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Biogeographical and analytical implications of temporal variability in geographically diverse soundscapes

Dante Francomano*, Benjamin L. Gottesman, Bryan C. Pijanowski

Center for Global Soundscapes and Department of Forestry and Natural Resources, Purdue University, 203 S. Martin Jischke Drive, West Lafayette, IN 47907, USA

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ABSTRACT

Unprecedented rates of biodiversity loss and intensifying human attempts to rectify the biodiversity crisis have heightened the need for standardized, large-scale, long-duration biodiversity monitoring at fine temporal resolution. While some innovative technologies such as passive acoustic monitoring are well suited for such monitoring challenges, many questions remain as to how they should be scaled out and optimally implemented across ecosystems.

Our research questions center on temporal sampling regimes—how frequently and how long one should collect data to represent biodiversity conditions over a given timeframe. Addressing this concern in the context of passive acoustic monitoring, we investigated whether temporal soundscape variability—the characteristic short-term acoustic change in an environment—is consistent across ecosystems and times of day, and we considered how various temporal subsampling schemes affect the representativeness of resultant acoustic index values, relative to continuous sampling. We quantified soundscape variability at eight sites across four continents based on temporal autocorrelation ranges and standard deviations of acoustic index values, and we created a heuristic model to classify types of soundscape variability based on those two variables.

Drawing on values derived from three distinct acoustic indices, we found that the characteristic temporal variability of soundscapes varied between sites and times of day (dawn, daytime, dusk, and nighttime). Some sites exhibited little difference in variability between times of day whereas other sites exhibited greater within-site differences between times of day than many inter-site differences. Daytime soundscapes generally tended to exhibit more temporal variability than nighttime soundscapes.

We also compared potential subsampling schemes that could be advantageous in terms of power, data storage, and data analysis costs by modeling subsample error as a function of total analysis time and number of subsamples within a larger block of time. Greater numbers of evenly distributed subdivisions drastically increased the representativeness of a sampling scheme, while increases in subsample duration yielded fairly minimal gains in representativeness between 33 and 67% of the full time one wishes to represent. Generally, our results show that for a long-term, fine temporal resolution monitoring program, one should record in evenly distributed durations at least as short as 1 min while only recording up to a third of the time one wishes to represent. While more continuous monitoring can be advantageous and necessary in many cases, current economic and logistical limitations in power, data storage, and analysis capabilities will often warrant optimized subsampling designs.

1. Introduction

Animal biodiversity is in global decline, and some have stated that Earth's sixth mass extinction event is in progress (Barnosky et al., 2011; Ceballos et al., 2015; Kolbert, 2014). As we try to monitor and address such significant global environmental changes, governments, nongovernmental organizations, and private landowners need to better understand how and why ecosystems change over time in response to management initiatives and ecological disturbances (Block et al., 2001; Fancy et al., 2009; Spellerberg, 2005). For each monitoring effort, those conducting the monitoring must determine the overall duration of the monitoring program and the manner in which sampling will be

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Abbreviations: ACI, Acoustic complexity index; AR, Autocorrelation range; BI, Bioacoustic index; CGS, Center for Global Soundscapes; DF, Dante Francomano; H_f, Spectral entropy; NS, Number of subdivisions; PAM, Passive acoustic monitoring; SD, Standard deviation; TAT, Total analysis time; WA, Wildlife Acoustics

* Corresponding author.

E-mail addresses: dfrancom@purdue.edu (D. Francomano), bgottesm@purdue.edu (B.L. Gottesman), bpijanow@purdue.edu (B.C. Pijanowski).

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scheduled within that overall duration. At the heart of these decisions is the concept of temporal variability. Ecosystems change over time in response to a vast array of interdependent ecological variables, and those changes occur at varying rates (Landres et al., 1999). Ecological monitoring must employ temporal sampling schemes designed to identify a signal (the change related to a driver of interest) amongst noise (change related to other inherent system variability) at the relevant temporal scale.

To maximize comprehensiveness and the chance of signal detection, monitoring would be continuous and of infinite duration. Unfortunately, such comprehensiveness is currently unattainable for most variables due to numerous constraints including funding, labor costs, fieldwork logistics, equipment, data storage resources, and data analysis resources (Caughlan and Oakley, 2001). As a result of the inherent tradeoff between monitoring cost and comprehensiveness, many monitoring programs are conducted with wide temporal gaps between monitoring events (e.g., biennial or decennial measurements) and limited temporal extent of monitoring events (e.g., measurements only occurring during 1 week of summer mornings). Wide temporal gaps preclude gaining information at fine temporal resolution. For example, while the North American Breeding Bird Survey (USGS Patuxent Wildlife Research Center, 2018) and Audubon Christmas Bird Count (National Audubon Society, 2019) provide rich datasets on avian diversity and spatial distributions at two points in the year (and just one time of day for the Breeding Bird Survey), similar data are not available for the rest of the year or additional times of day. Moreover, such wide temporal gaps could misrepresent the system if monitoring events coincide with a series of highs or lows in a quickly fluctuating variable or are periodic with a different frequency than a periodic variable being measured. Mannocci et al. (2017) highlight the importance of interannual variability in the California Current ecosystem due to the El Niño Southern Oscillation, and they emphasize the inadequacy of modeling based on low-resolution (e.g., decadal) measurements of variables in that system. Similarly, limited temporal extent only provides snapshots of variables that likely fluctuate outside of the temporal extent of the monitoring event. A 2-year study in the California Current would yield an incomplete picture of that system's states and dynamics.

Periodic monitoring events are not inherently problematic, particularly when there is preexisting knowledge of a system's temporal dynamics. For example, it is widely acknowledged that spring mornings are optimal times for assessing populations of most songbird species in temperate ecosystems (Ralph et al., 1995). That being said, continuous or near-continuous monitoring can be desirable for increased resolution when possible and can be necessary when little is known about the temporal variability of a system. Recent technological advances have facilitated the development of several methods of biodiversity or wildlife monitoring that generate continuous or near-continuous datasets. GPS tracking, camera trapping, and passive acoustic monitoring (PAM) are several examples of such promising emerging technologies that will be enhanced by refined analytical approaches with a greater focus on the temporal aspects of the data they produce (Cushman, 2010; Frey et al., 2017; Gage and Axel, 2014).

In the past decade, the emergence of soundscape ecology and/or ecoacoustics has taken PAM from its origins in bioacoustics and applied it to animal community biodiversity assessment and monitoring, based on the principle that aspects of biophony (sound from biological sources) are reflective of animal community biodiversity (Pijanowski et al., 2011b; Sueur et al., 2014; Sueur and Farina, 2015). A number of studies have begun to test the relationship between acoustic indices (empirical soundscape measurements) and biodiversity, and while results have been inconsistent, some indices have shown promise in certain situations, with both simulated and field recordings. Various acoustic indices have been shown to be correlated with: the number of biological sounds in a recording, species richness (derived from a recording or observed *in situ*), species evenness, Shannon diversity of species, individual abundance, or measures of functional diversity (Boelman et al., 2007; Buxton et al., 2018; Eldridge et al., 2018; Elise et al., 2019; Fuller et al., 2015; Harris et al., 2016; Jorge et al., 2018; Machado et al., 2017; Mammides et al., 2017; Pieretti et al., 2011; Sueur et al., 2008b; Zhao et al., 2019). The validation of acoustic indices is an ongoing process, but should not impede attempts to explore their PAM functions at this moment, as PAM has realized and potential applications for spatio-temporal monitoring of distribution patterns, phenology, and disturbance impacts from species to community levels (Sueur and Farina, 2015).

PAM is a method for which continuous monitoring is possible, and such monitoring could be necessary in certain contexts, such as when one is interested in short-duration, infrequent sound events (Towsey et al., 2014a; Yoccoz et al., 2001). If triggered recording is impossible or impractical for example, continuous monitoring would be desirable to ensure that rare sounds of interest are captured. Technological advancements of the past 2 decades have reduced power consumption and increased capacity for storage and analysis of acoustic data from PAM, making continuous monitoring feasible in studies with limited overall duration and few spatial replicates (Hill et al., 2018; Merchant et al., 2015). Reduced size and cost of PAM units are also making spatial replication much easier (e.g., the Frontier Labs "Bioacoustic Audio Recorder" (Frontier Labs, 2019), the Wildlife Acoustics "Song Meter Mini" (Wildlife Acoustics, Inc., 2019), and especially the Open Acoustic Devices "AudioMoth" (Open Acoustic Devices, 2019)). Applications with increased duration and spatial coverage or resolution like the Australian Acoustic Observatory (Roe et al., 2018) are becoming increasingly realistic, and more such projects can be expected in the near future.

