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Simultaneous passive acoustic monitoring uncovers evidence of potentially overlooked temporal variation in an Amazonian bird community

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The vocal activity and detectability of tropical birds are subject to high levels of temporal heterogeneity, but quantifying patterns of diel and day-to-day variation in complex systems is challenging with traditional point count methods. As a result, research concerning stochastic temporal effects on tropical bird assemblages is limited, typically offering only broad conclusions, such as that overall activity is highest in the first few hours of the morning and some species are active at different times of the day. Passive acoustic monitoring introduces several advantages for studying temporal variation, particularly by enabling simultaneous and continuous data collection across adjacent sites. Here, we employed autonomous recording units to quantify temporal variation in bird vocal activity and observed species richness at an Amazonian reserve in Madre de Dios, Peru, a region featuring some of Earth's richest, most complex bird assemblages. We manually annotated 18 dawn hour recordings, collected simultaneously from three separate days at the same six sites, which represent various microhabitats and bird community compositions. We documented significant and consistent temporal variation in avian vocal activity levels and observed species richness within the dawn hour and across days. We found that temporal effects were stronger for vocal activity than for observed species richness and that vocal activity patterns over the course of the dawn hour varied between species. Our results indicate that overlooked temporal variation in Amazonian soundscapes may obfuscate the results of surveys that do not sufficiently account for temporal variables with simultaneous monitoring. While manual analysis of large volumes of soundscape data remains challenging, such data should be collected to supplement traditional surveys whenever possible. Rapid advances in the automated processing of acoustic data could lead to more efficient methods for reducing temporal bias and improving the calibration and accuracy of tropical bird surveys.

Keywords: Amazon rainforest, avian biodiversity, bioacoustics, bird surveys, temporal variation.

The tropics account for an overwhelming share of Earth's avian diversity, with more than 75% of all species and over 90% of terrestrial birds (Barlow *et al.* 2018). Still, tropical regions are underrepresented in ornithological literature relative to temperate regions, even though tropical birds have fundamentally different life history strategies, behavioural ecology and vocal patterns than temperate birds, requiring separate study (Stutchbury & Morton 2008). The largest intact tropical system on the planet is the Amazon basin (Allan *et al.* 2017), which is the epicentre of global biodiversity (Antonelli *et al.* 2018). Like

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most of the tropics, the Amazon is undergoing rapid ecological change, primarily the result of agricultural expansion (Lapola *et al.* 2023), exacerbated by the increasing impacts of climate change (Xu *et al.* 2020). These anthropogenic impacts are significantly outpacing natural processes in Amazonia (Albert *et al.* 2023), threatening the resilience and stability of the region (Lovejoy & Nobre 2019, Boulton *et al.* 2022). Despite its importance, however, the Amazon's avifauna remains poorly documented and is subject to flawed baseline species occurrence data and significant knowledge gaps (Lees *et al.* 2014), which are exacerbated by systemic barriers to researchers from the Global South (Soares *et al.* 2023). Efforts to increase ornithological survey coverage in the region are complicated by the difficulty of tropical field surveys. Overwhelming bird species richness, including many rare and similar species, challenging logistics and poor visibility conditions contribute to the unreliability of bird surveys in Amazonia, where upwards of 95% of birds are heard but never seen by a field observer (Robinson *et al.* 2018).

The vocal activity and detectability of Neotropical birds are subject to high levels of temporal heterogeneity. Possible drivers of this variation include seasonality (Pérez-Granados & Schuchmann 2022), weather and feeding opportunities (Metcalf *et al.* 2021), foraging strata (Berg *et al.* 2006), temporal partitioning to avoid signal masking from other birds (Luther 2008, 2009, Planqué & Slabbekoorn 2008, Hart *et al.* 2021) and vocalizing insects (Hart *et al.* 2015, Alvarez-Berríos *et al.* 2016, Aide *et al.* 2017, Metcalf *et al.* 2020), along with a wide range of poorly understood floristic, geographical and spatial variables (Menger *et al.* 2017). Some broad patterns of diel variation in the detectability and vocal activity of tropical birds are well established; for example, birds are most vocally active during the first 2–3 h after dawn (Lynch 1995, Woltmann 2005). However, the temporal variation of tropical soundscapes is more complex than hour-long intervals can capture (Verner & Ritter 1986, Rodriguez *et al.* 2014, Metcalf *et al.* 2021). Many Amazonian species are only aurally detectable within strict temporal niches (Gil & Llusia 2020). These species may only vocalize during a single 5-min period in the morning, perhaps accompanied by an even shorter bout in the evening (Parker 1991). Some Amazonian species have been shown to sing as infrequently as twice in 50 days (Jirinec *et al.* 2018). In addition to affecting estimates of total species richness, this fine-scale temporal variation in vocal activity can also influence patterns of observed community composition. Temporal effects on detectability vary by functional or taxonomic group. For example, canopy species are known to reach their activity peak later in the morning compared with understorey species (Blake 1992), and species with high sensitivity to habitat fragmentation may have proportionately higher detection rates in pre-dawn surveys compared with less sensitive species (Woltmann 2005).

Quantifying the fine-scale patterns of temporal variation in tropical bird communities, both within and across days, is difficult. Non-simultaneous survey methods are subject to a litany of spatial, temporal and observer biases, and capturing such granular effects can therefore require infeasibly large sample sizes (Lynch 1995). For example, Esquivel and Peris (2008) found that four visits per point are necessary to account for the temporal variation in bird activity in the Atlantic Forest of Paraguay. This sampling design does not account for possible variation in vocal activity levels between different days, between different observers (Robinson *et al.* 2018) or travel time between sites. Additionally, Rodriguez *et al.* (2014) found that temporal effects on acoustic activity patterns were spatially heterogeneous at adjacent recording sites in French Guiana. Therefore, precise assessments of temporal variation may be required at individual sites.

More costly and labour-intensive approaches, for example using a team of point count technicians to visit multiple points simultaneously, may also introduce observer effects. 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 level of competence attainable in just 1–2 weeks of field experience in temperate systems (Parker 1991). Observer error rates have been experimentally quantified in relation to aural identification (Simons *et al.* 2007), visual identification (Hull *et al.* 2010) and the subjectivity of abundance estimates (Cerqueira *et al.* 2013). These dynamics are not limited to inexperienced surveyors; established ornithologists can also be subject to non-trivial identification error rates in environments as complex as Amazonia (Lees *et al.* 2014). Overlooked species tend to reflect non-random subsets of assemblages, and the

specific nature of these biases may differ between individual observers, even among experts (Blackburn & Gaston 1998). Therefore, standardized surveys that do not produce archivable raw data and seek to uncover subtle spatiotemporal variation in avian vocal activity, observed species richness and community structure should ideally be conducted by a single observer (Blake & Loiselle 2015, Robinson *et al.* 2018).

