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Mitchell,, Simon L., Bicknell, Jake E., Edwards, David P., Deere, Nicolas J., Bernard, Henry, Davies, Zoe G. and Struebig, Matthew J. (2020) *Spatial replication and habitat context matters for assessments of tropical biodiversity using acoustic indices.* Ecological Indicators, 119 . ISSN 1470-160X.

Ecological Indicators 119 (2020) 106717

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Spatial replication and habitat context matters for assessments of tropical biodiversity using acoustic indices

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ARTICLE INFO

Keywords:
Bioacoustics
Soundscape
Acoustic index
Biodiversity
Birds
Spatial replication, LiDAR

ABSTRACT

Approaches to characterise and monitor biodiversity based on the sound signals of ecosystems have become popular in landscape ecology and biodiversity conservation. However, to date, validation studies of how well acoustic indices reflect observed biodiversity patterns have often relied on low levels of either spatial or temporal replication, while focussing on habitats with similar underlying anthropological and geophysical sound characteristics. For acoustic indices to be broadly applicable to biodiversity monitoring, their capacity to measure the ecological facets of soundscapes must be robust to these potential sources of bias. Using two contrasting recording approaches, we examined the efficacy of four commonly used acoustic indices to reflect patterns of observed bird species richness across a tropical forest degradation gradient in Northeast Borneo. The gradient comprised intact and logged forests, riparian forests, remnants, and oil palm plantations, thus providing a highly variable anthrophonic and geophonic soundscape. We compared the degree to which acoustic indices derived from automated versus point count recording methods detected variation in inter-habitat species richness, as well as their capacity to capture changes in species diversity as a consequence of forest degradation quantified by high-resolution LiDAR derived forest canopy heights. We found *Acoustic Diversity Index* was associated with forest canopy height as measured by both automated recorders and recordings from point counts, whereas the association between canopy height and *Acoustic Complexity Index* was only detected using point count recordings. For both types of recordings, *Acoustic Complexity Index* exhibited the strongest relationship with observed bird richness in old growth and logged forest, whereas *Acoustic Diversity* was not linked, suggesting avian richness does not drive its association with canopy height. No acoustic indices were associated with observed bird richness in oil palm riparian areas. Our findings underscore the potential utility of soundscape approaches to characterise biodiversity patterns in degraded tropical landscapes, and may be used as a proxy for human inventories of bird communities. However, we also show that for acoustic indices to be effective on landscape-wide studies of environmental gradients, adequate spatial replication is required, and care must be taken to control for non-target elements of soundscapes in different habitats.

1. Introduction

Global ecosystems are changing rapidly due to anthropological pressures, resulting in wildlife population declines and extinctions (Ceballos et al., 2017). In turn, biodiversity loss weakens the stability of ecosystems upon which human populations depend (Hautier et al., 2015). As the number, extent, and severity of threats to biodiversity continue to increase, conservation practitioners are seeking more efficient, cost-effective, and scalable ways to monitor biodiversity, so they can identify and respond to emerging ecological crises (Bustamante et al., 2016; Anderson, 2018).

Recent advances in monitoring include the application of new remote sensing technologies (Pettoretti et al., 2014), such as Light Detection and Ranging (LiDAR) (Guo et al., 2017) and Synthetic Aperture Radar (Villard et al., 2016). These technologies allow biodiversity, human pressures and management interventions to be assessed over spatiotemporal scales that would be logistically unfeasible via ground-based methods alone, providing repeatable and standardised information on a suite of biodiversity indicators (Pettoretti et al., 2014). When combined with powerful new statistical approaches, robust estimates of species occupancy and habitat associations can be derived (Royle et al., 2007).

Further, the mass availability and reduced cost of sound-recorders has opened up an entirely new field of conservation research and practice (Beason et al., 2019). Now that it is feasible to deploy multiple sound-recorders within a given area, soundscape approaches are being

https://doi.org/10.1016/j.ecolind.2020.106717
Received 28 February 2020; Received in revised form 4 July 2020; Accepted 9 July 2020

used increasingly to address landscape-scale problems and questions - for example, how acoustic signals associated with biodiversity change with time, habitat-disturbance, and patterns of biological and human activity (Gasc et al., 2017). Such work is implemented across a wide variety of habitats and environmental contexts, including studies of species diversity in tropical (Mammides et al., 2017) and marine environments (Harris et al., 2016), responses of wildlife to forest fire smoke (Lee et al., 2017), and monitoring freshwater lakes for invasive species (Kottege et al., 2015).

Despite this, it remains unclear whether associations between acoustic indices and species richness are retained over large spatial scales and/or complex environmental gradients. In general, studies investigating these relationships have been relatively restricted in terms of spatial replication. For example, studies examining the link between acoustic indices and tropical avian richness, have typically been limited to a discrete habitat type (e.g. Machado et al., 2017; Mammides et al., 2017; Eldridge et al., 2018; Izaguirre et al., 2018). More recently Bradfer-Lawrence et al., (2019) made recommendations for the level of temporal and spatial sampling required to fully capture tropical forest soundscapes. However, this study focussed on capturing patterns of temporal and spatial variability within soundscapes, rather than whether acoustic indices measured patterns of biodiversity across multiple habitats, as captured via other survey methods. de Camargo et al., (2019) addressed spatio-temporal scaling of acoustic monitoring with respect to diversity, but assessed unsupervised learning techniques applied to only a subset of the community, rather than acoustic indices.