The potential continuous application of PAM is an asset when used to address certain questions (e.g., determining when rare sounds occur or considering how sounds may be triggered by the sounds preceding them), but continuous PAM is likely unnecessary and undesirable for the majority of applications in which researchers are interested in ecological change occurring over time scales of weeks to years. Continuous long-term PAM provides rich, potentially valuable data, but the preservation and use of that data requires technology that is often expensive to install and maintain, and those costs may outweigh the benefits of the additional data. Replacing power sources and data storage units in PAM units can be a time consuming and costly endeavor, particularly in multi-year studies and hard-to-access environments like marine systems, so such applications require well-informed decisions about sampling schedules. Less comprehensive temporal sampling schemes would reduce the number of field excursions needed to change batteries and memory cards, potentially allowing time and money to be redirected towards increased spatial replication or the collection of additional relevant data about local flora and fauna. Limiting temporal sampling schemes would also reduce the logistical and financial challenges associated with data storage and processing.

The temporal variability of ecosystems is reflected in the variability of biophony emitted from them. Temporal variability in biophony stems from a variety of biological and ecological factors operating over a wide range of time scales that PAM practitioners must consider (Table 1). On the order of minutes, individual animals' patterns and characteristics of sound production are relevant. Over hours, weather events, changing light levels, tides, and animals' endogenous clocks may trigger changes in biophony like the widely recognized dawn and dusk choruses (Gottesman et al., 2018; Rodriguez et al., 2014). On longer scales, lunar cycles can affect biophony in marine systems (Staaterman et al., 2014) and for some terrestrial taxa like bats and katydids (Lang et al., 2006), and patterns of mating, reproduction, and migration can cause seasonal changes in biophony (Rice et al., 2017; Towsey et al., 2014b). Population dynamics, climate change, and certain disturbances can bring about even slower rates of change in biophony (Buxton et al., 2016; Campos-Cerqueira and Aide, 2017; Krause and Farina, 2016). Characterizing temporal soundscape variability across ecosystems and spatiotemporal scales would provide important biogeographical

Table 1
Drivers of biophonic temporal variability across scales.

Temporal scale	Drivers	Consequences
Seconds – hours	● Individual repertoire size	● Individuals emit more or less types of sounds
	● Sound characteristics (amplitude envelope and frequency modulation)	● Single sounds contain more or less variability
	● Sound production patterns (continuous, repetitive, or sporadic)	● Individuals produce a consistent or highly variable composition of biophony
	● Acoustic community abundance and diversity	● Higher-diversity assemblages likely produce higher-variability biophony
Hours – days	● Animal movement causing short-term changes to acoustic community abundance and diversity	● Higher-diversity assemblages likely produce higher-variability biophony
	● Endogenous clocks regulating acoustic activity	● The acoustically active community changes over time
	● Changing light levels	● Individuals produce more or less sound
	● Changing temperature	● Individuals produce more or less sound, sometimes at different frequencies
	● Changing precipitation	● Individuals produce more or less sound
Days – seasons	● Animal movement causing short-term changes to acoustic community abundance and diversity	● Higher-diversity assemblages likely produce higher-variability biophony
	● Weather system movement	● Individuals produce more or less sound
	● Lunar cycles affecting light levels	● Individuals produce more or less sound
	● Lunar cycles directly affecting sound production	● Individuals produce more or less sound
	● Pulse disturbances (disturbing influences of short duration that begin and end rapidly)	● Individuals produce more or less sound
Seasons – years	● Emergence and breeding phenology of soniferous species	● Composition of acoustic communities change and higher-diversity assemblages likely produce higher-variability biophony
	● Animal movement and migration causing seasonal changes to acoustic community abundance and diversity	● Higher-diversity assemblages likely produce higher-variability biophony
	● Changes in repertoires and sound production patterns	● Individuals produce a more consistent or variable composition of biophony
	● Press and ramp disturbances (disturbing influences that are continuous and of long duration (press) or slowly increase in intensity (ramp))	● Composition of acoustic communities change or individuals produce more or less sound
	● Phenological changes in habitat structure	● Biophony propagates differently
Inter-annual	● Population changes	● Individual species account for more or less of the contributions to overall biophony
	● Press and ramp disturbances (disturbing influences that are continuous and of long duration (press) or slowly increase in intensity (ramp))	● Composition of acoustic communities change or individuals produce more or less sound

contextualization for the development of soundscape-based disturbance indicators—a primary research objective of soundscape ecology (Gasc et al., 2017; Lomolino et al., 2015). Of course, such indicators are dependent on baseline measurements that could simply represent average index values or even typical diel dynamics. Those baseline measurements must be grounded in a thorough understanding of the temporal variability that could bias them and must be obtained with an appropriate sampling schedule according to that potential bias (Almeira and Guecha, 2019). This study represents an attempt to characterize within-day temporal variability of acoustic indices and determine how the nature of that variability can influence the representativeness of various subsampling schedules. The acoustic indices we employed do not necessarily correlate with any specific measure of biodiversity in every environment, but they can still provide meaningful information about the temporal variability of soundscapes more broadly.

In this study we analyzed acoustic recordings from eight sites across four continents to characterize short-term (within-2-hour) and diel (within-24-hour) soundscape variability and to provide sampling schedule guidance to PAM practitioners. Using a set of three complementary acoustic indices, we addressed two principal questions: 1) is temporal soundscape variability consistent across ecosystems and times of day? and 2) considering any spatiotemporal differences in temporal variability, how do various temporal subsampling schemes affect the representativeness of resultant acoustic index values, relative to continuous sampling?

Regarding the first question, we hypothesized that temporal soundscape variability would be inconsistent across ecosystems because different ecosystems host characteristic animal assemblages that exhibit characteristic temporal patterns of sound production. Additionally, we hypothesized that temporal soundscape variability would be higher during daytime relative to nighttime, as nocturnally acoustically active taxa like insects and amphibians tend to produce sound repetitively and consistently, whereas diurnal taxa like birds tend to produce sound more sporadically. In terms of our second question, we expected that more subdivisions within sampling schedules would reduce “subsample error” (deviation from a “true” full-duration value caused by subsampling) by maximizing the chance of capturing rare sound events, while minimizing their influence (Cook and Hartley, 2018). Despite the inherent loss of precision due to subsampling, we also hypothesized that subsampling would yield acceptably small subsample errors and that subsampling could efficiently and adequately represent values derived from continuous recording.

2. Methods

2.1. Goals

Our goals related to each question were as follows: For Question 1 (variability characterization), we sought to a) measure soundscape variability at diverse sites based on temporal autocorrelation ranges and standard deviations of acoustic index values and b) compare soundscape variability between sites and times of day. For Question 2 (subsampling implications), we sought to model subsample error as a function of total analysis time and number of subdivisions.

2.2. Site selection

For each question, we employed acoustic data from eight sites in diverse ecosystems on four continents. A site was included in this study if: 1) there were acoustic recordings from that site in the archives of the Center for Global Soundscapes (CGS) at Purdue University, 2) the recordings spanned at least 5 complete, consecutive days, 3) each recording was at least 59 min in length, and 4) aural assessment of sample recordings did not reveal predominance of geophony or technophony.

Table 2

Site information, recording parameters, and data coverage. Under "Recorder model", "WA" indicates "Wildlife Acoustics". Ecoregions are classified as by Olson et al. (2001) and Spalding et al. (2007).