Simultaneous passive acoustic monitoring (PAM) conducted with autonomous recording units (ARUs) can eliminate much of the temporal bias in surveys by collecting continuous data from adjacent locations simultaneously (Tegeler *et al.* 2012, Venier *et al.* 2012). Such effects are difficult to quantify with traditional surveys, and establishing their presence and magnitude may be useful for improving the calibration of point count studies, even with relatively small volumes of ARU data. PAM can also address observer bias, as data collection is independent of technician skill level, and recordings collected simultaneously can be annotated by a single observer, replayed and reanalysed, archived publicly, and distributed to experts for an independent review of identifications (Rempel *et al.* 2005, Robinson *et al.* 2018). PAM has been shown to present a suitable supplement or alternative to point counts, both in Amazonia (Haselmayer & Quinn 2000) and in general (Shonfield & Bayne 2017, Darras *et al.* 2019, Blake 2021), while providing numerous other advantages (Acevedo & Villanueva-Rivera 2006, Newson *et al.* 2017, Darras *et al.* 2018, Jorge *et al.* 2018, Pillay *et al.* 2019, Sugai & Llusia 2019).

This study aimed to investigate the hypothesis that Amazonian soundscapes may be subject to overlooked temporal variation in avian vocal activity, both between days and throughout a single dawn hour. In the absence of simultaneous survey methods, such variation could mask important differences in vocal activity levels, community composition and observed species richness between sites. We tested this hypothesis by deploying an array of ARUs at a single Amazonian reserve in Madre de Dios, Peru, and manually annotated a subsample of the resulting bioacoustic data. We predicted that stochastic effects of diel and day-to-day variation in vocal activity and observed species richness would be consistent across sites and therefore possible to control for with simultaneous monitoring.

METHODS

Study area

We conducted this study 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 approximately 200 m along the Madre de Dios River, directly opposite the Reserva Nacional de Tambopata, one of the most biodiverse regions on the planet (Foster *et al.* 1994; Fig. 1). 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.

Acoustic monitoring

We collected acoustic data from 14 January to 2 February 2019, using six ARUs (Swift recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA). We deployed the ARUs across the entire reserve, at a minimum distance of 350 m from each other and 450 m from the river, to limit spatially overlapping detections (pseudoreplication) and background noise (Ralph *et al.* 1995, Yip *et al.* 2017, Darras *et al.* 2018, Haupert *et al.* 2022), respectively. Deployment locations were chosen to represent a gradient of intactness and forest habitat type, including edge habitat adjacent to clearings for small-scale agriculture (Site A), forest degraded by selective logging outside of the reserve's boundaries (Site F), mature *várzea* in the reserve's interior (Site C and Site E) and mixed palm swamp (*aguajal*)-*várzea* habitat (Site B and Site D; Fig. 1). Placed at 1.5 m above the ground to maximize the sound detection space and minimize sound shadows (Darras *et al.* 2018), the six ARUs recorded continuously (mono, WAV format) throughout the deployment period using a sampling rate of 48 kHz (16-bit resolution) and a gain setting of 35 dB. The microphone sensitivity of the Swifts was -44 dBV/Pa ($\pm$ 3 dB) and featured a flat frequency response ($\pm$ 3 dB) in the frequency range of the vocalizations of interest. The clipping level of the analog-to-digital converter (ADC) was $\pm$ 0.9 V.
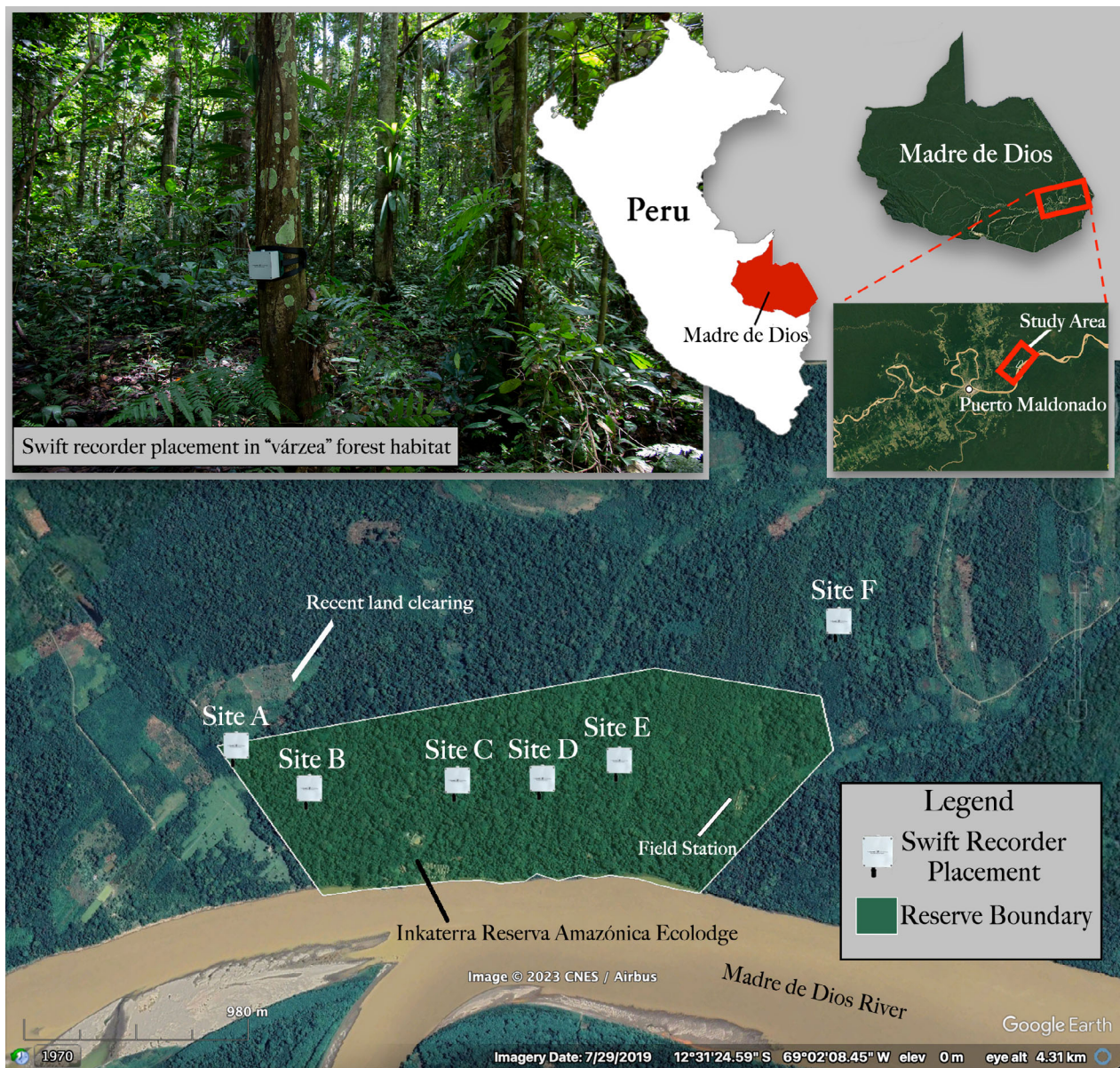
Figure 1. Swift recorder locations and typical forest habitat at Inkaterra Reserva Amazónica, Madre de Dios, Peru. Recorder locations covered a range of habitats, including edge habitat adjacent to clearings for small-scale agriculture (Site A), forest degraded by selective logging outside of the reserve's boundaries (Site F), mature *várzea* in the reserve interior (Site C and Site E) and mixed palm swamp (*aguajal*)-*várzea* habitat (Site B and Site D).

