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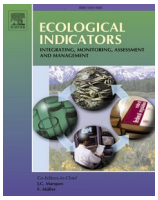

Soundscapes show disruption across the diel cycle in human modified tropical landscapes

Jenna Lawson [a,*], Andrew Whitworth [c], Cristina Banks-Leite [b]

[a] Science and Solutions for a Changing Planet DTP and Department of Life Sciences and Science and Solutions for a Changing Planet DTP, Imperial College London, UK
[b] Department of Life Sciences, Imperial College London, UK
[c] Osa Conservation, Conservation Science Team, Washington, DC 20005, USA

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ABSTRACT

1. Fluctuations in the diel cycle, especially when compared across different land-use types, can reveal key changes in acoustic activity and the biological community. Yet few studies have assessed the effects of land use change on soundscapes across the diel cycle. The emergence of passive acoustic monitoring (PAM) allows us to monitor landscapes over longer and continuous periods, providing data on temporal variability across the diel cycle.

2. Using AudioMoth acoustic recorders we collected data at 120 sites on the Osa Peninsula, Costa Rica, across a gradient of land use intensity. Information was extracted from recordings using a suite of nine acoustic indices. Principal component analysis reduced the indices into two axes, the first reflecting acoustic activity in the mid frequency bands, where the majority of biotic sound is present, and the second, representing acoustic activity in the upper frequency bands and the ratio of activity between the lower and mid-frequency bands.

3. In disturbed land use types we found reduced acoustic activity during the characteristic dawn and dusk peaks in the diel cycle; known as the dawn and dusk chorus. Palm oil plantations showed a complete loss of these peaks, while teak plantations retained evidence of a weaker dawn and dusk chorus. Restricting the analysis to narrower temporal windows masks these differences among habitats.

4. Synthesis and applications. Evaluating acoustic diversity at specific times of the day, which is common practice in bioacoustics studies, may be misleading, as pronounced changes in acoustic activity at dawn and dusk were obscured. By assessing trends across the diel cycle, we can gain a much better representation of the changes in acoustic activity. Our results show that in disturbed ecosystems there is a deviation in acoustic activity from that seen in a healthy native forest ecosystem, suggesting that there are likely changes within the biotic community in these ecosystems.

1. Introduction

Sound production across the diel cycle is a complex organisation of species activity, whereby shifts in activity can reveal important changes in the biological community and species behaviour resulting from anthropogenic activity (Francomano et al., 2021). Yet due to limited funding and people power, monitoring is often infrequent and spatially limited, thus precluding analyses of species activity and providing only a snapshot of variables that can fluctuate greatly between samples.

The emergence of passive acoustic monitoring (PAM) has improved our ability to noninvasively monitor landscapes across large regions and allowing the study of temporal variability at a fine scale (Pijanowski et al., 2011a; Ducrettet et al., 2020). Acoustic sensors can be deployed in the field for long periods of time and monitor continuously, without the need for the researcher to be present, allowing understanding of the impacts of anthropogenic disturbance across much wider temporal and spatial scales at a reduced cost (Gibb et al., 2019; Sugai et al., 2019). Yet listening to and analysing large datasets can be challenging and automated analyses are essential (Towsey et al., 2014). Computational approaches from the field of soundscape ecology provide one method for such automated analysis.

Soundscape ecology is the study of the interaction between animals (biophony), humans (anthrophony) and the environment (geophony) and is useful for studying spatial–temporal patterns (Pijanowski et al.,

* Corresponding author.
E-mail address: j.lawson17@imperial.ac.uk (J. Lawson).

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2011b). Soundscape ecology uses indices of acoustic diversity to determine measures of acoustic activity across space and time (Pijanowski et al., 2011b; Sueur et al., 2014). Each index measures a different aspect of the soundscape, including pitch, saturation and amplitude across time and frequency bands, with most indices being sensitive to the characteristics of biophony (Sueur et al., 2008; Napoletano et al., 2011; Bradfer-Lawrence et al., 2019), thereby providing measures of richness, evenness and heterogeneity of biotic sounds (Sueur et al., 2014).

By comparing acoustic diversity to biodiversity measured through standard sampling (e.g. point counts), a variety of indices have been related to the number of biological sounds in a recording, measures of species richness and abundance and functional diversity, mainly with birds (Joo et al., 2011; Mammides et al., 2017; Buxton et al., 2018b; Bradfer-Lawrence et al., 2020; Smith et al., 2020; Dröge et al., 2021), but also other taxa, including amphibians, orthopterans and mammals (Sueur et al., 2008; Fairbrass et al., 2017; Holgate et al., 2021). Soundscape studies have also used indices of acoustic diversity to demonstrate the effects of land use change on biodiversity. For example, Hao et al., (2021) found increased biophony in areas with more complex vegetation structure and a taller, denser canopy and Burivalova et al., (2021) found that biophony dropped when forested areas had been logged. In general studies have found that biophony increases and anthrophony decreases with reduced anthropogenic disturbance (Sueur et al., 2008; Tucker et al., 2014; Burivalova et al., 2021; Hao et al., 2021; Holgate et al., 2021).

However, there is some inconsistency in results with some studies failing to find any differences between landscapes (Mammides et al., 2017; Ng et al., 2018) and others reporting opposite results using the same index (Bradfer-Lawrence et al., 2019). This is perhaps due to lack of a standardised approach across the field, with over 60 different indices being used across very different temporal sampling regimes (Bradfer-Lawrence et al., 2019) and the inherent variation that exist across different environments around the world (Gibb et al., 2019). Indices are also sensitive to abiotic factors resulting from rain and wind and from poorly understood biotic sound, which is often not accounted for (Pijanowski et al., 2011b; Sánchez-Giraldo et al., 2020). It has been proposed that using multiple indices and continuous recording could help mitigate these issues (Bradfer-Lawrence et al., 2019; Dröge et al., 2021; Francomano et al., 2021; Hao et al., 2021).

Another reason why studies may find inconsistent results is because acoustic activity varies substantially across the day, reflecting species' diel cycle. The organisation of the acoustic space across diel cycles has developed over evolutionary timescales and major disruptions to this system may alter species' ability to communicate (Francomano et al., 2021). Effective intraspecies communication is directly linked to survival (Kleyn et al., 2021), and inability to communicate can disrupt important behaviours such as mating, recognition, predator avoidance and territoriality, ultimately interfering with population fitness (Luther, 2009). Changes across the diel cycle can also reveal differences in species behaviour and assemblages since loss of, or change in species composition, will alter activity and sounds produced (Bradfer-Lawrence et al., 2019; Francomano et al., 2021). For this reason, sampling at just one period in the day could lead to misrepresentation of or missing key changes in these patterns and processes.