The reliability of acoustic indices as proxies for species richness depends upon sufficient spatiotemporal replication to capture both variation in the biological community itself, as well as the factors affecting the acoustic indices (e.g. Jorge et al., 2018). One of the much-lauded advantages of monitoring using automated sound-recorders is that they allow data to be collected over long time periods, which would be necessary to capture temporal variation (Darras et al., 2018). However, spatial replication is equally important when considering sampling design (Bradfer-Lawrence et al., 2019), particularly when the research aims to assess the relative biodiversity value of contrasting habitats. First, the variation in both alpha and beta diversity of trees is especially high in tropical forests (Duivenvoorden et al., 2002; Molino and Sabatier, 2001), and contributes to substantial variation in animal communities, including those that vocalise. Second, acoustic signals might be influenced unduly by vegetation structure affecting noise attenuation (Gasc et al., 2015), the degree of anthropogenic sound in the environment (e.g. vehicle engines or chainsaw noise, Fuller et al., 2015), and the presence of geophonic sound (e.g. running water or rainfall, Fuller et al., 2015). Indeed, studies in urban environments counter the widely held view that acoustic indices reflect biodiversity patterns, due to strong and disruptive anthrophonic signals in highly disturbed environments (Fairbrass et al., 2017).

Birds are highly responsive bio-indicators of environmental change and, therefore, excellent surrogates for wider patterns of biodiversity (Lewandowski et al., 2010; Gardner et al., 2008). They are also one of the most dominant terrestrial taxonomic groups in terms of their contribution to soundscapes (Gasc et al., 2017). As such, birds are frequently a focal taxon to document or monitor via acoustic recordings. The central tenet underpinning this decision is that greater diversity of acoustic signals reflects more vocal species in a given community (Gage et al., 2001). Preliminary validations that compared acoustic indices with observed bird diversity from point counts or expert identification from recordings have yielded encouraging results. Indeed, acoustic indices tend to correlate with avian richness in temperate (Depraetere et al., 2012; Eldridge et al., 2018), sub-tropical (Burivalova et al., 2019) and some tropical environments (Mammides et al., 2017).

Here, we assess the performance of five commonly used acoustic indices, and two recording approaches at capturing variation in bird communities across a tropical forest degradation gradient. We compare acoustic outputs over extended time periods (i.e. the general convention in acoustic studies, particularly those using autonomous recording techniques), with those generated during point count recordings which tend to have higher levels of spatial replication. We compare the efficacy of these two sampling designs in terms of how the acoustic indices detect variation between habitat types, as well as their capacity to capture changes in species diversity as a consequence of forest degradation, as quantified by high-resolution LiDAR derived forest canopy heights. Boelman et al., (2007) previously combined field surveys, bioacoustics and LiDAR in the context of impoverished island communities of Hawaii, but made no assessment of the levels of spatial or temporal replication required for acoustic indices to be useful in such studies. Other studies demonstrated relationships between LiDAR-derived metrics and acoustic indices (Pekin et al., 2012), but without assessing how they are mediated by species richness of any particular taxonomic group. We verify selected acoustic indices against the number of species recorded during traditional point counts (i.e. conducted simultaneously with the point count sound-recordings and within the same landscapes), and to richness estimates from occupancy models that control for detection probability. Variation in detection probability between species has yet to be accounted for within acoustic indices. We undertake our validation in a hyper-diverse but hyper-disturbed tropical forest system, where the performance of acoustic indices is less well studied than in temperate regions. We discuss the implications of our findings across the indices, contrasting recording approaches, and in relation to spatial replication in acoustic monitoring.

2. Methods

2.1. Study system

Bird and acoustic surveys were conducted in four landscapes in Sabah, Malaysian Borneo: Danum Valley, Maliau Basin, Sepilok and Kalabakan. We undertook simultaneous point counts and sound-recordings at 296 sites within five habitat types, covering a gradient of habitat degradation and increasing human presence, from unlogged old growth dipterocarp forest through to oil palm plantations (Fig. 1). Old growth forest was sampled at Danum Valley, Maliau Basin and Sepilok ('old growth'; 20, 10 and 19 sites, respectively). At Kalabakan, surveys were implemented in and around the Stability of Altered Forest Ecosystems (SAFE) Project (https://www.safeproject.net) in logged riparian forest ('riparian forest'; 80 sites), isolated riparian forest remnants within oil palm plantations ('riparian reserve'; 90 sites), and riparian areas without natural vegetation in oil palm estates ('oil palm'; 20 sites). We also sampled continuous logged forests at SAFE and in the adjacent Ulu-Segama Forest Reserve in non-riparian areas ('logged forest'; 123 sites).

Anthropogenic noise varied for each habitat. Mostly it comprised distant machinery from adjacent logging, agricultural operations, and/or road and trail maintenance, the latter being especially prominent within oil palm. Old growth and logged forests were characterised by low geophonic sound, whereas riparian forests included fast-flowing streams, thus high levels of background geophonic noise. In comparison, the streams in riparian forest sites were typically slower-flowing, resulting in lower levels of geophonic noise. Although oil palm riparian sites were located along watercourses, they were all very small and slow-flowing, providing minimal acoustic signal in recordings. The biophonic contribution to the soundscape was typical of that a tropical forest landscape, incorporating a wide variety of taxa such as birds, insects and frogs.

2.2. Bird point count sampling

Birds were sampled via 15-minute, 50 m radius point counts with three or four visits to each site between 2014 and 2017 (1146 counts in total). Surveys were undertaken by a single experienced surveyor (SLM)

