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RESEARCH ARTICLE OPEN ACCESS

Acoustic Indices Reveal Fundamental Differences in Daily Phenology of Tropical and Temperate Forest Soundscapes

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ABSTRACT

Aim: Forests support the majority of the planet's terrestrial biodiversity, and in recent years the characterisation of soundscapes has emerged as a powerful tool for understanding forest ecosystems, both in terms of ecology and for the purpose of conservation. But it is still poorly understood to what extent generalisations can be made about soundscapes in different parts of the world, and to what extent we should expect soundscapes to differ regionally. Here, we characterise the dominant acoustic features of forest soundscapes on a global scale and establish baseline expectations for how acoustic indices vary among biogeographic realms and biomes.

Location: Forests in Brunei, Ecuador, Gabon, Germany, Peru, Singapore, Sierra Leone and the USA, a dataset spanning two biomes and five out of six global biogeographic realms where forests occur.

Time Period: Two to five weeks of continuous audio data from each site collected between 2020 and 2024.

Major Taxa: Birds, amphibians, insects and mammals.

Methods: Stratifying data by time and frequency, we calculated four acoustic indices. Principal components analysis was used to compare the similarity of soundscapes across sites.

Results: Temperate and tropical forest soundscapes clustered separately in principal component analysis. Temperate forests had soundscapes which were uniformly loud during the day across all frequencies and were generally quiet at night. In contrast, all tropical locations had complex soundscapes during both day and night and had banding patterns suggestive of a high diversity of soniferous insects. These banding patterns were created by the unique soniferous community at each site, causing the 'acoustic

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fingerprint' of each site to be most similar to other sites in the same ecoregion and in the same biogeographic realm. The 'acoustic fingerprints' of temperate forest differentiated between ecoregions only when dawn was considered separately.

Main Conclusions: Our results stress the importance of using regional specific baseline data, as soundscapes are not necessarily comparable. Ecoacoustics is growing in popularity as an ecosystem monitoring tool, and understanding how forest soundscapes vary naturally across the globe can provide much needed context for studies that seek to understand factors that may disrupt or alter those soundscapes.

1 | Introduction

Forests support the majority of the planet's terrestrial vertebrate biodiversity (Pillay et al. 2022) and store much of its carbon (Malhi et al. 2002; Schimel 2014). Anthropogenic climate change and other human activities such as landscape modification, logging, and hunting can alter forest ecosystems (Gardner et al. 2009). Human disturbances can influence biodiversity, perceptible through altered metrics of species richness, evenness and community composition (Johnson et al. 2017), lead to species endangerment or invasions (Prakash and Verma 2022) and alter ecological interactions like pollination, herbivory and predation (Fischer and Lindenmayer 2007). To fully understand these changes, we must first have comprehensive measures of the baseline characteristics of intact ecosystems and how they vary naturally across ecoregions and biogeographic realms. A close understanding of such ecological baseline attributes of forest ecosystems and their differences across spatial scales can also provide valuable insights into macro-ecological patterns, including latitudinal diversity gradients (Mittelbach et al. 2007) and biogeographic legacies (Cavender-Bares et al. 2016).

In recent years, soundscape analysis has emerged as a powerful tool for both conservation and ecological research (Dumyahn and Pijanowski 2011). Soundscapes are composed of all the sounds in a landscape, including wind and rain (geophony), human-made sound (anthropophony), as well as the vocalisations, stridulations, and tymbalizations of the species community (biophony) (Pijanowski et al. 2011). The biophony in a soundscape can be used to make inferences about species diversity, differences in species composition, and phenology, among others, if the assumption that vocalising diversity correlates with overall diversity holds (Farina 2014; Eldridge et al. 2018; Bradfer-Lawrence et al. 2020; Alcocer et al. 2022). For that reason, soundscape recording and analysis have become important ecosystem monitoring tools (Gibb et al. 2019). Soundscapes are now used for rapid biodiversity assessments (Bradfer-Lawrence et al. 2020), the detection of invasive or endangered species (Amorim et al. 2023; Dema et al. 2020), monitoring gunshots and poaching in nature reserves (Hedley et al. 2022; Yoh, Mbamy, et al. 2024), tracking phenological shifts (Buxton et al. 2016; Berman et al. 2025), detecting patterns of acoustic niche partitioning (Berman et al. 2024), distinguishing between intact and degraded forest habitats (Rappaport et al. 2022), and to track restoration success in tropical forests (Müller et al. 2023). The scientific community is in the process of building an understanding of the baseline acoustic characteristics of intact forests, to be able to differentiate between expected temporal and spatial variance versus signs of human-induced change (Somervuo et al. 2025).

Passive acoustic monitoring (PAM) is a non-invasive monitoring method using autonomous recording devices to collect environmental soundscapes. The expansion of PAM networks is increasingly making it possible to examine soundscapes at a global scale (Darras et al. 2025; Somervuo et al. 2025). PAM can generate large amounts of data, which are typically analysed using either acoustic indices or machine-learning species classifiers. Acoustic indices summarise features of audio recordings to infer meaningful ecological information about the soundscape as a whole (Sueur et al. 2014). Currently, more than 60 acoustic indices have been proposed (Alcocer et al. 2022; Bradfer-Lawrence et al. 2019; Buxton et al. 2018), and each index measures a different aspect of the soundscape. For example, the Acoustic Complexity Index (ACI) is designed to measure the complexity of biotic song while ignoring anthropogenic background noise by computing the variability in sound intensities (Pieretti et al. 2011). The inverse temporal entropy index (ENT) is highest for long pure tones like whistles and lowest for brief atonal sounds (Sueur et al. 2008; Towsey and Zhang 2014). The acoustic events index (EVN) counts the number of times the sound intensity passes a certain threshold per second as an approximation for the number of animal vocalisations. And power minus noise (PMN) measures the overall loudness of the soundscape above baseline background noise (Towsey 2017). In conjunction, indices like these can be used to gain a general understanding of the types of vocalisations and noises occupying the soundscape at different frequencies and times, based on their loudness, complexity, tonality, and call rate even when the exact species vocalising cannot be identified. In contrast, species classifiers are used to detect and classify individual vocalisations as belonging to a particular species, taxa or even individual (Hanf-Dressler et al. 2026). Acoustic indices and species classifiers each have their strengths and limitations, and both methods can be used in complementary ways to gain a holistic understanding of the soundscape (Bradfer-Lawrence et al. 2025). When compared to species classifiers, one of the main advantages of acoustic indices is their breadth. Acoustic indices are particularly useful for studies spanning sites across biogeographic realms, where there is little to no overlap in species composition, especially considering species classifiers are not equally available across regions and taxa (Pérez-Granados 2023; Funosas et al. 2026). Indices can also more effectively explore the use of acoustic niche space (Krause 1993) - to what extent different frequencies or times of day are saturated with complex sounds (Planque and Slabbekoorn 2008; Robert et al. 2019).