It has therefore been recommended that soundscapes are assessed across the diel cycle (Bradfer-Lawrence et al., 2019; Francomano et al., 2021; Hao et al., 2021), with studies to date having consistently found higher acoustic diversity during the day compared to the night, (Villanueva-Rivera et al., 2011; Pieretti et al., 2015; Gage et al., 2017; Bradfer-Lawrence et al., 2019; Dröge et al., 2021; Francomano et al., 2021) and variation in dominant taxa across different time periods based on the separation of frequency bins (Metcalf et al., 2021). Despite this, few studies have been able to monitor soundscapes across the diel cycle and in different land uses (Burivalova et al., 2018; Furumo and Aide, 2019; Bradfer-Lawrence et al., 2020; Dröge et al., 2021), with those that have revealing increases in acoustic index values during the day in forested habitats compared to disturbed land uses (Dröge et al., 2021) and a stronger chorus or soundscape saturation in forested areas at dawn and dusk compared to areas affected by anthropogenic disturbance (Burivalova et al., 2018; Furumo and Aide, 2019).

Although studying the whole diel cycle is recommended, no studies have yet compared diel cycle analysis with soundscapes from narrower temporal windows.Using data collected across 120 sites in the Osa Peninsula in Costa Rica, one of the most biodiverse regions of the world (Sanchez-Azofeifa et al., 2009), we address this research gap by using a suite of nine acoustic indices to analyse changes in acoustic activity across the diel cycle, over a gradient of land use change. Here we ask: 1. Can soundscape indices reveal changes in acoustic activity across the diel cycle and between land use types? 2. Does restriction of the soundscapes to narrower temporal windows obscure differences among habitat types?

2. Methods

2.1. Study site

Our study area, the Osa Peninsula, covers 1093 km^2 in the South Pacific coast of Costa Rica. The terrain is generally low altitude, with a maximum elevation of 792 m. Mean annual rainfall ranges from 3,000–6,500 mm and mean yearly temperature is 27 °C, with high levels of humidity throughout the year. There are distinct wet and dry seasons, with the highest rainfall occurring September through December (Gilbert et al., 2016). The Osa Peninsula contains the last remnants of tropical broadleaf evergreen lowland rainforest on the Central American Pacific (Gilbert et al., 2016), imbedded within a mosaic of pasture, plantations and urban centres (Fig. 1). Due to the geology and geography of the area, the peninsula contains high levels of biodiversity and endemism (Arturo Sánchez-Azofeifa et al., 2003). There are three national parks (Corcovado, Piedras Blancas and the Terrebe-Sierpe Wetlands) and one forest reserve, the Golfo Dulce. (Arturo Sánchez-Azofeifa et al., 2003). A map with highlighting the boundaries of these protected areas has been included in the Supplementary Material (Supplementary Fig. 1).

2.2. Sampling design

Land use at each site was calculated using land use maps created by NASA, created at a scale of 5 × 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha et al., 2018) (Fig. 1). The NASA map has nine land use categories, however we only sampled old growth, secondary forests, palm and teak plantations (Fig. 1). The land use maps used in this study defined secondary forests as 40 years+ (Shrestha et al., 2018).

We aimed for a uniform distribution of sampling locations across the Osa Peninsula to ensure even coverage, but this was not always possible due to access issues. Therefore, sampling sites were chosen across each land use category using a stratified sampling approach. We calculated the percentage cover of each land use category across the region and placed a representative number of recorders in each category. Due to access issues it was not possible to randomly choose sampling locations in all areas, therefore, to ensure independence among sampling locations, the first recorder in each area was placed by walking 500 m in a random direction and the remaining placed at a minimum of 500 m apart. Where possible, trails were not used to avoid bias, however, where this was not possible, devices were placed a minimum distance of 200 m perpendicular to a trail. Non-audio data were collected for each point including GPS location, elevation and land use, to verify data from NASA land use maps. Given that the majority of biotic sounds do not travel further than 200 m (Figueira et al., 2015), we used a minimum distance of 500 m between recorders to maximise independence between samples and avoiding pseudo-replication. Recording devices were also placed at a minimum distance of 200 m from habitat boundaries, to