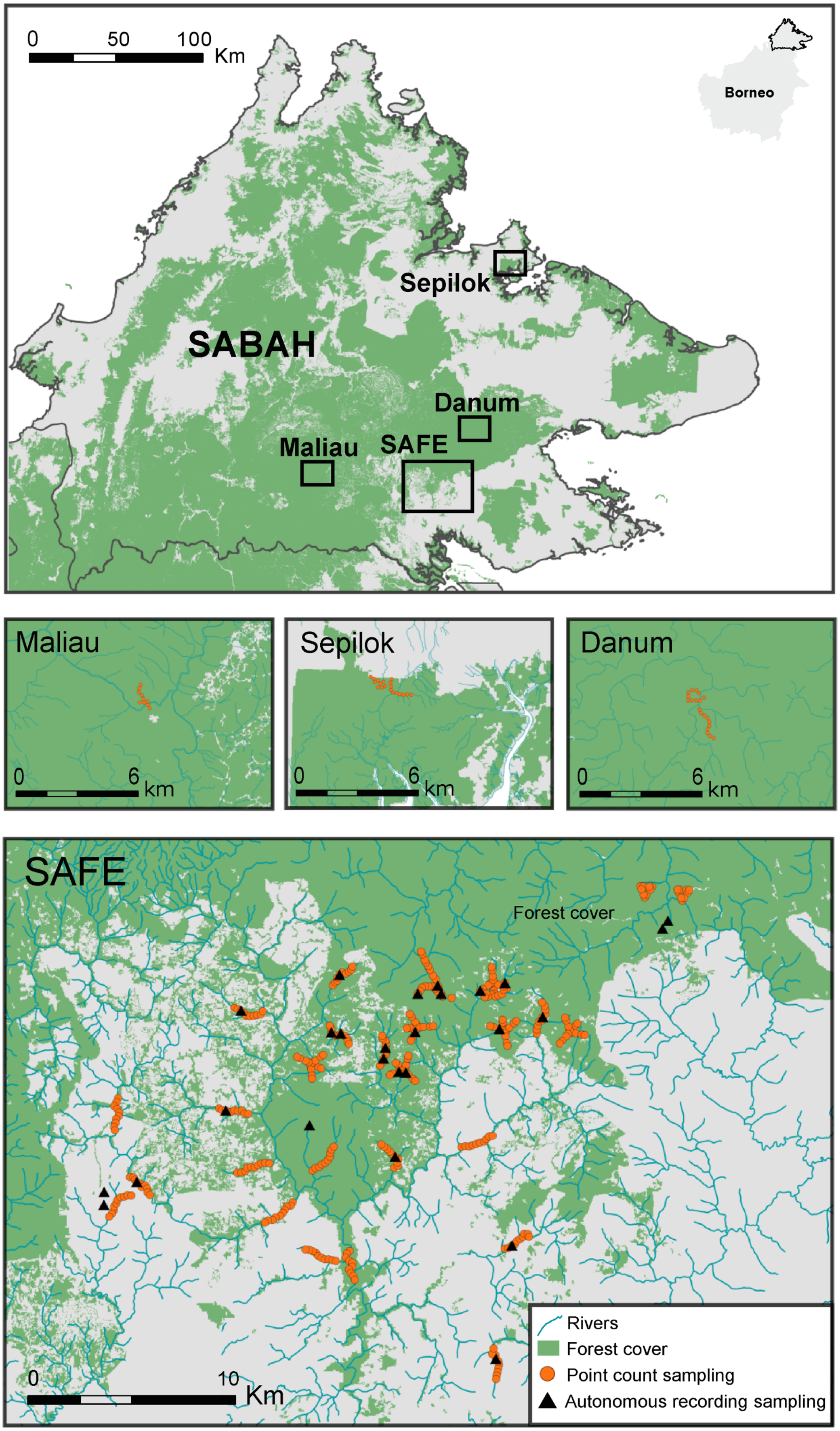

Fig. 1. Map of Eastern Sabah with the location of study areas inset: a) SAFE project at Kalabakan; b) Danum Valley; c) Sepilok; and d) Maliau Basin. Locations of automated sound-recorder deployments are labelled with black triangles whilst point count locations are marked with orange circles.

between 06:00 and 11:00 on days without rain. Sampling reflected seasonal variation across the whole forest degradation gradient as far possible given access constraints. Repeated point counts at a given site where done on different days to ensure temporal independence. Sites were located at least 180 m apart to maintain spatial independence.

2.3. Sound-recorder samples

To best measure the elements of the soundscape most reflective of the bird community, we focussed both types of acoustic recordings during the hours of the dawn chorus, when forest soundscapes tend to be dominated by birdsong (Eldridge et al., 2018).. However, our analyses do not allow for the complete exclusion of non-focal biophonic sounds.

During each bird point count a matched sound recording was made, using a single field recorder (Olympus LS-11/LS-12) and dual cardioid microphones positioned perpendicular to one another. In the riparian sites, the microphone was placed a minimum of 10 m from the watercourse and oriented away from areas producing the most noise. We recorded for the 15-minute period of the point count, following the convention for the duration of such counts generally used in tropical forests (e.g Mitchell et al., 2018; Hatfield et al., 2020). A total of 1146 recordings from the 296 sampling locations amounted to 286 h of recording time.

Automated sound-recorders were deployed at 26 sites across Kalabakan in logged forest (11 sites), riparian forest (9), riparian reserves (4) and oil palm (2) in order to capture a broad variation in the soundscape along a gradient of vegetation structure (Fig. 1). Deployment of automated acoustic devices took place during the same seasons as point count surveys. At each site we set the recorders for five mornings, which we determined to be the number of mornings required to fully capture the variation in the dawn chorus soundscape (Supplementary Materials). We used SM2 automated recorders (Wildlife Acoustics) with an omnidirectional microphone (SMX-II; sampling rate 48 kHz) positioned at a height of 1.5 m via a supporting pole. The units were configured to record the first three and half hours after 06:00am to coincide with the dawn chorus and with our point count surveys, and were split into 30 min segments, reflecting the length of analytical subunits commonly used in the automated recording literature (e.g. Burivalova et al., 2018, Tucker et al., 2014). This amounted to 455 h of recording time.

The differing durations of our analytical subunits were chosen to reflect those most typical of the contrasting recording methods, which also differ in a number of other key respects including microphone type, positioning and processing (see Supplementary Materials).

2.4. Acoustic indices

Multiple indices are available to statistically describe the distribution of acoustic information related to biodiversity in a given sound recording. Most are designed to gauge the richness and complexity of ecological communities, such as *Acoustic Complexity Index* (hereafter *Acoustic Complexity*) or bioacoustic activity (e.g. Pieretti et al., 2011; Sueur et al., 2008a; Sueur et al., (2008b; Depraetere et al., 2012). Others are designed to evaluate specific facets of soundscapes that could be useful for decision makers, such as anthropogenic disturbance (i.e. ‘anthrophony’; Kasten et al., 2012), while indices that measure acoustic dissimilarity (i.e. expressing the difference between multiple recordings; Sueur et al., 2008a; Sueur et al., 2008b) are potentially useful in studies seeking to measure beta diversity across landscapes.