Baseline information is needed to use acoustic indices effectively as an ecosystem monitoring tool. Monitoring studies frequently have assumptions about which times, frequencies, and indices are most important built into their sampling design, but assumptions based in one biogeographic region do not necessarily hold in another (Alcocer et al. 2022). It is still poorly

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understood to what extent biogeographic legacies lead to inherent differences in the structure of soundscapes, or to what extent similar ecological drivers lead to the convergence of soundscape structure in similar forest types across different biogeographic realms. Acoustic indices are impacted by the acoustic characteristics of local soniferous fauna (Sagar et al. 2024) which can lead to inherent differences between biogeographic realms (Dröge et al. 2021; Izaguirre et al. 2021). Additionally, canopy structure, humidity, and temperature have frequency-dependent influences on sound propagation (Pekin et al. 2012; Farina 2013; Larsen and Radford 2018), which in combination with known differences in species richness may lead to distinctive biome-specific acoustic characteristics of temperate and tropical forests respectively. Most studies have been carried out in either temperate (Buxton et al. 2018; Eldridge et al. 2018; He et al. 2022) or tropical forests (Opaev et al. 2021), but there are few truly comparative studies of global datasets collected and analysed in a uniform way (Darras et al. 2025). Evaluating acoustic indices in intact habitats can help establish baseline values and determine which acoustic features best reflect patterns in those environments (Gaspar et al. 2023; Kotian et al. 2024).

Our study aims to characterise the dominant acoustic features of forest soundscapes on a global scale, establish baseline expectations for how acoustic indices vary among biogeographic realms and biomes, and determine the extent of similarity among global forest soundscapes. Specifically, we investigate the following questions: (1) How do soundscapes of intact temperate deciduous forests differ from those of tropical rainforests? (2) How do forest soundscapes vary across biogeographic realms?

2 | Methods

2.1 | The Soundscape Baselines Project

The core dataset used in this study originates from the Soundscape Baselines Project (Buřivalová et al. unpublished manuscript), an international collaborative effort to collect long-term soundscapes from intact forests worldwide. While truly undisturbed forests are rare, this project defines intact forests as those with minimal human influence, limited to low levels of hunting and no commercial timber extraction. All sites were in mature forests that had not been logged for at least 40 years. Most of these sites were in protected areas or on research station land. Long-term study sites for the Soundscape Baselines Project were established in Brunei, Ecuador, Gabon, Germany, Peru and the USA. Additionally, we incorporated compatible data from Singapore and Sierra Leone, which were not part of the Soundscape Baselines Project, for a more comprehensive global scope (Figure 1). Ideally, future studies will compare more locations per realm to confirm if the patterns we observe here hold.

2.2 | Data Collection

Locations were selected to span a globally representative set of forest ecoregions. Our locations included five out of six biogeographic realms where forests occur: Nearctic, Palearctic, Neotropic, Afrotropic and Indomalayan (Figure 1). Biogeographic realms, biomes, and ecoregions were defined according to the Resolve Ecoregions framework (Dinerstein et al. 2017), where broad biogeographic realms are further subdivided into smaller ecoregions. Our dataset encompasses both temperate broadleaf and mixed forests (Nearctic and Palearctic) and moist tropical and subtropical forests (Neotropic, Afrotropic and Indomalayan). Within each tropical realm, we sampled two ecoregions, with 2–6 individual recording sites per ecoregion (Table 1).

2.3 | Acoustic Sampling

Each recording site was spaced at least 1 km away from the nearest site (Figure 1) and had one autonomous recording unit (ARU) recording continuously without subsampling. Most sites used BAR-LT (Frontier Labs, Australia) with a 44.1 kHz sampling rate, 22.05 kHz Nyquist frequency and 40 dB gain saved as 16-bit WAV files, except for Singapore, which used AudioMoth (Open Acoustic Devices, UK) recording with a 16 kHz sampling rate, 8 kHz Nyquist frequency and medium gain saved as 16-bit WAV files. All audio files were 30-min in duration, starting on the hour or half hour, for a total of 48 audio files per site per day. While different ARU models and sampling rates have an influence on the soundscapes recorded (Corvus 2024), we prioritised maximum ecoregion coverage. This study represents an early analysis of what will become a long-term monitoring dataset, with a year or more of continuous audio data from each study location. Here, we limited the dataset to a maximum of 5 weeks per site so that all sites were represented by a similar amount of data, and to minimise the confounding effects of seasonality and shifting photoperiod. Not all sites reached the preferred 5 weeks, but each site had a minimum of 2 weeks of continuous audio data, exceeding the recommended 120-h minimum per site to ensure within-season variance stabilisation (Bradfer-Lawrence et al. 2019). To account for strong seasonality at temperate sites, we selected audio data from the Nearctic and Palearctic realms collected in May to capture avian vocal activity during the breeding season. At tropical sites, data were collected to correspond with the local avian breeding season. We excluded days when researchers were on-site for deployment or revisiting of the recorders to minimise confounding disturbance in the audio files (Jorge et al. 2018), resulting in a dataset with full days only. No audio files were filtered, as filtering can impact acoustic index values (Hyland et al. 2023). Further details on individual sites can be found in Table 1.

2.4 | Acoustic Index Calculation

Acoustic indices were calculated using AP.exe version 23.9.0.2 (Towsey, Truskinger, et al. 2018), developed by Queensland University of Technology (QUT) Ecoacoustics for long-duration environmental recordings. We chose to calculate indices using the QUT Ecoacoustics AP package over similar methods, such as the R package soundecology (Villanueva-Rivera and Pijanowski 2016), due to its efficiency with large datasets. AP.exe segments audio into 1-min bins with a 43.1 Hz bandwidth, calculating indices for each bin from 0 to 11 kHz. All indices were calculated using FFT = 512 and had identical bin boundaries. In this study, we used four indices: Power Minus Noise (PMN), which measures approximate loudness as the difference between

