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Loss of temporal structure of tropical soundscapes with intensifying land use in Borneo

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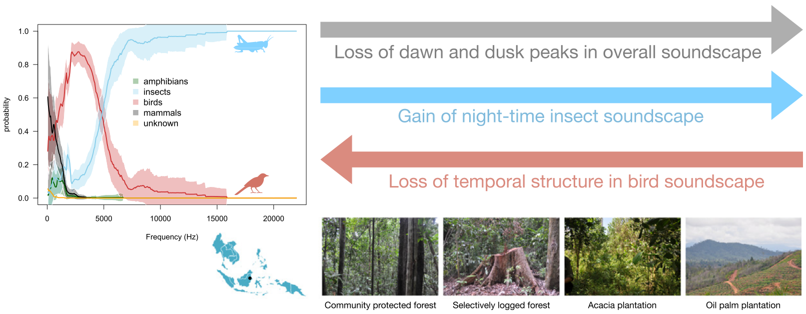
HIGHLIGHTS

- We develop a method to divide rainforest soundscape to broad taxonomic groups.
- With intensifying land use, soundscapes lose dawn and dusk peaks.
- Bird acoustic communities lose recurrent diurnal patterns in soundscapes.
- Insect soundscape saturation increases at night in disturbed forests.
- Conservation projects can use the indicators of intact soundscapes for monitoring.

GRAPHICAL ABSTRACT

Partitioning soundscape to broad taxonomic groups reveals changes due to land use



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ABSTRACT

Conservation and sustainable management efforts in tropical forests often lack reliable, effective, and easily-communicated ways to measure the biodiversity status of a protected or managed landscape. The sounds that many tropical species make can be recorded by pre-programmed devices and analysed to yield measures of biodiversity. Interpreting the resulting soundscapes has developed along two paths: analysing the whole soundscape using acoustic indices, used as a proxy of biodiversity, or focusing on individual species that can be either manually or automatically recognized from the soundscape. Here we develop an intermediate approach to divide the soundscape into frequency categories belonging to broad taxonomic groups of vocalizing animals. While the method was unable to distinguish between amphibian and mammal communities, it was successful in assigning parts of the soundscape as likely produced by birds and insects. Applying the approach in Borneo revealed that, with increasing land use intensity, *i)* the spectral saturation of the soundscape, a proxy of species richness, loses dawn and dusk peaks, *ii)* bird acoustic communities lose recurrent diurnal patterns, becoming less synchronized across sites, and that *iii)* insect Soundscape Saturation increases at night. If soundscapes are partitioned similarly in different regions, our method could be used to bridge soundscape-level and individual-species level analyses. Regaining dawn and dusk peaks, the synchrony of bird acoustic communities, and losing nocturnal dominance of insect could be used as a set of simple indicators of tropical forest retaining high levels of biodiversity.

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1. Introduction

Many countries with tropical forests are undergoing rapid shifts in land use, with profound consequences for the biodiversity within the changing landscapes, leading to local or even global extinctions of species (Betts et al., 2017; Curtis et al., 2018; Lambin et al., 2001). Understanding the impacts of land use change on biodiversity is a central enquiry of conservation biology (Bregman et al., 2014; Gibson et al., 2011; Koh et al., 2010). This knowledge is needed to inform decision makers about the likely consequences of land use change, and to outline alternative scenarios that might prevent large losses of biodiversity (Griscom et al., 2018; Phalan et al., 2011).

At the same time, countries and companies are implementing various conservation and sustainable management efforts to minimize losses of biodiversity (Burivalova et al., 2019a). Such efforts often require case-specific biodiversity monitoring to track and demonstrate success, or adapt management (Gillson et al., 2019). For example, a logging company needs to periodically prove that it is managing its forestry concession according to certain standards, in order to maintain its sustainability certification (Romero et al., 2015). Similarly, ecosystem restoration projects should be able to demonstrate their actual effect on biodiversity, rather than simply a predicted gain from modelling studies or meta-analyses (Fidelino et al., 2020; Helms et al., 2018).

Land use change and conservation affects species richness and community composition through altering demographic processes (i.e. birth, death, immigration, emigration) that are costly to monitor, especially when considering multiple taxonomic groups and when monitoring needs to be done periodically (Barlow et al., 2007; Burivalova et al., 2019b; de Castro Solar et al., 2015; Edwards et al., 2011). The recording and analysis of soundscapes - the sounds that result from acoustic communities within a landscape – is revolutionizing such case-by-case biodiversity monitoring (Farina, 2014; Sueur and Farina, 2015). This is particularly pertinent in tropical forest, where visibility is low and many vertebrate and invertebrate species make sounds (Campos-Cerqueira et al., 2019; Darras et al., 2018; Furumo and Mitchell Aide, 2019; Rappaport et al., 2020).

Currently, the analysis of soundscapes progresses in two principal directions: *i)* identification of selected individual species within the wider soundscape, either manually, through various templates or machine learning tools (Kahl et al., 2021; Stowell et al., 2018; Stowell and Plumbley, 2014; Towsey et al., 2012), and *ii)* characterization of a soundscape with the use of various soundscape indices, which are mostly agnostic about the sounds' sources (Buxton et al., 2018; Furumo and Mitchell Aide, 2019; Phillips et al., 2018; Sethi et al., 2020). Individual species recognition in tropical forests is more challenging than in many other habitats due to a large number of vocalizing species, many of which are poorly known or rare; continuous, overlapping insect sounds; and a dense vegetation structure that causes fast and non-uniform sound attenuation (Darras et al., 2016; Sun et al., 2021). Likewise, even though the use of soundscape indices in rainforests is promising, it yields little insight about the composition of the vocalizing biodiversity, as one index value typically describes a property of the whole soundscape (Bradfer-Lawrence et al., 2019).