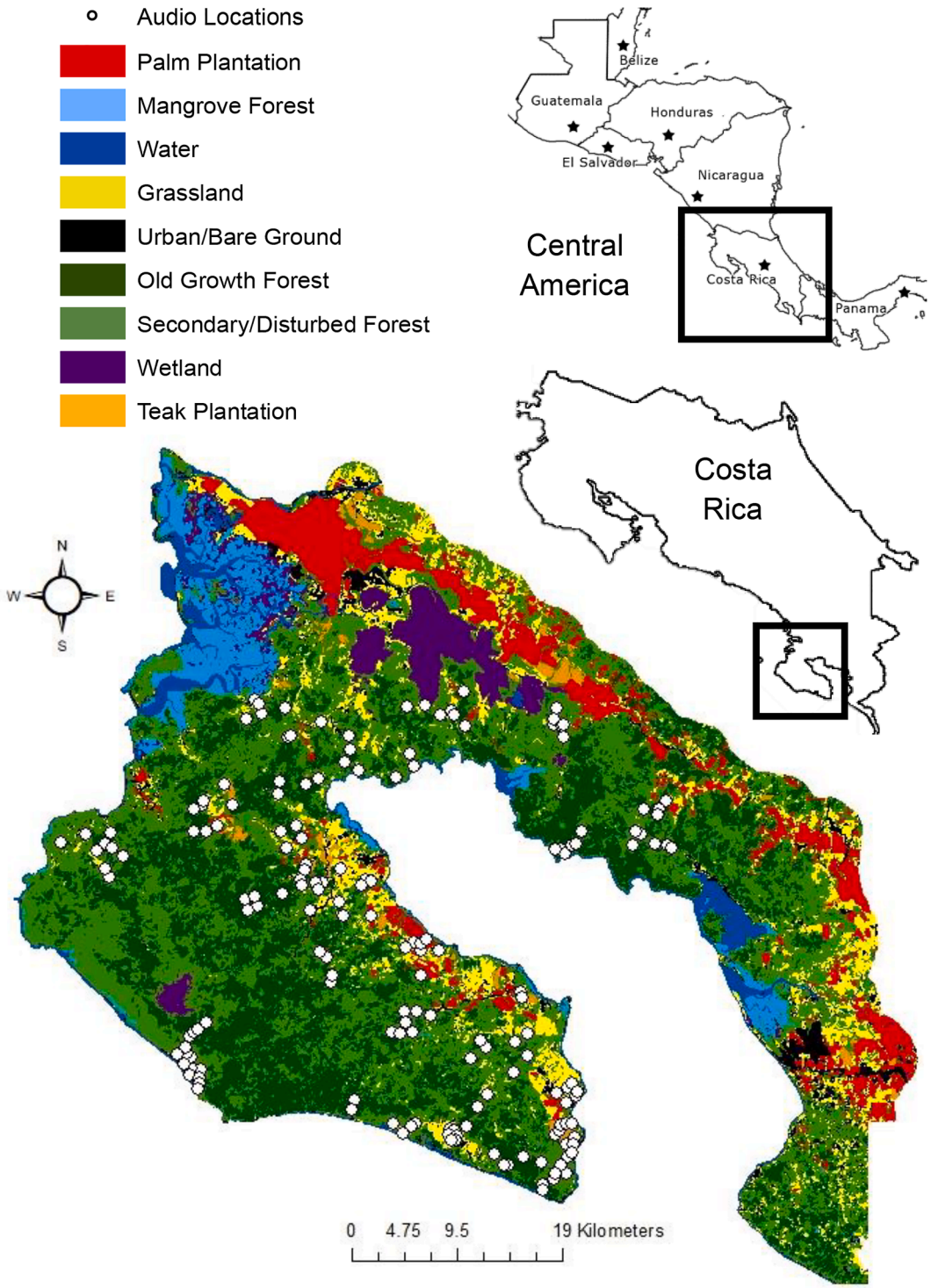

Fig. 1. Shows the nine land use categories, created at a scale of 5 × 5 m using Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) (Shrestha et al., 2018). White circles represent the sample sites where each audio recorder was placed.

ensure sounds were solely from the classified habitat.

Recordings were obtained using Audio Moth devices (Open Acoustics Devices, UK). Recorders ran for seven consecutive days to allow for variability in activity across different days and to allow for sufficient sampling effort. The devices were set to record on a schedule of 05.00–09 30, 14:00–18:30 and 21:00–03:00, a total of 15 h each day. We recorded constantly during these periods at a sample rate of 48 kHz based on best practice guidelines (Bradfer-Lawrence et al., 2019). Sampling was conducted during the dry season (December-August) to avoid extreme seasonal differences, and because of restricted access to many areas of the study site during wet season.

2.3. Acoustic indices

To extract acoustic information from the raw data we used a suite of nine complementary acoustic indices. which, depending on study design, can be used together to provide a comprehensive picture of the soundscape (Towsey, 2017). In combination these indices provide a

Table 1
Description of each acoustic index used, together with the reference to the paper where the indices were first developed and presented.

Index	Measure	Reference
Acoustic Complexity Index (*ACI*)	A spectral index that calculates the difference between two adjacent values of amplitude within a frequency band. It measures fluctuations in amplitude, with larger indicating a more complex and variable environment. Analysis is restricted to the mid frequency bands 1–8 kHz	(Pieretti et al., 2011)
Temporal Entropy	Measures the entropy of energy values of the signal waveform to provide a measure of energy concentration. Analysis is restricted to the mid frequency bands 1–8 kHz	(Towsey, 2017)
Normalised Difference Soundscape Index (NDSI)	This index produces a value between −1 and + 1 based on the distribution of sounds across frequency bins, with a value of + 1 indicating that there are no sounds in the anthrophony range and more sounds being present within the 2–8 kHz frequency bands.	(Kasten et al., 2012)
Events per Second (EVN)	Calculates the number of acoustic events per second above 3 dB	(Towsey, 2017)
Low Frequency Cover (LFC)	The number of spectrogram cells exceeding 3 dB in the low frequency band (1–1000 Hz)	(Towsey, 2017)
Mid Frequency Cover (MFC)	The number of spectrogram cells exceeding 3 dB in the mid frequency band (1000–8000 Hz)	(Towsey, 2017)
High Frequency Cover (HFC)	The number of spectrogram cells exceeding 3 dB in the high frequency band (8000–11025 Hz).	(Towsey, 2017)
Cluster Count (CLS)	Calculates the number of distinct spectral clusters in the mid frequency band. This index measures the amount of internal acoustic structure within the mid frequency band 1–8 kHz.	(Towsey, 2017)
Three Gramm Count (ThreeG)	Derived from calculation of spectral clusters in the mid frequency band and the number of sequences that occur more than once.	(Towsey, 2017)

good representation of the spatial–temporal variation that exists across the soundscape (Towsey, 2017). Additionally, using multiple indices that represent different parts of the soundscape helps to avoid incorrect interpretations that may occur due to competing explanations or sensitivities in different environments for a particular index value (Bradfer-Lawrence et al., 2019). Table 1 briefly describes each index, for a full description of how indices are calculated refer to (Towsey, 2017).

2.4. Statistical analysis

2.4.1. Pre-processing

Geophony is known to inflate the values of some indices and reduce others (Depraetere et al., 2012; Bradfer-Lawrence et al., 2019; Sánchez-Giraldo et al., 2020). We selected 20 sites, five from each land use, and reviewed the response of the indices to geophony in the recordings by simultaneously listening to the recordings and viewing the spectrograms and associated indices. To do this we generated Long Duration False Colour Spectrograms (LDFC Spectrograms) using Analysis Programmes software developed by (Towsey, 2017). This process combines the spectral data from five indices, *ACI*, EVN, *ENT*, BGN and PMN, to visually summarise the content of 24 h of audio recording, allowing sections of geophony, such as rain and wind, to be identified visually (Towsey et al., 2020). It was not possible to remove all wind from the recordings, nor did we want to remove all aspects of geophony, since they are a key component of natural soundscapes (Bradfer-Lawrence et al., 2019), however, we determined that heavy rain inflated values across the NDSI and reduced values across all other indices, similar to the findings of previous studies (Sánchez-Giraldo et al., 2020). Whenever rain obscured other acoustic activity within the spectrogram, these sections were removed. Since recordings across sites were performed on different days, rain had the potential to bias results and was therefore isolated and removed before calculating index values. To do this we used the LDFC spectrograms to determine roughly where rain was located across each 24-hr period and then matched these times to the associated index values to pinpoint the exact time that the index values either increased or decreased. In total approximately 500 h of rain were removed from recordings, mostly from recordings in secondary forests taken at the end of the dry season, leaving over 12,000 h of recordings for analysis.