Site name	State/province, country	Ecoregion	Coordinates	Recorder model	Sample rate	Gain	Preamplifier gain	Filtering	Frequency analysis range	Start date	End date	Number of complete days	Percent missing files
Penguin Colony	Tierra del Fuego, Argentina	Magellanic Subpolar Forests	54.9075° S, 67.3756° W	WA SM4	48 kHz	+12 dB	+26 dB	none	0.15 – 24 kHz	2016/02/24	2016/03/19	15	18
Tropical Rainforest	Heredia, Costa Rica	Isthmian-Atlantic Moist Forests	10.4237° N, 84.0144° W	WA SM4	44.1 kHz	+20 dB	+26 dB	none	1 – 22.05 kHz	2016/07/27	2016/08/02	5	0
Mongolian Grassland	Tšv, Mongolia	Mongolian-Manchurian Grassland	47.6917° N, 105.8835° E	WA SM3	48 kHz	0 dB	unpublished	none	0 – 24 kHz	2015/06/01	2015/07/06	22	9
Coral Reef	Puerto Rico, United States of America	Greater Antilles	17.9349° N, 67.0485° W	WA SM3M	48 kHz	0 dB	unpublished	none	0 – 24 kHz	2017/07/03	2017/08/11	37	0
Miombo Swamp	Rukwa, Tanzania	Central Zambezian Miombo Woodlands	5.4312° S, 30.5775° E	WA SM4	48 kHz	+18 dB	+26 dB	high-pass at 220 Hz	0.15 – 24 kHz	2017/03/25	2017/04/08	14	0
Nebraska Prairie	Nebraska, United States of America	Central and Southern Mixed Grasslands	40.7292° N, 98.5856° W	WA SM4	48 kHz	+12 dB	+26 dB	high-pass at 220 Hz	0.15 – 24 kHz	2017/08/17	2017/08/27	9	0
California Woodland	California, United States of America	California Interior Chaparral and Woodlands	38.42° N, 122.592° W	WA SM4	44.1 kHz	+18 dB	+26 dB	high-pass at 220 Hz	0.3 – 22.05 kHz	2017/08/18	2017/08/25	7	0
Magellanic Forest	Tierra del Fuego, Argentina	Magellanic Subpolar Forests	54.8473° S, 68.5442° W	WA SM4	48 kHz	+12 dB	+26 dB	none	0.4 – 24 kHz	2016/02/17	2016/03/15	19	15

Biophony-dominated sites were chosen in order to predominantly measure the temporal variability of biophony. Locations and details for the eight sites meeting the above conditions are presented in Table 2 and Fig. 1. All sites were terrestrial with the exception of Coral Reef, which was located underwater near a coral reef off the coast of Puerto Rico. While these sites do not represent random locations, they are stratified across an assortment of biomes and a range of latitudes and longitudes.

2.3. *Data preparation*

We first converted any recordings that existed as .flac files in the CGS archives to .wav format using R (R Core Team, 2018) and the R packages "tuneR" and "seewave" (Ligges et al., 2016; Sueur et al., 2008a). All code associated with this study is available on GitHub at https://github.rcac.purdue.edu/PijanowskiGroup/Francomano_et_al_2019. We then removed corrupted files and files with durations below 59 min. Files from the site Nebraska Prairie did not begin at the start of each new hour, so consecutive files for that site were combined and cut to a duration of 59 min with a top-of-the-hour start time. Other files that did not begin precisely at the top of the hour had their start times rounded (by up to 2 min and 18 s) to consider them as beginning precisely at the top of the hour. An evident DC-offset was removed from files from Mongolian Grassland and Coral Reef. The left channel was used for all analysis (aside from Coral Reef, which was recorded in mono). Data coverage over time is shown in Figs. S1–S8. 24-hour spectrograms for each site are presented in Fig. 2, and 1-minute versions of the corresponding audio files are provided on GitHub.

2.4. *Acoustic index calculation*

The acoustic complexity index (ACI; Pieretti et al., 2011), bioacoustic index (BI; Boelman et al., 2007), and spectral entropy (H_f; Sueur et al., 2008b) were calculated in 59 consecutive 1-minute windows within each 59-plus-minute file, beginning at the beginning of the file. The 60th minute of each hour was assigned a value of N/A, and those values were ignored in subsequent analyses (the recorders wrote files to the memory cards during this minute, so a few seconds were typically lost). The R package "seewave" was used for the ACI and H_f, while "soundecology" (Villanueva-Rivera and Pijanowski, 2016) was used for the BI. DF determined a separate frequency range for index calculation on files of each site by visualizing and listening to short sections of those files in Audacity (Audacity Team, 2015). He examined 24 files—one from each hour of the day on days that were randomly selected from all the complete days present for each site. He noted the minimum and maximum frequencies of biophony in each file and decided on per-site frequency ranges that would include almost all biophony that might be present at each site. Those frequency ranges are presented in Table 2. Geophony and technophony were not considered in this frequency range determination, except to determine if a predominance of those sounds warranted excluding a site from further analysis. The above indices were selected due to their prominence in the soundscape ecology and/or ecoacoustics literature, their use in past considerations of study design (Pieretti et al., 2015; Quiroz et al., 2017), and their complementary nature. The BI provides a good measure of biophonic contributions to soundscape amplitude, H_f offers insight into the spectral composition of a soundscape, and the ACI incorporates information on changes in the spectral distribution of sound over millisecond-level time scales (using its default parameters).

2.5. *Question 1 (variability characterization) analysis*

We addressed Question 1 through two methods based on subsets of the same data. For both methods, we operationalized the concept of temporal variability by calculating standard deviations and autocorrelation ranges of acoustic index values. We calculated these for

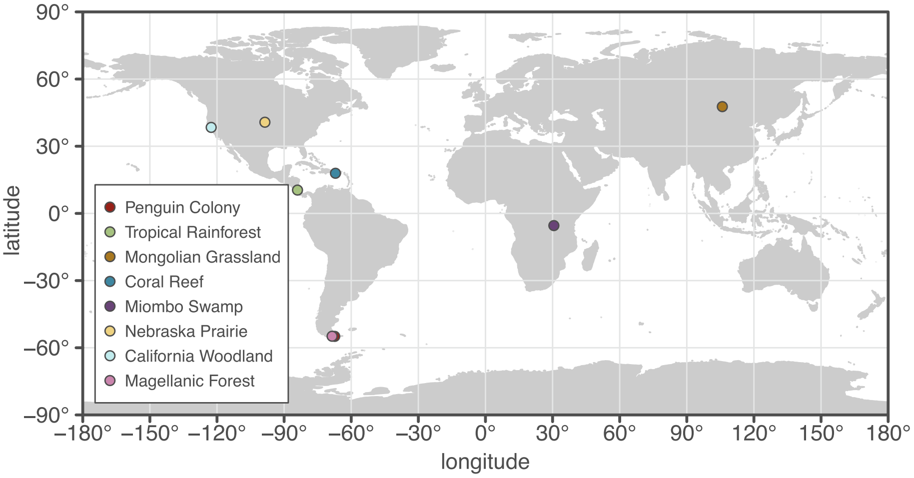

Fig. 1. Site locations. Penguin Colony and Magellanic Forest overlap substantially on this map, as they are in close proximity relative to a global scale.

different "value lengths" (durations over which 1-minute index values were averaged) and "analysis windows" (temporal windows limiting the values included in each calculation). We employed value lengths of 1 min, 5 min, 15 min, and 60 min, and we employed analysis windows of 5 min, 15 min, 60 min, dawn (a 2-hour window centered on sunrise), daytime (the time from 1 h after sunrise to 1 h before sunset), dusk (a 2-hour window centered on sunset), and nighttime (the time from 1 h after sunset to 1 h before sunrise), and 24 h (Fig. 3). To make standard deviations and autocorrelation ranges from daytime and nighttime analysis windows comparable with those from dawn and dusk analysis windows, as many 2-hour segments as possible were selected within daytime and nighttime windows (centered between sunrise and sunset), and standard deviations and autocorrelation ranges were calculated on each segment and then averaged to produce single values that are representative of any 2-hour segment within each daytime or nighttime analysis window. Because autocorrelation ranges are not robust when calculated on short time-series, value length-analysis window combinations were not considered if the analysis window was less than four times the value length (e.g., 5-minute value length in 15-minute analysis window) or if the autocorrelation ranges for all acoustic indices were 0 for at least four sites. We calculated standard deviations using the "sd" function and autocorrelation range using the "acf" function, both from the "stats" package of R. We defined the significance threshold of the autocorrelation function as:

$$\frac{qnorm\left(\frac{1+(1-\alpha)}{2}\right)}{\sqrt{n}}$$

where $qnorm$ is the quantile function of the normal distribution, α is the significance level (0.05 in this case), and n is the number of values in the time series. We defined the autocorrelation range (in minutes) as the product of the lag at which the autocorrelation function of the given time series first becomes less than the significance threshold and the value length (in minutes).

For the first method of addressing Question 1, we visualized within- and between-site differences by plotting standard deviations against autocorrelation ranges for each site (using inter-day averages). We constructed two plots for each index—one showing 1-minute value lengths within dawn, daytime, dusk, and nighttime analysis windows and another showing 1-hour value lengths in 24-hour analysis windows (Fig. 6). This method allowed for visual comparison of a) sites and their values at different times of day over a relatively short timeframe (2 h) and b) sites over a longer timeframe (24 h). While one could consider any value length and analysis window, we believe that these combinations provided useful snapshots of temporal variability on various within-day scales.