We used the R packages soundecology (Villanueva-Rivera et al., 2018) and seewave-R (Sueur et al., 2008a; Sueur et al., 2008b) to quantify five common acoustic indices for each recording from each sample design: *Acoustic Complexity*; *Bioacoustic Index*; *Acoustic Diversity Index* (hereafter *Acoustic Diversity*); and the *Normalised Difference in Soundscape Index*. *Acoustic Complexity* is designed to capture the intricacy of biophonic signals (sounds created by living things), while ignoring the influence of anthropological and geophysical noises. It is based on the premise that biotic sounds intrinsically encompass a large variety of intensities, whereas sounds such as overflying airplanes or running water are associated with constant intensity values (Pieretti et al., 2011). *Bioacoustic Index* describes mean spectral power between 2,000 kHz and 8,000 kHz, as this frequency range covers most ecologically important sound, but excludes many anthropogenic noises which, in general, register below 2,000 kHz (Boelman et al., 2007). *Acoustic Diversity* calculates Shannon’s diversity index (akin to the Shannon-Wiener index) for each recording, according to the power (i.e. measurable sound energy detected) of each 1 kHz frequency band (Jost, 2006). *Acoustic Evenness*, based on the Gini-Simpson index (Gini, 1912), measures evenness between ten equal frequency bands 0 – 22,050 kHz, as the proportion of the power in each band above a −50 dBFS (decibels relative to full scale) threshold (Villanueva-Rivera et al., 2011). Finally, we also computed the *Normalised Difference in Soundscape Index* (NDSI), which is simply the ratio of biotic to anthropogenic signal (Kasten et al., 2012). *Acoustic Diversity* and *Acoustic Evenness* characterise inverse soundscape properties to one another (Eldridge et al., 2018), and so after confirming this was the case in our data (Table S1), we limit analysis to just *Acoustic Diversity* (for further details on the settings used for the acoustic indices see Supplementary Materials).

2.5. LiDAR forest canopy height metric

To assess the impact of forest degradation on acoustic indices we estimated canopy height, which is known to strongly influence tropical bird communities in the region (Mitchell et al., 2018), and is correlated with other measures of forest structure, such as tree density, biomass and vegetation complexity (Deere et al., in press). Higher canopy corresponds with old growth, carbon-rich forest that has experienced little or no logging in our study. We extracted average canopy height within a 50 m radius of each sampling site using LiDAR data, generated in November 2014 using protocols described by Jucker et al. (2018). Surveys employed a Leica ALS50-II sensor aboard a light aircraft (Supplementary Materials).

2.6. Raw species richness

Using the raw point count data, we counted the total number of species for each location and habitat type. However, these types of species lists are not necessarily indicative of the numbers of species regularly using them, as some species are rare or transient in particular habitats. To make comparisons with acoustic indices we counted the raw number of species per 15-minute visit, and analysed this relative to index scores from the simultaneous recordings.

2.7. Modelled species richness

We used occupancy modelling to estimate species diversity at every point count location, based on the occupancy probabilities of each species and controlling for differing detection probabilities between species. Occupancy was estimated using a Bayesian hierarchical community model, whereby each species could be affected by five structural vegetation metrics and overall community means, and detection probability was influenced by time-of-day and survey date (see Supplementary Materials for model formulation and specification). Modelled richness was calculated as the sum of the median probabilities of each species being present at a particular site.

2.8. Statistical analyses

To understand the relationship between different acoustic indices and raw point count species richness, we fitted a series of bivariate linear regressions. Similarly, linear regressions were used to explore relationships between time-of-day and each acoustic index.

To test the relative performance of acoustic indices (calculated separately for point count and automated recordings) in reflecting habitat, time-of-day and raw species richness from the point counts, we ran GLMs using the appropriate link function for each acoustic index derived from the R package 'fitdistrplus' (Delignette-Muller & Dutang, 2015). We fitted *Acoustic Complexity* and *Bioacoustic Index* with Gamma family models, while *Acoustic Diversity*, *Acoustic Evenness,* and *NDSI* were fitted with Beta distribution models. Beta distributions were standardised using the package 'reghelper' (Hughes and Core, 2017.

Using linear mixed-effects models, we assessed the relationships between each of our indices and modelled species richness, canopy height and time-of-day, while controlling for site identity as a random factor. Species richness and canopy height were modelled separately from one another as they were correlated (Table S2), but time-of-day was included fixed effect in both cases, to provide comparable model structure between the former two variables. Site identity was included as a random effect in each set of models. This process was undertaken for point count recordings and autonomous samples separately. All statistical analyses were undertaken using R (R Core Team, 2014).

3. Results

3.1. Species richness

We recorded 221 bird species across all point count locations (Fig. 2e). Of these, 173 were observed in old growth, 185 in logged forest, 166 in riparian forest, 177 in riparian reserves and 49 in oil palm. Over 90% of species detections were acoustic identifications by the surveyor, so would also have been recorded as vocalisations by the simultaneous point count sound-recordings.

Our occupancy model represented 173 species sampled in the community, with any species recorded fewer than three times excluded. The model estimated species richness at every point count location, with a median of 78 species per location predicted in old growth, 68 in logged forest, 66 in riparian reserves and 52 in oil palm. The average number of species recorded per visit also varied between habitats: old growth (median = 12.5); logged forest (13.1), riparian forest (7.6), riparian reserves (9.6) and oil palm (6.9; Fig. 2j).

3.2. Acoustic indices from point count and autonomous sound-recording sampling designs

The broad differences apparent in acoustic indices between habitat types were similar, whether they were based on data from the point count or autonomous sound-recorders (Fig. 2). In both cases, the highest values for *Acoustic Complexity* were recorded in logged forests and oil palm (Fig. 2a, 2b), and the lowest were for riparian forests and riparian reserves. *Acoustic Diversity* (Fig. 2c, 2d) was lowest in riparian forests and riparian reserves, with higher values detected in oil palm and logged forest. *Bioacoustic Index* (Fig. 2e, 2f) was highest in oil palm, followed by logged forest, riparian forest and riparian reserves. *Normalised Difference in Soundscape Index* (NDSI) patterns were also consistent between point count recordings and autonomous recorders (Fig. 2g, 2 h). For Acoustic Complexity, Acoustic Diversity and NDSI we found that results from autonomous recorders demonstrated a greater overall variance than those from point count recordings (Fig. 2).

