Exploring spatio-temporal variation in soundscape saturation of an African tropical forest landscape

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ARTICLE INFO

ABSTRACT

Monitoring biodiversity calls for efficient monitoring techniques. Soundscape analysis is a landscape-level approach to acoustic monitoring whereby acoustic indices are calculated as proxies for biodiversity based on all sounds occurring in a landscape, i.e. a soundscape. However, it is not fully understood what the influence is of environmental, anthropogenic and temporal heterogeneity on soundscapes and what soundscapes mean in terms of species diversity. Here, we use soundscape saturation, a proxy for acoustic diversity which calculates the degree of use of acoustic niches. We study how soundscape saturation responds to forest management and seasonality in the tropical forests of Gabon, while taking into account distance to rivers, human accessibility, signs of hunting, elevation and slope. To study the contribution of medium to large mammals to soundscape saturation, we relate soundscape saturation to the abundance of several animal guilds as estimated with camera trap data. Soundscape saturation was higher in a multi-use forest vs. logging concessions, in the rainy reason vs. the dry season, and in proximity of rivers and human access points. Elevation, slope, and hunting were less important covariates. We did not find strong evidence for a relationship between soundscape saturation and the abundance of several mammal guilds derived from camera traps. The lack of this relationship highlights the opportunity for a joint approach of eco-acoustics and camera trapping due to complementary species coverage. Our study provides the first soundscape saturation study in African tropical forests and the first to combine soundscape saturation with camera trap data. Soundscape saturation is considered a useful additional index for quantifying biodiversity across a range of land-use types. Future studies may aim to improve species inference and the site-specific interpretation of saturation levels by investigating species-specific contributions to, and spatiotemporal variation in, acoustic activity.

1. Introduction

Human encroachment of natural ecosystems heavily impacts biodiversity (Lewis et al., 2015). Knowledge of our ecosystems and a thorough understanding of how they respond to human activity is fundamental for effective conservation actions (Pereira et al., 2012; Stephenson, 2019). Efficient, scalable biomonitoring methods are a prerequisite for this understanding (Stowell and Sueur, 2020), especially for landscape scale conservation (Reed et al., 2015). One increasingly used approach is soundscape analysis (Alvarez-Berríos et al., 2016; Merchant et al., 2015; Sueur et al., 2014; Sugai et al., 2019), whereby acoustic indices are calculated and used as proxies for biodiversity.

These soundscape analyses include all animal sounds emanating from a landscape and cover all vocally active species ranging from insects to elephants (Pijanowski, Farina, et al., 2011).

Acoustic indices are obtained at relatively low cost, are reproducible and objective, and provide a lasting image of the vocal footprint of a landscape. Soundscape analysis offers great potential for landscape level monitoring given its ability to accurately predict biodiversity (Buxton, McKenna, et al., 2018), with applications in measuring the impacts of forest fragmentation (Burivalova et al., 2018), climate change (Krause and Farina, 2016), traffic (Barber et al., 2011; Duarte et al., 2019; Pieretti and Farina, 2013), resource extraction (Burivalova, Purnomo, et al., 2019; Campos-Cerqueira et al., 2020; Deichmann et al., 2017),

agro-industrial operations (Furumo and Mitchell Aide, 2019) and conservation (Burivalova, Game, et al., 2019). Other potential applications involve tracking the impacts of reforestation on biodiversity and establishing biodiversity baselines for forest finance schemes. Thus, soundscapes may offer the potential to determine the state of, and track changes in, biodiversity at a landscape scale. Studying the potential applications for soundscape analyses is particularly relevant given the pervasive and increasing human presence in natural systems (Pijanowski et al., 2011) and requires knowledge of how anthropogenic activities affect soundscapes (Warren et al., 2006). Tropical forests, although rich in biodiversity and important for the provision of ecosystem services, are particularly understudied with regard to soundscapes (Scarpelli et al., 2020).

Landscape heterogeneity induces complex spatial and temporal acoustic partitioning, as species are non-randomly distributed along gradients of elevation (Caceres et al., 2011), slope (Nakashima et al., 2020), proximity to water (Rondinini et al., 2011), forest management type (Sollmann et al., 2017), roads (Stokes et al., 2010) and other human access points (Benítez-López et al., 2017). Sound also varies across time as species have variable activity patterns over the day and seasons (Depraetere et al., 2012; Haver et al., 2020; Vokurková et al., 2018). With changing seasons, the varying weather affects the sounds of the rain and the wind. Moreover, a changing moisture content also affects the overall acoustic properties of the environment, such as the reflectivity of wet versus dry surfaces and the distance that sound travels in relation to the denseness of the vegetation (Londhe et al., 2009). This variation makes soundscapes highly place and time specific, as each set of circumstances creates a unique spatio-temporal acoustic footprint (Fuller et al., 2015; Gasc et al., 2015; Lellouch et al., 2014). For soundscapes, these local effects are likely stronger than for other biomonitoring methods that target larger wildlife, e.g. walking line transects or camera trapping. This is because soundscapes also include smaller species like insects and amphibians, which respond more to localized heterogeneity. Given this influence of local variation on soundscapes, they can be used to detect subtle changes, enabling the tracking of biodiversity over time and space in changing landscapes. Conversely, the disadvantage is that a specific location and timing may exert a large influence on a soundscape, possibly complicating the interpretation of soundscapes (Sueur and Farina, 2015; Eldridge et al., 2016). For soundscape studies, this means that the heterogeneity in the landscape must be considered in the sampling design to prevent too much variation between the soundscapes of sampled sites. To account for this heterogeneity in the sampling design, it is important to understand how spatial and temporal variation affect soundscapes (Pijanowski et al., 2011).

Soundscapes include a wide variety of vocal animals, including birds, anurans, bats, primates, and several groups of insects (Ferreira et al., 2018). Acoustic indices reduce this diversity to a single value and for reliable ecological inference it is important to understand the relative contribution of different species groups to the soundscape (Fuller et al., 2015). Most acoustic diversity is driven by insects, due to their high abundance and their broad usage of both the time and frequency domains of the soundscape (Ferreira et al., 2018). While early soundscape research has primarily focused on birds, it has become evident that their contribution to acoustic diversity is relatively small compared to insects (Aide et al., 2017). Moreover, medium to large mammals have comparatively small bandwidths and short call durations. For the Neotropics it was found that these species contributed relatively little to soundscapes (Aide et al., 2017; Ferreira et al., 2018). Still, medium to large wildlife in Africa is comparatively more diverse and abundant than wildlife in other tropical forest regions and may therefore contribute differently to the soundscape. Studying which species contribute to the soundscape helps to understand which species can effectively be monitored with soundscapes. Species' contributions can be studied by corroborating species presence with other monitoring methods, such as camera trapping, at the sites where soundscapes are recorded.

A variety of acoustic indices for soundscape analysis are available (Buxton, McKenna, et al., 2018; Sueur et al., 2014; Towsey et al., 2014). One recently introduced index, soundscape saturation, is a promising, intuitive, and easy to understand proxy for acoustic diversity (Burivalova et al., 2018). Soundscape saturation is defined as the proportion of acoustically active frequency bins (i.e. arbitrary divisions of the frequency range) in a given minute of the spectrogram of a soundscape and calculates the degree of use of different acoustic bins. Soundscape saturation is based on the acoustic niche hypothesis, which states that species richness is strongly correlated with the total number of unique vocalizations (Krause, 1987), also referred to as 'sonotype' diversity (Ferreira et al., 2018). The reasoning driving this hypothesis is that time and frequency are resources over which vocalizing organisms compete to avoid acoustic interference. A species enhances its communication efficiency by occupying its own acoustic niche, thereby reducing overlap in time or frequency with other vocalizing species. As competition increases with increasing species richness, highly diverse systems see more acoustic niches filled. The total number of filled acoustic niches, measured as occupied frequency bins, can thus be used as a proxy for biodiversity which can be used for conservation management and translated into policy advice. As the index focuses on niche differentiation, it is particularly useful for species rich environments such as tropical forests (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019; Burivalova et al., 2021).