For the second method, we conducted non-metric multidimensional scaling to plot sites in multidimensional space and check for any obvious clustering that would warrant use of adonis and discriminant analysis. We used the "metaMDS" function in the R package "vegan" (Oksanen et al., 2018) and the Euclidean dissimilarity index. As there was no evident clustering (Fig. S9) with a low stress level (0.063), we did not pursue this analysis further.

2.6. *Question 2 (subsampling implications) analysis*

For question 2, we separately determined subsample error for "full file lengths" of 12 and 60 min. We assigned 1-minute index values to dawn, daytime, dusk, and nighttime as described above, and subdivided the times of day for each site and day into as many 12- and 60-minute blocks as possible. For each block and each index, we calculated cumulative means of index values and then defined the subsample error as the absolute value of the difference between each cumulative mean and the 12- or 60-minute mean for that block. This process resulted in vectors of length 12 and 60 that were averaged within each site-time of day combination. Additionally, we calculated similar averages of differences for non-continuous subsampling—i.e. subsampling with multiple subdivisions. We calculated average differences for all possible evenly distributed subsampling schemes with subdivision durations of full minutes (integer values; Fig. 4).

We then computed separate linear mixed models for each index and each full file length. The last value of each continuous subsample error vector was not incorporated in the models, as it was necessarily 0. Global models including all potential independent variables were constructed with subsample error as the dependent variable, site as an independent random intercept, and time of day, total analysis time, total analysis time squared, total analysis time cubed, number of subdivisions, and the interaction between total analysis time and number of subdivisions as fixed effects. All non-categorical independent variables were scaled and polynomials were orthogonal. Site was incorporated as a random intercept to account for the non-independence of the subsample errors from each site. Models were computed using the R package "lme4" (Bates et al., 2015). All models failed visual tests for normality of residuals and homogeneity of variance, so we conducted a natural log transform on subsample error and recomputed the models. Homogeneity of variance was then achieved for all models, and despite failing Shapiro-Wilk tests, qq-plots indicated that residuals were approximately normally distributed. Model selection was conducted using the "dredge" function of the R package "MuMIn" (Bartoń, 2018) with AICc as the evaluation metric. The result of the selection procedure was that all independent variables were included in all models. Finally, we recomputed models with non-scaled independent variables

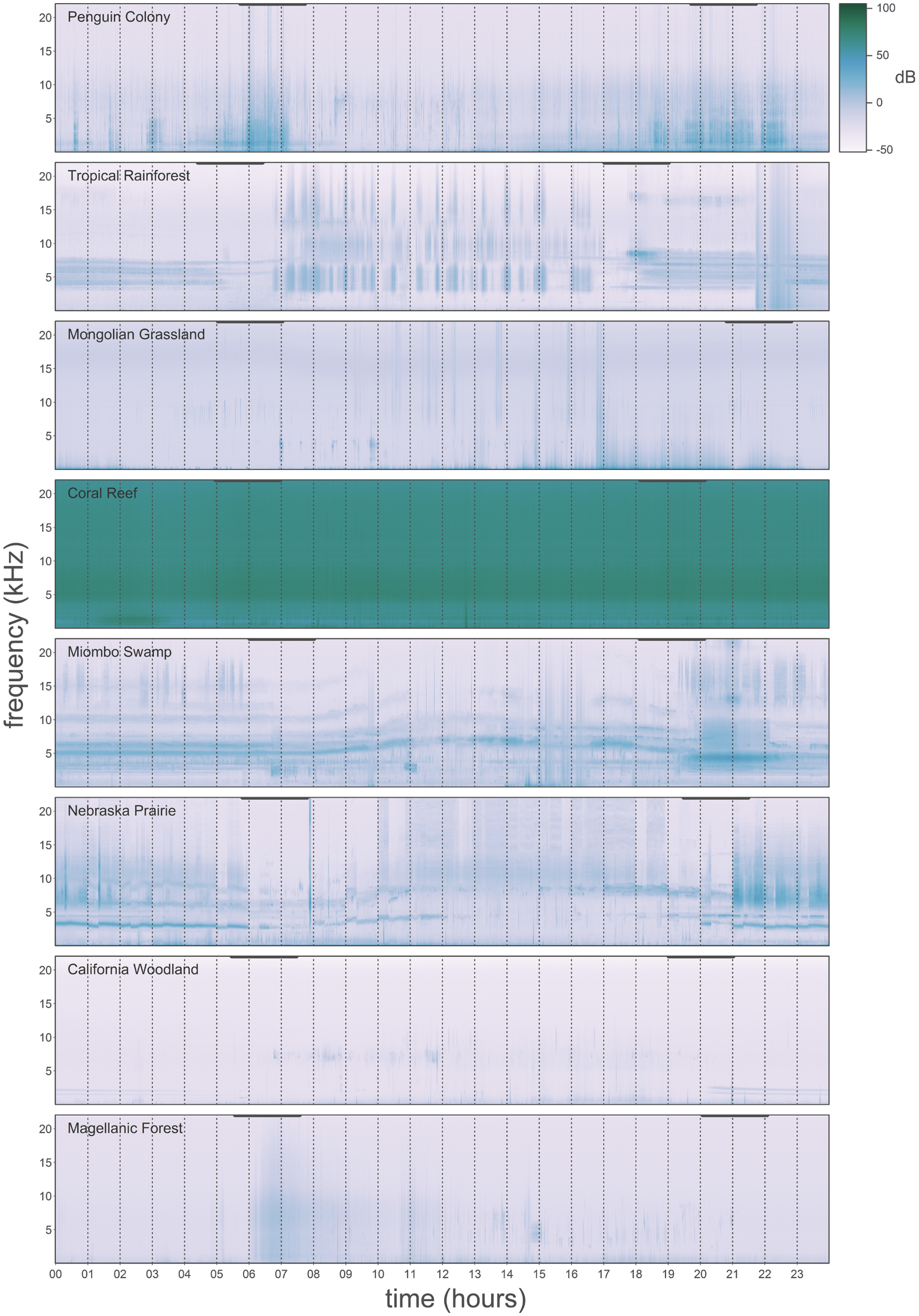

Fig. 2. 24-hour power spectral density spectrograms. These spectrograms show the first complete day of recordings from each site. Power spectral density was calculated following the methods described by Merchant et al. (2015) using a 1-second window length, Hann window, and root-mean-square (RMS) averaging to produce final spectrograms with 1-minute temporal resolution. Power is expressed as dB re (20 μPa)^{2}Hz^{-1} with the exception of the one marine site, Coral Reef, for which power is expressed as dB re (1 μPa)^{2}Hz^{-1}. All spectrograms have been cropped to a frequency range of 0 – 22.05 kHz, and the 60th minute of each hour is merely a duplication of the 59th minute. Horizontal lines at the top of each spectrogram represent the 2-hour dawn and dusk windows centered on sunrise and sunset for each day. The file splicing for Nebraska Prairie is evident where the spectrogram appears horizontally disjointed in places.

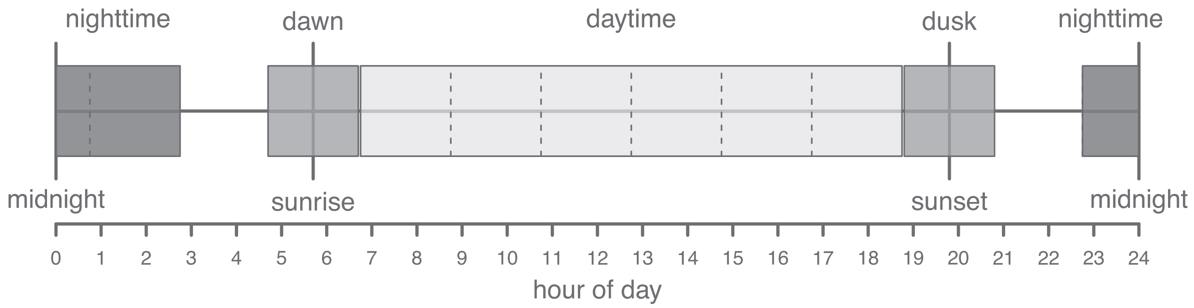

Fig. 3. Illustration of analysis windows situated within times of day.