Annotation process

We manually annotated 18 total dawn hours, from 05:00 to 06:00 h PET (10:00–11:00 h UTC), representing six sites on three days, using the Raven Pro Sound Analysis Software (version 1.6; K. Lisa Yang Center for Conservation Bioacoustics,

Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA). Annotations were performed by a single observer, the lead author, to control for observer bias. A local expert, Noe Huaraca-Charca, also annotated a subset of these recordings (*n* = 4) as a quality control measure. The three days – 16 January (Day 1), 20 January (Day

2) and 31 January (Day 3), 2019 – were randomly chosen from a subset of days that featured < 5 min of heavy rain during the dawn hour. The dawn hour was selected because it typically 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 time periods, reducing interference with bird species detection (Metcalf *et al.* 2020). Although annotating short, randomly selected samples spread out over a longer survey period can improve estimates of alpha and gamma diversity (Wimmer *et al.* 2013, Metcalf *et al.* 2021), this study was designed to assess temporal variation over the course of a contiguous hour, and annotations were therefore conducted in this format.

Spectrograms were viewed in 60-s increments split over two rows (Hann window, 3 dB bandwidth = 100 Hz, 690 FFT window size, 1024-sample DFT, 95% temporal overlap; Fig. 2). To reduce bias introduced by improved sound identification knowledge developed throughout the project, the order in which recordings were annotated was determined using a random number generator. Vocalizations were labelled 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 analysis. To account for interspecific 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 less than 5 s, they were included as part of the same annotation; otherwise they were treated separately. An assortment of unlabelled sound clips featuring identified and unidentified species was sent to regional experts for secondary verification. Annotations were reviewed repeatedly until unidentified vocalizations made up <10% of the total bird vocal activity on a given recording. We made considerable efforts to label accurately as many foreground and background vocalizations as possible to improve the value of this dataset for training soundscape-based automated identification algorithms.

Statistical analyses

To assess fine-scale temporal variation in dawn chorus vocal activity within recordings and across sampling sites and days, we subsampled each 1-h recording at 1-min intervals, totalling 1080 samples across all sites and days. For each 1-min interval, we calculated species richness (SR), vocal prevalence (VP) and total vocal prevalence (TVP). Species richness refers to the number of unique species detected, whereas vocal prevalence refers to the number of 10-s intervals featuring a vocalization of a given species. Therefore, a single species could attain a maximum VP of 6 per 1-min interval, or 360 per hour. TVP, a proxy for the total avian vocal activity in a soundscape, refers to the sum of VP for all detected taxa in a subsample. We assessed the relationship between TVP and SR using Pearson's *r* correlation analysis.

Certain taxa were excluded from species richness calculations for data quality reasons: parrots (Psittacidae sp.), because they occurred almost exclusively as calling flyovers, as well as 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. However, these species were included in calculations of TVP, as were vocalizations that were identified to a broader group but not at the species level (e.g. trogons). For a full list of species and exclusions for SR and TVP calculations, see Appendix S1.

Non-metric multidimensional scaling ordination and ANOVA

We used non-metric multidimensional scaling ordination (NMDS) and two-way repeated-measures ANOVA to assess evidence for significant effects of site-specific differences in community composition on SR and TVP. Substituting VP in place of abundance, we calculated NMDS using the 'bray' method, referring to Bray–Curtis dissimilarity, and metaMDS function from the 'vegan' package in R (Oksanen *et al.* 2019). One advantage of using Bray–Curtis dissimilarity is its ability to account for the relative abundances of different species or taxa (Ricotta & Podani 2017). We plotted NMDS ordinations on two axes and ensured that the output met minimum stress requirements (Kruskal 1964). To compare SR and TVP between sites,
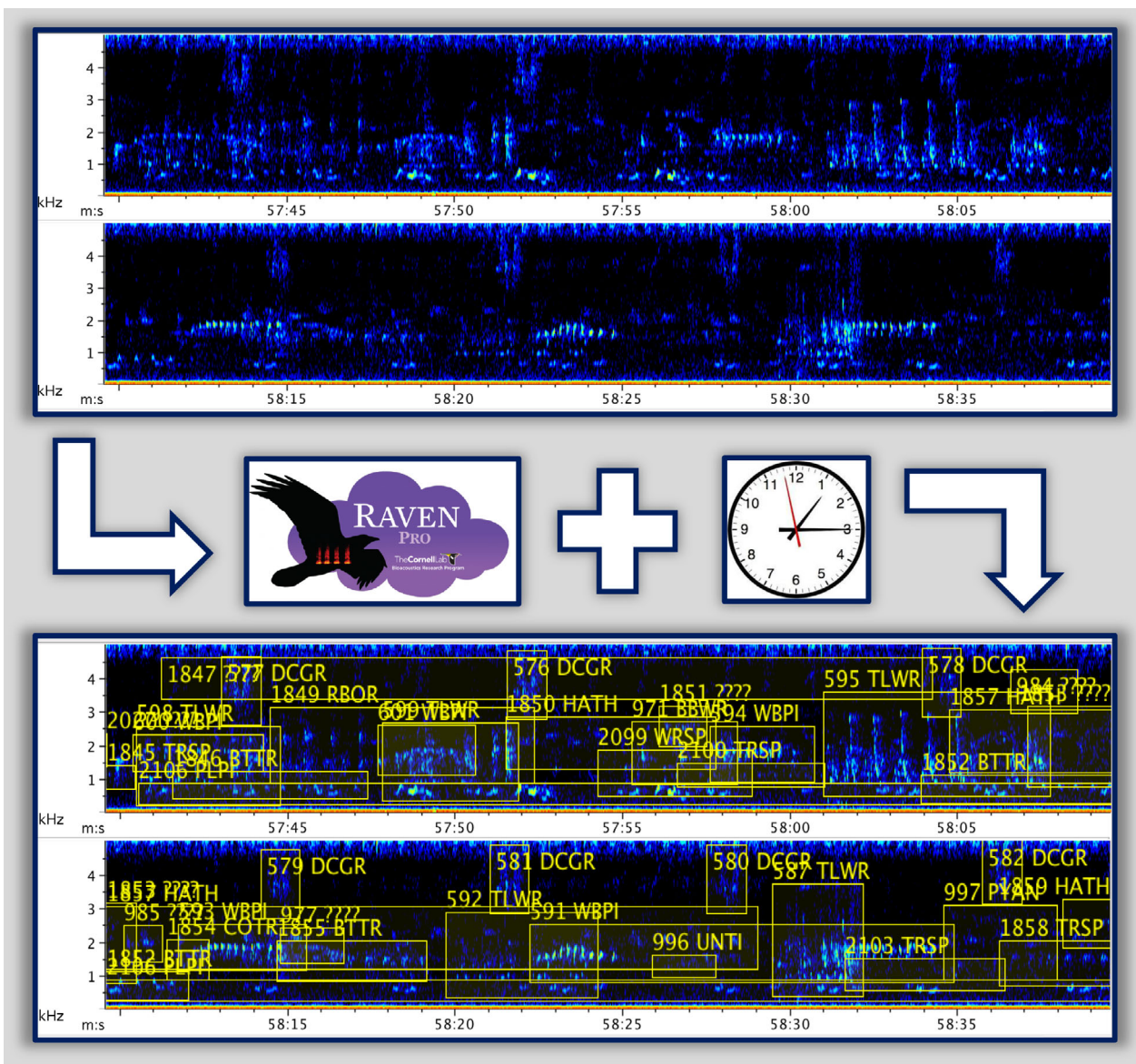
Figure 2. The annotation process. Spectrograms showing 1 min of sound from Site B, Day 2, before and after manual annotation in Raven Pro 1.6.