Migrant birds are present in the area during the North American winter between November and March (Desante et al., 2005). To account for the potential influence of changing avian choruses we included sampling month as a random effect in our models. Time of the day was used as an explanatory variable to understand changes in the soundscape throughout the diel cycle. Using Windows PowerShell 6.0 all data were processed using Analysis Programmes software and a value calculated for each of the nine indices for each 1-minute file (Towsey et al., 2020). We calculated the mean value for each minute across the seven days to give a value per minute per site. The data were then split into 30 categories, each corresponding to a 30-minute period during the 15-hour recording schedule each day. We then calculated a mean value for each 30-minute period during the diel cycle (i.e., each of the 30-minute categories was thus an average across 210 1-minute files). These 30-minute means were then used in the PC analysis.

2.4.2. Principal Component Analysis (PCA)

All statistical analysis were carried out in R 3.6.0. We used PCA to reduce the dimensionality of the nine acoustic indices using the *vegan* package (Oksanen et al., 2019), to find the best summary of the data in the Principal Components (PC's). Eigenvalues were extracted to determine the number of PC's to retain. We retained PC1 and PC2 as together they captured almost 70 % of the cumulative variance and both had eigenvalues of >1 (James et al., 2013).

To determine which combinations of indices are represented across the PC's, we used the loadings values for each index, with higher values indicating a larger effect from the index on that particular PC. PC scores, which represented a mean index value for each 30-minute period across the day per site, were then extracted for use in regression analyses. For a more detailed explanation of PCA analysis please see Supplementary Information (1.1).

2.4.3. Diel cycle and restricted time window analysis

In total we collected 105 h of data per site across the seven days, totalling 12,600 h of acoustic recording, 840 h in teak plantations (eight sites), 3,150 h in both in palm plantations and old growth forests (30 sites), and 5,460 h in secondary forests (52 sites). GAMM's (Generalised Additive Mixed Models) were used to assess how the soundscape varied across the diel cycle between land use type. We conducted two separate GAMM's, using regression values from the first two PCA axis, PC1 and PC2 as the response variables, where we included a smooth term to model time and an interaction term between time and land use to test whether the effect of time was dependent on land use. The variable month, which was included to account for migratory behaviour and variation in sampling season (Desante et al., 2005), reduced model AIC

and significantly improved loglikelihood for PC1, and was therefore added to the final model (SuppInfo 1.2. Table 3).

GAMM's were fitted using a thin plate regression spline smoother chosen for optimum RMSE performance. REML-restricted maximum likelihood method was used for smoothness selection (Wood, 2017) and degree of smooth was tested by fitting different basis functions and assessing fit, both visually, and using AIC. The optimum number of basis functions for PC1 GAMM was 12 ('Gam_k12′). Model AIC decreased for 15 and 20 basis functions ('Gam_k15′, Gam_k20′), but on visual inspection it was confirmed the model was overfitting to biologically irrelevant patterns. Optimum basis functions for PC2 GAMM were nine, as chosen by the mgcv package. Increasing the basis functions to 12, 15 or 20 ('Gam_k12′, 'Gam_k15′, Gam_k20′) did not improve model AIC (SuppInfo 1.2. Table 3) or change the smooth plots. GAMM's were fitted using the *mgcv* package (Wood, 2017). Models were fitted with a Gaussian error structure using an identity link function.

To understand if restriction of the soundscapes to narrower temporal windows obscures differences among habitat types, we used Linear Mixed Models (LMMs) to quantify the differences in PC1 and PC2 between land use types at key times in the diel cycle (i.e., dawn:06:30–07:00, mid-afternoon:14:00–14:30, dusk:16:30–17:00 and night:00:00–00:30). Two models were created for each time period using PC1 and PC2 as response variables. Fixed covariate was land use. We fitted models in the *nlme* (Pinheiro, Bates and DebRoy, 2020) and *lme4* package (Bates, Maechler and Bolker, 2015), assuming a gaussian distribution for normally distributed data. All models were tested for temporal autocorrelation of the residuals using the autocorrelation function (ACF). Temporal autocorrelation was found within GAMM's (SuppInfo 1.2. Fig. 4), therefore a correlation structure was included in the model. We tested three autocorrelation structures, auto-regressive model order-1 (AR-1), continuous auto-regressive (corCAR) and auto-regressive moving average (ARMA) (Pinheiro and Bates, 2000). The best model for both PC1 and PC2 included a corCAR correlation structure, producing time lags below the line of significance (See SuppInfo 1.2. Fig. 4) and improving model AIC and loglikelihood (SuppInfo 1.2., Table 3). ACF plots showed no significant temporal autocorrelation within LMM's across months for PC1 or PC2 (SuppInfo 1.3. Fig. 6). Due to the nested structure in the data we tested for spatial autocorrelation across all models by creating a distanced-based weight matrix using model residuals and sampling site coordinates. Moran's I Statistic and variogram plots indicated that there were no significant spatial autocorrelation in the final models for PC1 or PC2 across GAMM's (SuppInfo 1.2. Table. 4 & Fig. 5) or LMM's (SuppInfo 1.3. Table. 5 & Fig. 7).

Model performance was evaluated using Akaike Information Criteria (AIC) to select the model with the best fit and the likelihood ratio test (LRT) to test for goodness of fit (Zuur et al., 2009). Diagnostic plots for all models indicate model assumptions are met.