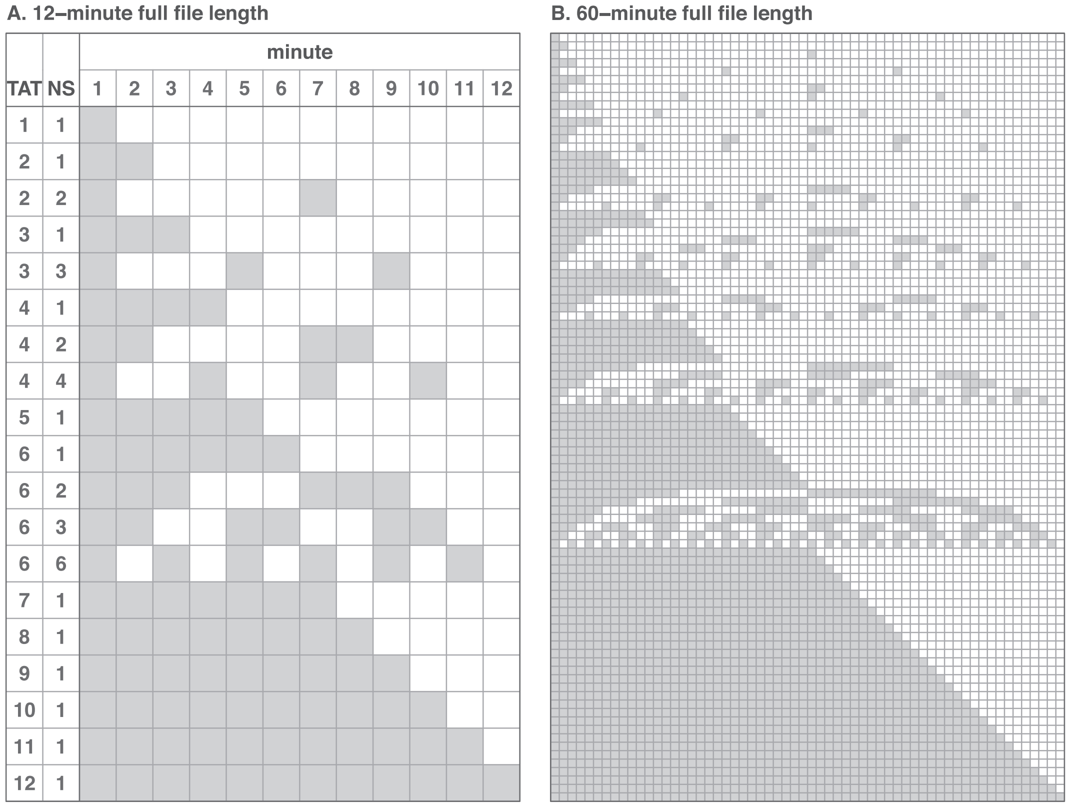

Fig. 4. Illustration of all possible subsampling schemes for 12- (A) and 60-minute (B) full file lengths with a minimum recording duration of 1 min and evenly distributed recording start times. "TAT" represents "total analysis time", and "NS" represents number of subdivisions. Grey blocks represent recorded minutes and white blocks represent unrecorded minutes. B is unlabeled for legibility, but the format is the same as A: columns represent minutes 1 – 60 (left to right), and rows represent increasing TAT and NS (top to bottom).

and non-orthogonal polynomials to obtain meaningful coefficients for predictive purposes.

3. Results and discussion

3.1. Question 1 (variability characterization)

As presented in Figs. 5 and 6, temporal variability as measured by standard deviation (SD) and autocorrelation range (AR) can be categorized in the four following non-discrete conceptual classes: I) high SD, high AR; II) low SD, high AR; III) low SD, low AR; and IV) high SD, low AR. Class I soundscapes vary substantially, but in a fairly predictable manner (e.g., the gradual emergence of an insect or amphibian chorus at dusk), whereas Class IV soundscapes vary substantially and unpredictably (e.g., sparse high-amplitude bird sounds). Class II soundscapes vary minimally and predictably (e.g., very quiet soundscapes or soundscapes with constant insect or amphibian choruses), while Class III soundscapes exhibit a small amount of fairly random variation (e.g., sparse low-amplitude bird sounds). While somewhat simplistic and based only on the means of standard deviations and autocorrelation ranges for the present data, this conceptual model is useful for interpretation of the following results.

One could define and measure temporal variability using a variety of metrics. We selected standard deviations to provide insight into the range and distribution of index values, and we chose autocorrelation ranges to highlight the consistency of index values between successive time windows. There are likely some aspects of temporal variability that are not captured in standard deviations and autocorrelation ranges (such as cyclicity), but the two concepts we employed proved useful in describing two distinct aspects of temporal variability. If standard deviations and autocorrelation ranges were measuring the same components of temporal variability, one would expect a predominance of points in Classes II and IV indicating a negative relationship between standard deviation and autocorrelation range. However, the fact that

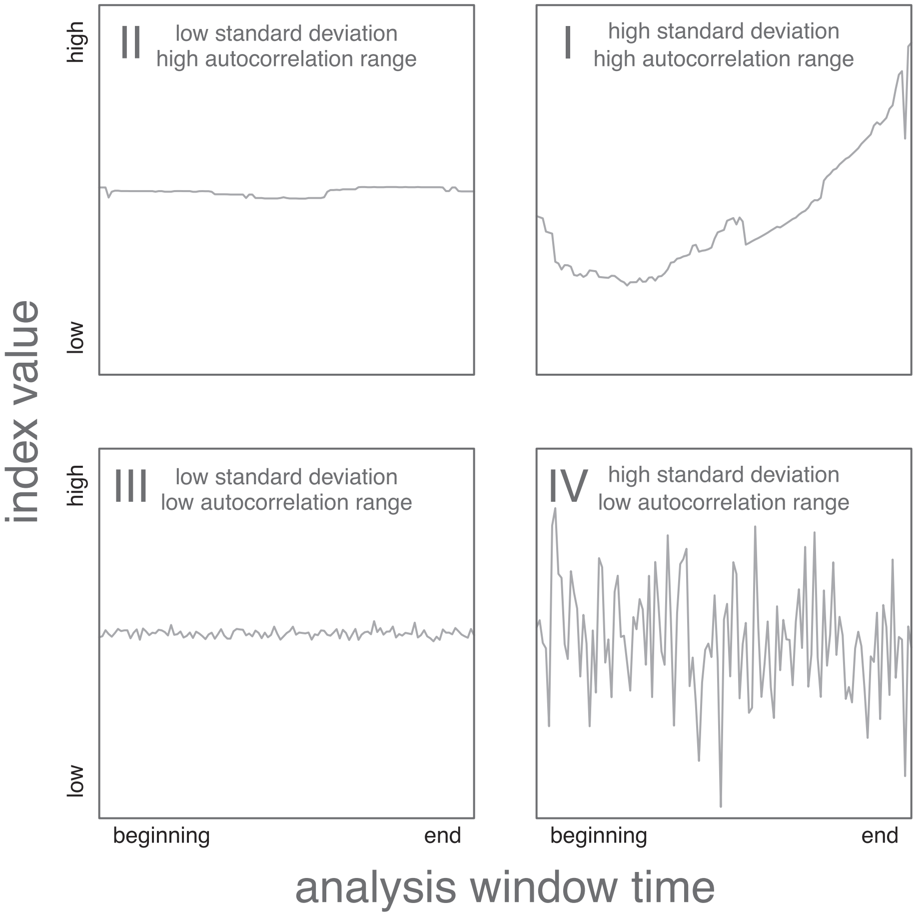

Fig. 5. Soundscape classes based on their temporal variability characteristics.

such a relationship is not apparent in any section of Fig. 6 indicates that standard deviations and autocorrelation ranges in fact represent distinct components of the concept of temporal variability. This lack of correlation is promising for the future application of these metrics in characterizing the temporal variability of soundscapes.