days and recordings, two-way repeated-measures ANOVA followed by Tukey's HSD tests for multiple comparisons were conducted in R, with site and day as interacting independent variables and the 1-min time interval as a blocking variable.

Generalized additive models

We then constructed a set of generalized additive models (GAMs) fit with Poisson distributions and restricted maximum likelihood estimations to account for the non-linearity of within-recording

response curves for SR, TVP and species-specific VP within the dawn hour. For both the SR and TVP models, we included a smoothing term for the interaction between time of day and recording to produce individual response curves for each recording, and a nested site–day random effects term to account for pseudoreplication. Similarly, to produce species-specific VP response curves across days and sites, we replicated this random effects structure, but removed the interaction for the time interval smoothing term. As the amount

of species present at time step *t* directly influences the number of species that are likely to be detected at time step *t* + 1, we accounted for this inherent temporal autocorrelation by fitting both models with a first-order autoregressive covariance structure (AR1; Yang *et al.* 2012). Because our model structure was biologically informed, we chose to forgo model selection and base inferences and predictions from this structure. We completed all statistical analyses in R (v. 4.2.0; R Core Team 2022) using functions from the 'tidyverse' (Wickham *et al.* 2019) and employing the 'mgcv' package to construct GAMs (Wood 2004, 2011, 2017, Wood *et al.* 2016).

RESULTS

We identified 127 species over the 18 dawn hours analysed, seven of which were recorded only as background vocalizations; 17 036 individual bounding-box annotations were drawn in Raven Pro 1.6, of which 94.8% were identified to species or taxon level. Site A had the lowest average species richness per 1-min interval (4.0; 43 total), followed by Site F (4.4; 42 total), Site D (4.8; 49 total), Site C (4.9; 46 total), Site E (5.3; 55 total) and Site B (6.1; 50 total), which was also the most active site by TVP. Aggregating detections across sampling sites, Day 1 featured 57 species, Day 2 featured 78 species and Day 3 featured 56 species, with average SR values per 1-min interval of 4.79, 6.18 and 3.81, respectively. At individual sites, the percentage of total vocal prevalence (TVP) that was not identified to a species or group ranged from 4.1% (Site E) to 7.1% (Site B) between sites, and from 5.1% (Day 3) to 5.4% (Day 1) between days.

Of the 120 foreground species detected, only two, Black-faced Antthrush *Formicarius analis* and Buff-throated Woodcreeper *Xiphorhynchus guttatus*, were detected on all 18 recordings, and six more, Hauxwell's Thrush *Turdus hauxwelli*, Little Tinamou, Thrush-like Wren *Camplyorhynchus turdinus*, Amazonian Motmot *Momotus momota*, Plumbeous Pigeon *Patagioenas plumbea* and Screaming Piha *Lipaugus vociferans*, were detected on at least 15 recordings. Most species were rare; more than half (*n* = 66, 55%) were detected on four or fewer 1-h recordings, and roughly a quarter (*n* = 27, 23%) on only a single recording (Appendix S2). Regarding total vocal prevalence, the most abundant species were Hauxwell's

Thrush, Black-faced Antthrush and Thrush-like Wren. TVP was highest at all six sites on 20 January (Day 2) and lowest on 31 January (Day 3) at every site except Site B.

Non-metric multidimensional scaling ordination and ANOVA

Individual sites were consistently separated from each other in terms of their species composition, as demonstrated by NMDS ordination (Fig. 3). Tukey's HSD tests indicated that a higher percentage of pairwise comparisons between sites were significantly different ($P < 0.01$) for SR (9/15, 60%) than for TVP (6/15, 40%), and all comparisons between days were significant for both TVP and SR. The rate that recordings from different days exhibited significant pairwise differences ($P < 0.01$) remained essentially identical whether they came from the same site or from different sites: 44.4% (8/18, same site) versus 42.2% (38/90, different sites) for SR and 55.6% (10/18) versus 56.7% (51/90) for TVP. In general, pairwise comparisons of recordings from different days were more likely to differ significantly ($P < 0.01$) than were recordings from different sites. For SR, 42.6% of recordings from different days (46/108) differed significantly, compared with 35.6% from different sites (48/135). For TVP, 56.5% of recording pairings from different days (61/108) differed significantly, compared with 45.2% from different sites (61/135). TVP and SR were least likely to differ between recordings that came from different sites on the same day; just 22.2% of these pairwise comparisons (10/45) differed significantly ($P < 0.01$) for each metric. For all Tukey's HSD pairwise comparisons between sites, days and individual recordings, see Appendix S3.