In this study, we aim to understand the spatial and temporal dynamics of soundscape saturation in the tropical forests of Gabon to establish which environmental, anthropogenic and temporal factors should be taken into account for future soundscape studies in Central Africa. Gabon harbors some of the most intact forests and richest communities of large wildlife in Central Africa (Abernethy et al., 2016), and is therefore a valuable study area for soundscape analyses, as future comparisons require baseline data of recorded soundscapes in relatively undisturbed sites. Gabon has an extensive logging industry that, although it is highly selective and its exploitation volumes are low (Karsenty, 2016), may affect acoustically active species (Burivalova et al., 2021). We sample various forest management types, including a FSC-certified logging concession, a non-certified logging concession, a multi-use forest which is used by local communities, abandoned and active slash and burn plantations, as well as a savanna area. We study the effect of distance to rivers, elevation, slope, distance to human access points, and signs of hunting on soundscape saturation. Furthermore, we compare saturation between the wet and the dry season. We then study how various management types affect saturation levels and calculate the dissimilarity of the soundscapes of the various land-use types. Last, given the rich forest wildlife of Gabon, we link acoustic data to camera trap data to study the relative contributions of the medium to large sized wildlife community to the soundscape.

2. Methods

2.1. Study area

We recorded the soundscapes of a mosaic of forest management types in Ngounie province, southwestern Gabon in November 2019 and January 2020 (Table 1) These forests are characterized as coastal dense evergreen tropical forests dominated by *Aucoumea klaineana* and *Sacoglottis gabonensis* (Caballé, 1978). Mean annual precipitation in the region is 1776 mm (Takenoshita and Yamagiwa, 2008). There are four seasons: a short dry season (January - February), a short rainy season (March - April), a long dry season (May – September), and a long rainy season (October – December). Most of the region, including what is now Moukalaba-Doudou National Park, has been selectively logged between 1962 and 1988 (Van Vliet and Nasi, 2008). In Gabon, logging cycles are 25 years and logging intensity is low compared to other tropical regions, with timber extraction volumes of ~ 4–8 m³ per hectare (Karsenty, 2016). These forests are of high conservation value and retain high

Table 1

An overview of the sampled sites, the number of Acoustic Recording Units (ARU) and camera traps placed at each site, the number of ARUs yielding at least 90% and 80% of daily recorded minutes after malfunction and rain removal, mean number of recording days per ARU and season. Superscripts indicate which sites were included in each analysis: 1 = Seasonality, 2 = Landscape heterogeneity, 3 = Forest management type, 4 = Comparison with camera traps, 5 = Land-use type.

Site	Number of ARUs	Number of ARUs yielding at least 90% of daily recorded minutes after malfunction and rain removal	Number of ARUs yielding at least 80% of daily recorded minutes after malfunction and rain removal	Mean recording days/ARU	Season
Concession 1 FSC-certified [1,4]	14 (+36 camera traps)	12	12	5.0	Long rainy season
Concession 2 Non-certified [1,4]	36 (+36 camera traps)	32	32	3.8	Long rainy season
Concession 1 FSC-certified [1,2,3,5]	44	39	41	4.0	Short dry season
Concession 2 Non-certified [1,2,3,5]	34	27	28	3.5	Short dry season
Multi-use forest [2,3,5]	18	15	15	4.1	Short dry season
Occupied subsistence (slash and burn) plantations [5]	4	3	3	4.9	Short dry season
Abandoned subsistence (slash and burn) plantations [5]	2	2	2	4.5	Short dry season
Savanna [5]	8	3	5	4.1	Short dry season

densities of critically endangered species such as western gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and approximately 10% of the African forest elephant (*Loxodonta cyclotis*) population worldwide (Maisels et al., 2013; Strindberg et al., 2018; Takenoshita and Yamagiwa, 2008).

2.2. Study sites

We sampled two logging concessions near the medium-sized town of Mandji which has approximately 3000 inhabitants, as well as a variety of land-use types around the town itself. In *concession 1*, which became FSC-certified in 2009, hunting is banned and prevented by manned road barriers, guard patrols, and obstructing access to unused logging roads. In *concession 2*, which is conventionally logged, hunting is officially prohibited but this is not strictly enforced. We did not quantify forest structure or other forest characteristics for the two concessions, and therefore are not able to link differences in soundscapes to specific causal determinants. Nonetheless, regional timber extraction volumes are low (Karsenty, 2016) in certified and non-certified concessions. We therefore feel safe to assume that differences due to forest certification mainly manifest themselves by decreased hunting levels rather than changes in forest structure. In addition to the logging concessions we recorded the soundscapes of four different land-uses: 1) a segment of *multi-use forest* where artisanal logging and hunting is allowed throughout most of the year and restrictions are not strongly enforced during the non-hunting season; 2) *currently utilized rotational subsistence* plantations at the edges of the town; 3) *abandoned and overgrown subsistence plantations* found between the currently utilized plantations; and 4) a *savanna* area near the town where forest encroachment is prevented by annual burning to allow for mushroom gathering (Table 1).

2.3. Data acquisition

Data were collected over two separate periods: in the long rainy season (November 2019); and the short dry season (January 2020), using AudioMoth Autonomous Recording Units (ARUs) (Hill et al., 2019) and camera traps (Bushnell Trophy Cam HD, Model 119876). In the long rainy season, we installed 14 ARUs and 36 camera traps in concession 1 and 36 ARUs with 36 camera traps in concession 2 (Table 1). The large difference in number of recorders between sites was partly caused by a high number of recorder failures and partly by a programming mistake which was only encountered upon recovery of the ARUs. In the short dry season, we set up 44 ARUs in concession 1 and 34 ARUs in concession 2, and 18 in the multi-use forest. We furthermore installed several recorders in non-forested sites including occupied (n = 4) and abandoned (n = 2) plantations, and the savanna (n = 8). Exact installation locations were chosen randomly following a predefined systematic grid pattern with a 1 km spacing. The detection distance of

sounds depends on the loudness with which a signal is produced. However, with one ARU per km2, it is unlikely that sounds are loud enough to be detected by multiple ARUs. ARUs were placed at breast height on trees and on one-meter-tall poles in the savanna area. Each ARU was placed in two ziploc bags to protect the device against rain. Devices recorded 1-min segments continuously at 48 kHz and 30.6 dB gain until battery power ran out, yielding 1.06–7.25 (mean: 4.40) recording days per ARU. All ARUs were programmed to start recording simultaneously. Camera traps were placed on the same trees with ARUs at a height of 30 to 45 cm and were required to have at least 4 m of unimpeded view and were operational for approximately two months.

2.4. Sound data processing

Segments that were corrupted due to recorder failure were removed. To improve processing speed and to conform to other studies (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019), we downsampled each 1-min segment to 22,050 Hz, as only few taxa vocalize above these frequencies. We excluded the 1-min segments whose maximum amplitude matched the amplitude limit of the recorder, as this was associated with either objects falling on the microphone or signal distortion caused by a cicada vocalizing on a tree too close to the recorder. Segments containing rain were classified using a threshold-based machine learning approach (Brown et al., 2019) and removed. To set the threshold, we manually annotated 650 files based on rain presence or absence and applied an MLP classifier with no MMSE STSA, all features, Relu activation, Adam solver, 50 iterations maximum, and no preprocessing (Brown et al., 2019). To each 1-min segment, the algorithm assigned a value between 0 and 1 indicating the probability that it contained rain. Segments with a classification threshold of 0.33 or higher were removed to produce a type-I error rate of 0.02. Together, the amplitude and rain filters removed 15% of the recorded segments. The remaining 1-min segments were converted to spectrograms using a short-time Fourier transform with a non-overlapping window of 512 samples. This divided each soundscape into 256 discrete frequency bins, each spanning approximately 43.0 Hz. The bin size is determined by dividing the Nyquist frequency (i.e. the maximum frequency beyond which aliasing will occur when transforming a sound signal into a spectrogram) of the signal (11,025 Hz) by the number of frequency bins.