We propose a method that bridges the species- and soundscape-level approaches, with the goal of yielding complementary insights at the level of broad taxonomic groups (amphibians, mammals, insects, birds). One of the four major hypotheses that proposes to explain patterns in a soundscape (Farina, 2014), the Morphological Adaptation Hypothesis (MAH), posits that species are limited in terms of the frequency they create by the size of the sound making structure (Neville, 2014). We therefore attempt to partition the soundscape to major taxonomic groups, based on the hypothesis that different taxonomic groups vocalize at different frequencies. Other major acoustic hypotheses, such as the Acoustic Adaptation Hypothesis, the Acoustic Niche Hypothesis, and the Species Recognition Hypothesis may better explain the soundscape partitioning *within* broad taxonomic groups, i.e. between species or related genera (Farina, 2014; Grant and Grant, 2010; Robert et al., 2019).

We apply our new soundscape partitioning approach to an existing soundscape dataset from an Indonesian forest and production landscape, and investigate whether different land uses alter the taxonomic soundscape components. We analyse soundscapes across a land use intensity gradient from intact protected forest, selectively logged forest, to clear cutting for monoculture plantations for two different kinds of crops.

2. Method

We used two existing datasets for our study (1 - raw soundscapes and 2 - soundscape annotations); both generated from the same lowland tropical forest landscape in Berau and East Kutai Regencies, in East Kalimantan, Indonesia.

2.1. Raw soundscapes

We analysed soundscapes from a previously published dataset collected between July and August 2016 in the Berau and East Kutai Regencies, in East Kalimantan, Indonesia (Purnomo et al., 2019). We used soundscapes collected at 84 sites (Fig. S1), across the following land use types: *i)* community protected forest (Hutan Lindung Wehea), which was a 38,000 ha large fully forested area, protected from 2004 by the local community. Parts of the protected forest had been selectively logged 15–20 years prior to data collection (Lhota et al., 2012). Throughout the forest, species typical of Kalimantan's lowland dipterocarp and montane tropical forests were present, such as the orangutan (*Pongo pygmaeus*), the Müller's gibbon (*Hylobates muelleri*), the great argus (*Argusianus argus*), or the rhinoceros hornbill (*Buceros rhinoceros*). This protected area was adjacent to *ii)* a selectively logged forest with Forest Stewardship Council (FSC) certification; and *iii)* a selectively logged forest working towards obtaining FSC certification. Both selective logging concessions extracted a similar set of tree species for timber at similar logging intensities (details in (Burivalova et al., 2019c)) and have other human uses, such as hunting and the collection of non-timber forest products. The second concession also had artisanal gold mining in its rivers using pumps, which are a substantial source of anthropogenic sound. For this analysis, we selected sites that had already been selectively logged twice (once in the last 1–3 years and once 31–34 years prior to data collection). The FSC certified selective logging concession was adjacent to *iv)* a monoculture oil palm plantation that had been cleared and planted 1–5 years ago; therefore, our sample does not include fully mature oil palm plantation with a closed canopy. The plantation harboured a limited diversity of vertebrates, with generalist bird species (yellow-vented bulbul, *Pycnonotus goiavier*) and some mammals (including *P. pygmaeus*) visiting from the nearby forest. Oil palm monoculture plantations in Southeast Asia have been found to have <15 % of species found in intact forests (Fitzherbert et al., 2008). Finally, *v)* not contiguous with the rest of the landscape, we included the soundscapes of a monoculture Acacia plantation ~100 km further north east, with sites cleared and planted 0–5 years ago. The Acacia plantation's biodiversity included generalist species such as oriental magpie robbin (*Copsychus saularis*), and southern pig-tailed macaque (*Macaca nemestrina*). Each land use type had at least 7 sites, at which soundscapes were recorded continuously for at least 48 h. The acoustic sampling was staggered over several weeks due to a limited number of recorders, meaning that not all sites overlapped in their recordings, however, the duration of the overall sampling period was short enough to rule out major seasonal effects. Weather-related changes in ambient sounds could nevertheless affect sites in different ways, and this is a limitation of our study (Farina et al., 2021).

2.2. Annotated soundscapes

The second dataset we used comprised 2780 sound annotations within 63 independent, exhaustively annotated minutes of passively recorded soundscapes from the same FSC-certified logging concession in East Kalimantan (Sun et al., 2021). The soundscapes for this dataset were recorded between June 2018 and July 2019 with the same devices, with identical settings and deployment techniques as for the raw soundscapes dataset (Burivalova et al., 2019c). The 63 min for annotation were randomly selected from a set of recordings collected at 15 sites within the logging concession, such that some sites were in areas that had never been logged before, and some at sites that had been previously selectively logged. At two sites, the same one-minute segment was randomly selected (using a random number generator in the program R, which yielded the numbers 8 and −4) within each of the two highest soundscape activity periods (Burivalova et al., 2019c): dawn (minute 8 after sunrise); and dusk (minute 4 before sunset), once a month, resulting in 48 min in total. Additionally, the same dawn minute (8 min after sunrise) was selected during one day across all 15 sites (15 min in total).