Generalized additive models

SR and TVP models accounted for substantial variation in dawn chorus vocal activity ($R^2 = 0.64$ and $R^2 = 0.83$, respectively, Fig. 4), in which smoothing terms for the interaction between time interval and recording, as well as site–day random intercepts, were often significant ($P < 0.05$; Appendix S4). The effect of time interval and day was generally stronger than the effect of site in explaining variation in observed SR and TVP, and TVP was strongly correlated with SR ($r = 0.85$, $P < 0.001$). We observed that diel variation in
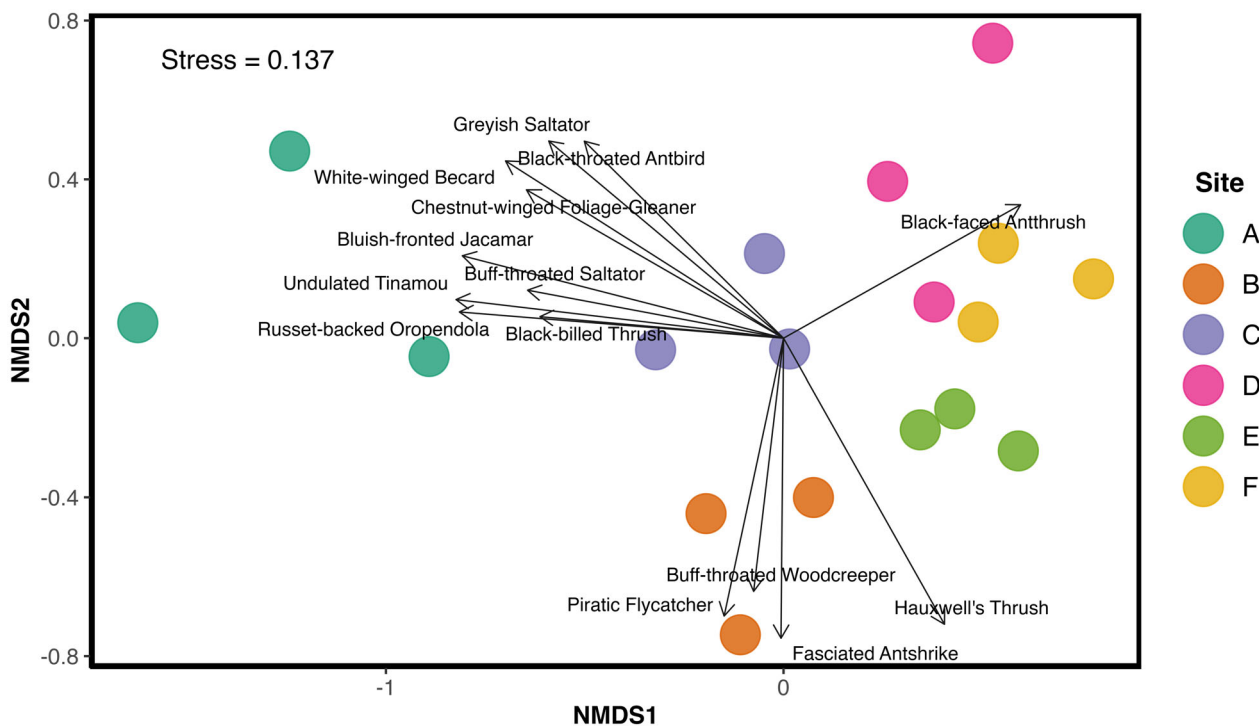
Figure 3. Non-metric multidimensional scaling (NMDS) ordination by site using Bray–Curtis dissimilarity, with vocal prevalence in place of abundance. Species significantly representative of their position along the ordination axes ($P < 0.02$) are shown with vectors. For site information, see Fig. 1.

avian vocal activity varied by species and taxonomic group, with the VP of different species peaking at different time intervals within the dawn hour (Fig. 5).

DISCUSSION

We used simultaneous PAM to quantify temporal variation in the vocal activity level and observed species richness of an Amazonian bird community. In line with our primary hypothesis, the magnitude of this temporal variation was sufficient to potentially mask, or even supersede, observed differences in species richness and vocal activity levels between sites and habitat types. Such variation may complicate the interpretation of point count studies and other non-simultaneous survey methods that fail to control for temporal variables. Although temporal variation in bird activity over

the course of the morning is well documented in the tropics, the limitations of traditional non-simultaneous survey methods mean that point count studies on temporal effects in these systems offer only broad conclusions, typically relating to maximum temporal resolutions of 1 h or more (Blake 1992, Lynch 1995, Woltmann 2005, Esquivel & Peris 2008). Fine-scale diel variation in the vocal activity and detectability of Amazonian birds has been referenced anecdotally for decades (Parker 1991). However, thanks to the development of ARUs, which allow for considerably easier repeat sampling than traditional methods, we are beginning to understand more about these effects at higher temporal resolutions (Gil & Llusia 2020, Blake 2021, Metcalf et al. 2021, Pérez-Granados & Schuchmann 2022). While prior temporal effects studies have focused primarily on diel and seasonal temporal variation, this is, to our knowledge, the

