, aerial insectivores

(swallows and swifts), nocturnal species, open habitat specialists, aquatic habitat specialists (including flooded forest obligates), and canopy, midstory, and understory forest species. Correlation analysis (Pearson's *r*) was employed to assess the relationship between vocal prevalence, species richness, and Shannon diversity. Using vocal prevalence as a stand-in for abundance data, a rank-abundance curve was plotted and compared with the results of Terborgh *et al.* 1990, a historical high-effort census conducted in the region using mist-netting and point counts, to evaluate the performance of ARUs as an alternative to traditional approaches. The total number of species recorded was summarized in a table for each site and day, along with average species richness.

2: Temporal analysis. Paired T-tests were used to compare variation in species richness, Shannon diversity, and vocal prevalence across the three days, and to compare variation in Bray-Curtis dissimilarity between parings of days.

3: Spatial analysis. Two-way repeated-measures ANOVA followed by Tukey's HSD tests for multiple comparisons were conducted in R (R Core Team, 2019), to assess differences in Shannon diversity, species richness, and vocal prevalence between habitat types. To evaluate whether or not community composition differed at edge sites compared to the forest interior, the Bray-Curtis dissimilarity between the edge Site (01) and all other sites was compared to the Bray-Curtis dissimilarity between non-edge sites. Relative soundscape representation (RSR) was assessed for each site day and habitat type by comparing the share of total vocal prevalence to the share of species richness contributed by habitat-preference groups. RSR has the potential to serve as a proxy for per-capita song rate, which is positively correlated with density and territory quality in birds (Pillay *et al.* 2019), therefore aiding in the characterization of habitat type and condition. Paired T-tests were used to assess the significance of representation. Patterns in community composition across sites were assessed using non-metric multidimensional scaling ordination (NMDS). NMDS analyses were calculated using the "bray" method and metaMDS function from the "vegan" package in R (Okansen *et al.* 2019), using vocal prevalence in place of abundance, for all species, interior specialists, and edge specialists, respectively. The NMDS ordinations were performed on two axes and checked to ensure that the output met minimum stress requirements (Kruskal 1964).

3 Results

3.1 Summary Information

We identified 134 species over 21 dawn-hours; 18,963 individual bounding-box annotations were drawn in Raven Pro, of which 94.8% were identified to the species or taxon level. At individual sites, the percent of total Vocal Prevalence that was not identified to a species or taxa group ranged from 4.1% (Site 06) to 7.1% (Site 02) between sites, and from 5.1% (Day C) to 5.4% (Day A) between days. Most annotations occurred in the frequency range 0.5-5

kHz, which features the highest diversity of Amazonian bird songs at dawn, and the least interference from insects, which contribute to significant signal masking between 4-12 kHz (Hart *et al.* 2015, Alvarez-Berríos *et al.* 2016, Aide *et al.* 2017, Metcalf *et al.* 2020). Seven species were recorded only as background vocalizations, and seven more were restricted to Site 08, which was excluded from the majority of analysis because of sustained interference from a Mealy Parrot (*Amazona farinose*), which obscured other vocalizations on Day B and severely impacted overall detections at the site (Supporting Information).

Of the 120 foreground species detected outside of Site 08, two, Black-faced Antthrush (*Formicarius analis*) and Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) were detected on all 18 site days, and six more were detected on at least two-thirds of site days. Most species were rare; more than half (66, 55%) were detected on 4 or fewer site days, and roughly a quarter (27, 23%) on only a single recording (Fig. 3). In terms of total vocal prevalence, the most abundant species were Hauxwell's Thrush (*Turdus hauxwelli*), Black-faced Antthrush, and Thrush-like Wren (*Camplyothynchs turdinus*), which were also the three most common species on eBird.

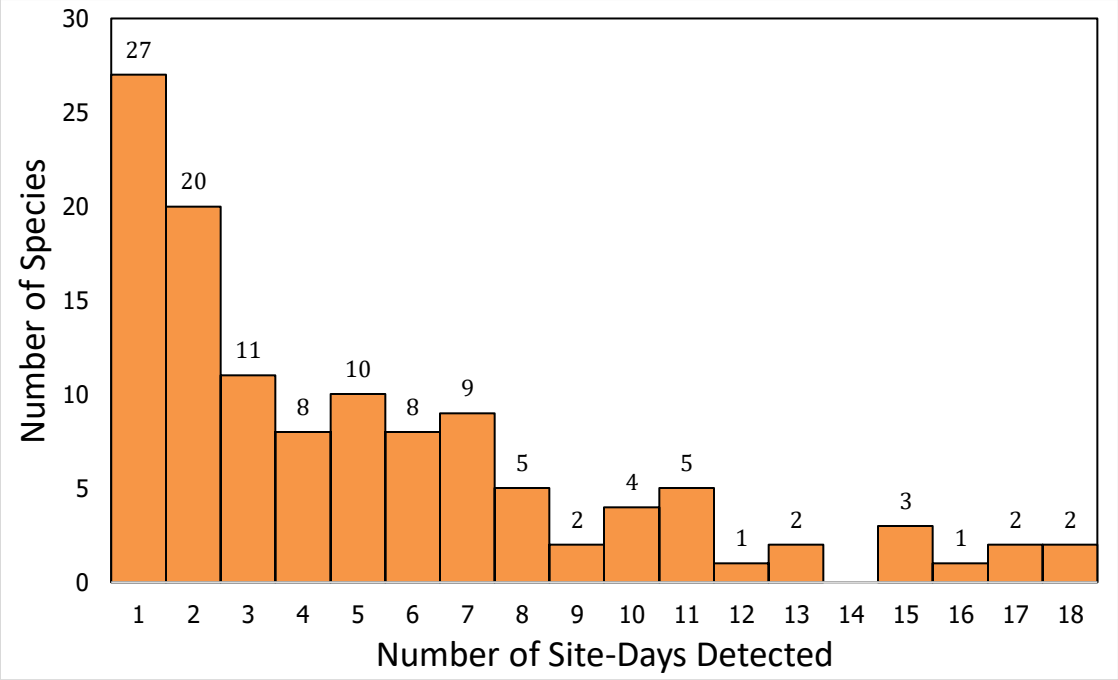

Figure 3: Number of site-days on which species were detected.