3. Results

3.1. Dimensionality reduction

The variable correlation plot shows that most indices are correlated, apart from HFC and NDSI (Fig. 2). The indices represented across PC1 (52.7 % variance) are generally restricted to measuring the soundscape between the mid frequency bands (1–8 kHz), as this is where the majority of biotic sounds occur (Towsey, 2017). The exception to this is the LFC index, which measures the distribution of sounds below 1 kHz, but only has a relatively small effect on PC1. NDSI and HFC index are represented across PC2 (13.7 % variance). The NDSI represents the distribution of sounds in the mid (2–8 kHz) vs lower (1-2khz) frequency bands and the HFC Index represents the sounds in the higher frequency bands

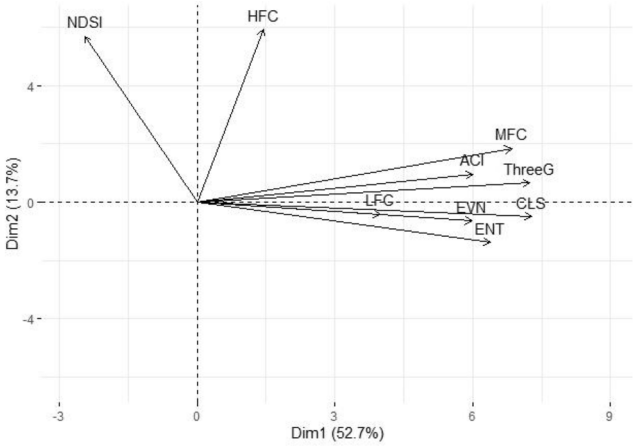

Fig. 2. Variable correlation plot showing the relationship between the indices to the PC's. Closer vectors are more highly correlated, those on opposite quadrants are negatively correlated and indices with longer vectors indicate increased strength on that PC. The x-axis represents PC1, controlled by mid-frequency indices and y-axis PC2, controlled by NDSI and HFC index.

(8–11 kHz). It has been suggested that the majority of anthropogenic sounds occur below 2 kHz, though this varies across soundscapes (Kasten et al., 2012). From this result we can conclude that PC1 can generally be considered a measure of sounds in the mid-frequency bands and PC2 a measurement of the distribution of sounds in the higher and lower-mid frequency bands.

3.2. Changes in PC1 across the diel cycle

PC1 and PC2 changed across the diel cycle, and these changes were significantly different depending on land use. The best models, with time and land use as predictor variables, month as a random effect and a corCAR1 correlation structure, explained a large proportion of the variation in the data across PC1 ($R^2 = 0.498$) and less so across PC2 ($R^2 = 0.195$) (SuppInfo 1.2. Table. 3).

3.2.1. PC1

The relationship between PC1 and time was significant in all habitats ($p < 0.001$), showing that it varied non-linearly throughout the day. However, the diel cycle varied with land use. PC1 varied substantially across the day in forested habitats, with clear dawn and dusk peaks in acoustic activity that are more prominent in old growth and secondary forests. Indeed, effective degrees of freedom (edf) were higher in forested habitats compared with palm and teak plantations, indicating that PC1 was more variable across the day in native forests (Fig. 3 & SuppInfo 1.4. Table 6). An edf score of one is a linear fit and anything over eight is considered to have a strong non-linear pattern (Zuur et al., 2009). Although edf values are similar between old growth and secondary forests, we can see more defined dawn and dusk peaks in old growth forests due to a more pronounced drop in acoustic activity during the day (Fig. 3). Teak plantations showed less distinctive dawn and dusk peaks, partially due to a reduction in acoustic activity (Figs. 3 & 5), but also due to a less pronounced drop in acoustic activity during the day. Palm plantations showed a small increase in the values of PC1 during the day, but with non-existent dawn and dusk peaks of activity (Fig. 3). Whilst it was difficult to determine the onset of the dawn chorus, the peak of activity was earlier in teak plantations, compared to native forests, being at 5:45 instead of 6:30. F-value was also lower in plantations, suggesting a weaker association, and less variance, between time and PC1 (Fig. 3).