3.1.1. *1-Minute values in 2-hour time of day windows*

3.1.1.1. Cluster dispersion and the relative importance of sites and times of day. As assessed visually, the dispersion of each single-site cluster (i.e. the area of a convex polygon with the points for each time of day as vertices) was variable between sites. For example, Miombo Swamp values were much more dispersed than those of Magellanic Forest for the BI, and California Woodland values were much more dispersed than those of Nebraska Prairie for H_f. In one respect, it is unsurprising that dispersion would differ between sites: it has been widely documented that soundscapes exhibit diel dynamics and that the patterns and magnitudes of those dynamics differ between locations (Gasc et al., 2018; Gottesman et al., 2018; Lomolino et al., 2015; Towsey et al., 2014a). However, these dynamics have been demonstrated through counts of acoustic events and raw acoustic index values, and such diel dynamics would not preclude diel constancy for measures of temporal variability on shorter time scales. To illustrate, consider a site with dawn soundscapes dominated by near-constant birdsong and extremely quiet nighttime soundscapes. The magnitudes of the ACI for this site would be high at dawn and low during nighttime, but the standard deviations and autocorrelation ranges for the ACI within each time of day could be quite similar. The fact that single-site dispersions differed indicates that some sites exhibited fairly constant temporal variability across times of day while others had more divergent variability for different times of day.

Single-site clusters almost always overlapped with each other, with the notable exceptions of Tropical Rainforest for the ACI (due to low standard deviations and high autocorrelation ranges) and Coral Reef and Mongolian Grassland for H_f (due to extremely low and high standard deviations, respectively). Given the fact that sites included in this study were widely distributed across continents and biomes it is perhaps surprising that single-site clusters were not more distinct. However, because the soundscapes of one site can be so variable between times of day, and acoustic indices provide quantitative as opposed to qualitative descriptions of soundscapes (e.g., spectral entropy as opposed to acoustic community composition), it is understandable that index-based measures of temporal variability would yield overlapping single-site clusters.

Within-site differences sometimes exceeded between-site differences. Considering H_f, the dispersion of Tropical Rainforest was greater than that of the combination of Penguin Colony, Miombo Swamp, Nebraska Prairie, and Magellanic Forest. For the BI, the dawn value of Miombo Swamp is closer to the dawn value of Magellanic Forest than any other Miombo Swamp values, and the daytime value of Tropical Rainforest is closer to the daytime values of Penguin Colony, Mongolian Grassland, Miombo Swamp, Nebraska Prairie, and Magellanic Forest (not to mention other times of day for those sites) than it is to other Tropical Rainforest values. The lack of spatial replicates in each location does not allow for statistical assessment of the relative importance of site- and time of day-based differences, but this initial graphical assessment with a single site for each general location suggests that both factors influence temporal soundscape variability. Some single site clusters are compact and/or distinct from those of other sites, but there is also substantial overlap between clusters with some clusters being relatively large. Generally, it can be assumed that there is greater change in the composition of the acoustically active animal community

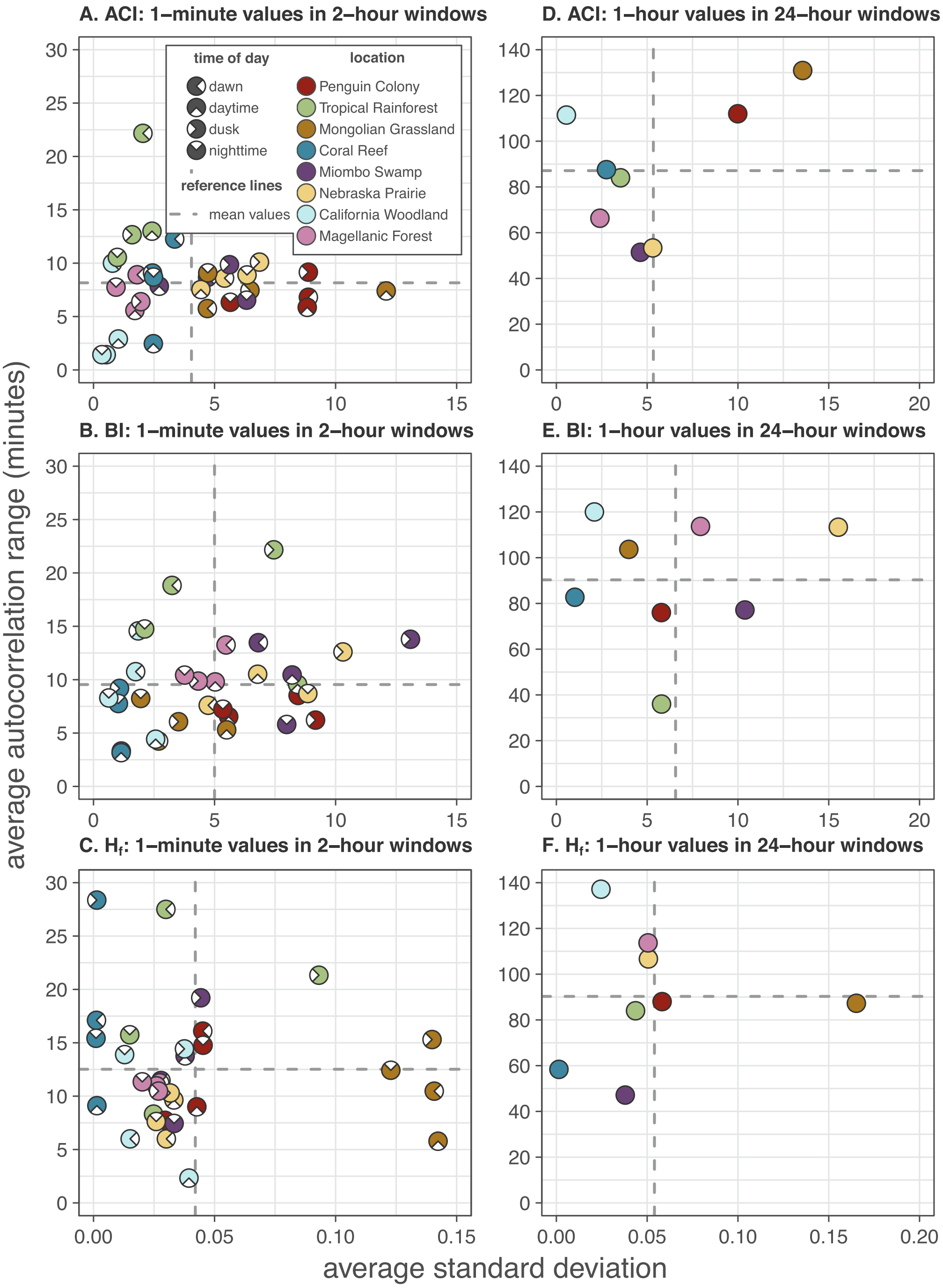

Fig. 6. Temporal variability of sites plotted based on standard deviations and autocorrelation ranges. Plots feature different scales, but the y-axes are the same within each column of plots.

over the course of a 24-hour period in sites with large clusters than those with small clusters. One could argue that large clusters result from temporal acoustic niche partitioning (Krause, 1993; Pijanowski et al., 2011a), but it is more likely that temporal partitioning of acoustic activity at such a coarse temporal scale is driven by non-acoustic factors (e.g., predator or prey activity patterns and light availability).

3.1.1.2. Trends based on time of day and sites. Within single-site clusters, dawn values exhibited no clear trends, but those for other times of day tended to exhibit consistent directionality within the clusters. Daytime values tended to have high standard deviations and low autocorrelation ranges, relative to the other times of day in the cluster, suggesting that daytime soundscapes are among the most highly variable within a given 2-hour window. Dusk autocorrelation ranges tended to be high, and nighttime standard deviations tended to be low, indicating that these soundscapes exhibit less short-term temporal variability. These results for daytime and nighttime soundscapes support our hypothesis that nighttime soundscapes would be less variable than daytime soundscapes due to the consistency of quiet or insect/amphibian-dominated nighttime soundscapes.

Standard deviation values were always below average for Coral Reef, California Woodland, nighttime and dawn for Tropical Rainforest, and dusk and nighttime for Magellanic Forest. Based on the authors' *in situ* and remote listening (both formal and informal), these sites—aside from Tropical Rainforest—all feature Class II and III soundscapes composed of little biophony and/or biophony from a small number of species.

The soundscapes of Coral Reef are dominated by broadband sounds from snapping shrimp and occasional low-frequency (< 2 kHz) fish choruses. This site is interesting in that its standard deviations were consistently low across indices and times of day whereas autocorrelation ranges were moderately to highly variable. Fig. 6C provides a prime example of this unusual feature; a probable explanation is that some times of day are dominated by extremely gradual, locally monotonic changes in index values while others are characterized by more random short-term fluctuations. The relatively high dawn and dusk autocorrelation ranges could be due to increases in temporally consistent snapping shrimp activity during those times, whereas the lower nighttime values could be attributed to more variable fish choruses.