3.2 Performance of Acoustic Sampling

A total of 134 species were identified from recordings across all sites, including background vocalizations and species only detected at Site 08. Through 2020, field observers in the reserve reported 360 species to the citizen science database eBird, spanning 253 complete checklists from December-February. Four species were detected exclusively with ARUs:

Cinereous Mourner (*Laniocera hypopyrra*), Royal Flycatcher (*Onychorhynchus coronatus*), Striped Cuckoo (*Tapera naevia*), and Blue-crowned Manakin (*Lepidothrix 11oronate*), a first record for the reserve, bringing the total species list from both methods to 364. Species reported on >2% and >5% of eBird checklists were considered "regular" and "expected," respectively, and the majority of species reported to eBird but missed by ARUs were neither (Table 1).

		All Species			Regular Species (>2% of eBird Checklists)			Expected Species (>5% of eBird Checklists)		
	Guild	**ARUs**	**eBird**	**% Coverage**	**ARUs**	**eBird**	**% Coverage**	**ARUs**	**eBird**	**% Coverage**
Target Groups	Canopy	29	91	31.9	28	61	45.9	21	40	52.5
	Midstory	36	52	69.2	28	34	82.4	22	25	88.0
	Understory	55	90	61.1	36	48	75.0	29	31	93.5
Non-target Groups	Parrots	5	16	31.3	5	11	45.5	5	6	83.3
	Aquatic	5	35	14.3	3	8	37.5	2	5	40.0
	Open	1	11	9.1	0	4	0.0	0	1	0.0
	Nocturnal	2	10	20.0	1	2	50.0	1	1	100.0
	Aerial Insectivores	0	16	0.0	0	7	0.0	0	2	0.0
	Hummingbirds	0	16	0.0	0	6	0.0	0	2	0.0
	Soaring Raptors	1	23	4.3	1	12	8.3	0	4	0.0
	Total	***134***	***360***	***37.2***	***102***	***193***	***52.8***	***80***	***117***	***68.4***

Table 1: Performance of ARUs vs eBird data by guild and rarity level. eBird detections are based on 253 complete checklists submitted within the reserve from December-February.

ARUs performed best with midstory and understory species, detecting 63% of all species in these foraging strata, including 91% of expected species, but were considerably less effective for canopy foragers, and, as expected, missed the vast majority of species in non-target groups (Table 1). There was a significant positive relationship between vocal prevalence and both species richness ($r = 0.83$, $p = 1.9e\text{-}05$) and Shannon diversity ($r = 0.75$, $p = 3e\text{-}04$) (Fig. 4). Using vocal prevalence as a stand-in for abundance, a rank-order curve was plotted; in line with the abundance-based results of Terborgh *et al.* (1990), we found that vocal prevalence was distributed equitably, fitting a log distribution ($R^2 = 0.84$), with a high proportion of total vocal prevalence contributed by only a few species (Fig. 5).

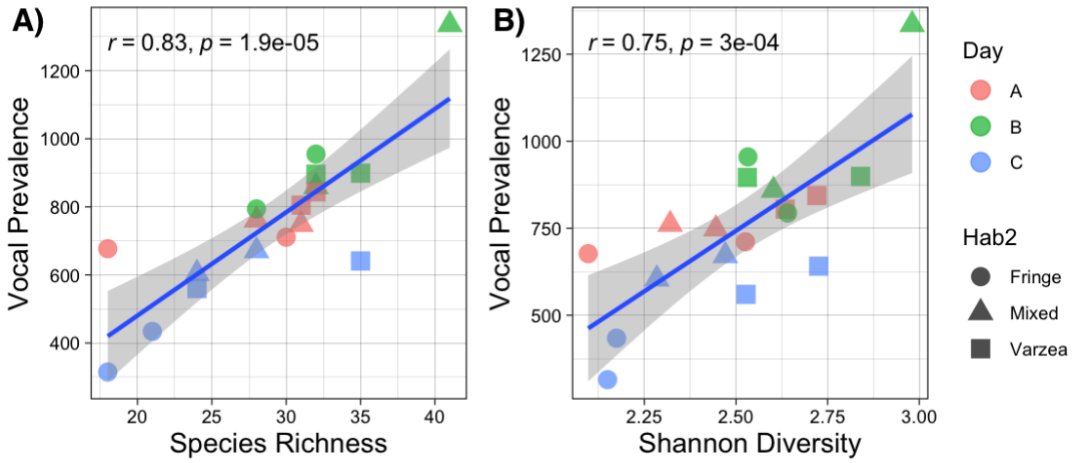

Figure 4: Vocal prevalence vs Species Richness (A) and Shannon Diversity (B).