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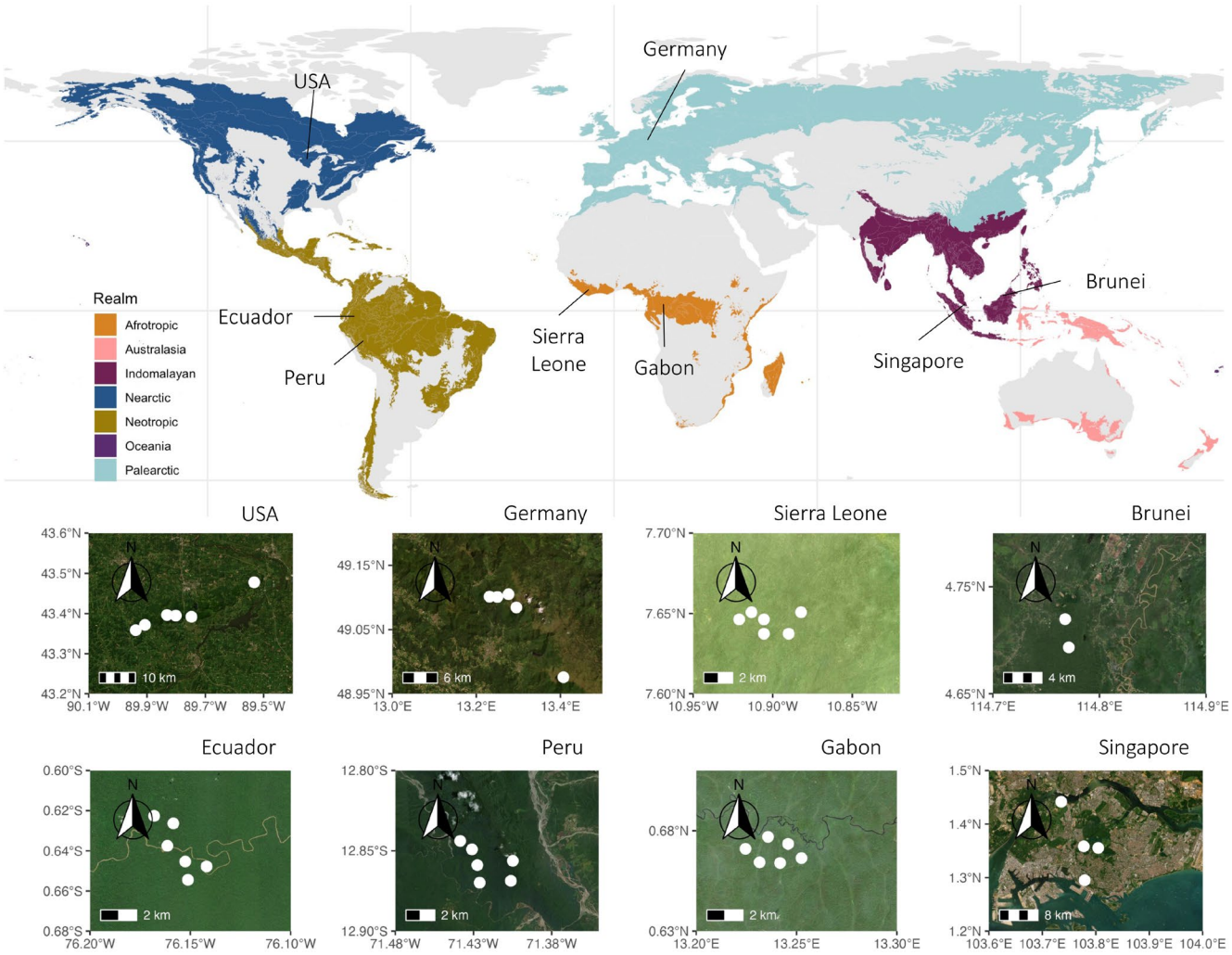


FIGURE 1 | Top: Global forested landscapes (Dinerstein et al. 2017) coloured by biogeographic realm. Non-forest landscapes were left blank (grey). Country labels indicate study locations. Bottom: White dots show specific recording sites. Basemap is esri world imagery.

the maximum decibel value and background noise (assumed to have a Gaussian distribution); inverse temporal Entropy (ENT), which quantifies temporal energy concentration or tonality, with higher values indicating more long, pure toned musical sounds like whistles and lower values indicating more short atonal sounds; Acoustic Complexity Index (ACI), which measures the relative change in acoustic intensity and is commonly used to assess biophony; and acoustic Events (EVN), which are detected when the spectrogram cell value crosses the 3 dB threshold, effectively measuring call rate (Sankupellay et al. 2015; Towsey, Truskinger, et al. 2018). The indices ENT, ACI and EVN were selected because they measure complementary characteristics of animal vocalisations (complexity, tonality, and call rate), making it possible to infer which taxa might be vocalising and are often used in false-colour spectrograms (Towsey et al. 2015). PMN was selected to provide a more transparently interpretable measure of loudness and measures the decibel level above background noise. False-colour spectrograms are a concise way to display soundscape information and help to highlight times and frequency bands which are high in some indices but low in others by mapping three indices to red, green, and blue in RGB colour space. Index values for frequencies below 0.2 kHz and above 10.7 kHz were excluded from analysis to avoid edge effects; these lowest and highest frequency bins sometimes contain artefacts which can lead to unreasonably high index values.

2.5 | Principal Component Analysis

We used principal component analysis to quantify the similarity of soundscapes among biomes, realms, ecoregions, and sites. For all four indices at all 41 sites, data were grouped by site, index, frequency bin (~43 Hz), and time (10 min), then averaged across days and 10-min bins, resulting in a 41 by 140,544 matrix, with one row per site and one column for each possible combination of index, frequency, and time. For example, average ACI at 2.155–2.198 kHz at 12:00–12:10 PM was one eigenvector. PCA handles missing data poorly, so sites which had high missingness (NUS and GRNP_811) were excluded from PCA. In analyses including Singapore, which had a 8 kHz maximum detected frequency, only frequencies up to 7.7 kHz were used to avoid edge artefacts which were sometimes seen in the top 0.2 kHz. After excluding sites and frequencies with high missingness, the data matrix input for PCA included 39 sites and 75,168 variables. Fifteen separate PCAs were performed, in which we subsetted the data in a variety of ways to focus on the differences

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TABLE 1 | Audio data collection details.

Biome	Biogeographic realm	Ecoregion	Country	Locality	ID	Lat	Lon	Start date	End date	Duration (days)	Sampling rate (kHz)
Temperate Broadleaf and Mixed Forest	Nearctic	Upper Midwest US Forest-Savannah Transition	USA	Baraboo Hills, Wisconsin	W1	43.3717	−89.9070	6-May-2024	1-Jun-2024	26	44
					W2	43.3588	−89.9385	6-May-2024	1-Jun-2024	26	44
					W3	43.3966	−89.8314	6-May-2024	1-Jun-2024	26	44
					W4	43.3951	−89.8012	6-May-2024	1-Jun-2024	26	44
					W5	43.4778	−89.5324	6-May-2024	1-Jun-2024	26	44
					W6	43.3920	−89.7475	6-May-2024	1-Jun-2024	26	44
	Palearctic	Western European Broadleaf Forests	Germany	Bavarian Forest National Park	D1	49.1009	13.2503	24-Apr-2024	31-May-2024	37	44
					D2	49.1014	13.2315	24-Apr-2024	31-May-2024	37	44
					D3	49.1051	13.2766	24-Apr-2024	31-May-2024	37	44
					D4	49.0846	13.2954	24-Apr-2024	31-May-2024	37	44
					D5	48.9758	13.4074	24-Apr-2024	31-May-2024	37	44

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TABLE 1 | (Continued)