3.3. Relationships between acoustic indices and raw point count species richness

Relationships between acoustic indices and raw species richness were strongly mediated by habitat type (Table S1; Fig. S1). Differences between habitat types were particularly strong for *Acoustic Complexity*, *Bioacoustic Index* and *Acoustic Evenness*. Bird diversity was associated with one or more acoustic indices in every habitat type, with the exception of riparian reserves.

3.4. Effects of time-of-day

The time period for point count and autonomous sound-recorder samples was highly consistent (998 of 1146 point count sound-recordings were made before 09:30). *Bioacoustic Index* and *Acoustic Complexity* were negatively related to time-of-day when the point count sound-recordings were analysed (Table 1, Table 2). No such significant relationships were found for *Acoustic Diversity*. For the acoustic indices estimated from the autonomous sound-recorders, *Acoustic Complexity* was again negative against with time-of-day, while *Acoustic Diversity* was positively related. Raw species richness was also affected by time-of-day (Table S2)

3.5. Performance of acoustic indices in reflecting changes in forest structure

Point count sound-recorder sample indices were related with changes in canopy height for *Acoustic Complexity* (negatively), *Bioacoustic Index* (positively) and *Acoustic Diversity* (positively) (Table 1). Only *Acoustic Diversity* was (positively) associated with changes in canopy height for autonomous sound-recorders. Controlling for the effect of habitat type within linear mixed models did not influence any of the relative results. For point count recordings the range of canopy height was 6–68 m, for autonomous recorders canopy height varied from 9 to 37 m.

3.6. Performance of acoustic indices in reflecting modelled species richness

Only *Acoustic Complexity* from point count sound-recordings was related to modelled bird species richness (negatively) (Table S2). Controlling for the effect of habitat type did not affect this finding. However, none of the between habitat type patterns derived from acoustic indices reflected estimated species richness from the occupancy models (Fig. 2i, 2j).

3.7. Performance of acoustic indices in reflecting raw point count species richness

Raw species richness derived from the point counts was significantly related to all acoustic indices derived from simultaneous sound-recordings (Table 3). Positive relationships with the strongest coefficient was evident for *Acoustic Complexity*, followed by *Acoustic Evenness*, *Bioacoustic Index* and *Normalised Difference in Soundscape Index*. The relationship with *Acoustic Diversity* was negative and weak. *Acoustic Complexity* and *Bioacoustic Index* were negatively related to time-of-day (Table 3), with the highest values observed shortly after dawn. *Normalised Difference in Soundscape Index* showed the inverse relationship.

4. Discussion

Given an appropriate sampling design and analytical framework, acoustic indices can reflect bird diversity patterns across tropical landscapes and, therefore, serve as a viable method to characterise and monitor avian biodiversity. We found *Acoustic Diversity* was positively related to canopy height, used as a proxy for forest structure, based on relatively limited spatial replication (n = 24) of autonomous sound-recordings. However, this relationship was not detected from point count sound-recordings (n = 296), despite greater spatial replication. Conversely, no association between canopy height and *Acoustic Complexity* was identifiable from automated recordings (despite greater temporal sampling), although a negative association existed with point