Figure 4. Comparisons of (a) species richness and total vocal prevalence detected by time of day across days and sites overlaid with generalized additive model (GAM) prediction curves ± 95% confidence intervals (CIs), along with (b) site-specific GAM prediction curves overlaid with day-specific mean GAM prediction curves ± 95% CIs of species richness and vocal prevalence across days.
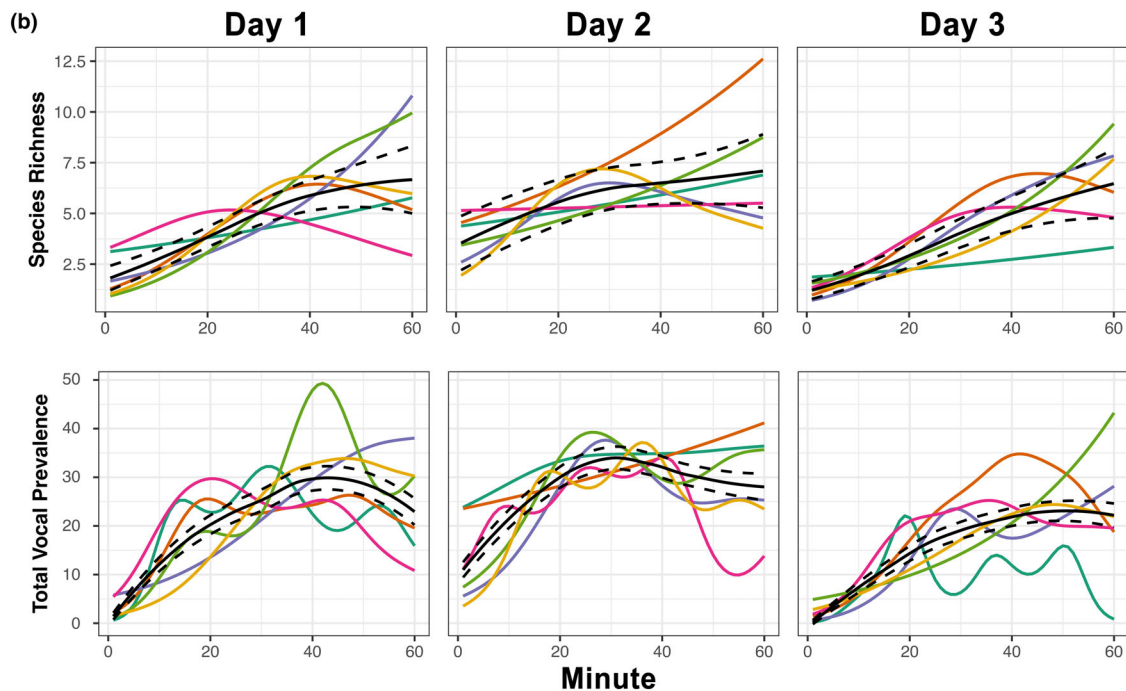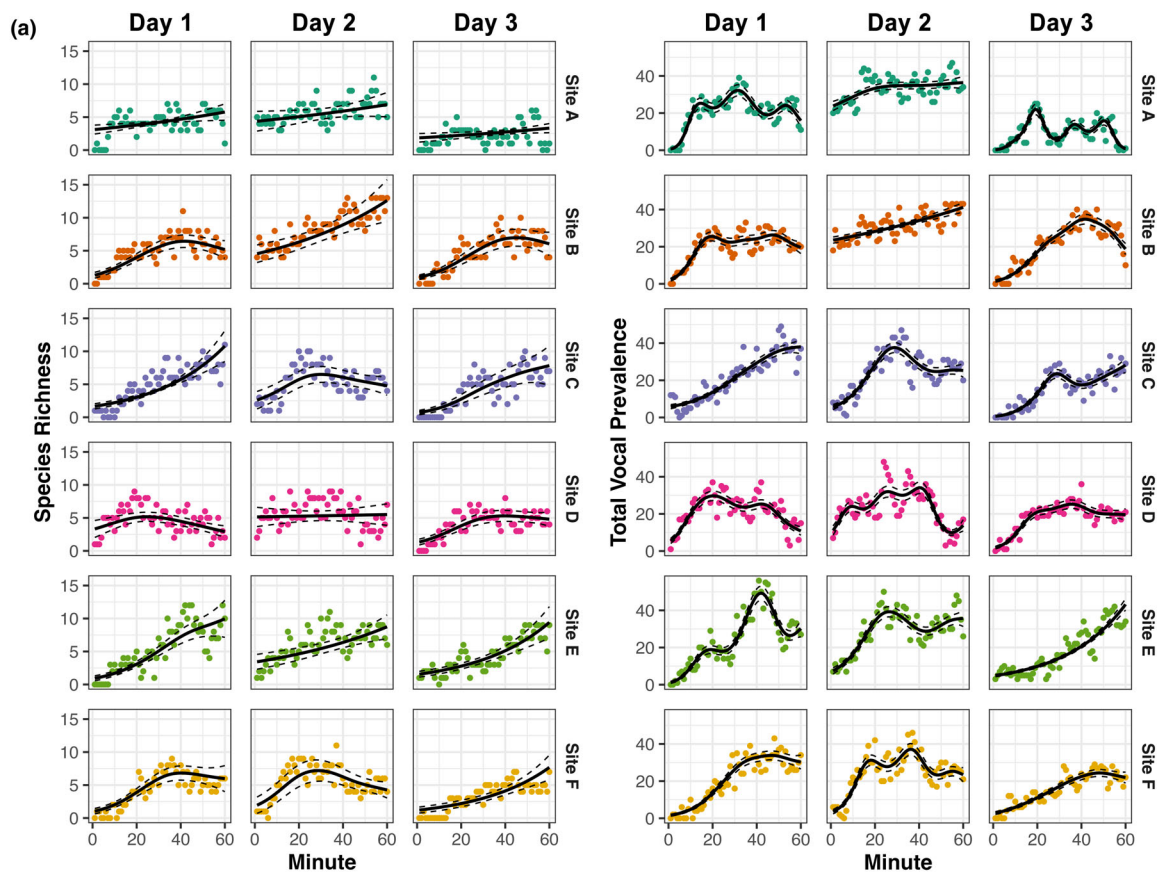
(a)

| Species	0-5min	5-10min	10-15min	15-20min	20-25min	25-30min	30-35min	35-40min	40-45min	45-50min	50-55min	55-60min
Cinerous Tinamou	5	15	69	59	29	46	61	17	22	3	8	1
Little Tinamou	7	34	43	39	25	18	10	17	8	3	0	1
Undulated Tinamou	9	33	39	38	51	44	50	47	58	47	53	43
Plumbeous Pigeon	0	1	3	1	31	15	26	26	18	42	40	67
Ruddy Pigeon	0	1	1	0	8	2	2	22	26	14	0	0
Grey-fronted Dove	0	1	1	13	15	40	79	88	39	13	12	20
Amazonian Pygmy-Owl	51	48	21	4	1	2	0	0	0	0	0	0
Black-tailed Trogon	0	0	0	1	3	2	17	7	11	23	13	18
Collared Trogon	0	0	0	21	20	3	15	20	48	53	47	21
Amazonian Motmot	38	31	52	90	69	54	42	14	15	10	15	0
Mealy Parrot	0	0	0	0	7	9	21	29	23	10	5	11
Fasciated Antshrike	4	5	1	2	8	31	21	49	35	31	3	6
Plain-winged Antshrike	0	0	19	46	39	39	20	15	3	1	0	8
Dusky-throated Antshrike	0	1	0	6	14	10	17	24	30	33	19	13
Spot-winged Antshrike	0	0	20	26	30	10	13	23	13	8	5	2
Pygmy Antwren	0	0	0	0	8	11	10	12	19	17	11	10
Long-winged Antwren	4	19	17	39	27	3	6	3	3	12	0	8
Grey Antbird	0	0	10	37	40	43	60	100	93	69	80	57
Plumbeous Antbird	0	0	0	0	2	2	36	76	75	59	60	43
Goeldi's Antbird	0	2	13	18	20	27	19	23	22	18	17	7
Black-throated Antbird	0	0	1	0	4	4	2	14	28	18	8	0
Black-faced Antthrush	7	29	55	114	118	148	164	194	163	184	190	148
Rufous-fronted Antthrush	0	0	0	0	1	4	17	24	19	15	19	21
Cinnamon-throated Woodcreeper	7	25	39	24	21	4	20	8	13	6	0	1
Long-billed Woodcreeper	0	6	10	25	14	9	12	6	3	6	12	9
Amazonian Barred-Woodcreeper	6	46	62	50	17	14	1	0	1	0	0	2
Striped Woodcreeper	0	6	17	41	36	47	27	21	15	11	0	1
Buff-throated Woodcreeper	25	58	86	104	67	60	52	38	34	16	10	8
Purple-throated Fruitcrow	0	0	0	0	9	8	22	17	18	9	16	9
Screaming Piha	2	3	2	10	24	31	27	30	32	54	57	54
White-winged Becard	0	6	31	54	65	54	33	48	52	44	31	26
Wing-barred Piprites	0	0	1	1	4	2	9	2	7	19	35	29
Yellow-margined Flycatcher	0	1	0	1	0	1	1	3	24	24	20	19
Dusky-capped Flycatcher	0	0	0	0	0	3	13	33	15	17	4	0
Piratic Flycatcher	2	2	7	14	24	13	8	12	15	13	12	8
Dusky-capped Greenlet	0	0	0	0	11	32	28	38	74	99	99	75
Thrush-like Wren	1	5	20	44	73	100	90	122	101	102	114	119
Buff-breasted Wren	0	1	5	13	14	30	65	76	36	38	40	54
Hauxwell's Thrush	18	40	46	46	67	63	79	68	74	82	88	88
Russet-backed Oropendola	0	0	0	1	0	0	8	22	25	48	41	14
Amazonian Grosbeak	8	24	55	58	57	46	52	52	48	30	25	0