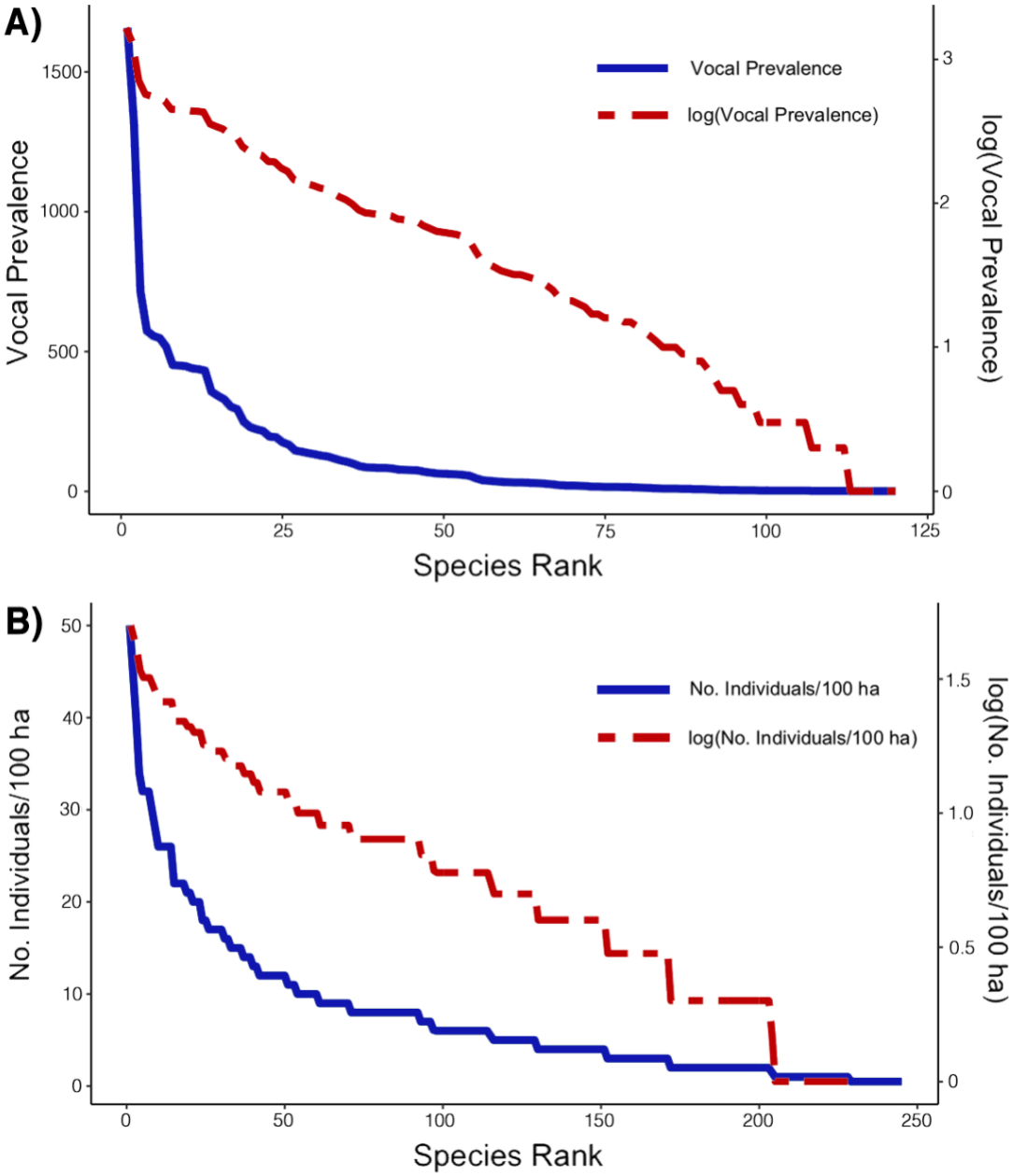

Figure 5: Rank-order curves for vocal prevalence (A), using our data, and no. individuals/100 ha (B), using the data from Terborgh *et al.* (1990), an avian census conducted with traditional methods over 12 person-months of effort at Cocha Cashu, another reserve in Madre de Dios.

3.3 Temporal Variation

We captured significant temporal variation in estimated avian species richness, Shannon diversity, vocal prevalence and inter-site community dissimilarity (Table 2). The three diversity and activity measures averaged highest on Day B, and temporal variation was especially consistent for vocal prevalence; at all six sites, vocal prevalence was highest on Day B and

lowest on Day C. Paired t-tests found that Day B had significantly higher average species richness (p = 0.024), Shannon diversity (p = 0.015), and VP (p = 0.0027) than Day C, which also had significantly lower average VP than Day A (p = 0.0026). Day B also featured consistently higher values than Day A for species richness (p = 0.094), Shannon diversity (p = 0.092) and VP (p = 0.059), but these results were not statistically significant. The compositional similarity between sites also differed across days; the average Bray-Curtis dissimilarity between Days A and B, 0.750, was significantly greater than the Bray-Curtis dissimilarity between Days A and C, 0.715 (p = 0.022), and between Days B and C, 0.710, (p = 0.044). The highest species total detected in an individual recording came from Site 02, Day B, which featured 41 species, 46% more than the 28 species identified at the site on Day A and C; adjacent Site 01 also featured significantly more species on Day B (32) than on Days A and C (18).

Metric	Day	Total	Mean/pt	SE/pt	Range	Highest Site	Lowest Site
Vocal Prevalence	A	4546	757.7	25	677-844	Site 06	Site 01
	B	5738	956.3	79	794-1335	Site 02	Site 10
	C	3225	537.5	56	315-671	Site 02	Site 01
Species Richness	A	57	27.5	2.1	18-32	Site 06	Site 01
	B	78	33	1.9	28-41	Site 02	Site 01
	C	56	25.7	2.5	18-35	Site 06	Site 01
Shannon Diversity	A	3.50	2.46	0.084	2.10-2.72	Site 06	Site 01
	B	3.57	2.69	0.068	2.53-2.98	Site 02	Site 10
	C	3.26	2.39	0.084	2.15-2.73	Site 06	Site 01

Table 2: Summary of Temporal Variation

3.4 Spatial Variation

Sites in fringe habitats averaged significantly lower species richness ($F_{1, 14}$ = 10.31, p = 0.0063), Shannon diversity ($F_{1, 14}$ = 6.98, p = 0.019), and vocal prevalence ($F_{1, 14}$ = 6.56, p = 0.023) than interior sites (Table 3). Site 01, in edge habitat, was the only site to feature significantly higher inter-site Bray-Curtis dissimilarity (0.83) than the average between other sites (0.66, p = 2.2e-16) (Fig. 6), and NMDS ordination showed clustering of interior sites in terms of species composition (Fig. 7).