2.5. Camera trap data processing

Species and number of individuals were manually identified from camera trap images. Photos taken more than ten minutes apart were considered to depict unique individuals. We calculated the relative abundance for each species as the number of unique individuals divided by the number of camera days. Species were then categorized into eight different animal guilds: apes, birds, carnivores, elephants, monkeys,

pangolins, rodents, and ungulates. The relative abundance index (RAI) of each guild at each camera trap was calculated as the mean RAI of its affiliated species.

2.6. Soundscape saturation

We calculated soundscape saturation following Burivalova et al. (2018) for each 1-min segment and took the average value for each minute in the 24-hour cycle across the multiple recording days, producing 1440 saturation values per ARU. ARUs that missed more than 10% of minutes due to malfunctions and rain (n = 27) were excluded from all analyses. For the soundscape dissimilarity comparison between the land-use types we included ARUs that missed up to 20% of the minutes of the day, to retain sufficient data points for the savanna recordings (Table 1). The remaining missing values were estimated as the average of the two adjacent minutes. All soundscape saturation code was written in R (R Core Team, 2020) and can be found in the Supplementary Information. We first studied whether the length of our recording period of five days was sufficiently long to capture the major acoustic variability, by plotting the range of soundscape saturation values of ARUs with recording periods of 2, 3, 4 and 5 days (n = 9). Ranges were plotted for eight different sets of randomly combined ARUs to ensure that the findings are consistent despite the small sample size. Next, to quantify the ability of soundscape saturation to predict biodiversity, we inspected the spectrograms of two randomly chosen sets of 100 consecutive minutes and counted the total number of sonotypes (unique vocalizations) for each minute. Some minutes experienced signal distortion due to a cicada too close to the device (24 of the 200 selected minutes) and were removed by the amplitude filter without replacement from other recordings. The first 100-minute segment began at 5 AM and the second at 5 PM. We opted for the annotation of longer consecutive 100-minute segments over randomly chosen 1-minute segments, because it allowed us to review sonotypes from start to end. Recognizing partially overlapping sonotypes thereby becomes easier and arbitrarily splitting sonotypes over multiple 1-minute segments is prevented. Verification was performed blindly, i.e. the person annotating did not know the metadata of the recording. The unique number of sonotypes was then cross-referenced with soundscape saturation by using a Pearson's correlation test to measure whether saturation correlated with the observed richness of the vocalizing fauna.

2.7. Statistical analyses

We first evaluated soundscape saturation in relation to the following covariates: elevation, distance to the nearest river, human accessibility defined as the shortest distance to a point of access with a car or canoe, hunting intensity, management/ land-use type, latitude, longitude, and slope (Table 2). The relative contribution of these covariates to soundscape saturation was estimated using Aikake's Information Criterion for adjusted sample size (AICc), which allowed us to select the combination of covariates that best explain the variation in soundscape saturation. Our study area contained a gradient of increasing elevation and distance to the nearest river from northwest to southeast. As a result, latitude and longitude masked a lot of the variation which we thought was better attributed to elevation and river proximity. We therefore excluded latitude and longitude from model selection, as done in other studies (Poulsen et al., 2011). Each minute of the 24-cycle was fitted separately, as acoustic activity naturally fluctuates throughout the day-night cycle. This produces the combination of covariates that best explain the variation in acoustic species richness for each minute of the day. The best models throughout the entire day are those that perform best for the most minutes of the 24-hour cycle (Burivalova et al., 2018).

To more closely investigate covariates relating to human impact, we compared soundscape saturation across three sites differing in the type of management (i.e. FSC-certified logging, non-certified logging, and multi-use forest). We did not include the plantations and savanna

Table 2

A description of the covariates of spatial variation used in this study.

Covariate	Description	Range or categories
Slope	Estimated slope at ARU in the field	0–5°, 5–20°, or > 20
Distance to river	Shortest Euclidean distance to a river (m)	Range 31–4876 m, mean 1890 m
Hunting	Wire snares, shell cases, and/or hunting camps found within 500 m of a ARU	Presence / absence
Human accessibility	Shortest Euclidean distance to either a road with vehicle access or a navigable river	Range 18–15475 m, mean 8040 m
Elevation	Elevation above sea level (m)	Range 38–417 m, mean 200 m
Management/ land-use type	Type of ecosystem.	FSC-certified logging, non-certified logging, multi-use forest, occupied subsistence plantations, abandoned subsistence plantations, savanna

recordings, because those sites are vastly different, non-forested ecosystems, which renders their acoustic diversity incomparable. As differences between forest management types were expected to be subtle, the comparisons for this analysis were made during dawn (05:00–06:00) and dusk (18:00–19:00) choruses, as these moments contain the highest acoustic activity and are therefore most likely to show differences in soundscape saturation following the acoustic niche hypothesis. The sample size differed between sites, which complicates drawing conclusions about whether the sites differ in soundscape saturation levels, or whether a potential difference is merely the result of a differential sampling size. We therefore compared the forested sites in two analogous analyses. In the first, we used all data available to decrease variation and increase statistical power. However, to confirm whether the same effect can be found with an equal sample size between the sites, we also did the same analysis using a randomly picked set of ARUs with an equal number per forest management type (n = 6). The latter analysis has a small sample size and therefore less statistical power. The analysis was therefore repeated eight times, each with a new random combination of ARUs to verify whether the outcomes are consistently similar to the analysis with all the available data.

Subsequently, to compare soundscape saturation sampled in both seasons, we used a paired-sample *t*-test of the locations that were recorded in both seasons (n = 22). The number of paired ARUs is lower than the overall number of ARUs installed in the rainy season because we did not resample all rainy season locations in order to capture more heterogeneity in the landscape in the dry season.

With large differences in ecosystems, species communities are less similar, which makes comparing soundscape saturation less useful as a proxy for biodiversity. We therefore also used another related index, the soundscape dissimilarity index (S_d) (Burivalova, Purnomo, et al., 2019), to compare the acoustic communities of all the recorded land-use types by ordinating all ARUs using non-metric multidimensional scaling (NMDS). This index characterizes each frequency bin of a 60 s soundscape as the maximum decibel value minus the background noise creating a daily soundscape grid of 1440 min by 256 frequency bins. Following Burivalova, Purnomo, et al. (2019), we split this grid into 192 non-overlapping segments of 32 frequency bins by 60 min. Each segment is in turn divided into subsegments of 8 bins by 10 min, each overlapping its neighboring subsegments by 4 bins and 5 min. Each soundscape is thus composed of 192 × 77 values. For two sites, the absolute difference of each corresponding subsegment pair is calculated. The mean of all these pairwise differences produces the final value for S_d between two sites.

Finally, we performed a second AICc model selection using only the locations where camera traps were placed together with acoustic recorders by using the RAI of the eight selected animal guilds as covariates

to compare soundscape saturation with camera trap data and to investigate the relative species' contributions and the degree of overlap between the two monitoring techniques. Interactions were not fitted due to the small sample size.