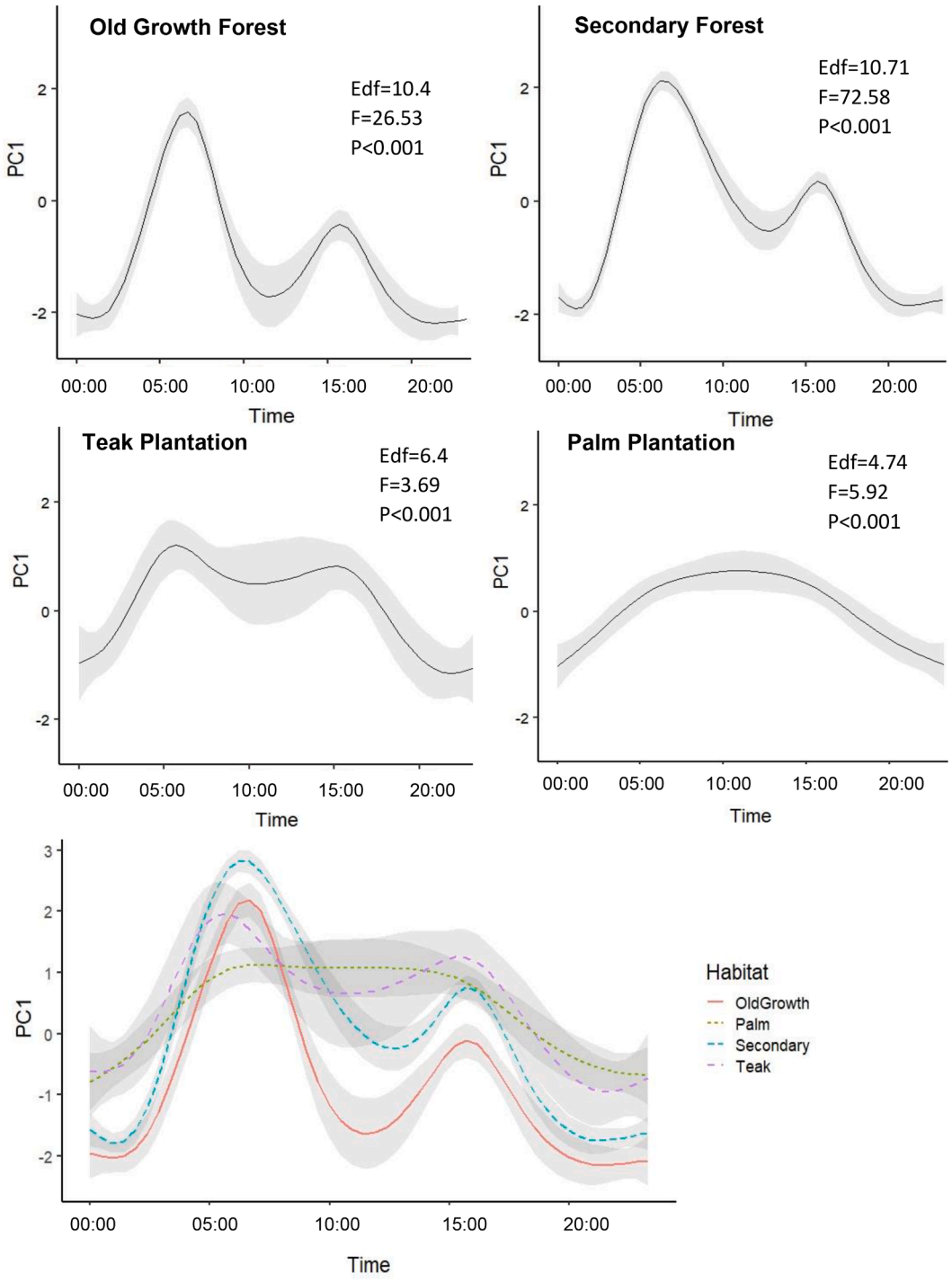

Fig.3. Estimated smoothing curves showing the change in PC1 across the diel cycle in different land uses. Shaded area represents 95% confidence bands. Edf, f and p values for each land use are marked on the plot. The final plot shows all land use types together.

3.2.2. PC2

As mentioned above, PC2 is associated with HFC and NDSI. The raw values for these indices show an increase in HFC in old growth and secondary forests at dawn, with all other habitats remaining stable and a drop in NDSI values in all habitats during the day, with a much more pronounced drop in plantation forests (SuppInfo 1.4. Fig. 8). Edf values were similar across all habitats, indicating similar variation in PC2 across the day (Fig. 4 & SuppInfo 1.4. Table 7). The relationship between PC2 and time is significant in all habitats ($p \leq 0.05$), showing that it varied non-linearly throughout the day. The F-value is lower in native forest habitats, suggesting a weaker association, and less variance, between time and values of PC2, likely due to the strong drop in NDSI in plantation forests (Fig. 4).

We observed a large drop in PC2 values during the day in palm and teak plantations and a slight drop in native forests, likely due to a drop in the NDSI (Fig. 4). This indicates that there is a larger proportion of sounds in the 1–2 kHz frequency bands compared to 2–8 kHz frequency bands plantation forests than in native forests. Plots also highlight an increase in PC2 at dawn in secondary forest, likely due to an increase in the HFC index at this time in this habitat (Fig. 4). This suggests that there are more sounds located in the higher frequency bands (8–11 kHz) in secondary forests at dawn than other habitats.

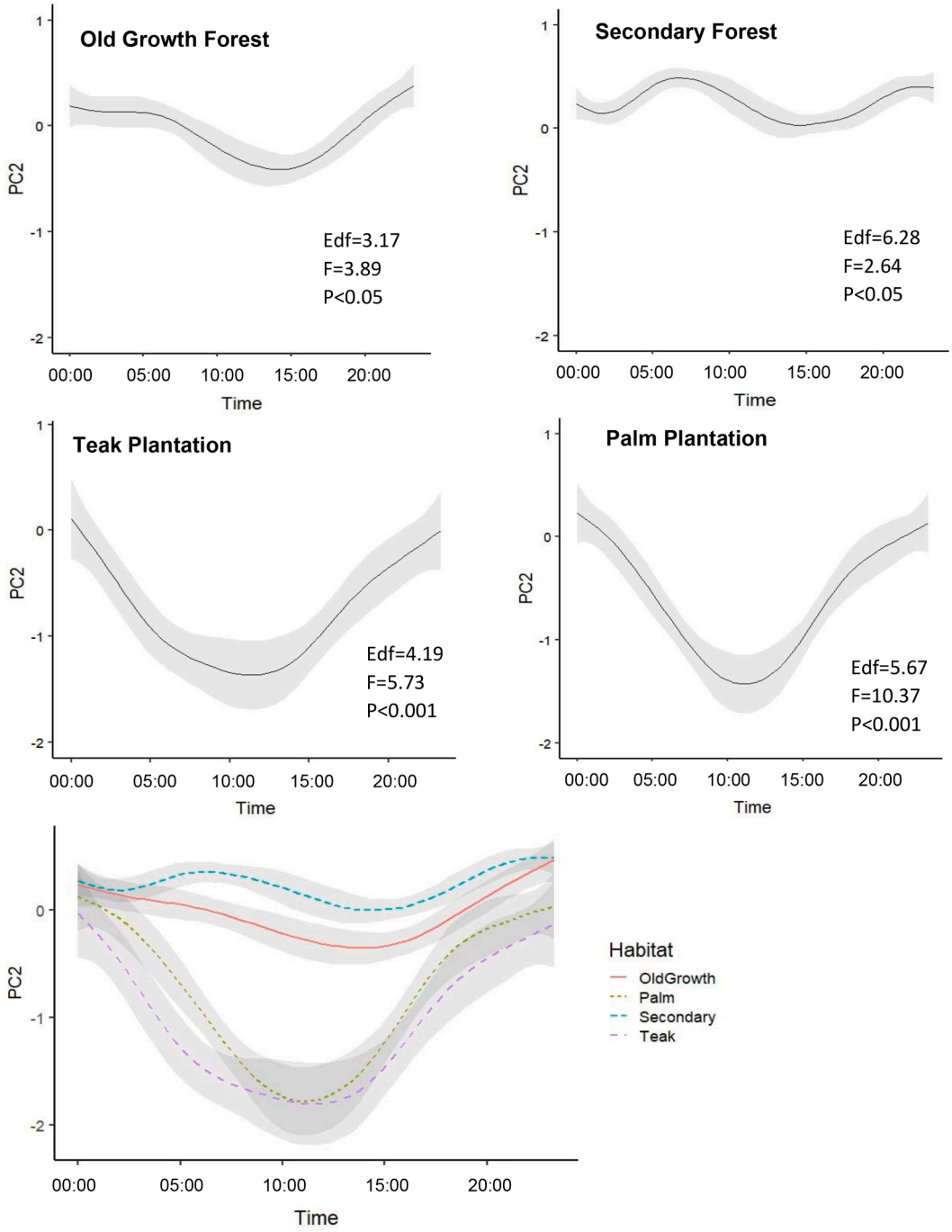

Fig. 4. Estimated smoothing curves showing the change in PC2 across the diel cycle in different land uses. Shaded area represents 95% confidence bands. Edf, f and p values for each land use are marked on the plot. Final plot shows all land use types together.