Metric	Site	Habitat	Total	Mean/day	SE/day	Range	Highest Day	Lowest Day	UnID%
Vocal Prevalence	01	Fringe	1947	649	185.3	315-955	Day B	Day C	6.5 (206)
	10	Fringe	1939	646.3	108.8	434-794	Day B	Day C	4.2 (119)
	02	Mixed	2767	922.3	208.0	677-1335	Day B	Day C	7.1 (244)
	05	Mixed	2211	737	73.8	604-859	Day B	Day C	4.5 (138)
	04	Várzea	2261	753.7	100.3	560-896	Day B	Day C	5.2 (154)
	06	Várzea	2384	794.7	78.5	641-899	Day B	Day C	4.1 (141)
Species Richness	01	Fringe	43	22.7	4.7	18-32	Day B	Day A/C	
	10	Fringe	42	26.3	2.7	21-30	Day A	Day C	
	02	Mixed	50	32.3	4.3	28-41	Day B	Day A/C	
	05	Mixed	49	29	2.5	24-32	Day B	Day A/C	
	04	Várzea	46	28	1.2	26-30	Day B	Day C	
	06	Várzea	55	34	1.0	32-35	Day B	Day A	
Shannon Diversity	01	Fringe	2.52	2.26	0.112	2.10-2.53	Day B	Day A	
	10	Fringe	2.65	2.45	0.115	2.17-2.64	Day B	Day C	
	02	Mixed	2.89	2.59	0.163	2.32-2.98	Day B	Day A	
	05	Mixed	2.64	2.44	0.075	2.28-2.60	Day B	Day C	
	04	Várzea	2.74	2.56	0.029	2.53-2.63	Day A	Day C	
	06	Várzea	3.02	2.76	0.032	2.72-2.84	Day B	Day A	

Table 3: Summary of Spatial Variation

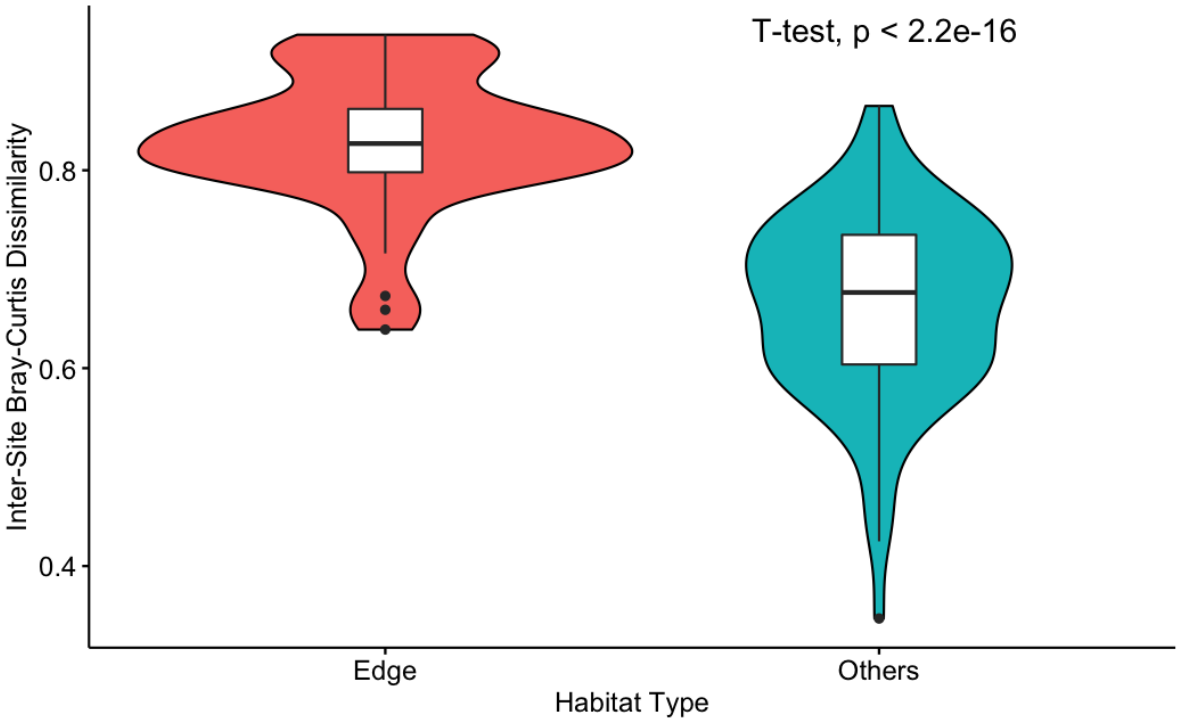

Figure 6: Bray-Curtis dissimilarity between the edge Site (01) and all other sites vs the Bray-Curtis dissimilarity between non-edge Sites. Same-site comparisons between days were excluded.