To create annotations, the analyst (TMM) manually examined the selected minutes using Raven Pro 1.6 (Center for Conservation Bioacoustics, 2019) and annotated all biophonies (sound produced by fauna), based on auditory and spectrum features (Sun et al., 2021). Adopting the definition of a sonotype or acoustic morphospecies as "[…] a note or series of notes that constitute a unique acoustic signal" (Aide et al., 2017), the analyst created selection boxes around each sound (here, we are using the word sound for any biophony), tracking as closely as possible the minimum and maximum frequency and the beginning and end of each sound. When repeating sounds were spaced by >2 s, separate selection boxes were created for each part, and labeled as the same sonotype. For sonotypes with continuous acoustic signals encompassing the entire sampling minute, a single selection box was created. Each sonotype was classified as likely produced by a bird, amphibian, insect, or mammal. Anthropophony and geophony were also labeled for all the sampled minutes. When the analyst was uncertain about a sonotype's group, three other specialists were consulted (P, TB, ZB) and consensus achieved. Sonotypes that could not be assigned to a category were classified as unknown.

2.3. Analyses

2.3.1. Signal processing

On the raw soundscape dataset, we calculated the soundscape index Power Minus Noise (PMN), following the methods described by Truskinger et al. (2014). The PMN acoustic index dataset has 256 values of acoustic maximum Power Minus Noise per minute, and can be thought of as a matrix with 1440 columns, representing minutes of the day, and 256 rows, representing frequency bins (Fig. S2). From PMN, we then calculated the summary index Soundscape Saturation, with a threshold of 1 dB, described in Burivalova et al. (2019a) and summarize here. The Soundscape Saturation index 'collapses' the PMN matrix to a single row (1 value per minute), which indicates the percentage of frequency bins that exceeded the 1 dB threshold (Fig. S2). Soundscape Saturation is positively correlated with the number of sonotypes per minute in our study area, as well as other tropical landscapes (Burivalova et al., 2019c; Gottesman et al., 2021; Zwerts et al., 2022).

2.3.2. Frequency probabilities from annotations

First, we tested whether mean frequencies of the annotated sounds ($n = 2780$, of which 114 were mammal, 1447 bird, 66 amphibian, 1002 insect, and 4 unknown sounds) differed between taxonomic groups, using an analysis of variance, and a post hoc pairwise test with Bonferroni correction. Then, we calculated the probabilities of each taxonomic group vocalizing at a given frequency, as follows. Using the minimum and maximum frequencies of all labeled sounds, we created a table with binary values (0, 1) for each frequency bin (43.1 Hz each, to match bin size for PMN calculation) and each sound (Fig. S2). The value of 1 signifies that a given frequency bin falls within the frequency range of the given vocalization. For example, a vocalization with a minimum and maximum frequency of 112 Hz and 168 Hz would receive the following bin values: 0–43 Hz: 0; 44–87 Hz: 0; 88–135 Hz: 1; etc.

Next, for each frequency bin, summing across all vocalizations, we calculated two probabilities: *i)* the probability that a given taxonomic group makes sound at a given frequency (area under curve = 1 for each taxonomic group); and *ii)* the probability that a vocalization at a given frequency bin was made by a given taxonomic group (probabilities of all taxonomic groups for a given frequency add up to 1). The first calculation is not affected by how commonly the different taxonomic groups make sound, whereas the second calculation is. For example, if for the 0–43 Hz bin there were a total of 100 vocalizations, of which 50 were mammals, 10 birds, and 40 amphibians, we assigned probabilities of 0.5, 0.1, and 0.4 to each of the taxonomic group, respectively (Fig. S2). To understand the influence of sampling, we bootstrapped the second calculation 10,000 times, each time randomly selecting 100 annotated sounds from our dataset. We plotted the mean plus or minus one standard deviation at each frequency.

2.3.3. Partitioning the soundscape dataset

We used our results on frequency probabilities generated from annotations (3.2) to divide soundscapes from our 84 sites into parts of soundscapes most likely produced by insects and birds, as follows (Fig. S2). First, because of the largely overlapping frequency distributions for amphibians, mammals, and anthropogenic sound (see Results for details), we pooled these groups together, under the term "remaining soundscape". For each minute and each of the 256 frequency bins whose PMN value crossed our threshold of 1 dB, we divided its value of 1 in matrix (Fig. S2) into three parts – insects, birds, remainder – according to the probability of each taxonomic group vocalizing at a given frequency. For example, at site 1, during the minute from 6:00 to 6:01, the PMN value at the frequency bin 2500–2543 Hz was 3 dB. This is higher than our threshold of 1 dB, therefore this frequency bin got the value of 1 in the matrix (Fig. S2). From frequency probabilities generated in Section 2.3.2, we know that at this frequency, a sound has a 0.6 probability of being produced by a bird, and 0.4 probability of being produced by an insect. Therefore, this frequency bin and minute got a value of 0.6 for bird soundscape, and 0.4 for insect soundscape (Fig. S2). Next, for each minute, we summed the values for birds, and divided by the number of frequency bins (256), yielding 1 value per minute, corresponding to the percentage of the soundscape that is likely saturated with bird sounds. We proceeded in the same way for insects, and for the remainder of the soundscape.