3. Results

3.1. Recording length and verification of soundscape saturation

We first examined whether our five-day recording period was sufficiently long by plotting the range of soundscape saturation values for ARUs that recorded various lengths (Fig. S1). This showed that the range of saturation values did not increase after three to four days (Kruskal-Wallis chi-squared = 7.4961, df = 3, p-value = 0.05766), indicating that five days of recordings were sufficient to capture the majority of short-term acoustic variability. To verify whether soundscape saturation is a true proxy for biodiversity, we tested whether its estimate of acoustic diversity corresponded to the number of unique vocalizations on an annotated subset of soundscapes and found that this was indeed the case (P < 2.5e-08, R = 0.40; Fig. S2). No occurrences of anthrophony were observed.

3.2. Landscape heterogeneity

To investigate the effect of covariates on soundscape saturation, we used AICc model selection for all ARUs that were installed in the forest (Table S1). This revealed three models that were dominant during more than 10% of the day: the null model (13.1%), the model only including human accessibility mostly during the nighttime (11.3%), and the model including human accessibility and distance to the nearest river (10.8%) (Fig. 1 and S3). Thus, shorter distances to the river and human access points correlated positively to soundscape saturation and were by far the most important covariates. Throughout the day, the total amount of dominance per covariate was 28.5%, 22.4%, 18.6%, 15.6% and 14.9% for human accessibility, river proximity, elevation, slope and hunting, respectively.

3.3. Forest management type

The mean soundscape saturation values of the three differently managed forests; FSC-certified, non-certified and a multi-use forest, were not significantly different during the dawn chorus (one-way ANOVA; F = 1.23, P = 0.30), but they differed during the dusk chorus

(one-way ANOVA; F = 8.27, P = 5.53e-04). Post-hoc comparisons with a Tukey HSD test revealed that the multi-use forest differed significantly from the FSC certified (P < 0.001) and non-FSC certified (P = 0.045) logging concessions during the dusk chorus. However, the covariate analyses indicated the importance of river proximity, and ARUs in the FSC-certified concession were on average much further away from rivers (mean = 2647 m), compared to those in the non-certified (mean = 1145 m) and multi-use forest (mean = 2573). We therefore decided to exclude all ARUs (n = 29) more than 2500 m away from a principal river. Again, acoustic diversity at dusk differed significantly between the multi-use forest (n = 6) and the FSC-certified (n = 19, P = 0.018) and the non-certified (n = 27, P = 0.022) logging concessions (F = 4.36, p = 0.018; Fig. 2 and S4). Also with small sample sizes (n = 6), a consistently similar pattern was found when the same analysis was performed eight times with randomly picked equal sample sizes between management types (Fig. S5). It should be noted that although human accessibility also was a dominant covariate, we did not discard any recordings based on this variable because it would result in removing the complete multi-use forest recordings as this forest was more closely situated to the town than the forest concession.

3.4. Seasonality

We used the combined data of the FSC and non-certified sites to study seasonal fluctuations in acoustic diversity between the long rainy season of 2019 and the short dry season of 2020. A pairwise comparison between sites in both seasons revealed that the rainy season exhibited significantly more acoustic diversity than the short dry season (t = 3.16, P < 0.0048; Fig. 3 and S6).

3.5. Land-use type

Using the acoustic dissimilarity index S_d (Burivalova, Purnomo, et al., 2019), we characterized the soundscape of each ARU to compare differences in acoustic activity between the recorded land-use types (Table 1; Fig. 4 and S7). The axes of Fig. 4 were chosen arbitrarily to best represent the dissimilarity of the ARUs. Based on this ordination, the soundscapes of the land-use types can be placed into three distinct groups: savanna, active subsistence plantations, and forested land-use types, which included both types of logging concessions, the multi-use forest, and the abandoned subsistence plantations.
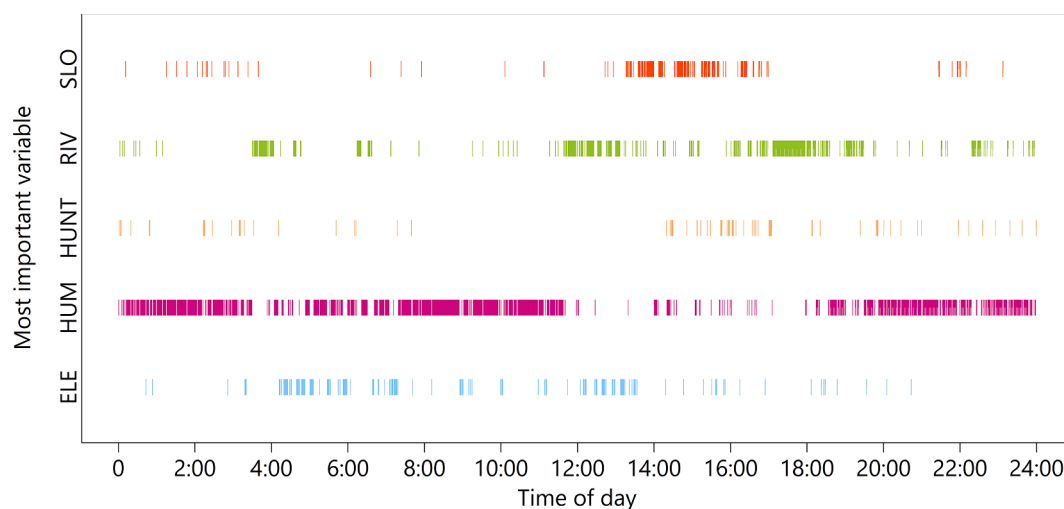

Fig. 1. The relative importance of spatial landscape gradients in explaining soundscape saturation throughout the 24-hour cycle. Each variable is colored when it the most relevant variable for explaining the soundscape saturation for a given minute of the day. Covariate abbreviations: SLO, slope; RIV, distance to nearest river; HUNT, presence/absence of signs of hunting; HUM, distance to either nearest human settlement or point of vehicle access; and ELE, elevation.
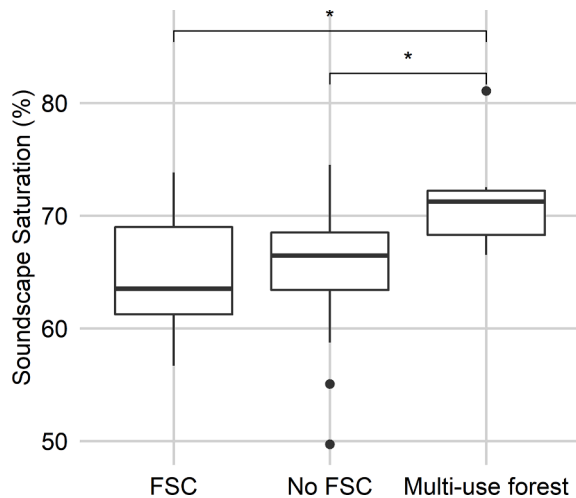
Fig. 2. Mean soundscape saturation during the dusk chorus in two logging concessions (FSC (n = 19 and non-certified (n = 27)) and a multi-use forest (n = 6). We excluded ARUs that were further than 2500 m away from a river because these were almost exclusively found in the FSC-certified concession. * = P < 0.05.
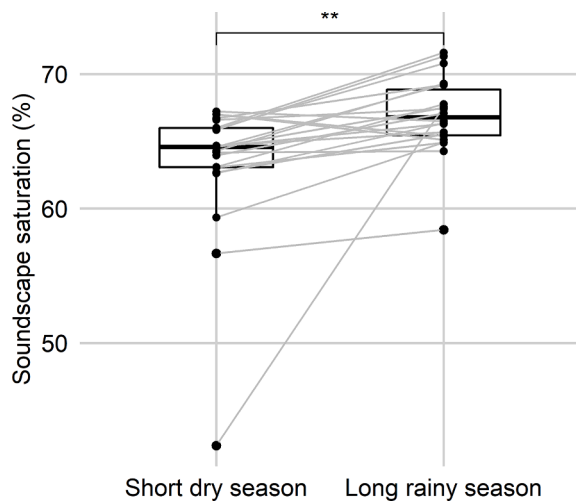

Fig. 3. Seasonal changes in soundscape saturation of the combined data of the FSC and non-certified sites. ** = P < 0.01.