(b)
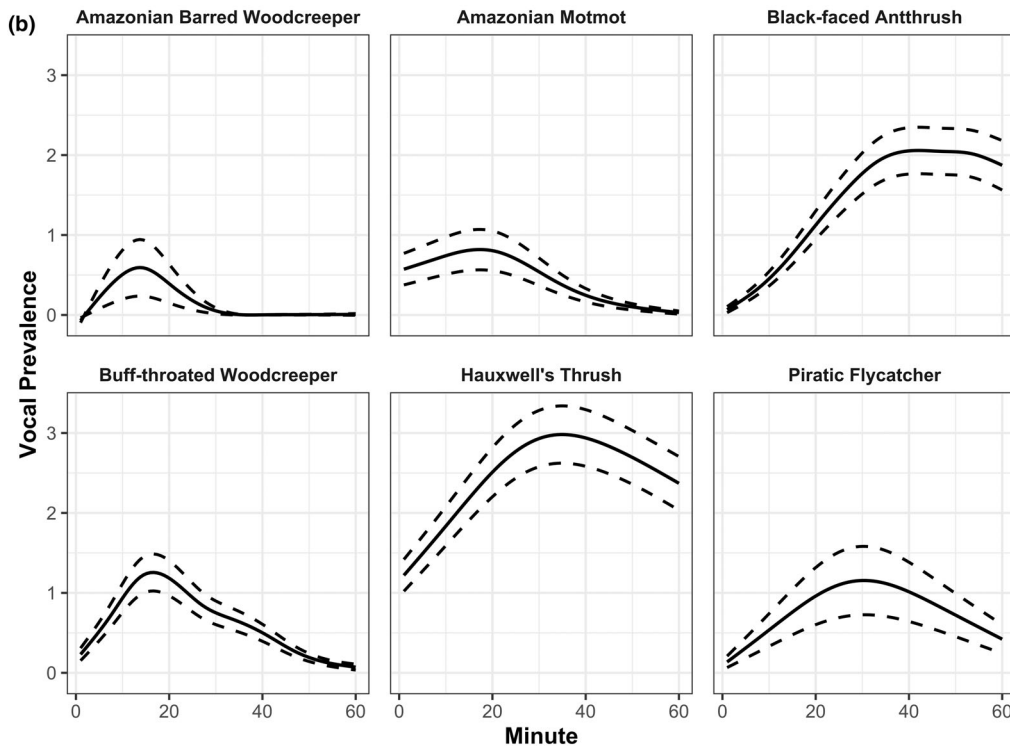
Figure 5. Species-level diel variation in vocal prevalence within the dawn hour. (a) Diel variation in vocal prevalence by 5-min interval for species with total vocal prevalence >75 from all sites and days, and (b) model-generated prediction curves ± 95% CIs of species-specific vocal prevalence within the dawn hour for six species.

first study to provide evidence that day-to-day temporal variation in the vocal activity and detectability of Amazonian bird communities may be strong enough to obscure statistically significant differences between sites in the absence of simultaneous data collection.

The variable diel patterns in avian vocal activity that we observed between species and taxonomic groups (Fig. 5) mean that visiting two sites with the same overall SR or TVP at different times in the morning could result in considerably different observations of community composition, even when both visits occur within the same hour. This species-to-species diel variation in vocal activity and detectability may partially or entirely explain why the diel variation patterns in SR and TVP that we documented within the dawn hour were spatially heterogeneous. Consistent with the findings of Rodriguez *et al.* (2014), these patterns varied between sites even in the same general habitat type and superficial condition. Because sites with differing communities should be expected to exhibit differing patterns of diel variation in overall vocal activity, the differing patterns of diel variation in TVP and SR that we documented between sites are plausibly the result of the spatial heterogeneity of bird community composition (Fig. 3).

The spatial heterogeneity in TVP and SR that we observed in contiguous lowland forest locations with superficially similar conditions may have been the result of cryptic habitat diversity. Though sometimes misrepresented as homogeneous, Amazonian habitats are highly heterogeneous (Pires & Prance 1985, Tuomisto *et al.* 1995), and important elements of their structural diversity remain poorly understood (Macía 2011, Borges 2013). Interactions between habitat features and avian community structure in the Amazon are extremely complex and are influenced by variables including soil type (Borges 2013), riverine sediment concentration (Laranjeiras *et al.* 2021), the condition of surrounding habitat (Latta *et al.* 2011, Laurance *et al.* 2011, 2012, Woltmann *et al.* 2012, Wolfe *et al.* 2015, Menger *et al.* 2017, Barlow *et al.* 2006, 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 generally rely on features discernible by field observers, can be overly simplistic (Milliken *et al.* 2010) and for this reason we avoided incorporating them in our analysis. The complexity of Amazonian systems increases the importance of controlling for temporal variables, which may obscure these effects.