Whereas during the manual annotations, the entire recorded frequency spectrum was annotated (0–22,050 Hz), we calculated the acoustic index PMN only for 0–11,025 Hz. Therefore, to apply the taxonomic probabilities to the soundscape index, we only used sonotypes with $f_{min} < 11{,}025$ Hz.

2.3.4. Differences in Soundscape Saturation between land use types

We estimated the difference in overall Soundscape Saturation, and in its components, between land use types, by carrying out an analysis of variance of daily mean values per site (Mean Soundscape Saturation ~ Land use type). Next, to visualize the diurnal trends in bird and insect soundscapes across the different land use types, we plotted the residuals of Soundscape Saturation for each minute of the day.

Finally, we wanted to quantify to what extent these diurnal patterns may be affected by different land uses. To this end, we calculated the synchrony of soundscapes at different sites within the same land use. The calculation of synchrony is typically used in community ecology to estimate whether the abundance of different species within a community rises and falls simultaneously (Gouhier and Guichard, 2014). We applied this analysis to the overall Soundscape Saturation, as well as separately to bird and insect Soundscape Saturation. Specifically, we calculated the correlation and its statistical significance via Loreau and de Mazancourt's ϕ and Monte Carlo randomizations between the time series of the Soundscape Saturation values at different sites within each land use type, by using the R package Synchrony (Gouhier and Guichard, 2014). Values range from 1, which signifies perfect synchrony, and $1/S$, signifying random fluctuations, where S is the number of sites. Since our land use types had different numbers of sites (Fig. S1), we standardized the results so that $1/S$ corresponds to 0.

3. Results

The four broad taxonomic groups in our dataset made sounds at different frequencies (Adj. R-squared = 0.49, p < 0.0001, Fig. 1), whereby each group differed from all other groups (p = 0.035 for mammals versus amphibians, p < 0.0001 for remaining pairs in a post-hoc pairwise test, using Bonferroni correction). Mammals had the lowest mean frequencies, followed by amphibians, birds, and insects (Fig. 1). Mammals and amphibians had, collectively as taxonomic groups, narrow and largely overlapping acoustic niches (Fig. 2A). Most bird vocalizations occurred around 2500 Hz, and insect sounds spanned the whole human audible range (Fig. 2A). Taking the abundance of different sonotypes into account, the lowest part of the frequency spectrum was dominated by mammals, until ~1 kHz, beyond which mammals and birds were equally common, with some insect and amphibian sounds (Fig. 2B). From ~2 to 5 kHz, the frequency spectrum was dominated by bird vocalizations, above which insects were the most common.

Applying the results on frequency distributions of the different taxonomic groups (Fig. S2), we divided the soundscapes of 84 sites across 5 land use types into Soundscape Saturation likely due to birds, saturation likely due to insects, and the remainder of the saturation (<0.8 kHz), which was likely due to any taxonomic group and human sound (Fig. S2). Average daily Soundscape Saturation differed between land use types, but had low explanatory power (p = 0.007, adj. R-squared = 0.12, F = 3.8, Fig. 3A). Average daily bird Soundscape Saturation did not differ between land use types (p = 0.14, adj. R-squared = 0.03, F = 1.8, Fig. 3A), whereas land use types explained a moderate amount of variance in mean daily insect Soundscape Saturation (p < 0.00001, adj. R-squared = 0.31, F = 10.6, Fig. 3A).

Throughout the day, total Soundscape Saturation was the most synchronized across protected forest sites, and the least synchronized across oil palm and acacia plantations (Fig. 3B). This trend was stronger when considering bird Soundscape Saturation: in protected and logged forests, bird saturation was more synchronized than overall saturation, whereas in plantations, bird saturation was less synchronized than the overall saturation. Insect Soundscape Saturation had the lowest synchrony in protected forest. In both types of monoculture plantation, synchrony was higher in terms of insect saturation than in terms of birds (Fig. 3B).

In natural forests (protected and selectively logged, Fig. 4A–C, Fig. S3A–C), bird and insect saturation had two peaks – one at 6:00 and one shortly after 18:00. These peaks were smaller in selectively logged sites that were not certified compared to protected and certified forests, and absent in the monoculture plantations, with the exception of a 6:00 peak in bird saturation in acacia plantations (Fig. 4D–E, Fig. S3D–E). Protected forests had a lower bird and insect Soundscape Saturation during the night compared to daytime (Fig. 4A, Fig. S3A). In selectively logged forests, this was also the case for birds, however, insect Soundscape Saturation showed the opposite trend: it was higher at night than during the day (Fig. 4B–C, Fig. S3B–C). In both types of monoculture plantation, bird Soundscape Saturation did not show a clear diurnal trend, and insect saturation was generally higher at night than during the day (Fig. 4D–E, Fig. S3D–E).