Biome	Biogeographic realm	Ecoregion	Country	Locality	ID	Lat	Lon	Start date	End date	Duration (days)	Sampling rate (kHz)
Moist Tropical and Subtropical Broadleaf Forests	Neotropic	Napo Moist Forests	Ecuador	Tiputini Biodiversity Station	E1	−0.6264	−76.1585	28-Oct-2023	28-Nov-2023	31	44
					E2	−0.6226	−76.1680	28-Oct-2023	28-Nov-2023	31	44
					E3	−0.6375	−76.1614	28-Oct-2023	28-Nov-2023	31	44
				Yasuni National Park	E4	−0.6453	−76.1525	28-Oct-2023	28-Nov-2023	31	44
					E5	−0.6544	−76.1512	28-Oct-2023	28-Nov-2023	31	44
				Tiputini Biodiversity Station	E6	−0.6478	−76.1419	28-Oct-2023	28-Nov-2023	31	44
		Southwest Amazon Moist Forests	Peru	Manu Biological Station	P1	−12.8687	−71.4061	18-May-2023	17-Jun-2023	30	44
					P2	−12.8562	−71.4048	18-May-2023	17-Jun-2023	30	44
					P3	−12.8438	−71.4385	18-May-2023	17-Jun-2023	30	44
					P4	−12.8491	−71.4310	18-May-2023	17-Jun-2023	30	44
					P5	−12.8589	−71.4275	18-May-2023	17-Jun-2023	30	44
					P6	−12.8698	−71.4261	18-May-2023	17-Jun-2023	30	44

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TABLE 1 | (Continued)

Biome	Biogeographic realm	Ecoregion	Country	Locality	ID	Lat	Lon	Start date	End date	Duration (days)	Sampling rate (kHz)
	Afrotropic	Northwest Congolian Lowland Forests	Gabon	Makokou, Massaha Community	GAB1	0.6770	13.2358	15-Oct-2022	11-Nov-2022	27	44
					GAB2	0.6735	13.2458	15-Oct-2022	11-Nov-2022	27	44
					GAB3	0.6664	13.2524	15-Oct-2022	11-Nov-2022	27	44
					GAB4	0.6640	13.2418	15-Oct-2022	11-Nov-2022	27	44
					GAB5	0.6643	13.2316	15-Oct-2022	11-Nov-2022	27	44
					GAB6	0.6710	13.2245	15-Oct-2022	11-Nov-2022	27	44
		Western Guinean Lowland Forests	Sierra Leone	Gola Rainforest National Park	GRNP_1	7.6508	−10.9133	12-Dec-2021	25-Dec-2021	13	44
					GRNP_12	7.6374	−10.9055	12-Dec-2021	25-Dec-2021	13	44
					GRNP_176	7.6508	−10.8822	12-Dec-2021	25-Dec-2021	13	44
					GRNP_369	7.6463	−10.9055	12-Dec-2021	25-Dec-2021	13	44
					GRNP_397	7.6374	−10.8900	12-Dec-2021	25-Dec-2021	13	44
					GRNP_811	7.6463	−10.9211	12-Dec-2021	25-Dec-2021	13	44

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TABLE 1 | (Continued)

Biome	Biogeographic realm	Ecoregion	Country	Locality	ID	Lat	Lon	Start date	End date	Duration (days)	Sampling rate (kHz)
	Indomalayan	Borneo Lowland Rainforest	Brunei	Kiudang	Kiudang 2	4.7197	114.7678	1-Jan-2024	1-Feb-2024	31	44
					Kiudang C	4.6933	114.7712	1-Jan-2024	1-Feb-2024	31	44
		Peninsular Malaysia Rainforest	Singapore	Central Catchment Nature Reserve	CCNR	1.3555	103.8045	23-Jun-2020	8-Jul-2020	15	16
				Dairy Farm Nature Park	DAFA	1.3584	103.7775	23-Jun-2020	8-Jul-2020	15	16
				National University of Singapore	NUS	1.2951	103.7793	23-Jun-2020	8-Jul-2020	15	16
				Sungei Buloh Wetland Reserve	SBWR	1.4416	103.7353	23-Jun-2020	8-Jul-2020	15	16

Note: Sample sites are distributed throughout two biomes, five biogeographic realms, and eight ecoregions. Soundscapes from all sites were recorded in 30-min long 16-bit WAV files starting on every hour and half hour, collecting the full 24-h period without subsampling.

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between specific groups: The dataset included either (a) all sites, (b) only temperate forest locations or (c) only tropical forest locations; and either (1) the full 24-h period, (2) only times from 07:00 to 18:00, which were daylight hours across all locations or (3) only the hours from 21:00 to 03:00, which were nighttime hours across all locations, (4) only the dawn chorus (2 h before sunrise—2 h after sunrise) or (5) only the dusk chorus (2 h before sunset—2 h after sunset). Sunrise and sunset times were aligned across sites using the getSunlightTimes function from the R package suncalc (Thieurmel and Elmarhraoui 2022). Versions of the PCAs which keep high frequencies but exclude Singapore can be found in the Supporting Information. PCA was calculated using prcomp in the stats package of R version 4.4.1 (R Core Team 2024).

2.6 | False Colour Spectrograms

Numerous indices have been developed to correlate with vocal activity, and each differs in its sensitivity to certain types of vocalisations. Indices differ particularly in their sensitivity to insect sound (Ross et al. 2021). A combination of three indices has been found to provide a more reliable representation of the soundscape than any single index (e.g., Scarpelli et al. 2023). We generated false colour spectrograms (Towsey, Znidersic, et al. 2018) by combining three indices to offer a more comprehensive visualisation of the soundscape. Each index describes a different characteristic of the soundscape, making it possible to infer which taxa are vocalising based on their call rate (EVN), tonality (ENT), and vocal complexity (ACI). The RGB colour scale was normalised to the overall minimum and maximum values of each index across all sites: ACI (red, 0.34–0.71), ENT (blue, 0.03–0.34) and EVN (green, 0–3). Indices were converted to RGB values using the rgb function in the R core package grDevices, and the matrix was rasterized using geom_raster from package ggplot2 (Wickham 2016). To provide a comprehensive overview of the typical soundscape at each study location, we calculated the average values of each acoustic index grouped by time (10-min bins), frequency (43 Hz bins) and location.