3.6. Comparison with camera trap data

We performed a second AICc model selection using only the soundscape saturation values of ARUs that were placed together with camera traps and with the RAI of the eight animal guilds as covariates (Table S1; Table S2). In this case, the null model without any of the species' covariates was the best fit during 31% of the 24-hour period (Figs. S8 and S9). The second-best performing model (21%) included the mean RAI of the great apes (i.e. *G. gorilla* and *P. troglodytes*), which was also the most important covariate across all models. The relative contribution of the bird guild RAI was low throughout most of the day but peaked during the dusk chorus.

4. Discussion

Here we report the first soundscape saturation analyses (Burivalova et al., 2018) of African tropical forests, to assess acoustic diversity in relation to environmental, anthropogenic, and temporal heterogeneity. The most important covariates contributing to soundscape saturation
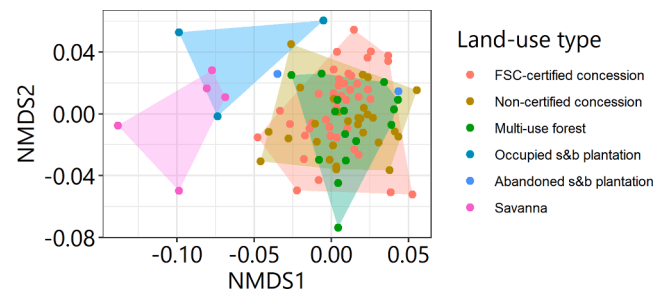

Fig. 4. NMDS ordination of the soundscapes recorded in various land-use types, using the soundscape dissimilarity index. Colored shapes indicate convex hulls. FSC certified logging concession (n = 41), non-certified logging concession (n = 28), multi-use forest (n = 15), occupied slash and burn plantation (n = 3), abandoned slash and burn plantation (n = 2) and savanna (n = 5).

were proximity to rivers and human accessibility, which were both associated with higher acoustic diversity. For the forest management types, we found no difference in soundscape saturation between the FSC-certified and non-certified forest, but found higher saturation in a multi-use forest. For the seasonal comparison, we found that acoustic diversity was higher during the rainy season than the dry season. Finally, using paired camera trap data, we did not find strong evidence that medium to large sized wildlife contributes significantly to soundscape saturation, highlighting the complementarity in species coverage between acoustical and visual monitoring and the benefits of a combined approach.

4.1. Landscape heterogeneity

Covariate analysis showed that shorter distances to human access points were positively correlated with soundscape saturation. The higher acoustic diversity in connection with human disturbance was unexpected and contrasts with studies that found less biodiversity closer to human access points, although these studies did not look at acoustic diversity (Benítez-López et al., 2017; Lhoest et al., 2020). It is unlikely that anthropogenic noise itself contributed much to soundscape saturation, as distances to human access points were at least 1 km. It is important to note, however, that traffic noise can affect the spectral structure of the soundscape by masking sounds and subsequent adjustments of song type and frequency by vocalizing species (Oden et al., 2015). This correlation can however best be explained by trophic disruptions of the ecosystem (see below). Hunting did not prove to be a large contributor to soundscape saturation, which can be explained, as hunting mainly affects larger and generally less vocally active wildlife.

We found that proximity to rivers positively affected soundscape saturation. Soundscapes near to rivers are likely more diverse due to the increased anuran and insect diversity, which are positively correlated with microhabitat gradients in riparian systems (Campos-Cerqueira et al., 2020; Depraetere et al., 2012). Insects are likely to constitute a prominent component of soundscapes which explains the impact of distance to rivers found here (Aide et al., 2017; Diepstraten and Willie, 2021). Fig. 1 showed that the relative variable importance of elevation is strongly correlated with distance to rivers, in line with rivers lying lower, which in turn explains the redundancy of elevation in the model selection. The same logic applies to slope, because it is also correlated with elevation. Moreover, there was only limited variation in elevation over our study sites (Table 2).

4.2. Forest management type

Contrary to our expectations but in line with Diepstraten and Willie (2021), we found that the more disturbed multi-use forest displayed higher acoustic diversity compared to the logging concessions, which is likely explained by several reasons. First, both forest-interior species and

edge species may coexist in the multi-use forest, increasing overall species richness (O'Dea and Whittaker, 2007; Welford, 2000). This effect may be enhanced in this forest as birds may be attracted by the opportunity to forage on the subsistence plantations nearby (Poulsen et al., 2011). Second, insects may be attracted to the increased light availability in the more disturbed multi-use forest. Cicadas, start to vocalize when the sun hits them and are likely to contribute a lot to the soundscape. In areas with abundant light gaps (roadsides, multi-use forests, river banks), the sun may hit the cicadas earlier than within the closed canopy forest, prompting them to sing. Third, the multi-use forest likely suffers from the highest hunting pressure of the three management types as it is closest to the town, which likely depleted higher trophic levels. Cascading effects in the ecosystem, such as a loss of top-down control by predators, may result in a release of species that are otherwise suppressed and that vocalize more than the hunted species (Abernethy et al., 2013; Terborgh, 2015). Future studies are necessary to elucidate the meaning of high acoustic diversity. While the higher soundscape saturation of the multi-use forest might initially appear positive, it is in fact likely to indicate severe defaunation of larger, silent species not captured by acoustic methods and the subsequent release of more vocal, smaller species. Increasing soundscape saturation in human disturbed systems would in such cases still be in line with the acoustic niche hypothesis, but does not represent an ecologically desirable situation from a conservation perspective. Thus, using soundscape saturation as a proxy for biodiversity in a conservation setting does not simply require maximization of saturation, but necessitates a more context-dependent understanding of what creates differences in soundscape saturation. This implies that comparing saturation levels is only useful when ecosystems are structurally similar and consist of comparable species communities. Examples include a comparison of forest management types in logged forests, or comparing oil palm plantations with and without pesticides, but does not include comparing a logged forest with an oil palm plantation.

We found no differences in soundscape saturation between the FSC-certified and non-certified sites. The most likely explanation for this is that soundscape saturation may not be the right method to gauge the environmental impacts from forest certification. That is, soundscape saturation is a measure of acoustic diversity, not of abundance. If an ecosystem is impoverished in species abundance, but not in species diversity, this is unlikely to be captured by soundscape saturation. Extraction volumes of logs in Central Africa, and therefore the overall environmental impact, are low compared to other tropical regions (Karsenty, 2016). Thus, if a site has not lost any species, the differences between two types of forest management may be too subtle to distinguish with soundscape saturation. Moreover, the most likely differences between the two types of forest management are potentially going undetected as larger species, that are expected to gain most from the protection of FSC's stricter hunting regulations, are generally less vocal (Ferreira et al., 2018). So even though our camera trap data indeed shows that the FSC-certified site boasts a higher abundance of wildlife (Table S2), this is not expressed in a significantly different level of soundscape saturation.

To correct for the influence of distance to rivers between the forest management types, we excluded sites with a distance larger than 2500 m from a river from the analyses. Even though human accessibility also had a high relative importance for saturation levels, we did not exclude recordings based on this covariate. Namely, sites with high human accessibility were heavily skewed to the multi-use forest and their exclusion would result in excluding the multi-use forest entirely. Thus, in this specific case the skewed anthropogenic covariate between various land-use types was of little consequence because the nature of the compared sites themselves implies that anthropogenic covariates are unevenly distributed. This would not be the case when soundscape saturation is compared within one management type and all other variables that may impact the soundscape should be roughly kept equal. The significance of the influence of covariates is thus context dependent.