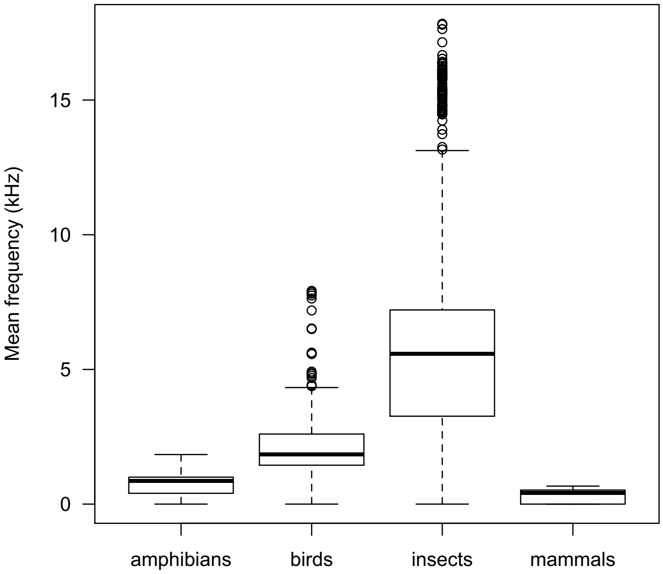

Fig. 1. Mean frequencies of sounds made by four broad taxonomic groups. Bars represent the median, whiskers 95th quantile. All groups were significantly different from each other based on post hoc pairwise comparison with Bonferroni correction.

4. Discussion

4.1. Partitioning soundscape based on frequency

Our frequency-based method can partially address the separation of bird and insect soundscape components. Whereas there is some overlap in the frequency niches of these taxonomic groups, particularly around 5 kHz (Fig. 2B), a large proportion of the frequency spectrum could be assigned to predominantly birds or insects. Above 10 kHz, >90 % of sounds in our dataset were insect sounds (Fig. 2B). An important limitation is that our dataset did not contain possible bat echolocating calls, which in our study area mostly occur above 22 kHz (Yoh et al., 2022).

Such broad separation, due likely to the large differences in the body size of the two groups as well different sound-making structures (Neville, 2014), can be useful in tropical forest biodiversity monitoring. Separate soundscape metrics for insects and birds could be used as an indicator of the state of forest biodiversity, such as degree of degradation caused by selective logging, or the progress towards a mature forest community in restoration projects (Bicknell et al., 2014; Burivalova et al., 2019b; Chaudhary et al., 2016; Helms et al., 2018; Hua et al., 2016).

4.2. Dawn and dusk peaks in natural forests

We found that the first hallmark of a natural forest soundscape was the presence of two peaks in the overall Soundscape Saturation, corresponding to the dawn and dusk chorus – periods of heightened bird vocalizing activity (Figs. 3–4). This corroborates previous findings from Papua New Guinea, whereby continuous forests had the dawn and dusk peaks and fragmented forests lost both (Burivalova et al., 2018). In this study, we build on this knowledge by showing that these peaks are due to both bird and insect Soundscape Saturation, and that these respond differentially to land use change (Fig. 4). The avian dawn chorus, and to a lesser extent the dusk chorus, are well known and documented in the scientific literature, in tropical, temperate and Mediterranean environments (Bruni et al., 2014; Farina et al., 2015; Gil and Llusia, 2020). Nevertheless, the question about what drives the dawn chorus has not been fully resolved, with many hypotheses, ranging from circadian hormonal changes to inter-specific competition, receiving variable support (Berg et al., 2006; Farina et al., 2015; Gil and Llusia, 2020; Kacelnik and Krebs, 1982).

Theoretically, the loss of the peaks could be driven by *i)* shifts in the timing of birds' vocalizations (behaviour shift), *ii)* population decline of species that vocalize during the dawn and dusk (local extinction), or *iii)* by reduced vocal activity (per capita vocalization decline). A shift in the timing of the peaks could occur if the original time of the dawn chorus became more dangerous due to human presence, if it incurred higher visibility by predators in a more open habitat, such as after selective logging, or due to anthropogenic sound interfering with signal transmission (Hua and Sieving, 2016). Existing literature shows mixed results on shifts in dawn chorus timing due to human disturbance. For example, in the neotropics, the timing of the first vocalization was not found to be affected by light pollution or urbanization (Marín-Gómez and MacGregor-Fors, 2019), but another study found that air traffic sound advanced the onset of dawn signing (Arroyo-Solís et al., 2013; Gil et al., 2015). At our study site, we did not observe a shift in the timing of dawn and dusk peak as a