Autocorrelation ranges for Tropical Rainforest tended to be much higher than average (with the exceptions of daytime values for the BI and H_f). This indication of low short-term temporal variability could come as a surprise, considering the fact that the site is a biodiversity hotspot within the global biodiversity hotspot of Mesoamerica (McDade et al., 1994; Myers et al., 2000) and contains a vast array of soniferous species. Moreover, those species' sounds span the frequency spectrum and are produced with a diversity of methods. Despite this diversity, the high autocorrelation ranges point to temporal consistency and categorization as Class I and II soundscapes. Despite the diversity of soniferous species at this site, its soundscapes are largely dominated by amphibian and insect sounds that are often consistent across any 2-hour analysis window, and this consistency likely explains the low standard deviations for this site.

The most distinctive site in terms of temporal variability for any one index is Mongolian Grassland for H_f. Its autocorrelation ranges hover around the global mean, but its standard deviations far exceed all values except that of Tropical Rainforest dusk. Recordings from this site featured a large amount of wind noise and occasional clipping, so that geophony could explain this outlying site. H_f represents the entropy of a mean spectrum, and clipping, or even just loud wind could drastically affect the shape of that spectrum. Because such gusts could either be absent from or be predominant in any given minute of a 2-hour period, wind could be responsible for the high standard deviations associated with H_f at this site.

3.1.2. 1-Hour values in 24-hour windows

On this longer time scale, several sites exhibit consistent relative temporal variability across indices. California Woodland is the most consistent, as it always displays low standard deviations and high autocorrelation ranges, indicating extremely low-variability Class II soundscapes. This result is unsurprising given the fact that the site featured very quiet soundscapes throughout the day. Tropical Rainforest and Coral Reef exhibited moderate to low standard deviations as well, but also exhibited moderate to low autocorrelation ranges, making their soundscapes Class III. Both sites featured some consistent biophony across a wide range of frequencies (e.g., birds, insects, and amphibians, at Tropical Rainforest and snapping shrimp at Coral Reef), but the soundscapes were also punctuated by less consistent biophonic and geophonic events like howler monkey sounds and rain at Tropical Rainforest and fish choruses at Coral Reef.

Other sites were far less consistent across indices. Soundscapes from Mongolian Grassland, Nebraska Prairie, and Magellanic Forest would be classed differently for each of the three indices used in this study. This inter-index discrepancy highlights the fact that these indices measure different soundscape features (Sueur et al., 2014). This multifaceted information can be beneficial, but must be paired with supplemental soundscape analysis methods for well-informed interpretation (Gottesman et al., 2018).

3.1.3. Implications of autocorrelation ranges

Average autocorrelation ranges were highly variable between sites and times of day. 1-minute values in 2-hour windows ranged from less than 2 min (the ACI for California Woodland at dusk) to nearly 30 min (H_f for Coral Reef at dusk), and 1-hour values in 24-hour windows ranged from below 40 min (the BI for Tropical Rainforest) to nearly 140 min (H_f for California Woodland). In this study we used autocorrelation ranges to characterize temporal variability, but the concept of temporal autocorrelation can also be considered problematic if one were to treat two autocorrelated measurements as independent. Hopefully this study has provided a baseline that researchers can reference if they wish to assume that two temporally separated soundscape measurements are independent. We do however advise caution in this situation, as thresholds for temporal correlation are clearly dependent on the value length and the analysis window considered. To truly derive benefits from the temporal richness of a continuous or near-continuous dataset, we recommend further investigation and application of time-series analysis methods.

3.2. Question 2 (subsampling implications)

We constructed six models (one for each combination of the three indices and the two full file lengths (12 and 60 min) for predicting subsample error based on total analysis time, number of subdivisions, and time of day. Model coefficients are presented in Table 3, and predicted values for several subdivision scenarios are presented in Fig. 7. While the subsample errors understandably differed between indices (mean raw 1-minute index values were 169.52 for the ACI, 53.19 for the BI, and 0.82 for H_f), the general shape of the predicted curves was similar across indices and 12-minute and 60-minute full file lengths. Initial increases in total analysis time yielded rapid decreases in subsample error that subsequently became more gradual. This finding corresponds with the conclusions of Pieretti et al. (2015), who found that sampling just 1 min per 60 min yielded ACI values that were highly correlated with values from continuous recordings, and Bradfer-Lawrence et al. (2019), who found that the variance in the standard error of seven different acoustic indices initially declined rapidly with increased recording time. In our study, increasing the number of subdivisions substantially reduced subsample error, especially at low values of total analysis time. This finding reflects those of Cook and Hartley (2018), who applied similar analytical methods, but used aural species identification as opposed to acoustic indices. As a whole, our results suggest that to maximize representation with subsampling, 1) the number of subdivisions should be maximized and 2) extensions of total analysis time between approximately 33% and 67% of the full file length will yield relatively negligible decreases in subsample error, especially with greater subdivision.

3.2.1. Relative magnitudes of subsample error

The magnitudes of subsample error differed across indices, relative to the global mean of raw 1-minute values for those indices. To illustrate, the approximate y-intercept for the ACI with one subdivision in 12- and 60-minute full file lengths is 3—less than 2% of its global mean; the approximate y-intercept for the BI with one subdivision in 12- and 60-minute full file lengths is 3.75—about 7% of its global mean; and the approximate y-intercept for H_f with one subdivision in 12- and 60-minute full file lengths is 0.03—about 4% of its global mean. While these values differed relative to means, they were fairly consistent with the mean standard deviations indicated in Fig. 6. Across indices, the approximate y-intercept with one subdivision in 12- and 60-minute full file lengths represented about 75% of the mean standard deviation for 1-minute values in 2-hour analysis windows and about 55% of the mean standard deviation for 1-hour values in 24-hour analysis windows. This fact suggests that the magnitude of subsample error, as one might expect, is directly related to the variability of the raw index values. No index appeared to have such substantially greater subsample error that

Table 3
Model coefficients for non-orthogonal polynomials with a log-transformed dependent variable.

Model identifiers		Independent variable coefficients						
Full file length (minutes)	Index	Total analysis time	Total analysis time squared	Total analysis time cubed	Number of subdivisions	Total analysis time * number of subdivisions interaction	Time of day	Location (intercept)
12	ACI	−0.37827	0.046928	−0.00331	−0.27349	0.019679	dawn: 0 daytime: 0.1397901 dusk: 0.0205532 nighttime: −0.255058	Penguin Colony: 2.1934119 Tropical Rainforest: 0.4805445 Mongolian Grassland: 1.8703637 Coral Reef: 1.0740979 Miombo Swamp: 1.5970559 Nebraska Prairie: 1.8136459 California Woodland: −0.4041180 Magellanic Forest: 0.3066004
12	BI	−0.37374	0.047173	−0.00335	−0.27495	0.018378	dawn: 0 daytime: 0.3826255 dusk: 0.2462057 nighttime: −0.1796268	Penguin Colony: 1.93628642 Tropical Rainforest: 1.21769318 Mongolian Grassland: 1.07445364 Coral Reef: 0.09519489 Miombo Swamp: 2.02254772 Nebraska Prairie: 1.88661536 California Woodland: 0.25286167 Magellanic Forest: 1.33907290
12	H_f	−0.35768	0.047183	−0.00349	−0.34002	0.021172	dawn: 0 daytime: 0.3902763 dusk: 0.2620727 nighttime: −0.09537009	Penguin Colony: −3.342225 Tropical Rainforest: −3.986364 Mongolian Grassland: −2.063402 Coral Reef: −7.060274 Miombo Swamp: −3.490599 Nebraska Prairie: −3.537867 California Woodland: −4.061918 Magellanic Forest: −3.985694
60	ACI	−0.08948	0.003088	−4.4E-05	−0.13719	0.002326	dawn: 0 daytime: 0.1279314 dusk: −0.01429503 nighttime: −0.3262839	Penguin Colony: 1.9359568 Tropical Rainforest: 0.4834979 Mongolian Grassland: 1.7101902 Coral Reef: 0.8451372 Miombo Swamp: 1.4602650 Nebraska Prairie: 1.7484148 California Woodland: −0.7803512 Magellanic Forest: 0.2901693
60	BI	−0.09001	0.003127	−4.5E-05	−0.1482	0.002517	dawn: 0 daytime: 0.3705776 dusk: 0.3913135 nighttime: −0.1893556	Penguin Colony: 1.6435870 Tropical Rainforest: 1.2333933 Mongolian Grassland: 0.7909718 Coral Reef: −0.2916607 Miombo Swamp: 1.9134693 Nebraska Prairie: 1.8047284 California Woodland: 0.1004181 Magellanic Forest: 1.3597102
60	H_f	−0.07903	0.002795	−4.2E-05	−0.17882	0.003096	dawn: 0 daytime: 0.1972703 dusk: 0.3115572 nighttime: −0.2105951	Penguin Colony: −3.365772 Tropical Rainforest: −3.565602 Mongolian Grassland: −2.179576 Coral Reef: −6.782412 Miombo Swamp: −3.469463 Nebraska Prairie: −3.682393 California Woodland: −4.098806 Magellanic Forest: −3.837981