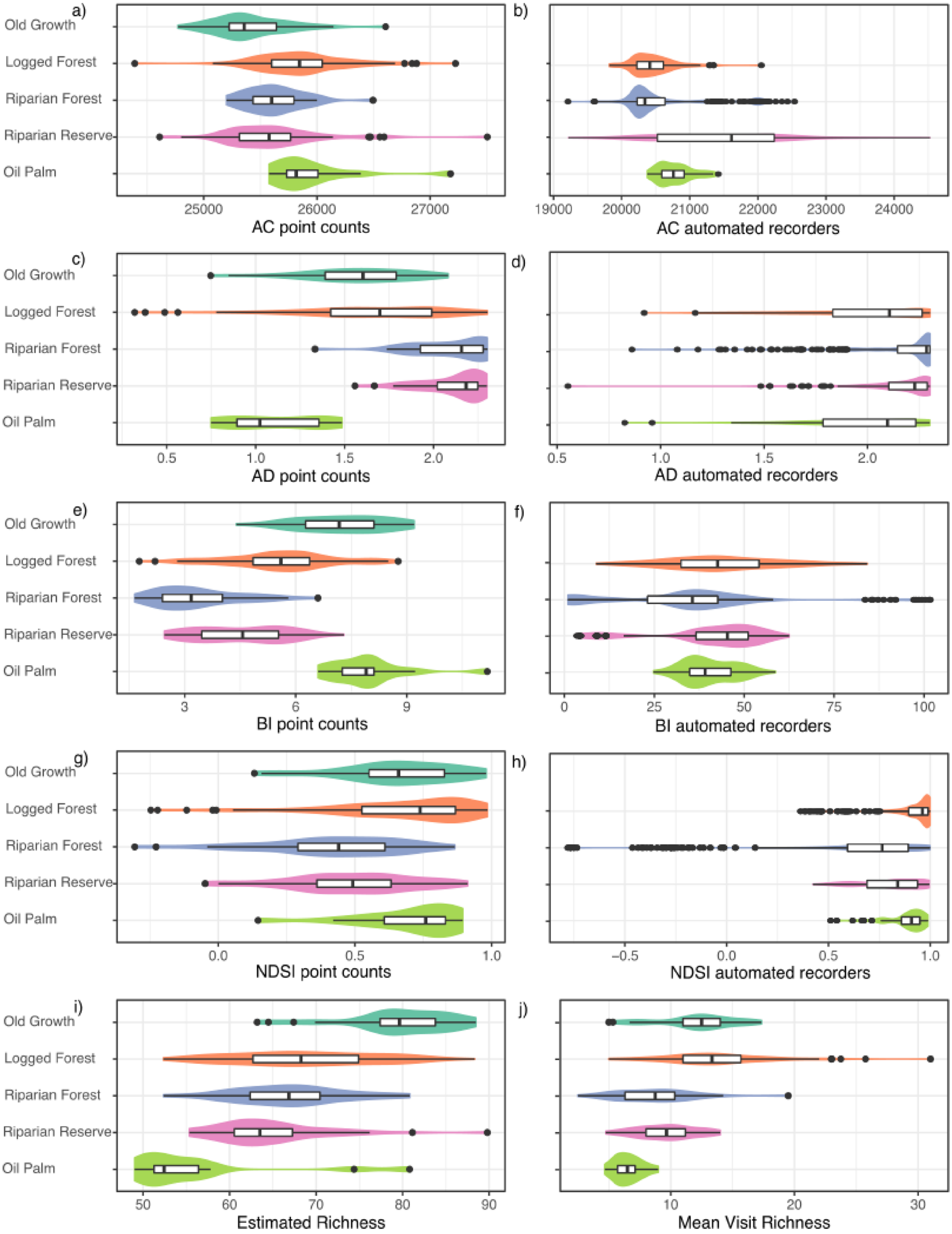

Fig. 2. Boxplots showing the variation between habitats in: a) *Acoustic Complexity* (AC) from point count sound-recordings; b) *Acoustic Complexity* (AC) from automated sound-recordings; c) *Acoustic Diversity* (AD) from point count sound-recordings; d) *Acoustic Diversity* (AD) from automated sound-recordings; e) *Bioacoustic Index* (BI) from point count sound-recordings; f) *Bioacoustic Index* (BI) from automated sound-recordings; g) *Normalised Difference in Soundscape Index* (NDSI) from point count sound-recordings; h) *Normalised Difference in Soundscape Index* (NDSI) from automated recordings; i) species richness derived from occupancy modelling; j) the raw mean number of species recorded per visit during point counts.

Table 1
Linear mixed models comparing two different survey methods (point count and autonomous sound-recordings) in capturing associations with time-of-day and canopy height. Indices assessed were: *Acoustic Complexity* (AC); *Acoustic Diversity* (AD); and *Bioacoustic Index* (BI).

Recording method	Acoustic index	Variable	Coefficient	Standard error	Degrees of freedom	t-value	p-value
Automated	BI	Intercept	51.37	12.85	590	3.998	< **0.001**
		Canopy height	−0.47	0.49	16	−0.964	0.349
		Time-of-day	0.13	0.17	590	0.739	0.460
	AC	Intercept	22394.70	749.36	590	29.885	< **0.001**
		Canopy height	−46.35	28.87	16	−1.606	0.128
		Time-of-day	−68.90	6.62	590	−10.407	< **0.001**
	AD	Intercept	1.66	0.15	590	10.923	< **0.001**
		Canopy height	0.01	0.00	16	2.247	**0.039**
		Time-of-day	0.01	0.00	590	3.967	< **0.000**
Point count	BI	Intercept	5.26	0.30	593	17.155	< **0.001**
		Canopy height	0.01	0.01	293	1.925	**0.050**
		Time-of-day	−0.00	0.00	593	−3.565	< **0.001**
	AC	Intercept	26407.42	60.87	593	433.824	< **0.001**
		Canopy height	−15.37	1.70	293	−9.045	< **0.001**
		Time-of-day	−1.65	0.20	593	−7.912	< **0.001**
	AD	Intercept	1.65	0.07	593	23.108	< **0.001**
		Canopy height	0.01	0.00	293	2.107	**0.036**
		Time-of-day	0.01	0.00	593	0.468	0.640

Table 2
Linear mixed models comparing two different survey methods (point count and autonomous sound-recordings) in capturing relationships with time-of-day and modelled species richness. Indices assessed were: *Acoustic Complexity* (AC); *Acoustic Diversity* (AD); and *Bioacoustic Index* (BI).

Recording Method	Acoustic index	Variable	Coefficient	Standard error	Degrees of Freedom	t-value	p-value
Automated	BI	Intercept	42.675	8.038	1955	5.309	< **0.001**
		Modelled richness	−0.019	0.044	16	−0.429	0.673
		Time-of-day	0.103	0.097	1955	1.066	0.287
	AC	Intercept	21140.75	455.578	6746	46.404	< **0.001**
		Modelled richness	−1.406	2.499	16	−0.563	0.581
		Time-of-day	−3.475	0.632	6746	−5.494	< **0.001**
	AD	Intercept	1.916	0.104	1955	18.382	< **0.001**
		Modelled richness	0.000	0.001	16	0.850	0.408
		Time-of-day	0.018	0.002	1955	7.723	< **0.001**
Point count	BI	Intercept	5.545	0.248	593	22.395	< **0.001**
		Modelled richness	0.001	0.001	293	1.189	0.235
		Time-of-day	−0.003	0.001	593	−3.548	< **0.001**
	AC	Intercept	26152.89	54.122	593	483.222	< **0.001**
		Modelled richness	−1.025	0.212	293	−4.822	< **0.001**
		Time-of-day	−1.663	0.212	593	−7.830	< **0.001**
	AD	Intercept	1.742	0.059	593	29.652	< **0.001**
		Modelled richness	0.000	0.000	293	0.787	0.432
		Time-of-day	0.000	0.000	593	0.491	0.624

count sound-recordings. This highlights the need for sufficient spatial, as well as temporal, replication in studies examining potential relationships between acoustic indices, patterns of biodiversity and environmental gradients.

4.1. *The influence of habitat context on acoustic indices*

Acoustic indices varied dramatically within habitats, but these differences did not always follow the same patterns as those evident from either raw or modelled richness data. Across multiple forest habitats,

Table 3
Linear regression model statistics of raw point count species richness and time-of-day. Results listed for each acoustic index, with intercept, F-statistic, p value, R^2, residual standard error, and degrees of freedom for each. Indices assessed were: *Acoustic Complexity* (AC); *Acoustic Diversity* (AD); *Acoustic Evenness* (AE); and *Normalised Difference in Soundscape Index* (NDSI).