Although this study was not designed to serve as a comprehensive census of the bird community at ITRA, our observations were generally consistent with those documented by previous census efforts in Madre de Dios's *várzea* forests (Terborgh *et al.* 1990, Martínez *et al.* 2023), namely that most species were rare, with a high proportion of TVP contributed by only a few species, and that sites were compositionally heterogeneous. The observation that the site in edge habitat (Site A) had the lowest average species richness per 1-min interval (4.03; 43 total), followed by Site F (4.41; 42 total), in degraded forest outside of the reserve boundaries, is consistent with the results of research focused on edge effects in Amazonia, which are known to have a pervasive impact on Amazonian bird communities (Terborgh *et al.* 1990, Laurance 2004, Barlow *et al.* 2006, Broadbent *et al.* 2008, Haddad *et al.* 2015, Laurance *et al.* 2011, Moura *et al.* 2016, Luther *et al.* 2020, Stouffer 2020). This habitat usage pattern differs from observed dynamics in temperate systems, where bird diversity tends to be higher in edge habitats than forest interiors (Baldi 1996, Lindell *et al.* 2007). Most annotations occurred in the frequency range of 0.5–5 kHz, suggesting possible signal masking from insects, which primarily occur between 4 and 12 kHz (Hart *et al.* 2015, Metcalf *et al.* 2020).

The temporal variation in avian vocal activity levels and observed species richness that we documented between days was greater and more consistent than we expected, generally influencing SR and TVP more than differences between sites. Supporting the idea that temporal effects may overwhelm statistically significant differences

between sites, sampling the same site on different days was more than twice as likely to result in significantly differing measures of SR and TVP than was sampling different sites on the same day, even though most site-to-site comparisons indicated significant differences in SR or TVP. That temporal variation was strongest for TVP 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 10-s window. Standard duration point counts should have higher rates of false absences on days with lower TVP, even with static species availability, because of the reduction in time windows where species vocalize.

We found that TVP was a useful metric for quantifying avian vocal activity and believe that it is worthy of further study and use. TVP is a more stable indicator of overall activity levels than raw call count, total number of annotations, or total annotation length because it is robust to natural differences in vocalization patterns across species. When annotation boxes are split, if the gap between vocalizations exceeds a set time interval (5 s in this study), alternative activity metrics are dependent on the innate vocalization rate of a given species. For example, Hauxwell's Thrush and Black-faced Antthrush were two of the most common species in this dataset but feature different vocalization styles; whereas Hauxwell's Thrushes often take only short breaks of fewer than 5 s between song bouts in the morning, Black-faced Antthrushes sing with gaps between song bouts that are generally >5 s. A Hauxwell's Thrush singing throughout the morning may only result in a small number of different annotation boxes but a large total annotation length that incorporates the time in-between song bouts, while a Black-faced Antthrush singing throughout the morning can feature a very high number of total annotations but will not include the gaps between song phrases because they exceed 5 s in length. In our data, Black-faced Antthrush had a total annotation length of 4456 s across 1500 individual bounding boxes, whereas Hauxwell's Thrush had a total annotation length of 25 308 s that constituted just 675 total bounding boxes. Using TVP eliminates this type of artificial species-to-species variability in vocal activity estimates. As a result, TVP can improve comparisons of annotated bioacoustic datasets that employ slightly different annotation protocols and can reduce manual analysis time by eliminating the need to measure

the distance between vocalizations. Whereas metrics that require species-level identification are highly contingent on observer skill level, driving inconsistencies in Neotropical bird surveys (Robinson *et al.* 2018), TVP supports using broader taxonomic groups for challenging identifications, potentially reducing time and experience barriers for researchers. We found that TVP correlated strongly with SR ($r = 0.85$, $P < 0.001$), meaning that it may be a viable proxy for species richness, even without requiring species identifications, and should be easier to generate with automated approaches than metrics that rely on species identifications. Because TVP essentially represents soundscape abundance, it can also enable the calculation of abundance-based indices such as Bray–Curtis dissimilarity and Shannon diversity with acoustic data.

Based on our collective results, we suggest that bioacoustic data should be collected to complement traditional bird surveys whenever possible. In addition to the short-term benefits of quantifying diel and day-to-day temporal variation, even small bioacoustic datasets serve as ecological time capsules (Sugai & Llusia 2019), particularly important in an era of rapid global change. ARUs can generate greater data volume than traditional methods without meaningfully increasing field time or cost (Hobson *et al.* 2002, Acevedo & Villanueva-Rivera 2006, Tegeler *et al.* 2012). Whereas manually analysing acoustic data can be time-intensive, limiting its utility, acoustic indices (Jorge *et al.* 2018, Metcalf *et al.* 2020) and automated identification programs such as BirdNET (Kahl *et al.* 2021) are continuously improving and could have a transformative effect on global ornithological research (Pérez-Granados 2023). Due to their relative rarity, fully annotated tropical soundscapes are critical for developing these automated programs, and this dataset has already been used for this purpose (Kahl *et al.* 2020). Studies focused exclusively on birds can come at the expense of developing knowledge of other groups (Gardner *et al.* 2008) but bioacoustic data collected for ornithological research often contain vocalizations of non-target taxa and other soundscape elements, enabling more holistic biodiversity research (Newson *et al.* 2017). To help advance these efforts, we encourage researchers collecting bioacoustic data to make use of open-access repositories such as Zenodo (European Organization For Nuclear Research & OpenAIRE 2013) to host their datasets, as we have (Hopping *et al.* 2022).

To conclude, we found that simultaneous PAM coupled with manual annotation revealed significant diel and day-to-day variation in the vocal activity and observed species richness of an Amazonian bird community, an ecological pattern that would be difficult to elucidate using traditional field methods. The magnitude of this temporal variation was large enough that it could mask meaningful differences between sites if temporal bias is not sufficiently accounted for in study designs. This research provides a case study for using PAM to quantify temporal variation in tropical bird surveys, even with a relatively small sample of sites and days. Future studies could help explain the mechanisms for this variation and improve methods for processing and interpreting large volumes of acoustic data in complex systems.

AUTHOR CONTRIBUTIONS

W. Alexander Hopping: Data curation; funding acquisition; writing – original draft; writing – review and editing; validation; visualization; investigation; conceptualization; methodology; formal analysis; software; resources; project administration. **Christopher J. Sayers II:** Data curation; writing – original draft; writing – review and editing; validation; software; formal analysis; visualization; methodology. **Noe Roger Huaraca-Charca:** Investigation; resources; validation. **Holger Klinck:** Supervision; resources; funding acquisition; writing – review and editing; conceptualization; methodology; project administration.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

Data Availability Statement

All software curated for this research are archived and available at https://github.com/csayers2/Inkaterra-ARU. The raw acoustic data and annotations referenced in this study can be found at https://zenodo.org/record/7079124 (DOI: 10.5281/zenodo.7079124).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Index of featured species and exclusions for TVP and SR calculations.

Appendix S2. The number of individual recordings that species were detected on.

Appendix S3. Tukey's HSD comparisons between sites, days and recordings.

Appendix S4. Model covariate summary statistics, including smoothing parameters (k), effective degrees of freedom (edf), F-statistics and P-values. Covariate effects highlighted in bold indicate statistically significant differences ($P < 0.05$) among groups based on analysis of variance (ANOVA).