3 | Results

3.1 | Temperate Versus Tropical Forest Soundscapes

The PCA of all forest soundscapes revealed a primary division between temperate and tropical forests (Figure 2i). Temperate soundscapes had uniformly high index values during the day and low values at night (Figures 3 and 4). Soundscapes

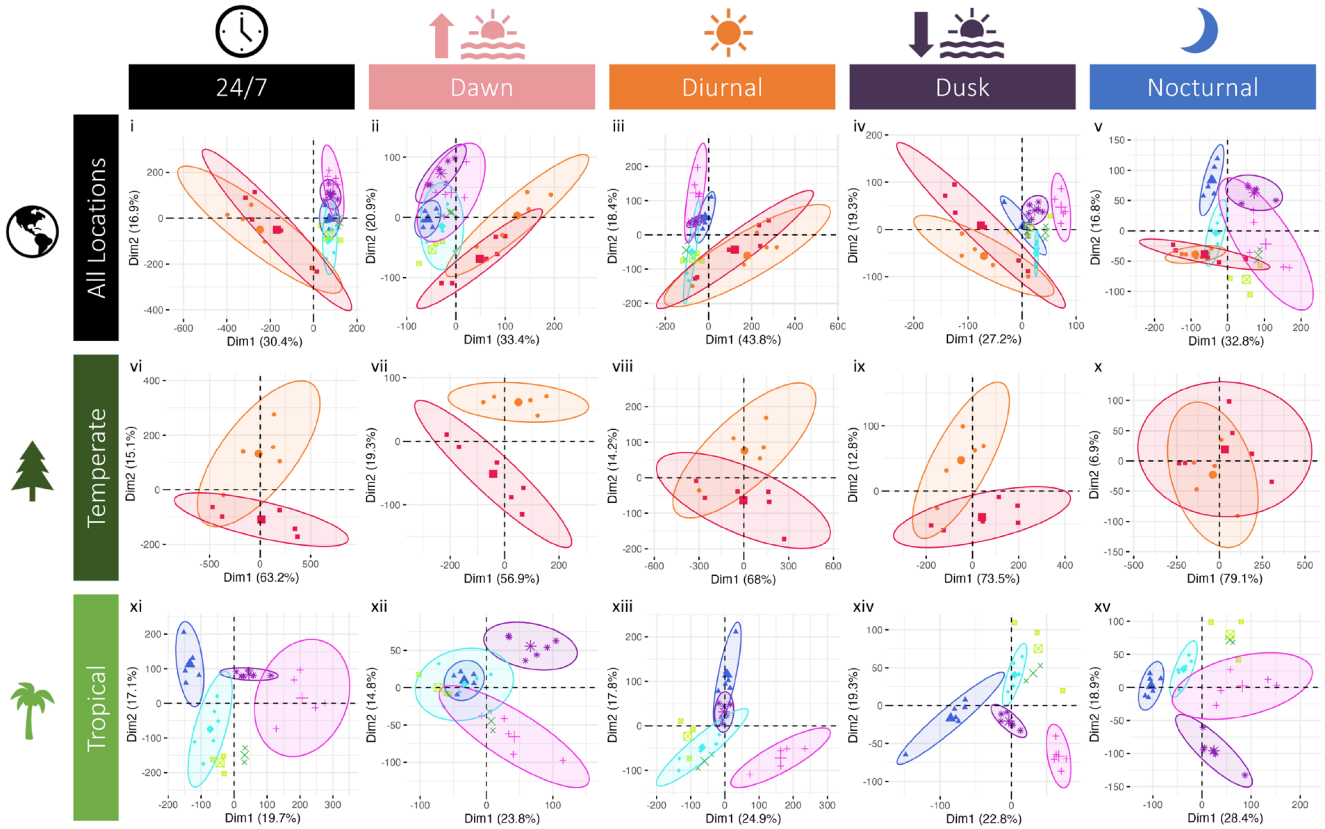


FIGURE 2 | Principal component analysis (PCA) showing similarity of soundscapes across all locations (row 1, panels i–v), temperate forest locations (row 2, panels vi–x) and tropical forest locations (row 3, panels xi–xv), using either the entire 24-h period (column 1, panels i, vi, xi), only data from the dawn chorus (2 h before sunrise—2 h after sunrise, panels ii, vii, xii), the diurnal period (07:00–18:00, panels iii, viii, xiii), the dusk chorus (2 h before sunset—2 h after sunset, panels iv, ix, xiv) or the nocturnal period (21:00–03:00, panels v, x, xv). Each point is one recording site, and sites are colour-coded by recording location (country). Eigenvectors are composed of each possible combination of acoustic index, frequency bin and 10-min window. Sites NUS and GRNP_811 were excluded due to high missingness. Singapore and Brunei had too few points to calculate an ellipse.

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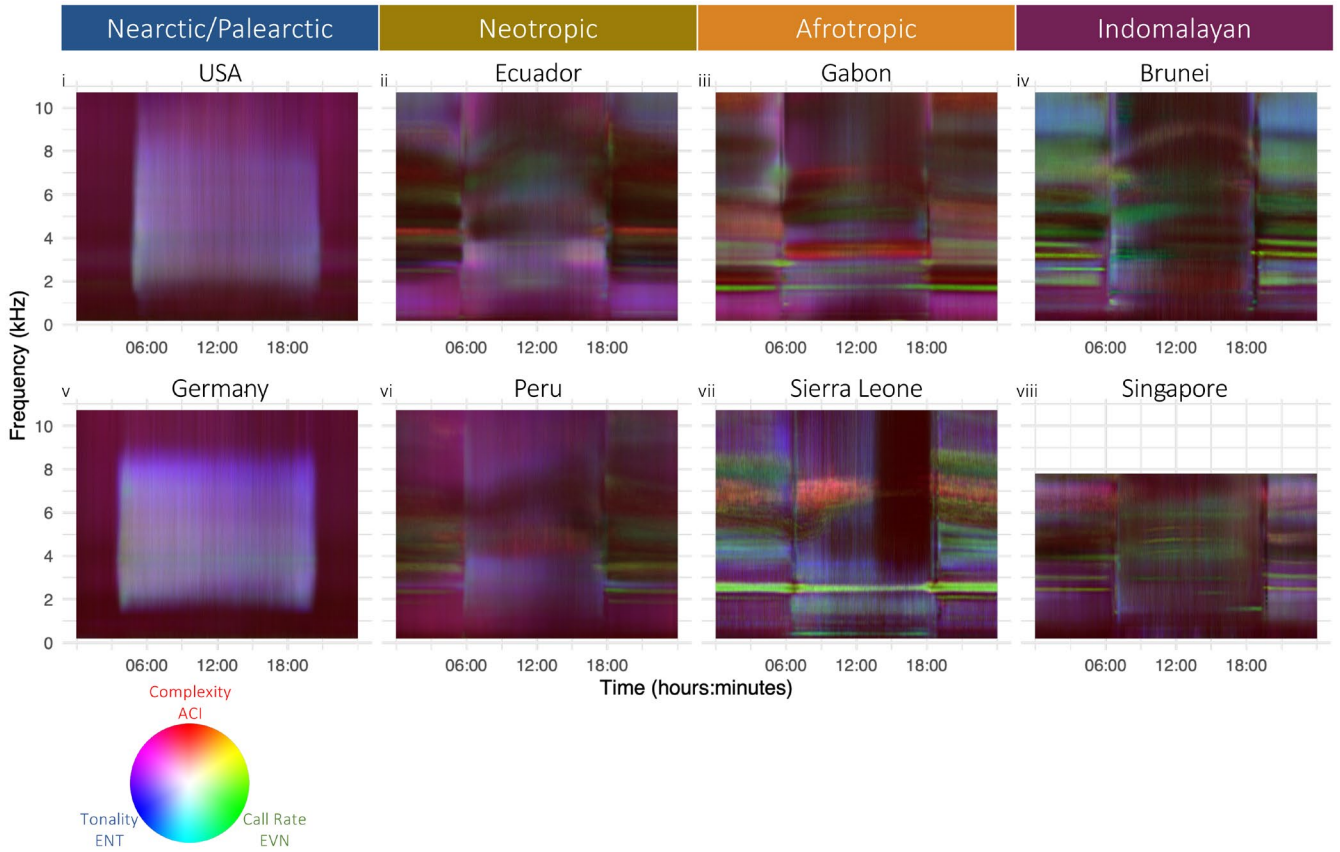