3.3. Changes in acoustic diversity at key times during the diel cycle

We quantified the differences in PC1 and PC2 between land use types at key times in the diel cycle, namely: dawn:06:30–07:00, mid-afternoon:14:00–14:30, dusk:16:30–17:00 and night:00:00–00:30.

PC1 was higher in old growth and secondary forests at dawn when compared to palm and teak plantations, however this difference was only significant in palm plantations (Fig. 5). During the day and at dusk, the only significant difference was that old growth forests had lower PC1 values at dusk than other land use types (Fig. 5). At night, PC1 was significantly lower in native forests when compared to plantation forestry (Fig. 5).

PC2 was higher in old growth and secondary forests at dawn when compared to palm and teak plantations, however this difference was only significant between secondary forests and plantations (Fig. 5). During the day this difference became stronger and native forests showed significantly higher values of PC2 when compared to plantation forests (Fig. 5). At dusk and during the night PC2 remained similar across habitats (Fig. 5).

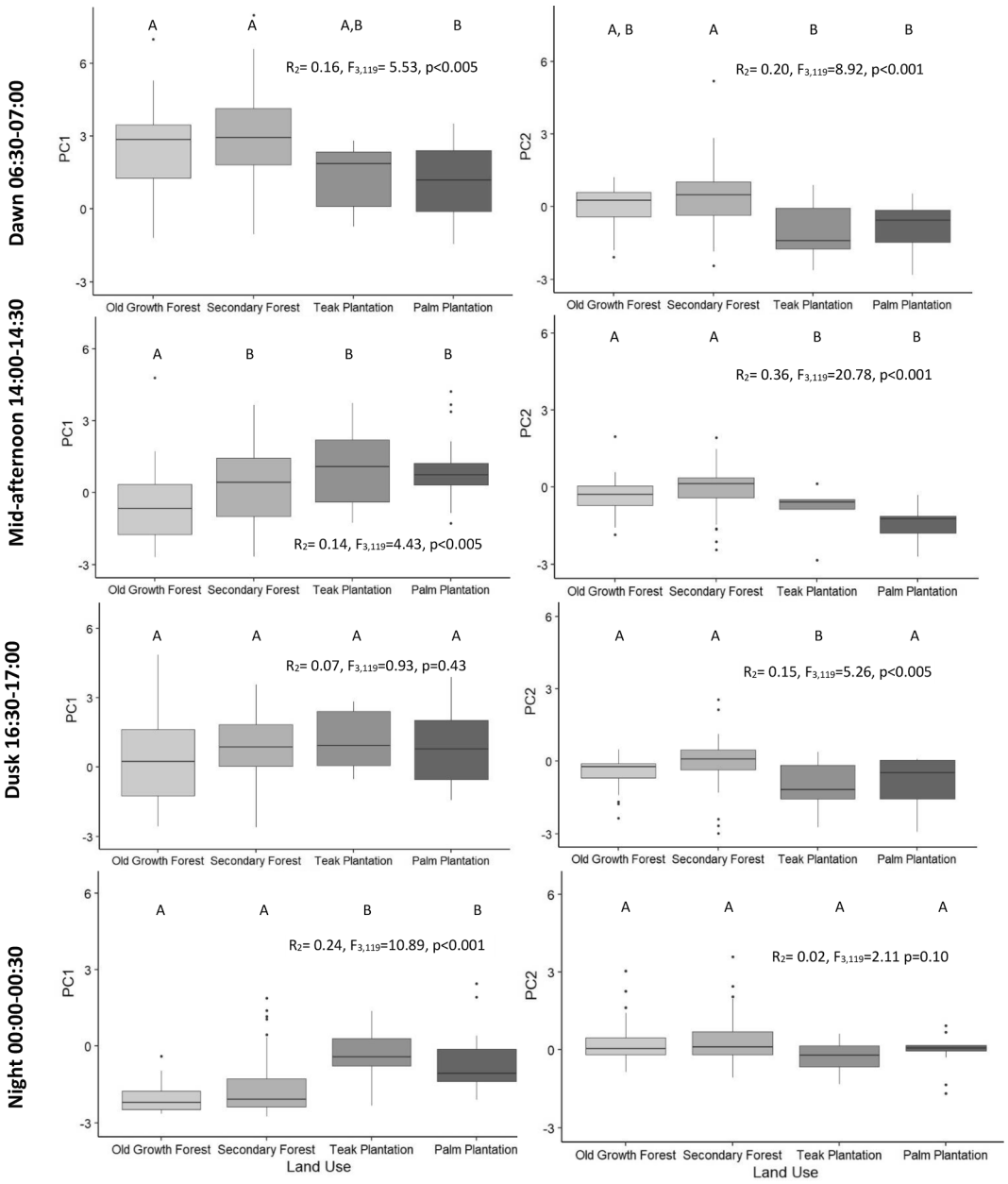

Fig. 5. Boxplots showing the differences in PC1 and PC2 between land use types at key times during the day (dawn: 06:30–07:00, mid-afternoon:14:00–13:30, dusk:16:30–17:00 and night:00:00 00:30). R^2, F and p values for each model are marked on the graphs. Pairwise differences between land use are indicated with letters A and B, where the different letters represent a significant difference between land use.

4. Discussion

By using a soundscape approach across 120 sites, we found that acoustic indices were able to separate sites temporally and by land use. We see distinctive peaks in acoustic activity (PC1) at dawn and dusk in native forest habitats where we would expect a dawn and dusk chorus to be present. Yet in teak plantations, and to some degree in secondary forests, these peaks are less prominent, in part due to diminished acoustic activity in teak plantations, but also due to a less pronounced drop in acoustic activity during the day. In palm plantations dawn and dusk peaks in activity are entirely eliminated. These changes were masked when analysing the data at reduced temporal windows, suggesting that studies not taking the diel cycle into account may be missing important changes both spatially and temporally. Changes in acoustic activity within plantation forests suggest that these habitats are not functioning in the same way as native forest habitats.