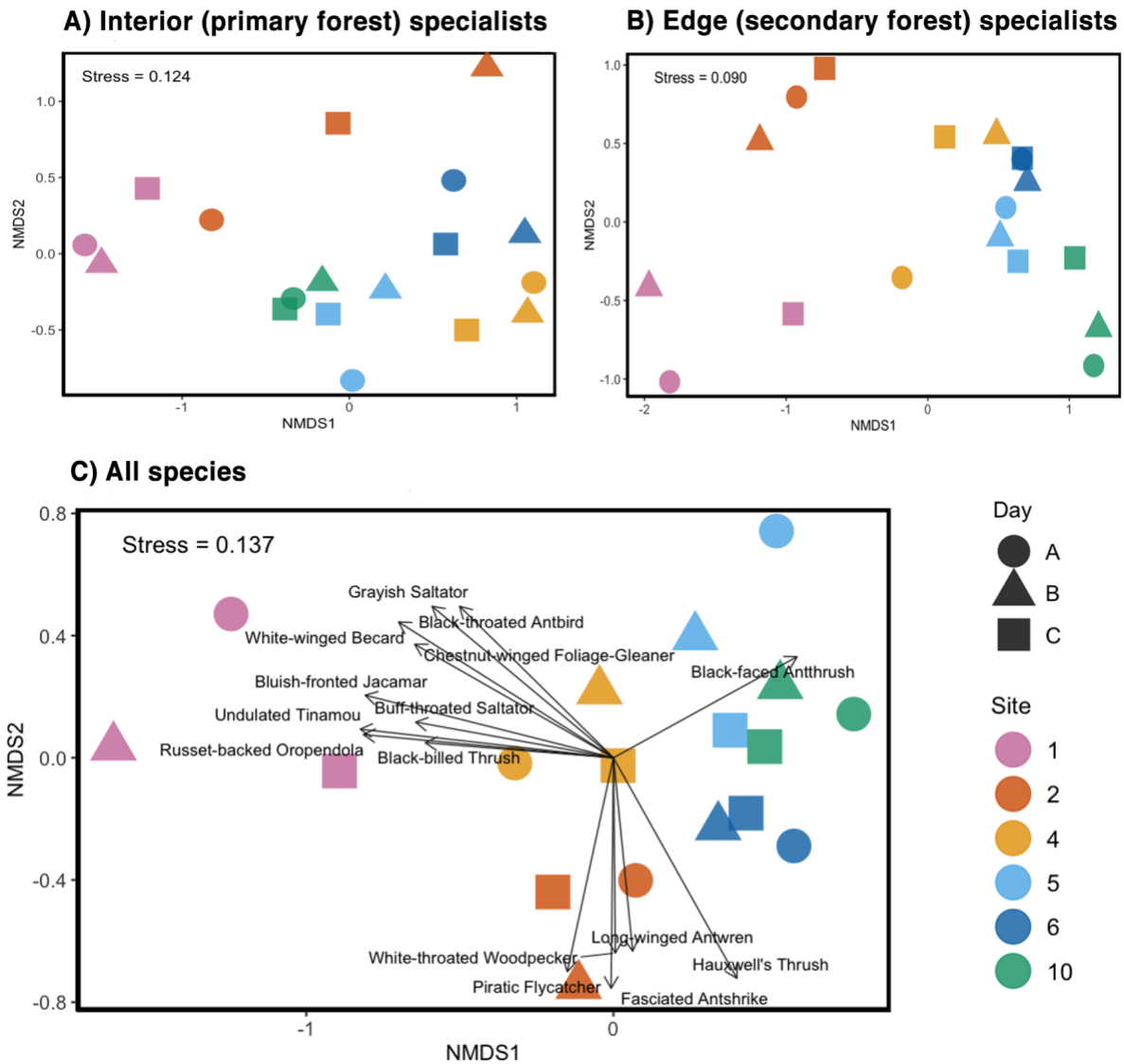

Figure 7: Nonmetric multi-dimensional scaling (NMDS) ordinations using Bray-Curtis dissimilarity, with vocal prevalence in place of abundance for interior specialists (A), edge specialists (B), and all species (C). Significantly representative species ($p < 0.02$) are shown with vectors on (C).

Relative soundscape representation (RSR) (Fig. 8) indicated that interior specialists were significantly underrepresented as a share of vocal prevalence (23.8%) relative to their share of overall species richness (41.2%) across the reserve (p = 1.56e-06). While consistent across all habitat types, this effect was strongest in fringe habitats, where interior specialists made up 25.8% of average species richness but only 4.7% of average vocal prevalence (p = 5.28e-05), followed by mixed habitats (S% = 43.0, VP% = 18.6, p = 0.0011) and *várzea* (S% = 54.9, VP% = 48.1, p = 0.74). Across all interior habitats, interior specialists made up 49% of species richness and 33.4% of VP (p = 0.0009). In contrast with interior specialists, generalists were relatively overrepresented in ITRA's soundscape, making up 38.7% of average species richness and 51.5% of vocal prevalence across all site days (p = 0.0017). In fringe habitats, generalists

were proportionally represented, making up 39.7% of species richness and 44.6% of VP, but they were significantly overrepresented in the soundscape of interior habitats, making up 38.2% of species richness and 55.0% of VP ($p = 0.00054$). Soundscape overrepresentation of generalists was strongest in mixed habitats, where they made up 64% of VP compared to 41.1% of species richness ($p = 0.008$). Generalists were also significantly overrepresented in the soundscape of *várzea* sites, accounting for 35.3% of species richness and 45.9% of VP ($p = 0.02$). Edge specialists made up 22.9% of VP and 17.3% of species richness across all sites, but this difference was not statistically significant ($p = 0.10$). In fringe habitats, however, edge specialists made up a significantly higher share of average vocal prevalence, 49.0%, than species richness, 29.4% ($p = 0.012$). Edge specialists contributed 11.2% of species richness and 9.8% of VP at interior sites.