FIGURE 3 | Red-green-blue false colour spectrogram combining three acoustic indices, acoustic complexity index (ACI, red), inverse temporal entropy (ENT, blue) and acoustic events (EVN, green). High ACI indicates more complex song. High ENT indicates long pure tones, as opposed to short atonal sounds. High EVN indicates high call rates. Colour approaches white as all indices increase, and approaches black when all indices decrease. Data is averaged across all sites for each location. Missing data from Singapore is due to a lower sampling rate.

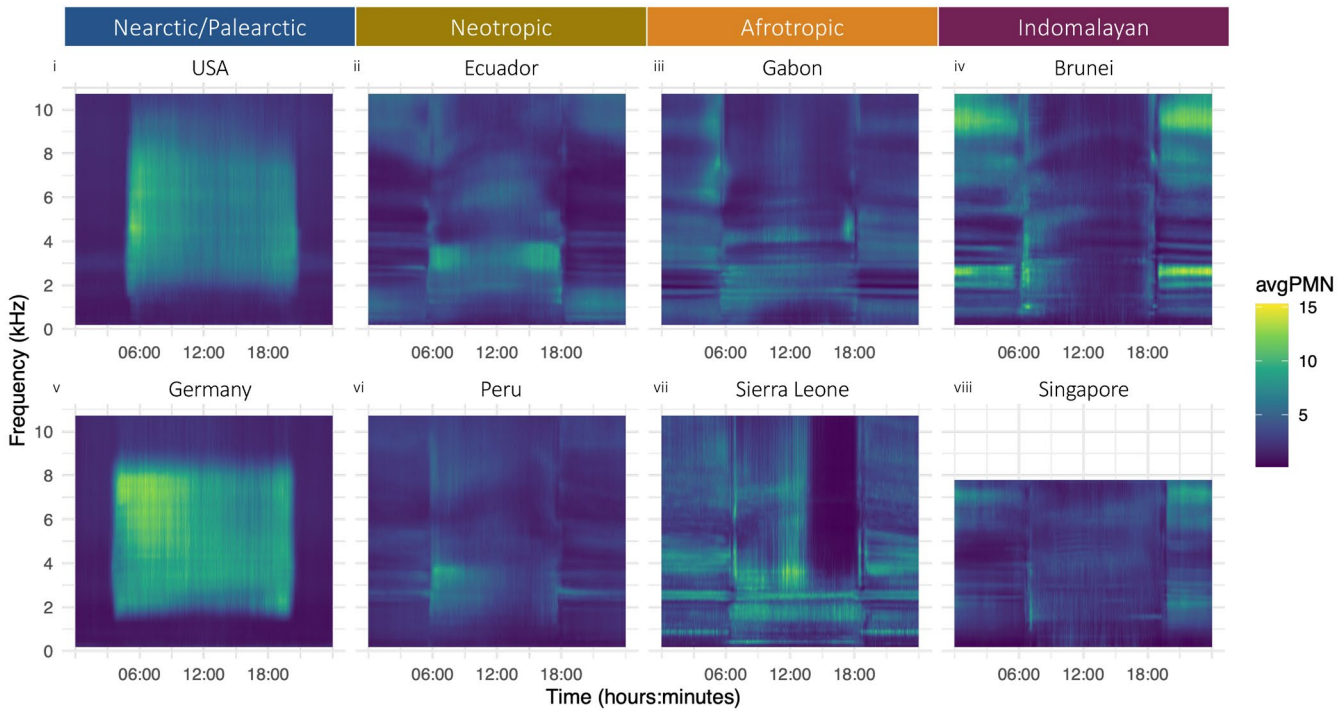


FIGURE 4 | Average power minus noise (PMN) across frequency and time of day for each study location in decibels. PMN is a measure of loudness above baseline background noise. Data are averaged across all sites for each location. Missing data from Singapore is due to a lower sampling rate.

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from temperate forests in the USA and Germany were very similar as measured by acoustic indices, despite their locations in distinct biogeographic realms (Figure 2), especially at night (Figure 2x) when ACI, ENT, EVN and PMN values were uniformly low (Figures 3i,v and 4i,v). In all tropical forest soundscapes, but in none of the temperate ones, there was distinct frequency stratification, a horizontal banding pattern (Figures 3 and 4). Tropical soundscapes could be as loud or louder at night as compared to during the day, while temperate soundscapes were generally quiet at night (Figure 4). Above 8 kHz, in temperate forests, all indices tended to taper off, while in tropical forests, the soundscape was still saturated at higher frequencies.

3.2 | Differences Among Biogeographic Realms and Ecoregions

Tropical forest soundscapes clustered separately by ecoregion, with locations from the same realm adjacent to one another (Figure 2xi). The differences between ecoregions among tropical forest soundscapes were generally diagnostic, with distinguishing information between ecoregions present in both the diurnal (Figure 2xiii) and nocturnal (Figure 2xv) periods, with the nocturnal periods being especially distinct. Tropical forest sites tended to have banding patterns most similar to those from the same ecoregion (Figure 5). The banding patterns of each ecoregion were most similar to those from the same biogeographic