4.3. Seasonality

Soundscape saturation was higher in the long rainy season of 2019 than in the short dry season of 2020, which contrasts earlier findings by Burivalova et al. (2021). The increased vocal activity in our rainy season recordings is likely caused by increased insect (mainly cicadas) and anuran activity during the rainy season (Galoyan et al., 2017; Rodriguez et al., 2014). Primates are also known to be far noisier in the wet season. They can afford to be more active because more food is available (Poulsen et al., 2001). In the dry season, primates move little to conserve energy when food is less abundant. Finally, the physical properties of the forest, e.g. the reflectance which causes sound to travel farther, also change during the rainy season. Given the site-specific seasonal variation, it is paramount that future soundscape studies take the timing of recordings into account when comparing sites. Although it is often logistically difficult to install recorders at various sites simultaneously, care should be taken to avoid large gaps in time between different sites of interest. It will also be valuable to record for longer time periods to capture more temporal variation, which will aid in understanding cyclical soundscape patterns or impacts of events undetectable by this short-term study (Burivalova et al., 2021). To achieve the necessary battery power, recordings could be made only at the most ecologically relevant times, such as the dusk chorus. During this time the soundscape saturation was the highest in our data and competition for time–frequency niches is likely the most severe. Furthermore, it is important to report how rain is dealt with in the analyses in detail, as the number of recordings that are retained that contain rain, directly affect the index that is calculated over a soundscape.

4.4. Land-use type

We used the soundscape dissimilarity index (S_d), to characterize and compare the soundscapes of all our recorded land-use types (Fig. 4. The savanna and active subsistence plantations formed two distinct groups, although the sample sizes are too small to establish statistically significant differences as was done for land-use types in an oil palm landscape in Colombia (Furumo and Mitchell Aide, 2019). Despite of the lack of replication and therefore statistical power, we chose to analyze the active and abandoned subsistence plots separately in the dissimilarity analysis. This was done because the active subsistence plots clearly display dissimilarity from the forested sites, while the abandoned subsistence plots show greater acoustic similarity to the forested sites. This similarity nicely illustrates how soundscapes of abandoned subsistence plots quickly revert to their original acoustic state. These findings also indicate that soundscape dissimilarity can be a highly suitable method for tracking coarse-scale acoustic changes in the landscape, which can potentially be applied in monitoring and quantifying the biodiversity of reforestation efforts, or in quantifying recovery of degraded or fragmented forests.

There was little dissimilarity between the soundscapes recorded in the two logging concessions, the multi-use forest, and the abandoned subsistence plantations. Note that this does not immediately imply that soundscape saturation levels between these land-use types are equal, as the structure of the soundscape can be largely similar in terms of which time–frequency segments are filled resulting in high similarity, even when acoustic diversity differs strongly. Soundscape dissimilarity is a coarser index than soundscape saturation and is more informative for detecting larger differences between acoustic communities. This merits further research into which land-use changes can effectively be monitored and quantified either using soundscape saturation or soundscape dissimilarity. Future studies can use a combined approach to address how soundscape saturation and dissimilarity changes over a temporal gradient of slash and burn subsistence plots to shed light on the acoustic recovery of soundscapes of this dominant land-use type in tropical Africa (Nasi et al., 2012).

4.5. Comparison to camera trap data

We found very little evidence for a correlation between the relative abundance of wildlife guilds as observed by camera traps and soundscape saturation, except for some evidence for the contribution of great apes (Table S1). The relative contribution of great apes was highest during the night when apes are predominantly inactive (Figs. S8 and S9). This finding suggests that the correlation between ape abundance and soundscape saturation was not caused directly by their sounds contributing to soundscapes. A plausible explanation is that the habitat preference of these species is related to acoustic diversity through environmental conditions such as vegetation structure or distance to water. Our results thus seem to corroborate that medium to large forest wildlife, mostly mammals, provides a relatively small contribution to the soundscape of African tropical forests (Diepstraten and Willie, 2021), as was previously also found for the neotropics (Aide et al., 2017; Ferreira et al., 2018). It is important to note, however, that camera traps are not very suitable for observing birds, limiting our ability to draw conclusions about their contribution to the soundscape. Moreover, our camera traps were in the field for a much longer period (approximately two months) than the ARUs (five days). The difference in deployment period is linked to the ability of the two devices to detect animals. On the one hand, collecting camera trap data over only five days would not be useful, as cameras only have a very small spatial observation window which needs to be compensated with a longer observation period to capture a representative image of the wildlife community. ARUs, on the other hand, can capture sounds from larger distances, and thus require less time to capture diversity. Yet, it is not sure whether large animals with large home ranges were present in the area around the ARU in the five days of the recording, even though they might have been observed multiple times on the camera in the subsequent two months.

4.6. Outlook

We studied how soundscape saturation is affected by land-use/ management type, environmental heterogeneity, seasonality, and how saturation correlated to camera trap data. Regional soundscape explorations are required to understand how spatio-temporal variation is reflected in soundscapes and to provide guidance for future studies for which factors should be controlled in relation to installation locations (Burivalova, Game, et al., 2019). Soundscape saturation has presently only been applied in the tropical forests of Papua New Guinea and Indonesian Borneo (Burivalova et al., 2018; Burivalova, Purnomo, et al., 2019; Burivalova et al., 2021). We answer the call to focus acoustic research on terrestrial, tropical wildlife, and how it is affected by human pressures (Scarpelli et al., 2020). We showed that soundscape saturation can be effectively used to track and quantify vocally active species across various types of forest management with potential applications for biodiversity monitoring in reforestation, rehabilitation, or degradation settings. We also showed that not all species can be effectively monitored using this method and that soundscape saturation requires a context-dependent interpretation of species' contributions and of the importance of spatial and temporal variation. Overall, given that spatiotemporal variation is carefully considered, soundscape saturation may be highly suitable for tracking vocal biodiversity through time and space. Spatiotemporal variation implies that to compare soundscapes, all factors affecting a soundscape need to be identified. They then either need to be standardized across the sampling units, or controlled during the analysis.

The field of eco-acoustics is still developing, with many promising avenues for future research. With our study, we highlight the opportunities and challenges of soundscape saturation studies. Opportunities include the potential to monitor landscape level changes in biodiversity, and the complementarity of species coverage to other monitoring methods. Challenges include correctly dealing with landscape heterogeneity and increasing our understanding which species make up the soundscape. Both soundscape saturation and soundscape dissimilarity can be used to discern changes within and between land-use types. Having an effective way of quantifying landscape level quality and changes in biodiversity can be an important asset for the implementation of verifiable controls for conservation efforts. Considering the large quantity of acoustic indices (Buxton, McKenna, et al., 2018), much remains to be learned about which indices are most relevant for particular land-use types, ecosystems, and species representations. Which species group contributes also depends on the acoustic index (Ferreira et al., 2018; Fuller et al., 2015; Gasc et al., 2015) and although generalizing metrics like soundscape saturation can serve as proxies for vocal biodiversity in general, they do not represent all species equally well. The most vulnerable species, those with large body sizes, require other monitoring methods to inform conservation actions (e.g. Zwerts et al., 2021). Combined approaches of acoustic monitoring with camera trapping are desirable, as both methods share similar logistical benefits, while being complementary in species coverage (Buxton, Lendrum, et al., 2018).