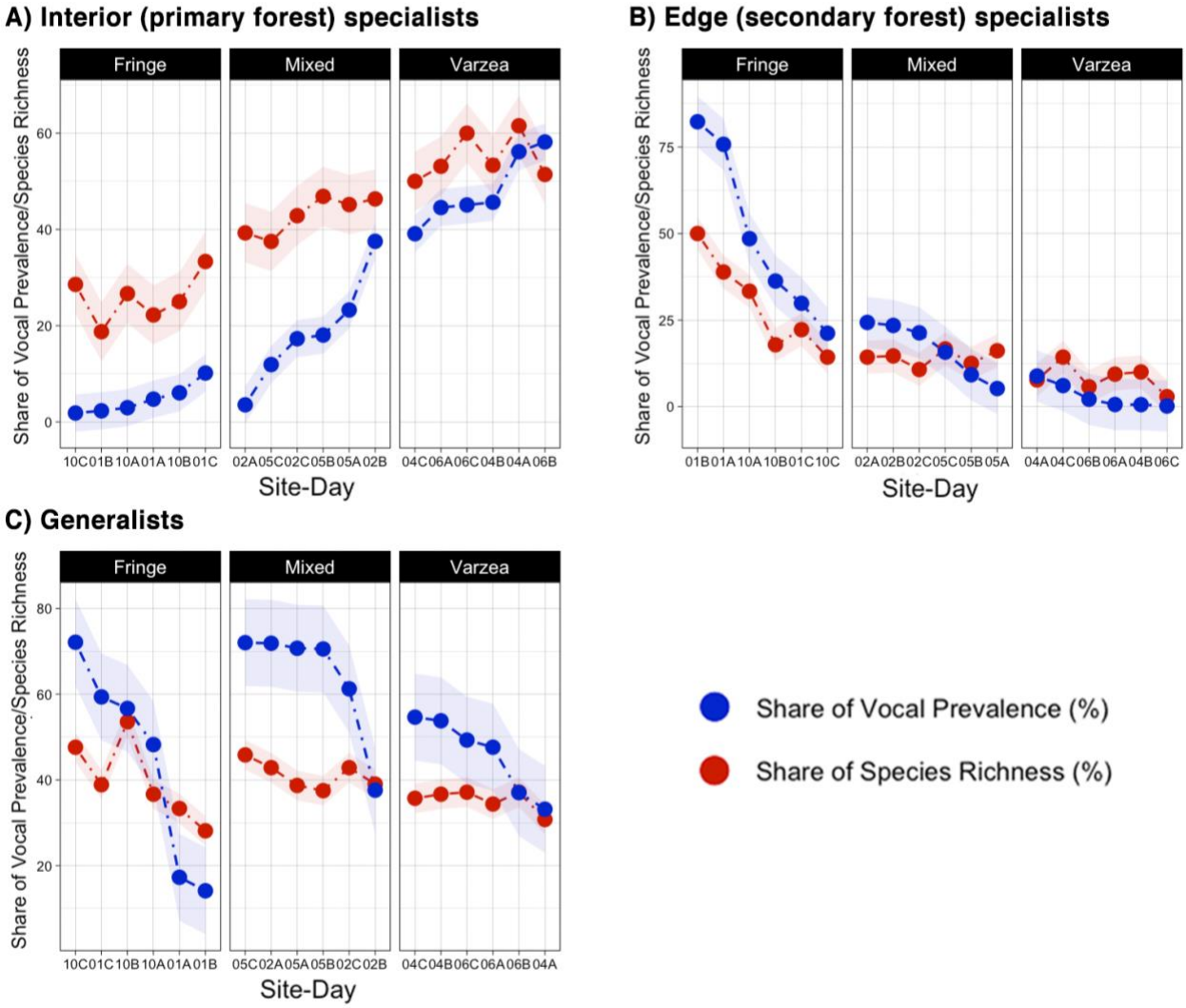

Figure 8: Relative soundscape representation (RSR) of interior (primary forest) specialists (A), edge (secondary forest) specialists (B), and generalists (C) by habitat type. Shaded areas represent one standard deviation of intra-site variation, averaged for each habitat preference group.

4 Discussion

4.1 Performance of Acoustic Sampling

ARUs and manual annotation performed exceptionally well for understory and midstory species in the reserve, but was less effective for canopy foragers. With only 3 days of dawn recordings, we detected almost half (27/63) of the rare (<2% of checklists) midstory and understory species reported to eBird over 13 years, but only one of the 30 rare canopy species, Chestnut-winged Foliage-gleaner (*Philydor erythropterum*). The high-pitched calls of many Amazonian canopy-foraging passerines are extremely challenging to identify to species; even experienced observers are typically unable to use them as a primary identification method in the field. Such calls are poorly represented in acoustic databases like Xeno-canto and the Macaulay Library, making them even harder to learn. Additionally, detection of canopy species was almost certainly impacted by the 1.5 m average placement height of ARUs, especially in a region where canopy heights regularly exceed 30 m (Asner *et al.* 2014). Stevens *et al.* (2019) used ARUs at heights of 2-5m and documented decreased detection rates of canopy-dwelling mixed flock species relative to point counts, but found no such effects in habitats with shorter, smaller trees, supporting the idea that the distance between recorder and canopy height meaningfully influences detection rates of canopy species. Placing recorders in both the canopy and understory would likely improve the detection of species across multiple foraging strata (Bradfer-Lawrence *et al.* 2018, Darras *et al.* 2018, Castro *et al.* 2019). Including annotations from later in the morning is also likely to increase detection rates of canopy foragers, which are known to reach their vocal activity peak in the second or third hour after dawn, and time windows with lower activity would be easier to annotate (Blake 1992, Woltmann 2005, Esquivel & Peris 2008).

Passive acoustic monitoring and manual annotation were an effective avian census method for the forest species that were the focus of this study, detecting 75% of the canopy, midstory, and understory species present on >5% of the 253 December-February eBird checklists in only 21 hours of acoustic data (Table 1). The majority of missed species were rare at the study site or belonged to non-target groups, e.g., species of aquatic and open habitats. A larger sample of habitat types would capture more of these species, but we restricted our ARU placements for consistency. Detections of hummingbirds, aerial insectivores, and soaring raptors, which are primarily visual, are notoriously random in Amazonia and poorly suited for ARUs; only 8/55 (15%) of these species were featured on more than 5% of eBird checklists at ITRA, mostly coming from open areas and the reserve's canopy tower, compared to 96/236 (41%) of canopy, midstory and understory forest species. Additionally, soaring raptors and aerial insectivores have large foraging ranges and are observed primarily as flyovers, meaning that their detection rate can have more to do with visibility conditions than the characteristics of a site on the ground (Kułaga & Budka 2019). As a result, flyover species are of only limited value for assessing differences between sites, and regularly excluded from general point count studies, even though their detectability is one of the biggest advantages of visual survey methods over ARUs (Ralph