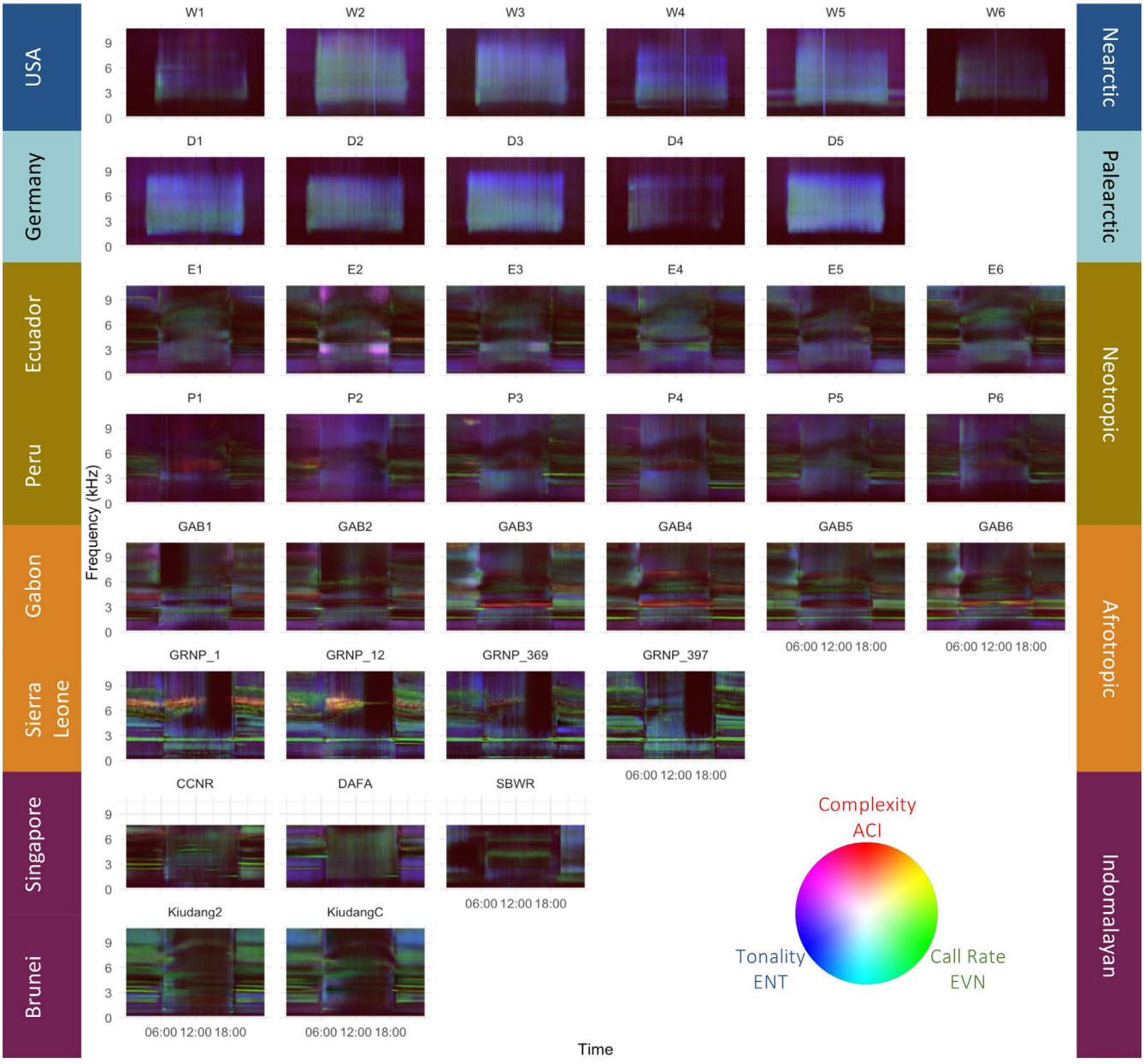


FIGURE 5 | Within-realm variation. Each false colour (ACI/ENT/EVN) spectrogram represents the average values over 2–5 weeks at each recording site. Sites NUS, GRNP_811 and GRNP_176 were excluded due to partial missingness. ACI, Acoustic Complexity Index; ENT, inverse temporal Entropy; EVN, events. High ACI indicates more complex song. High ENT indicates long pure tones (whistles), as opposed to short atonal sounds (clicks). High EVN indicates high call rates.

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realm (Figures 3–5). Differences between Nearctic and Palearctic soundscapes were not as well delineated; there was elliptical overlap between the German and USA clusters during both diurnal and nocturnal periods (Figure 2). The differences between Nearctic and Palearctic soundscapes disappeared almost entirely at night (Figure 2x). The dawn chorus was the only time period when Nearctic and Palearctic soundscapes had no elliptical overlap (Figure 2vii).

4 | Discussion

We provide a quantitative baseline dataset to describe how intact forest soundscapes vary across the globe. While it is well established that forests in different regions do of course sound different (Sethi et al. 2020, 2023; Somervuo et al. 2025), the comparative strength of the opposing influences of biogeographic legacies and ecological convergence is still poorly understood. In other words, there is not yet a baseline understanding of what assumptions we can make about a soundscape based on the region where it occurs. This understanding is important in both conservation and ecological contexts. Some features of the soundscape clearly differed between temperate versus tropical forest, like the quiet nights of temperate forests. Other features distinguished between biogeographic realms, like the distinct banding patterns found at each of our tropical forest sites. There were also some patterns that held true across temperate and tropical soundscapes globally—most notably, all soundscapes had distinct inflection points at dawn and dusk, likely due to distinct cohorts of nocturnally and diurnally active soniferous species. Future studies with data from additional ecoregions and across the annual cycle will continue to build this essential baseline knowledge on the variation of global forest soundscapes.

4.1 | Noisy Tropical Nights

While temperate forests tended to be quiet at night, tropical forests across all biogeographic realms exhibited loud, complex nocturnal soundscapes (Figures 3 and 4). The nocturnal tropical soundscape contains a robust soniferous community. The majority of frogs (Villanueva-Rivera 2014), katydids (Symes et al. 2016) and crickets (Gomez-Morales and Acevedo-Charry 2022) are acoustically active at night, particularly during the first few hours after sunset. Bats are also important contributors to the nocturnal soundscape (López-Baucells et al. 2021), although most bat (and some orthoptera) vocalisations occupy frequencies above our recording settings. The nocturnal soundscape with the highest PMN was Brunei (Figure 4), home of the Empress Cicada (*Megapomponia imperatoria*), which can reach up to 120 dB at close range (Riede 1996). Whereas the PMN index (power minus noise) expresses loudness (power) across time and frequency, the background noise removed during the calculation of this index can sometimes include biotic sound that is long and even in nature, such as some invertebrate choruses (e.g., Figure S3). Temperate forests are generally understood to have quiet nights due to the lower overall diversity of amphibians, katydids, and crickets, which all have their centres of diversity in tropical regions (Song 2018; Duellman 1999), and because of their colder temperatures, which are an additional physiological limiting factor on nocturnal vocalisations of amphibians and insects (Sanborn 2005; Oseen and Wassersug 2002). Physical characteristics of the forested landscape like vegetation density and humidity can also influence the soundscape by altering sound propagation, but this effect is likely much weaker than the influence the faunal diversity has on the soundscape.