The difficulty in connecting soundscape indices to species groups does not negate their usefulness given their efficacy in monitoring overall ecosystem structure and stability. Any form of disturbance that affects biodiversity will likely also have an impact on the soundscape and can thus be measured and quantified. Elucidating species' contributions is an important part of future soundscape work. One approach to disentangle the relative importance of taxonomic groups in the soundscape, may be to identify the frequency ranges and activity patterns characteristic to different groups of interest and use this as a basis for classification, as has been done to distinguish biophony from anthrophony (Kasten et al., 2012). Insight derived from such studies may help to further elucidate species' contributions. Soundscape research is still new and looking ahead we see much value in studies addressing species' contributions in a range of land-use types to strengthen our understanding of how soundscapes relate to biodiversity.

CRediT authorship contribution statement

Joeri A. Zwerts: Conceptualization, Writing – original draft, Project administration, Resources, Funding acquisition. **J.N. (Yannick) Wiegers:** Writing – original draft, Formal analysis. **E.H.M. Sterck:** Supervision, Writing – review & editing, Funding acquisition. **M. (Marijke) van Kuijk:** Supervision, Writing – review & editing, Funding acquisition.

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.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2022.108712.

References

Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E., Maisels, F., 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. Philos. Trans. Royal Soc. B: Biol. Sci. 368 (1625), 20120303. https://doi.org/10.1098/rstb.2012.0303.

Abernethy, K., Maisels, F., White, L.J.T., 2016. Environmental Issues in Central Africa. Annu. Rev. Environ. Resour. 41 (1), 1–33. https://doi.org/10.1146/energy.2016.41.issue-110.1146/annurev-environ-110615-085415.

Aide, T.M., Hernández-Serna, A., Campos-Cerqueira, M., Acevedo-Charry, O., Deichmann, J.L., 2017. Species richness (of insects) drives the use of acoustic space in the tropics. Remote Sens. 9 (11), 1–12. https://doi.org/10.3390/rs9111096.

Alvarez-Berríos, N., Campos-Cerqueira, M., Hernández-Serna, A., Amanda Delgado, C.J., Román-Dañobeytia, F., Aide, T.M., 2016. Impacts of small-scale gold mining on birds and anurans near the Tambopata Natural Reserve, Peru, assessed using passive acoustic monitoring. Trop. Conserv. Sci. 9 (2), 832–851.

Barber, J.R., Burdett, C.L., Reed, S.E., Warner, K.A., Formichella, C., Crooks, K.R., Theobald, D.M., Fristrup, K.M., 2011. Anthropogenic noise exposure in protected natural areas: Estimating the scale of ecological consequences. Landscape Ecol. 26 (9), 1281–1295. https://doi.org/10.1007/s10980-011-9646-7.

Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. Science 356 (6334), 180–183. https://doi.org/10.1126/science.aaj1891.

Brown, A., Garg, S., Montgomery, J., 2019. Automatic rain and cicada chorus filtering of bird acoustic data. Appl. Soft Comput. J. 81, 105501. https://doi.org/10.1016/j.asoc.2019.105501.

Burivalova, Z., Game, E.T., Butler, R.A., 2019. The sound of a tropical forest. Science 363 (6422), 28–29. https://doi.org/10.1126/science.aav1902.

Burivalova, Z., Purnomo, Orndorff, S., Truskinger, A., Roe, P., Game, E.T., 2021. The sound of logging: Tropical forest soundscape before, during, and after selective timber extraction. Biol. Conserv. 254, 108812. https://doi.org/10.1016/j.biocon.2020.108812.

Burivalova, Z., Purnomo, Wahyudi, B., Boucher, T.M., Ellis, P., Truskinger, A., Towsey, M., Roe, P., Marthinus, D., Griscom, B., Game, E.T., Mukul, S., 2019. Using soundscapes to investigate homogenization of tropical forest diversity in selectively logged forests. J. Appl. Ecol. 56 (11), 2493–2504. https://doi.org/10.1111/jpe.v56.1110.1111/1365-2664.13481.

Burivalova, Z., Towsey, M., Boucher, T., Truskinger, A., Apelis, C., Roe, P., Game, E.T., 2018. Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea. Conserv. Biol. 32 (1), 205–215. https://doi.org/10.1111/cobi.12968.

Buxton, R.T., Lendrum, P.E., Crooks, K.R., Wittemyer, G., 2018a. Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. Global Ecol. Conserv. 16, e00493. https://doi.org/10.1016/j.gecco.2018.e00493.

Buxton, R.T., McKenna, M.F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L.M., Crooks, K., Wittemyer, G., 2018b. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Conserv. Biol. 32 (5), 1174–1184. https://doi.org/10.1111/cobi.2018.32.issue-510.1111/cobi.13119.

Caballé, G., 1978. Essai sur la géographie forestière du Gabon.

Caceres, N.C., Godoi, M.N., Hannibal, W., Ferreira, V.L., 2011. Effects of altitude and vegetation on small-mammal distribution in the Urucum Mountains, western Brazil. J. Trop. Ecol. 27 (3), 279–287. https://doi.org/10.1017/S0266467410000854.

Campos-Cerqueira, M., Mena, J.L., Tejeda-Gómez, V., Aguilar-Amuchastegui, N., Gutierrez, N., Aide, T.M., Pettorelli, N., Lecours, V., 2020. How does FSC forest certification affect the acoustically active fauna in Madre de Dios, Peru? Remote Sens. Ecol. Conserv. 6 (3), 274–285. https://doi.org/10.1002/rse2.v6.310.1002/rse2.120.

Deichmann, J.L., Hernández-Serna, A., Delgado, C.J.A., Campos-Cerqueira, M., Aide, T.M., 2017. Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on biodiversity in a tropical forest. Ecol. Ind. 74, 39–48. https://doi.org/10.1016/j.ecolind.2016.11.002.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., Sueur, J., 2012. Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. Ecol. Ind. 13 (1), 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006.

Diepstraten, J., Willie, J., 2021. Assessing the structure and drivers of biological sounds along a disturbance gradient. Global Ecol. Conserv. 31, e01819. https://doi.org/10.1016/j.gecco.2021.e01819.

Duarte, M.H.L., Caliari, E.P., Scarpelli, M.D.A., Lobregat, G.O., Young, R.J., Sousa-Lima, R.S., 2019. Effects of mining truck traffic on cricket calling activity. J. Acoust. Soc. Am. 146 (1), 656–664. https://doi.org/10.1121/1.5119125.

Eldridge, A., Casey, M., Moscoso, P., Peck, M., 2016. A new method for ecoacoustics? Toward the extraction and evaluation of ecologically-meaningful soundscape components using sparse coding methods. PeerJ, 4, e2108.

Ferreira, L.M., Oliveira, E.G., Lopes, L.C., Brito, M.R., Baumgarten, J., Rodrigues, F.H., Sousa-Lima, R.S., 2018. What do insects, anurans, birds, and mammals have to say about soundscape indices in a tropical savanna. J. Ecoacoust., 2, 1–17.

Fuller, S., Axel, A.C., Tucker, D., Gage, S.H., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Ecol. Ind. 58, 207–215. https://doi.org/10.1016/j.ecolind.2015.05.057.

Furumo, P.R., Mitchell Aide, T., 2019. Using soundscapes to assess biodiversity in Neotropical oil palm landscapes. Landscape Ecol. 34 (4), 911–923. https://doi.org/10.1007/s10980-019-00815-w.

Galoyan, E., Vassilieva, A., Poyarkov, N., 2017. Seasonal activity of terrestrial amphibians in the monsoon lowland forest of southern Vietnam. Herpetol. J. 27 (2), 189–199.

Gasc, A., Pavoine, S., Lellouch, L., Grandcolas, P., Sueur, J., 2015. Acoustic indices for biodiversity assessments: Analyses of bias based on simulated bird assemblages and recommendations for field surveys. Biol. Conserv. 191, 306–312. https://doi.org/10.1016/j.biocon.2015.06.018.