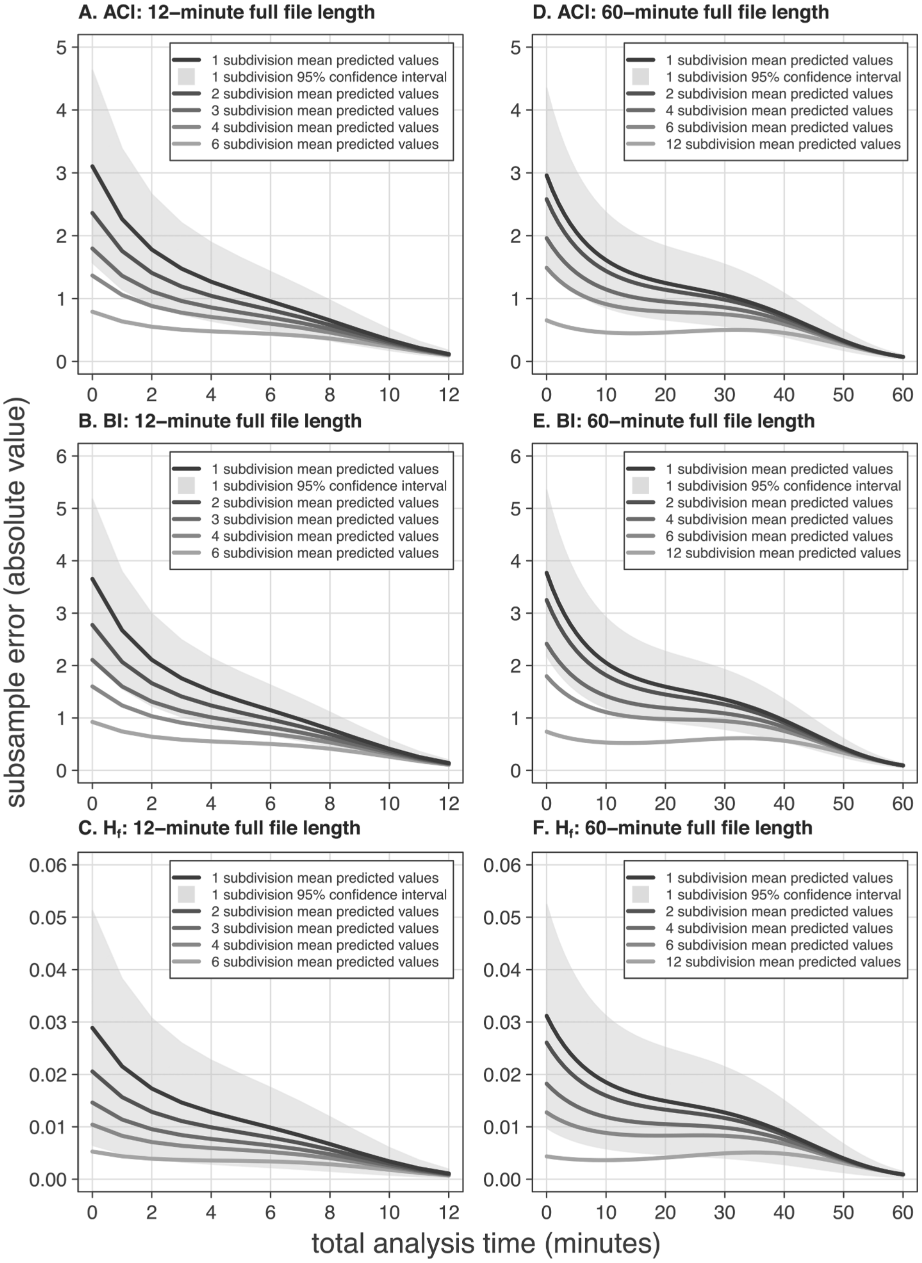

Fig. 7. Predicted subsample error for different subsampling schedules. Values are based on inter-site and inter-time of day means, and the 95% confidence intervals for the 1-subdivision schedule are based on treating sites as replicates. For context, mean values for all 1-minute segments used in the calculation of these models were as follows: ACI—169.52; BI—53.19; H$_f$—0.82.

it would be problematic for representation through subsampling. Notably, we did not define an explicit threshold for acceptable error, as such a threshold would likely vary between studies. However, as stated above, the errors we documented are fairly small relative to the global means for each index.

3.2.2. Implications for sampling schedule design and limitations for application

We suggest that a "sweet spot" for maximizing soundscape representation and efficiency in terms of battery life and storage consumption would be a schedule in which one records for about a third of the time they wish to represent and in which they subsample as much as possible, at least until a minimum recording duration of 1 min. As the Wildlife Acoustics SM4, one of the leading terrestrial automated field recording systems, does not allow scheduling for recording durations below 1 min, we did not analyze such subsampling schemes in this study. There is reason to suspect that the relationships we found could be extrapolated for recording durations below 1 min, especially for spectral indices that do not consider within-recording-duration temporal variability. However, for some indices like the ACI, one must set a minimum recording duration, if only to ensure that there are multiple temporal windows in a single file for appropriate calculation of the index.

Subdividing, and especially extreme subdividing (sub-minute), comes with several notable drawbacks. First, it means that certain sound events may extend beyond the recording duration. This is the case for any recording duration if one considers long enough sound events, but if one considers the recognized units of biophony emitted by most animals, one might not capture those full units when recording durations drop below several minutes (or longer for exceptional taxa like whales). At extreme values below around 10 s, some sounds may become unrecognizable for human listeners, potentially impeding any manual aural analysis. Additionally, the context of sounds is lost; extreme subdividing would obviously be inappropriate for studies considering the relationships between short-duration (approximately less than 10-second) sounds or acoustic triggers. It is also worth considering that storage and analysis technologies will likely improve in the future, so the financial and logistical constraints that encourage subsampling today may become less relevant, and it could eventually be desirable to have the most complete archive possible of our contemporary soundscapes. Subdividing also decreases the duration of each recording, increasing the influence of whatever short-term sound event is recorded. Despite these drawbacks, it does yield increased temporal resolution, and it increases the chances of capturing segments of longer sound events that might be otherwise missed (e.g., a 2-minute period of avian alert calls following a predator detection that begins in the 42nd minute of an hour would be missed if one was recording 10 min every 30 min).

In a recent paper on the topic of PAM study design, Bradfer-Lawrence et al. (2019) argue in favor of continuous recording, but their hypothetical use case seems to center around infrequent studies designed to characterize the soundscape of a given location as rapidly as possible, rather than long-term monitoring. While they consider seasonality a potential complication, it may well be the topic of interest in a different type of study. PAM can be employed to address an impressive diversity of ecological questions, some of which, like phenology or population dynamics, require long-term monitoring. While there seems to be a fairly universal desire for standardization of PAM methods, the diverse tools in the PAM jackknife often require different techniques in order to carve out an answer to the question at hand.

4. Conclusions

The vast diversity of Earth's soundscapes makes them a fascinating topic of study and a compelling motivator for global conservation. While the findings of this study have revealed some consistency in their short-term temporal variability, this consistency lends support to the case for using soundscapes as ecological indicators. Differences in temporal variability between times of day and sites are of largely secondary importance to the fact that based on acoustic index values, substantial subsampling is still highly representative of full-duration recordings, at least when quantifying soundscapes through the limited set of fairly general metrics we employed. While the big data concerns associated with PAM remain (Gasc et al., 2017)—and are of especial importance in political and economic climates that are not supportive of scientific research—the findings of this study suggest that judiciously applied subsampling can still yield valid results while minimizing the physical and financial restraints associated with big data storage and processing. The utility of soundscape-based research is greatly enhanced through global involvement and the potential for biogeographically important findings, and optimized subsampling may help promote such involvement and discovery.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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