et al. 1995, Van Wilgenburg *et al.* 2017). Avian censuses in Amazonia typically find that a high percentage of species occupy only a small share of sites, which our results reinforced (Terborgh *et al.,* 1990, Menger *et al.,* 2017, Blake 2021) (Fig. 3). That 23% (27/120) of the species in our study were featured on just one recording site, and 32% and 27% at one site and day, respectively, suggests that ARU performance should be expected to improve continuously over a larger sample (Wood *et al.* 2021). Annotating many short-duration time blocks, representing a broader range of temporal windows than contiguous dawn-hours, can reduce requisite analysis time or improve results, including higher detection rates of uncommon and rare species, more complete estimates of alpha and gamma diversity, and fewer false absences (Shonfield & Bayne 2017, Metcalf *et al.* 2021).

Vocal prevalence correlated strongly with estimates of both species richness ($r = 0.83$, $p = 1.9e\text{-}5$) and Shannon diversity ($r = 0.75$, $p = 3e\text{-}4$). VP is a better indicator of overall activity levels than raw call count, total number of annotations, or total annotation time, because it smooths out natural differences in vocalization patterns across species. While metrics that require species-level ID are highly contingent on observer skill level, driving inconsistencies in neotropical bird surveys (Robinson *et al.* 2018), total VP supports the use of broader taxonomic groups for challenging identifications, lowering time and experience barriers for researchers. Skill-driven variation in results from bioacoustic surveys is further reduced by the ability to replay, review, and distribute recordings to other experts, which is impossible to do with point counts. Substituting 'number of individuals/100 ha' with VP, we found that a rank-order curve of our data closely mirrored the results of Terborgh *et al.* (1990), a traditional, high-effort avian census conducted in Madre de Dios by skilled Neotropical field ornithologists (Fig. 5). This comparison validated the effectiveness of VP a proxy for abundance, enabling the calculation of abundance-based indices like Bray-Curtis dissimilarity and Shannon diversity with acoustic data.

4.2 Temporal Variation

We documented significant temporal variation between days, which was controlled for with simultaneous monitoring but could distort the results of traditional surveys. While temporal variation over the course of a morning is well documented in the tropics (Blake 1992, Woltmann 2005, Esquivel & Peris 2008, Blake 2021), the variation that we observed between days was much greater and more consistent than expected. Though evident in all featured metrics, these effects were strongest and most uniform for VP, which was highest on Day B and lowest on Day C at all six sites. Day B was major outlier at adjacent Sites 01 and 02, likely the result of a single large mixed flock that moved past both sites during the same hour. Plots comparing VP to Shannon diversity and species richness showed clear clustering by day (Fig. 4).

Stochastic vocal activity levels across days mean that temporal variation may obscure, or even exceed, differences in richness and diversity between sites and habitat types, complicating

the interpretation of point count studies. That temporal variation was strongest for VP is relevant for point counts because aural detection probability for a field observer is a direct function of VP, which reflects the probability that a species vocalizes during a given 15-s window. Standard duration point counts are much more likely to record false absences on days with lower total VP, even with static species presence. Esquivel & Peris (2008) estimated that it would take four 10-min visits per point, strategically spread out over different hours of the morning, to sufficiently cover the hourly variability in avian activity levels, even without considering variation between days, between different observers (Robinson *et al.* 2008), and travel time between sites. As a result, Amazonian point count studies seeking to do more than compile species lists may require sample sizes that are not practical, or risk drawing erroneous conclusions.

Many Amazonian bird species vocalize only in brief temporal windows, especially those surrounding dawn and dusk (Scott *et al.* 1986, Parker 1991, Metcalf *et al.* 2020, pers. obs.). These effects also apply to broader groups: for example, canopy species are known to reach their activity peak later in the morning than understory species (Blake 1992, Esquivel & Peris 2008), and species with high sensitivity to habitat fragmentation may have proportionately higher detection rates in pre-dawn surveys than less sensitive species (Woltmann 2005). More detailed data on the specific temporal activity patterns of species and groups will be informative for selecting annotation windows, estimating avian presence/absence and abundance, and interpreting the results of point count studies. ARUs are uniquely suited for answering these questions, because their capacity for simultaneous monitoring can precisely quantify temporal variation between days, meaning that bioacoustic surveys can draw comparable conclusions with less field time and/or higher precision than point counts.

4.3 Spatial Variation

Intact forest outperformed edge and degraded sites ("fringe" habitats) in all featured diversity and activity metrics. On all three days, the edge Site (01) featured the lowest species richness, and the lowest values for vocal prevalence and Shannon diversity came from either Site 01 or Site 10, in degraded forest. These results are consistent with the findings of previously conducted Amazonian avian inventories using traditional methods, such as point counts and mist-netting (Terborgh *et al.* 1990, Laurence 2004), demonstrating the viability of ARUs as an alternative method. This habitat usage pattern differs from observed dynamics in temperate systems, where avian diversity tends to be higher in edge habitats than forest interiors (Baldi 1996, Lindell *et al.* 2007). Acoustic data is likely superior to point counts for comparing tropical habitat types with variable visibility conditions; visual detection rate is a direct function of vegetation density and other habitat characteristics, which can lead to relative overestimation of avian diversity and abundance in more open habitats (Kułaga & Budka 2019), obscuring the magnitude of degradation-induced biodiversity loss in the tropics (Celis-Murillo *et al.* 2012, Darras *et al.* 2018, Darras *et al.* 2019). While sound transmission and auditory detection rate are

also influenced by habitat structure, this impacts both point counts and acoustic monitoring (Darras *et al.* 2016, Castro *et al.* 2019). Mist-netting surveys are likewise impacted by habitat; Karr (1981) found that capture rates of canopy-foraging bird species were higher in successional habitats with low canopy heights than in tall primary forest (Remsen & Parker 1983, Remsen 1996).