4.1. Does acoustic diversity represent changes in biodiversity?

Soundscape studies, by their nature, cannot directly link acoustic index values to changes in species diversity, nonetheless, previous studies have continually demonstrated a strong correlation between acoustic values and measures of species richness, abundance and biomass (Sueur et al., 2008; Joo et al., 2011; Fairbrass et al., 2017; Buxton et al., 2018a; Bradfer-Lawrence et al., 2020; Smith et al., 2020; Dröge et al., 2021; Holgate et al., 2021). However, many studies find contrasting results (Mammides et al., 2017; Ng et al., 2018), and it has been suggested that the reason for this inconsistency is due to lack of a standardised approach across both field and analysis methods (Bradfer-Lawrence et al., 2019; Sugai et al., 2019), combined with the inherent differences that exist among landscapes (Bradfer-Lawrence et al., 2019; Gibb et al., 2019). Indeed, most soundscape studies to date have only analysed data at specific points during the day, not taking the diel cycle

into account. Here we have shown that if we had compared data from certain times of the day, we would have missed key changes in the soundscape that have occurred in disturbed land use types (Fig. 5). In fact, our results show that PC1 values were lower in old growth compared to non-native habitats in the afternoon and at night, showing that the actual values of acoustic activity are highly context-dependant. We propose that future soundscape studies utilise the breadth of the diel cycle, which may prevent changes in diversity being missed and go some way to providing consistency across the field.

4.2. Changes in patterns of acoustic activity

In our study we found that PC1, which represents acoustic activity in the mid-frequency bands where the majority of biotic sounds are thought to be present, shows clear dawn and dusk peaks in acoustic activity in native forests. Firstly, we can see that the soundscape in secondary forests is quitesimilar to old growth forests, suggesting that these two habitats are similar and highlighting the value of secondary forests in regenerating landscapes as previously found in other studies (Dent and Joseph Wright, 2009; Matos et al., 2020). Despite these similarities there is a more prominent drop in acoustic activity during the day in old growth forests when compared to secondary forests, suggesting that there are some differences in the soundscape between these habitats. It is worth noting that secondary forests in this study were classified as forests of 40 years+ and that differences between old growth and secondary forests will depend on the age and structure of secondary forests, which can vary greatly in age and composition. Whilst teak plantations retained some of the characteristic dawn and dusk peaks, the variation in acoustic activity was much less prominent due to reduced acoustic activity at dawn and a less pronounced drop in acoustic activity during the day, and palm plantations lost all evidence of a dawn and dusk chorus. This suggests that teak plantations share a more similar soundscape to native forests sites than do palm plantations. This finding agrees with traditional biodiversity studies that show native forests to be most structurally complex and to hold the highest bird diversity, followed by teak plantations and finally oil palm, which has consistently been found to be the least structurally complex habitat and hold the poorest bird diversity (Mandal and Raman, 2016; Bennett et al., 2018). Although a different set of forestry plantations were studied, our results agree with those of Burivalova et al., (2018), where areas with higher human disturbance, such as cacao plantations, showed less acoustic activity during the dawn and dusk chorus.

As a result, it is plausible that there are changes in species diversity, composition or acoustic behaviour in palm and teak plantations where we see little or no evidence of a dawn or dusk chorus. This would agree with previous soundscape studies that have demonstrated reduced species diversity in areas of reduced forest quality (Sueur et al., 2008; Tucker et al., 2014), in rice paddies and pasture (Dröge et al., 2021), in forests with less complex vegetation structure (Hao et al., 2021) and in logged forests (Burivalova et al., 2021). But it is crucial to stress that this interpretation from our results can only arise because we showed the diel cycle pattern varying across habitats, rather than because the acoustic indices were generally greater in native forests than in plantations.

The drop in PC2 during the day seen in plantation forests suggests a larger amount of energy in the lower frequency bands compared to the mid frequency bands. This could be linked to the observed decreases in PC1 or an increase in biotic or abiotic sounds in these lower frequency bands. Considering the observed increase in human presence in these forests and the natural changes in geophony resulting from changes in vegetation structure in forestry plantations, it is plausible that both geophony and anthrophony are affecting this result, however the direction and magnitude of these effects remain understudied (Towsey et al., 2014; Sánchez-Giraldo et al., 2020).

Our results showed that the peak in acoustic index values at dawn was earlier in teak plantations, compared to native forests. Research suggests that both increased light (Berg et al., 2006; Da Silva et al., 2016; Da Silva and Kempenaers, 2017) and anthropogenic sound (Arroyo-Solís et al., 2013; Dorado-Correa, Rodríguez-Rocha and Brumm, 2016) can cause earlier onset of the dawn chorus as birds try to maximise their signal transmission. If anthropogenic sound or altered abiotic conditions resulting from changes in vegetation structure are affecting the acoustic space in plantations, impairing or changing acoustic behaviour, it is possible that this will reduce population fitness, since communication ability is directly linked to species survival (Kleyn et al., 2021), and has been found to interfere with mating, egg laying, provision of young and fledging success (Halfwerk et al., 2011; Schroeder et al., 2012).

4.3. Conservation and management implications

This study has shown that conversion of native forests in the tropics into forestry plantations causes changes in the soundscape across the day, most notably causing a suppression or loss of acoustic activity during the dawn and dusk chorus. The different patterns of acoustic activity throughout the day in plantation forestry, and indeed in secondary forests, could signal loss or change in species diversity or composition, reinforcing the importance of old growth native forests for biodiversity (Gibson et al., 2011). Future work should focus on ground truthing the data to better understand what taxa and species are driving these changes across the diel cycle.

4.4. Statement of inclusion

This research has been in collaboration with stakeholders in the region from the outset. We have worked closely with a local NGO in the region, Osa Conservation, who's director is a co-author on the paper. We have regularly discussed the research with staff of the Ministry of Environment and Energy (Ministerio de Ambiente y Energia) (MINAE) and have received both administrative and field support from this department, which was financially compensated. All results will be made available in an appropriate format for their use.

CRediT authorship contribution statement

Jenna Lawson: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Visualization. **Cristina Banks-Leite:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Andrew Whitworth:** Funding acquisition, Resources, Supervision, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109413.

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