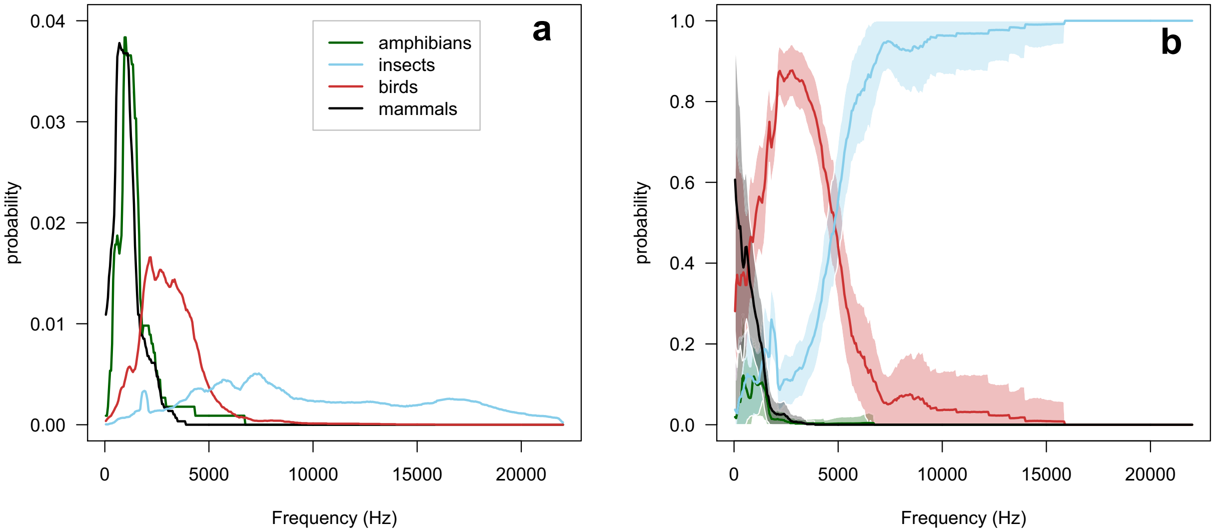

Fig. 2. Probabilities of sounds by four broad taxonomic groups at different frequencies. (a) Probability that a given taxonomic group makes sounds at a given frequency. The area under each curve adds to 1, i.e. the probabilities are independent of how frequent vocalizations by e.g. amphibians were compared to birds. (b) Probability that a sound at a given frequency emanates from a given taxonomic group. At any given frequency, probabilities for the four taxonomic groups add to 1.

consequence of human activity (Fig. 4). This maybe be because logging activity typically begins at least an hour after the dawn chorus, nevertheless, the road sound from plantation activity is common throughout the whole day.

It is well documented that selective logging affects bird species richness and abundance, including decreases in the abundance of some species and increases in others (Burivalova et al., 2014, 2015; Newbold et al., 2013), and that intense land uses including oil palm and acacia plantations result in sharp declines of bird species richness (Gibson et al., 2011). Population decline may therefore be a more likely cause for the loss of the dawn and dusk peaks in Soundscape Saturation. Interestingly, a lower density of a given species may result into lower per capita singing rate, due to a diminished need to defend territory (Goretskaia, 2004; Laiolo and Tella, 2008; Pillay et al., 2019). In Malaysia, selective logging altered the vocalizing behaviour of approximately half of the song bird species studied: for these species, when occupancy decreased with selective logging, per capita rate of singing also decreased, and vice versa (Pillay et al., 2019). Overall, we speculate that it is more likely that the loss of the dawn and dusk peak results from changes in species abundance and the amount vocalizing behaviour, rather than radical shifts in timing of the vocalizations, however, demographic surveys would be needed to confirm this.

4.3. Disturbance leads to high nocturnal insect activity

A second sign of a minimally disturbed forest was bird and insect Soundscape Saturation that is higher during the day than at night (Fig. 4). As forests become degraded, insect, and to a lesser degree bird soundscapes became more saturated at night (Fig. 4). This corroborates the findings of a study from FSC-certified forest concessions in Peru, whereby even lightly logged forests had a higher insect sound activity at night (Campos-Cerqueira et al., 2019). This could be because forest disturbance creates microclimatic conditions or new habitat and resources for nocturnal species of insects that make sounds. It is challenging to identify species of insects from their sounds due to the lack of existing insect sound libraries. For

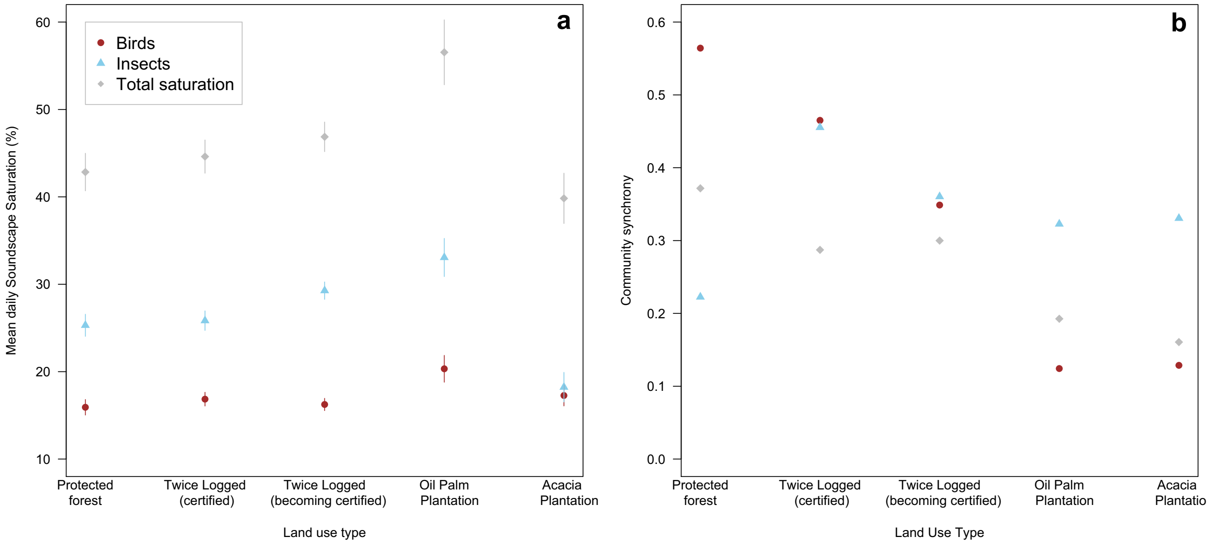

Fig. 3. (a) Mean daily total, bird, and insect Soundscape Saturation across different land use types. Symbols show parameter estimates, lines show 95 % Confidence Intervals, (b) Synchrony of Soundscape Saturation values throughout the day across sites within the same land use type. High values mean that Soundscape Saturation rises and falls simultaneously over time across sites. Low values mean that Soundscape Saturation fluctuates randomly over time across sites.