Linear Model	Intercept	F	p-value	R^2	Residual standard error	Degrees of freedom
BI ~ Raw species richness	0.04	6.537	0.05	0.005	2.69	1145
AC ~ Raw species richness	23.76	54.79	< 0.001	0.046	517.7	1132
AD ~ Raw species richness	−0.009	7.374	< 0.001	0.006	0.562	1132
AE ~ Raw species richness	0.007	25.74	< 0.001	0.021	0.27	1145
NDSI ~ Raw species richness	0.006	14.17	< 0.001	0.012	0.295	1145
BI ~ Time-of-day	−0.004	15.98	< 0.001	0.013	2.679	1145
AC ~ Time-of-day	−1.515	56.97	< 0.001	0.047	517.2	1132
AD ~ Time-of-day	0.0001	0.487	0.485	< 0.001	0.563	1132
AE ~ Time-of-day	−0.0002	3.508	0.061	0.003	359.4	1132
NDSI ~ Time-of-day	0.0009	58.71	< 0.001	0.049	0.289	1132

index values were associated with raw species richness derived from point counts. However, this was not the case in oil palm sites, where the highest levels of *Bioacoustic Index* and *Acoustic Complexity* of any habitat type were found, contrary to the lowest levels of raw bird diversity (Fig. 1; Fig S1).

Bird communities in oil palm, as in other intensively managed farmland or urban systems, are species-poor, comprising only a few generalist species that occur at almost all sites sampled (Mitchell et al., 2018; Edwards et al., 2010). In practice, this limits variation in both the raw diversity and acoustic indices, therefore lowering the statistical probability of detecting significant association between the two. This is supported by the fact that we observed only 3–16 species per point count in oil palm, compared to up to 29 species per point count in old growth forest. In addition, non-focal acoustic signals (e.g. anthropogenic and geophonic sounds) are likely to strongly influence the overall soundscape in this habitat context. In urban environments, for example, human speech is known to exert a significant bias upon acoustic indices, resulting in higher than expected value of *Acoustic Complexity* and *Bioacoustic Index* and lower than expected values of *Acoustic Diversity* and *Normalised Difference in Soundscape Index* (Fairbrass et al., 2017). Since workers could often be heard in oil palm sound-recordings, it is possible that these acoustic signals at least partially obscured differences in acoustic indices driven by bird vocalisations.

The association between *Acoustic Complexity* and raw bird richness also broke down in riparian forests (Fig. S1), where sites were typically steep stream gullies with substantial background noise from running water. Again, we suspect these sound signals undermined the capacity of this index to detect differences in bird diversity at these sites. As *Acoustic Complexity* is based upon absolute differences in signal power within each frequency band over time it should, in theory, account for constant background noise (Pieretti et al., 2011). However, if such noise is sufficiently loud to override signals of bird vocalisations, this would significantly dampen the variations in signal power over time and, therefore, reduce the capacity of the index to reflect overall *Acoustic Complexity*.

By comparing patterns of acoustic indices across habitats from two different acoustic survey methodologies, we are able to highlight that these demonstrate broadly similar patterns of variation between habitats (Fig. 2), despite the two protocols using differing analytical subunits, microphones and deployment regimes (Supplementary Materials). However, relationships to bird species richness across a whole gradient of forest degradation may not be effectively captured without sufficient spatial replication. This is highlighted by the fact that we found autonomous recorders did not detect any associations between acoustic indices and species richness modelled from point counts, whereas point count recordings did (Table 2). One potential avenue for future exploration is whether it is possible to 'calibrate' recordings from different habitats and acoustic contexts to better reflect bird species richness. This could, in theory, be done using noise reduction processing to remove the majority of extraneous acoustic signals prior to analysis..

4.2. Potential influence of cicada calls

Across the entire dataset, we found a weak but significant association between the *Bioacoustic Index* and raw species richness (Table 3), yet when partitioned by habitat-type this was only statistically robust in riparian forest (and not in old growth, logged forest, riparian remnants or oil palm sites; Fig S1). A possible explanation is the influence of insect sounds, primarily from cicadas, which are common in Asian rainforests and can make a substantial contribution to the overall soundscape (Gogala & Riede, 1995). Cicadas tend to call at constant frequencies within the range of 2–8 kHz (e.g. Presern et al., 2004), which coincides with most bird vocalisations (Goller and Riede, 2013), and hence the frequency range applied in the calculation of the *Bioacoustic Index* (Boelman et al., 2007). Gasc et al. (2018) demonstrated that reductions in cicada abundance due to wildlife in the three Macrean habitats corresponded to significantly reduced *Bioacoustic Index* values during certain periods of the day. It is therefore difficult to discriminate between high *Bioacoustic Index* values arising from cicada- versus bird-derived sounds. Some endothermic species of tropical forest cicada are known to limit calls until a certain temperature is reached (Sanborn et al., 1995). Since old growth forests have a greater thermal buffering capacity than logged forests (Frey et al., 2016), it is possible that the onset of certain cicada calls is delayed in the former habitat.

The cicada chorus may have also affected measures of *Acoustic Diversity*, leading to the lack of association with raw bird richness, contrary to expectations. *Acoustic Diversity* values can be affected by other sources of acoustic heterogeneity, such as the distance of the sound sources from sensors or the presences of variations in the intensity of animal vocalisations (Gasc et al., 2013). In our dataset more cicada taxa calling at frequencies coinciding with straddling multiple different 1 kHz frequency bands would increase evenness (and therefore Shannon diversity across bands and resulting *Acoustic Diversity* values).