4.2 | Tropical Frequency Stratification

Another salient distinction between tropical and temperate soundscapes was the stratification of frequencies. All our tropical sites had narrow horizontal green (high EVN index values) stripes throughout the nocturnal period. These green stripes show sounds that have characteristics most stereotypical of frog and cricket choruses: a simple (low complexity, less red) atonal (low inverse temporal entropy, less blue) chirp, repeated many times per minute (high number of events, more green), always at the same narrow frequency, continuously from sunset to sunrise (horizontal stripe). Some tropical sites also had red bands with characteristics stereotypical of cicadas: complex (more red) atonal (less blue) continuous drones (less green). The fact that this banding pattern is evident in tropical forests but not temperate ones can likely be attributed to the higher diversity of insects and anurans in tropical regions (Song 2018; Duellman 1999). Likely because each species occupies its own acoustic niche in terms of frequency and time, there was a strong biogeographic signal when comparing the similarity of tropical soundscapes. Shared bands and similar soundscapes among sites from the same ecoregion likely result from sites being similar in terms of species composition (Figure 5). Bird song has different acoustic characteristics and tends to appear as wide, pale-coloured bands in our false-colour spectrograms. Bird song tends to be complex (high ACI, more red), musical (high inverse temporal entropy, more blue), with many notes per minute (high number of events, more green) and have different types of notes at different frequencies (wider frequency band). Song with these characteristics appears as whitish (high value across all indices) in Figures 3 and 5 and can be seen throughout the day at our temperate locations, and during the dawn chorus in particular at our tropical sites.

4.3 | Index Variance May Be an Indicator of Sound Stratification

It is possible that this pattern of stratification has previously been underappreciated, and may be the reason why some studies observed that the variance in indices in frequency and time is often a more powerful indicator of biodiversity than the average value (e.g., Bradfer-Lawrence et al. 2019). Many studies using acoustic indices make use only of the average value for a site, both across time and frequency (e.g., Allen-Ankins et al. 2023), which can be problematic due to strong daily phenology of soundscapes (Yoh, Haley, and Burivalova 2024). Coming from a temperate forest paradigm (Figures 3 and 4), there would be little reason to separate out the frequencies when analysing soundscape patterns. However, our results clearly show that in tropical forests, frequency is a well-partitioned parameter. A higher degree of acoustic partitioning in frequency and time, resulting in a banding pattern like the one we observe at tropical sites, would lead to higher measured variance across acoustic indices. Higher species diversity is often associated with a greater degree of

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niche partitioning, including partitioning of acoustic space and frequency bands (Carscadden et al. 2020; Robert et al. 2019).

4.4 | Acoustic Indices May Be Better Applied to Insects and Anurans Than to Birds

Many studies have used acoustic indices to estimate avian biodiversity and species richness (e.g., Bradfer-Lawrence et al. 2020). However, considering the availability of more refined tools for avian monitoring, future studies may find that acoustic indices are a tool better suited to the monitoring of acoustically active insects and frogs instead. Machine learning species identification of more than 6000 out of the approximately 10,000 known species of birds is already possible with convolutional neural networks like BirdNET (Kahl et al. 2021). The accuracy and breadth of contexts in which species-specific bird song identification can be applied is improving rapidly every year (Shen et al. 2023). However, this type of species identification is still difficult in tropical forests (Müller et al. 2023), and is not expected to be workable for insects for many years to come (Bradfer-Lawrence et al. 2025; Kyalo et al. 2025). Similarly, machine learning methods for frog identification are still largely under development (e.g., Khalighifar et al. 2021) and while the comparatively simple call types of frogs make future classifiers promising, many recent studies still rely on acoustic indices to identify frog choruses (Gan et al. 2021). This is because birds are one of the best-known animal groups on Earth, and audio libraries have much more comprehensive records of birds compared to insects, frogs and even mammals. Many insect species are undescribed, or are described based solely on dead specimens with no or only theoretical knowledge of the matching stridulation/tymbalization (Gomez-Morales and Acevedo-Charry 2022, Riede 1998). Much more research is needed to make accurate species classifiers for even a fraction of the known soniferous insects. New tools (e.g., Rivas et al. 2024) and libraries (Branding et al. 2024) are being developed for the analysis of insect sounds, in the meantime, acoustic indices can be an effective measure of insect acoustic activity (Aide et al. 2017). Studies attempting to correlate indices with avian diversity have often found their results more strongly impacted by insect choruses rather than birds (Aide et al. 2017). Insects have great potential as models for the study and monitoring of acoustic assemblages due to their sensitivity to environmental change (Gomez-Morales and Acevedo-Charry 2022).

4.5 | Implications for Acoustic Monitoring

The ways in which acoustic indices can appropriately be used may differ between temperate and tropical forest ecosystems. In our study, acoustic indices in temperate forests in the USA and Germany generally had higher values across all frequencies at times when birds are most vocally active. That comparatively simple pattern in the data lends itself well to studies monitoring phenological changes in acoustic indices in order to make inferences about the intensity of vocal activity of the soniferous community (e.g., Bradfer-Lawrence et al. 2020), but there is little information that could be used to infer species composition or diversity (Figure 2), with the exception of the dawn (Figure 2vii). In contrast, tropical forest soundscapes had very distinct acoustic fingerprints diagnostic of their ecoregion and biogeographic realm, but that information-rich acoustic complexity makes it impractical to use overall higher average index values as an indicator of factors like avian vocal activity. Studies that have attempted to do so have been met with mixed success (Sethi et al. 2023; Giuliani et al. 2024) but are more likely to succeed in temperate forest soundscapes, and would not be expected to give intuitive results in most tropical forests (e.g., Moreno-Gómez et al. 2019; Bicudo et al. 2023). In contrast, studies which attempt to track shifts in species community would be expected to work well in tropical forests where insect species create distinct banding patterns, but would struggle to differentiate between sites in a temperate forest context.

5 | Conclusion

Environmental disturbances can alter soundscapes in various ways, through the loss of sensitive species, increases in anthropophony, shifts in species composition towards generalist species and shifts in the timing and frequency of vocalisations to avoid saturating noise (Gindhart et al. 2025). Our results emphasise that ecoregion-specific baselines are necessary, especially in tropical regions, to detect these types of shifts in the soundscape. Acoustic indices can provide valuable insights into soundscapes as a whole, and facilitate comparison of sound characteristics even among regions and biomes with no overlap in species composition. Some characteristics, such as a dichotomy between diurnal and nocturnal soundscapes, were common to all forests. Other characteristics, such as a highly partitioned frequency space, clearly distinguished tropical from temperate forests. As such, acoustic indices may be less effective at detecting species community shifts in temperate forests compared to tropical forests. There are inherent differences between forest soundscapes across the globe, and region-specific baseline data are required to draw informed comparisons between sites and measure changes due to accelerating environmental shifts with global climate change and habitat degradation. Soundscape science is growing in popularity as a tool for monitoring ecosystems, and understanding the baseline characteristics of forests worldwide can provide much needed context for studies that seek to understand factors which may disrupt or alter those soundscapes.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code created for this manuscript are publicly available on GitHub (https://github.com/KalmiaLatifolia/Soundscape_Baselines) and archived on Zenodo (https://zenodo.org/records/18165143).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70224-sup-0001-supinfo.docx.

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