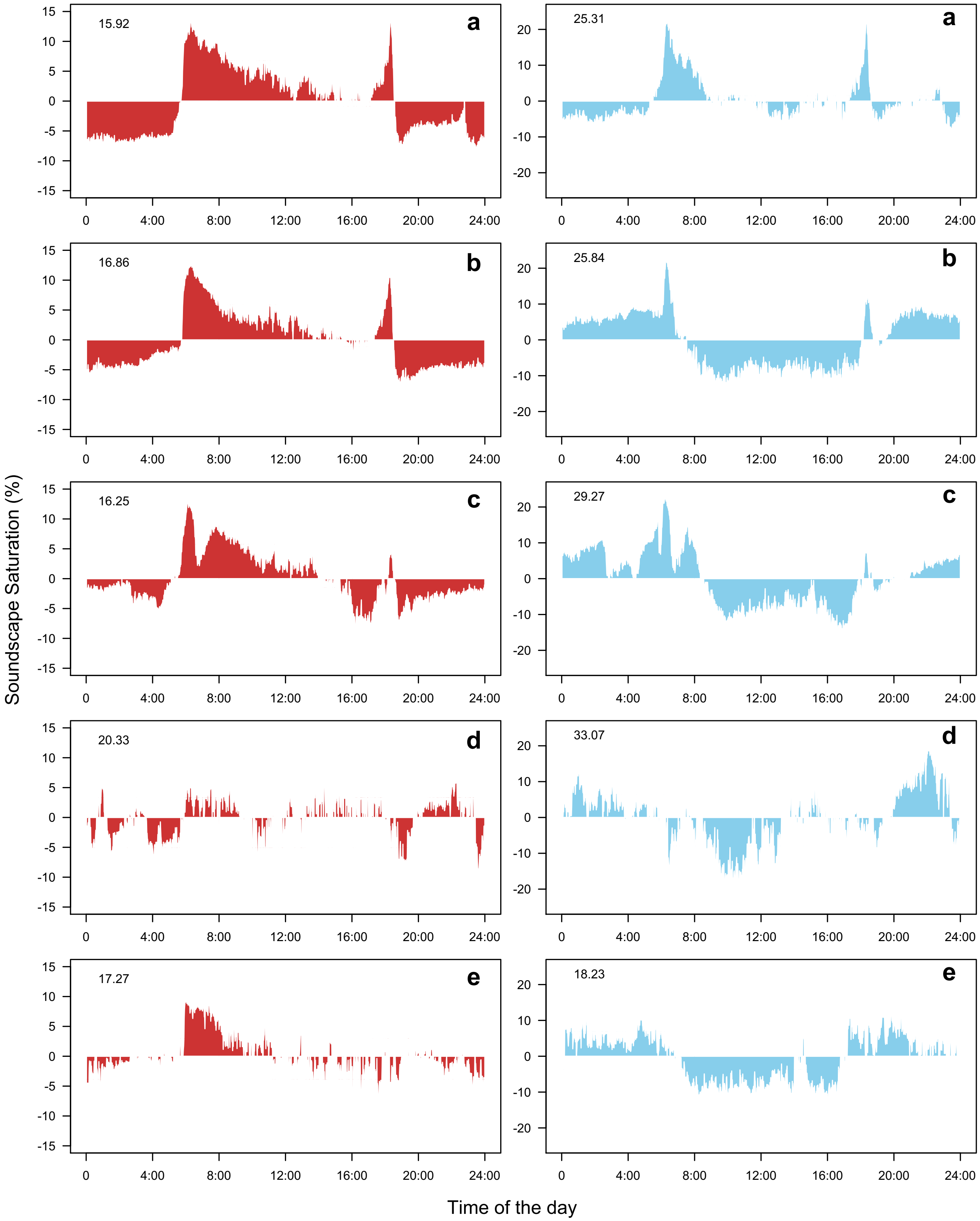

Fig. 4. Daily demeaned trends in bird (red) and insect (blue) Soundscape Saturation in different land use zones (undisturbed forest – a; certified selectively logged forest – b; non-certified selectively logged forest – c; oil palm monoculture plantation – d; acacia monoculture plantation – e). Daily means for each land use type, corresponding to 0 on the y axis, are shown in top left corner of each panel.

example, for Orthoptera – a major sound producing group – the acoustic signature of only about 10 % of species is documented, and these are predominantly from Europe and North America (Noda et al., 2019; Riede, 2018). Empirical surveys from selectively logged forests have typically focused on less commonly vocalizing groups, such as butterflies, dung beetles, and ants (França et al., 2017; Gustafsson et al., 2012; Hamer and Hill, 2000; Nichols et al., 2007), overall finding a modest increase in richness with logging intensity (Burivalova et al., 2014). Whereas nocturnalization of wildlife in response to human pressure is well-documented (Gaynor et al., 2018), individual species analysis would be needed to confirm this in our study area.