Although some studies have attempted to exclude cicada choruses prior to analysis (Towsey et al., 2014), the uneven temporal distribution of such signals means doing so adds new biases based on the time-of-sampling. Previous research has also found that temporal differences in cicada chorus introduced bias in entropic indices, resulting in higher index values in degraded than intact tropical forest (Sueur et al., 2008a; Sueur et al., (2008b). The loud insect chorus characteristic of Bornean rainforests is also thought to result in 'jamming avoidance', whereby some taxa sing less frequently during the loudest choruses of others (Riede, 1997). Therefore, understanding how changes in cicada choruses effect acoustic indices is therefore a major research priority for optimising their utility in tropical forests, particularly those in Asia.

4.3. Potential influence of species detection rates

Bioacoustic Index values were greater in old growth forest, followed by logged forests, then riparian reserves and riparian forest (Fig. 2e, f). This pattern (excluding for oil palm) mirrored the aggregated habitat richness findings from our previous analysis of the landscape (Mitchell et al., 2018), and more broadly show that old growth forests support more bird species than logged forests (Edwards et al., 2014) or isolated fragments (Edwards et al., 2010). Associations between *Bioacoustic Index* values and observed richness from individual point counts may have been weak due to the raw species richness being a poor reflection of actual diversity patterns. This is because most birds in tropical forest are relatively uncommon, with some not calling every day (Robinson et al., 2018) and therefore, are more likely to be missed due imperfect detection.

We found fewer and weaker associations between acoustic indices and modelled point count richness (Table 2), than between acoustic indices and raw species richness (Table 3), even when time of day was controlled for. This suggests that one issue acoustic indices have yet to overcome is accounting for imperfect detection to better capture avian species richness. It may be difficult to do this for indices that analyse acoustic variation across windows of a few seconds. However, indices the development of machine learning techniques and acoustic classifiers which identify individual species could potentially be used in conjunction with an occupancy modeling approach in order to control for detection probability.'

Incomplete sampling of some species due to imperfect detection contributes to the discrepancy between acoustic indices and raw richness patterns. This is supported by the negative relationships found between several indices and time-of-day (Table 1). Similar patterns have been noted in previous studies (Wimmer et al., 2013). Since raw species richness from point counts can be based on upward of 95% aural encounters in tropical forests (Robinson et al., 2018), this metric also decreases with time-after-dawn. However, the effect of time upon acoustic indices and raw species richness is not the same, since point counts do not rely solely upon vocalisations. This means that the differing effects of time upon the two metrics introduces a further source of bias. We detected effects of time-of-day upon both acoustic indices (Table S1) and raw species richness (Table S2) and therefore included time as a covariate in the occupancy model we developed to estimate species richness (see Supplemental Methods). By modelling species richness from point counts whilst controlling for the influence of time-of-day upon the detection probability of each species, we were able to demonstrate an effect of time-of-day upon acoustic indices independent of the changes in detection probability (Table 2). We therefore recommend controlling for time-of-day in any sampling designs that base their acoustic indices upon samples from different times of day, even in the case of stratified samples limited to particular part of the day.

4.4. Acoustic indices as measures of biodiversity across landscapes

Although previous studies have demonstrated the capacity of acoustic indices to reflect changes in species richness in response to landscape configuration (Fuller et al., 2015), their ability to reflect patterns associated with environmental or structural gradients across multiple habitats remains uncertain. In fact, we know of only one study to date (Farina & Pieretti, 2014) that has assessed the relationship between vegetation structure and acoustic indices and even in this case, indices were applied to habitat categories, rather than using a continuous gradient approach.

The way in which correlations between vegetation metrics and acoustic indices are mediated by species richness is also still poorly understood, and may be contingent upon a number of other factors such as bird community composition or vegetation structure (Boelman et al., 2007). For acoustic indices to be of similar utility to existing wildlife monitoring tools they must be able to reflect biological patterns at a comparable or improved level to conventional methodologies. Although the effect of canopy height upon *Acoustic Complexity* was weak (though significant), this effect was similarly weak between raw species richness and canopy height (Table S3). Associations between acoustic indices and raw bird diversity were stronger and more consistent across indices than those with canopy height, suggesting that the failure to detect strong associations between indices and canopy height was partly due to the weak association between canopy height and observed species

Though recent studies have provided useful recommendations for how to design soundscape studies (Bradfer-Lawrence et al., 2019), these have focussed on the levels of sampling effort needed to fully capture spatial and temporal variation within soundscapes, rather than the effort required to assess ecological patterns. A primary ecological application of ecoacoustic technologies is to document and monitor biodiversity. Therefore, appropriate spatial and temporal scales can be considered as those that sample sufficiently to reveal biodiversity patterns. Our study demonstrates that despite a high level of temporal sampling from autonomous records, associations between both biodiversity (as measured observed and estimate richness from point counts) and environmental gradients (as measured by LiDAR-derived canopy height) can be missed without sufficient levels of spatial replication. This issue should be kept in mind as acoustic approaches further develop, and as the field advances from community-level indices to species-level species identification.

Authors contributions

S.L.M. J.E.B. M.J.S. D.P.E. H.B. and Z.G.D. conceived and designed the methodology; S.L.M. and N.J.D. collected autonomous acoustic data; S.L.M processed and analysed acoustic data and collected bird point count data. J.E.B. processed the autonomous recordings. S.L.M. M.J.S. Z.G.D. J.E.B. and D.P.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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.

Acknowledgments

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/ and http://bali.hmtf.info; NE/K016377/1), and a Newton-Ungku Omar Fund grant from the British Council and Malaysia Industry-Group for High Technology (MIGHT) (216433953). SLM was supported by a PhD scholarship jointly funded by University of Kent and NERC. We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby, Benta Wawasan, Sabah Softwoods and Innoprise Foundation for permitting site access. We are grateful to Unding Jami, David Hemprich-Bennet and the LOMBOK research assistant team for their field assistance, Suzan Benedick, Joseph Tobias, and Ryan Gray for facilitating fieldwork, and David Coomes, Tomasso Jucker, David Milodowski and Thomas Swinfield for providing the data that informed the occupancy model.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106717. All data utilised is freely available at the University of Kent academic repository: https://kar.kent.ac.uk/82363/.

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