We found that relative soundscape representation (RSR), comparing the share of VP to the share of species richness contributed by habitat-preference groups, was a viable and significantly more efficient alternative to per-capita song rate. Bird species are known to vocalize more frequently in preferred habitats and where they are abundant (Pillay *et al.* 2019); song rate is used by females as an indicator of territory quality (Møller 1991, Gil & Gahr 2002), is positively associated with density-dependent competition between males (Penteriani 2003, Goretskaia 2004), and may also increase conspecific immigration from surrounding areas (Fletcher 2007, Laiolo & Tella 2008). While per-capita song rate can be calculated with ARUs through careful, manual analysis of individual variation between vocalizations (Pillay *et al.* 2019), doing so is labor-intensive and difficult to scale. Mirroring expected patterns for per-capita song rates, RSR was highest in preferred habitats of both interior and edge specialists. Even in the reserve's most intact *várzea* forest, however, interior specialists made up a smaller share of VP than their share of species richness, and they were significantly underrepresented across all interior sites ($p = 0.0009$). Generalists, conversely, were overrepresented in the soundscapes of interior sites, an indicator of fragmentation; Amazonian fragments tend to disproportionately feature generalists, which possess strong dispersal abilities and high tolerance for deforested habitats (Sekercioglu *et al.* 2002, Lees & Peres 2008). Site 01 was the only site to significantly differ in community composition compared to all other sites (Fig. 6). The lack of significant compositional differences between interior sites is another potential symptom of degradation; Burivalova *et al.* (2019) found that the soundscapes of selectively logged forests in Borneo were less heterogenous than the soundscapes of a never-logged forest, likely the result of subtractive homogenization. Together, the soundscape overrepresentation of generalists, soundscape underrepresentation of interior specialists, and relative compositional homogeneity of interior sites suggest that the entire 191 ha reserve is degraded, and in the process of becoming a fragment.

Edge effects are known to pervasively impact Amazonian bird communities and ecosystem function, stretching deep into forest interiors (Terborgh *et al.* 1990, Gascon *et al.* 2000, Laurence 2004, Barlow *et al.* 2006, Broadbent *et al.* 2008, Laurence *et al.* 2011, Whitworth *et al.* 2015, Wolfe *et al.* 2015, Haddad *et al.* 2015, Moura *et al.* 2016, Stouffer 2020), but we did not expect RSR to illustrate these dynamics so clearly. Based on its performance in this study, we suggest that RSR, which can only be calculated with ARUs, has the potential to be a useful, efficient tool for remotely characterizing habitat features and quality. RSR has applications for both long-term biodiversity monitoring and rapid assessment, without requiring

established baseline data. Though frequently misrepresented as homogenous, Amazonian habitats are highly heterogeneous (Pires & Prance 1985, Tuomisto *et al.* 1995), and important elements of their vegetational diversity remain poorly understood (Milliken *et al.* 2010, Macía 2011, Borges 2013). Interactions between habitat features and avian community structure in the Amazon are extremely complex, influenced by variables like soil type (Borges 2013), riverine sediment concentration (Laranjeiras *et al.* 2021), the condition of surrounding habitat (Stouffer 2006, Latta *et al.* 2011, Laurence *et al.* 2011, Woltmann 2012, Laurence *et al.* 2012, Wolfe *et al.* 2015, Barlow 2016, Menger *et al.* 2017, Hernández-Palma & Stouffer 2018), the presence of large animals (Redford 1992, Estes *et al.* 2011), and climate change (Blake & Loiselle 2015, Stouffer *et al.* 2020). As a result, Amazonian habitat assessments, which are generally reliant on features discernable by field observers, can be overly simplistic. Under global change, RSR and other approaches that assess nuanced habitats based on their use by species may be particularly valuable.

5 Synthesis & Applications

Developing a better understanding of the effects that deforestation, fragmentation, and degradation have on biodiversity in tropical biodiversity hotspots is a major international conservation priority (Gardner *et al.* 2008, Barlow *et al.* 2016, Stouffer 2020), particularly analyses that go beyond presence/absence and that can be applied at landscape scales (Hernández-Palma & Stouffer 2018). The results of this study support the potential of simultaneous passive acoustic monitoring as a cornerstone of biodiversity assessment, for both birds and other taxa. We found that annotated acoustic data can replicate the results of historical avian censuses, characterizing community structure, species richness, Shannon diversity, and vocal activity levels across habitat types. We documented significant temporal variation between days, which may be missed with non-simultaneous survey methods, distorting their results.

Acoustic data can generate informative, novel metrics that are impossible to produce with human observers, including effective proxies for abundance data and per-capita song rate. Such metrics, namely VP and RSR, can efficiently characterize complex habitats based on species usage patterns, rather than relying on visible features. In the future, passive acoustic monitoring's scalability, permanent storage, and ability to integrate with new and developing technologies could have a transformative impact on global conservation efforts (Kahl *et al.* 2020). Rampant habitat destruction and climate change threaten to destabilize the Amazon basin, and long-term, perhaps cascading declines in biodiversity and ecosystem function have already been documented, even in structurally intact habitats (Bird & Lees 2011, Laurence *et al.* 2012, Blake & Loiselle 2015, Brienen *et al.* 2015, Lovejoy & Nobre 2019, Stouffer 2020). If we wish to save, or at least document, these imperiled systems, furthering cutting-edge approaches like bioacoustics should be a central research priority.

Authors' Contributions

Both authors designed the methodology. H.K. helped to secure the funding to conduct the study; W.A.H. collected and annotated the recordings, analyzed the data, and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Statement

All data collected is available on request and will be made publicly available upon acceptance.

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