4.4. Degraded forests are less synchronized

Third, we found that the soundscapes of undisturbed, protected forest sites were more synchronized, in terms of their saturation, than those of degraded sites (Fig. 3B). The level of synchrony decreased with selective logging, and was close to random in monoculture plantations. This trend was even stronger when considering the component of the soundscape that can be attributed to the bird community. Based on our limited dataset, we propose a preliminary threshold of 0.5 for community synchrony of bird Soundscape Saturation across sites to signify an undisturbed or regenerated forest.

Synchrony in bird Soundscape Saturation across sites could result from several processes: Sites could have the same set of species (low beta diversity across sites), which would occupy the same frequencies, and begin and end vocalizations at the same time, resulting in a synchronized bird Soundscape Saturation. In this scenario, a decrease in synchrony could result from some species missing from some sites due to disturbance, but not from others, or new species emigrating to some of the disturbed sites but not to others. This is likely, because selective logging affects the forest heterogeneously, depending on the location of target trees, skid trails, roads, and log landings (Ellis et al., 2016). Beyond the spatial heterogeneity of disturbance, human impact may also vary over time. Asynchrony could result from an anthropogenic factor altering the acoustic habitat, such as by sound from machinery, which changes throughout the day as workers progress through the forest, have breaks, etc.

Alternatively, sites could have sets of different species (high beta diversity across sites), filling in temporal and frequency acoustic niches that are common to all sites, resulting into a chorus of a locally synchronized bird community (Malavasi and Farina, 2013). Land use, regardless of being applied homogeneously or not, could affect some species and not others, resulting in less synchronized Soundscape Saturation across sites. Previous work from the same landscape showed that soundscapes across selectively logged sites were more homogeneous compared to protected sites, in terms of frequencies filled with sound (Burivalova et al., 2019c). Together with the results presented here, a complex picture emerges, suggesting that undisturbed forests have diverse but highly synchronized soundscapes, and disturbed forests and plantations have more homogeneous soundscapes that lack synchrony.

4.5. Limitations

We were unable to reliably distinguish amphibians and mammals from the other taxonomic groups based purely on frequency. Whereas our dataset does not allow the study of temporal overlap, we hypothesize that, instead of frequency partitioning, there may be a temporal portioning of the soundscape between mammals, birds, and amphibians (Oliveira et al., 2021). Whereas amphibians typically vocalize at night, mammals that vocalize in East Kalimantan (gibbon, orangutan, etc.) do so largely during the day.

Our sensitivity analysis suggests that the soundscape partition between birds and insects is robust to the number of sounds sampled, however, we expect that the exact frequency profiles may differ across geographies and forest types. This could be due to different species extinction histories and biogeographic patterns that may result in different levels of acoustic competition, or island syndromes, which could alter frequency ranges through body size (Losos and Ricklefs, 2009; Robert et al., 2019). Therefore, our results should not be used for soundscape partitioning in other regions without additional tests. Exhaustively labelling soundscapes is resource-intensive, however, beyond enabling the partitioning of a soundscape, it can also be useful in training automated classification models, such as Convolutional Neural Network (Sun et al., 2021). The minutes from which we drew the frequency probabilities were sampled from the dawn and dusk forest soundscapes, in order to capture the maximum sonotype diversity. However, this could be problematic if the frequency patterns of nocturnal fauna, or species only present in monoculture plantations are different (Oliveira et al., 2021). For example, it is possible that sampling night-time minutes would have improved our estimate of the amphibian frequency distribution. Additionally, both types of plantations were adjacent to mature tropical forest, and a lot of species recorded in the soundscapes were likely non-resident visitors from the nearby forests. This, we believe, makes the acoustic biodiversity differences between plantations and natural forests described here conservative.

4.6. Conclusion

We present a soundscape partitioning approach, which could be considered intermediate between a soundscape index and individual species analysis. This approach may be useful for conservation or sustainable management projects that need to monitor biodiversity, such as certified logging or agricultural operations maintaining high biodiversity areas, restoration initiatives, or protected areas. Based on our findings from Indonesian Borneo, we suggest that the three indicators of a recovering or minimally disturbed forest are prominent peaks in Soundscape Saturation during the dawn and dusk, higher bird and insect Soundscape Saturation during the day compared to the night, and high synchrony in bird Soundscape Saturation.

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CRediT authorship contribution statement

Zuzana Burivalova: Conceptualization, methodology, formal analysis, Writing – Original draft, Visualization, Supervision.

Tatiana M. Maeda: Conceptualization, Validation, Investigation, Data curation, writing – review & editing.

Purnomo: Investigation, project administration, resources, writing – review & editing.

Yaya Rayadin: Conceptualization, writing – review & editing.

Tim Boucher: Investigation, visualization, writing – review & editing.

Pooja Choksi: Conceptualization, writing – review & editing.

Paul Roe: software, data curation, writing – review & editing.

Anthony Truskinger: software, data curation, writing – review & editing.

Edward T. Game: Conceptualization, funding acquisition, project administration, writing – review & editing.

Data availability

Data is already publicly available on www.ecosounds.org

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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