Haver, S.M., Rand, Z., Hatch, L.T., Lipski, D., Dziak, R.P., Gedamke, J., Haxel, J., Heppell, S.A., Jahncke, J., McKenna, M.F., Mellinger, D.K., Oestreich, W.K., Roche, L., Ryan, J., Van Parijs, S.M., 2020. Seasonal trends and primary contributors to the low-frequency soundscape of the Cordell Bank National Marine Sanctuary. J. Acoust. Soc. Am. 148 (2), 845–858.

Hill, A.P., Prince, P., Snaddon, J.L., Doncaster, C.P., Rogers, A., 2019. AudioMoth: A low-cost acoustic device for monitoring biodiversity and the environment. HardwareX 6, e00073. https://doi.org/10.1016/j.ohx.2019.e00073.

Karsenty, A., 2016. The contemporary forest concessions in West and Central Africa: chronicle of a foretold decline? In: Forestry Policy and Institutions Working Paper, 1–90. http://www.fao.org/forestry/45021-04023cd52f4619cd28fe747b7e42c167f.pdf.

Kasten, E.P., Gage, S.H., Fox, J., Joo, W., 2012. The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology. Ecol. Inf. 12, 50–67. https://doi.org/10.1016/j.ecoinf.2012.08.001.

Krause, B., 1987. Bioacoustics, habitat ambience in ecological balance. Whole Earth Rev. 57 (Winter).

Krause, B., Farina, A., 2016. Using ecoacoustic methods to survey the impacts of climate change on biodiversity. In: Biological Conservation (Vol. 195, pp. 245–254). Elsevier Ltd. https://doi.org/10.1016/j.biocon.2016.01.013.

Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H., Sueur, J., Giuggioli, L., 2014. Monitoring temporal change of bird communities with dissimilarity acoustic indices. Methods Ecol. 5 (6), 495–505. https://doi.org/10.1111/2041-210X.12178.

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science, 349(6250), 827 LP – 832. https://doi.org/10.1126/science.aaa9932.

Lhoest, S., Fonteyn, D., Daïnou, K., Delbeke, L., Doucet, J.L., Dufrêne, M., Josso, J.F., Ligot, G., Oszwald, J., Rivault, E., Verheggen, F., Vermeulen, C., Biwolé, A., Fayolle, A., 2020. Conservation value of tropical forests: Distance to human settlements matters more than management in Central Africa. Biol. Conserv. 241(July 2019), 108351. https://doi.org/10.1016/j.biocon.2019.108351.

Londhe, N., Rao, M.D., Blough, J.R., 2009. Application of the ISO 13472–1 in situ technique for measuring the acoustic absorption coefficient of grass and artificial turf surfaces. Appl. Acoust. 70 (1), 129–141.

Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba'a, R., Abitsi, G., Ambahe, R.D., Amsini, F., Bakabana, P.C., Hicks, T.C., Bayogo, R.E., Bechem, M., Beyers, R.L., Bezangoye, A.N., Boundja, P., Bout, N., Akou, M.E., Bene, L.B., Fosso, B., Greengrass, E., Grossmann, F., Ikamba-Nkulu, C., Ilambu, O., Inogwabini, B.-I., Iyenguet, F., Kiminou, F., Kokangoye, M., Kujirakwinja, D., Latour, S., Liengola, I., Mackaya, Q., Madidi, J., Madzoke, B., Makoumbou, C., Malanda, G.-A., Malonga, R., Mbani, O., Mbendzo, V.A., Ambassa, E., Ekinde, A., Mihindou, Y., Morgan, B.J., Motsaba, P., Moukala, G., Mounguengui, A., Mowawa, B.S., Ndzai, C., Nixon, S., Nkumu, P., Nzolani, F., Pintea, L., Plumptre, A., Rainey, H., de Semboli, B.B., Serckx, A., Stokes, E., Turkalo, A., Vanleeuwe, H., Vosper, A., Warren, Y., Kolokotronis, S.-O., 2013. Devastating Decline of Forest Elephants in Central Africa. PLoS ONE 8 (3), e59469. https://doi.org/10.1371/journal.pone.0059469.

Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P., Parks, S.E., Hodgson, D., 2015. Measuring acoustic habitats. Methods Ecol. Evol. 6 (3), 257–265. https://doi.org/10.1111/mee3.2015.6.issue-310.1111/2041-210X.12330.

Nakashima, Y., Hongo, S., Akomo-Okoue, E.F., 2020. Landscape-scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. Biol. Conserv. 241, 108381. https://doi.org/10.1016/j.biocon.2019.108381.

Nasi, R., Billand, A., van Vliet, N., 2012. Managing for timber and biodiversity in the Congo Basin. For. Ecol. Manage. 268, 103–111. https://doi.org/10.1016/j.foreco.2011.04.005.

O'Dea, N., Whittaker, R.J., 2007. How resilient are Andean montane forest bird communities to habitat degradation? In: Vertebrate Conservation and Biodiversity. Springer, Netherlands, pp. 305–333.

Oden, A.I., Bomberger Brown, M., Burbach, M.E., Brandle, J.R., Quinn, J.E., Foster, S., 2015. Variation in avian vocalizations during the non-breeding season in response to traffic noise. Ethology 121 (5), 472–479. https://doi.org/10.1111/eth.2015.121.issue-510.1111/eth.12360.

Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global biodiversity change: The Bad, the good, and the unknown. In: Annual Review of Environment and Resources, Vol. 37, pp. 25–50. Annual Reviews. https://doi.org/10.1146/annurev-environ-042911-093511.

Pieretti, N., Farina, A., 2013. Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. J. Acoust. Soc. Am. 134 (1), 891–900. https://doi.org/10.1121/1.4807812.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L., Krause, B.L., 2011. What is soundscape ecology? An introduction and overview of an emerging new science. Landscape Ecol. 26 (9), 1213–1232.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011. Soundscape Ecology: The Science of Sound in the Landscape. Bioscience 61 (3), 203–216. https://doi.org/10.1525/bio.2011.61.3.6.

Poulsen, J.R., Clark, C.J., Smith, T.B., 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (Lophocebus albigena) in Cameroon. Am. J. Primatol.: Off. J. Am. Soc. Primatol. 54 (2), 91–105.

Poulsen, J.R., Clark, C.J., Bolker, B.M., 2011. Decoupling the effects of logging and hunting on an afrotropical animal community. Ecol. Appl. 21 (5), 1819–1836. https://doi.org/10.1890/10-1083.1.

R Core Team, 2020. A Language and Environment for Statistical Computing. In: R Foundation for Statistical Computing, 2, https://www.R-project.org. http://www.r-project.org.

Reed, J., Deakin, L., Sunderland, T., 2015. What are "Integrated Landscape Approaches" and how effectively have they been implemented in the tropics: A systematic map protocol. In: Environmental Evidence, Vol. 4, Issue 1, p. 2. BioMed Central Ltd. https://doi.org/10.1186/2047-2382-4-2.

Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P., Sueur, J., 2014. Temporal and spatial variability of animal sound within a neotropical forest. Ecol. Inf. 21, 133–143. https://doi.org/10.1016/j.ecoinf.2013.12.006.

Rondinini, C., di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., Hoffmann, M., Schipper, J., Stuart, S.N., Tognelli, M.F., Amori, G., Falcucci, A., Maiorano, L., Boitani, L., 2011. Global habitat suitability models of terrestrial mammals. Philos. Trans. Royal Soc. B: Biol. Sci. 366 (1578), 2633–2641. https://doi.org/10.1098/rstb.2011.0113.

Scarpelli, M.D.A., Ribeiro, M.C., Teixeira, F.Z., Young, R.J., Teixeira, C.P., 2020. Gaps in terrestrial soundscape research: It's time to focus on tropical wildlife. Sci. Total Environ. 707, 135403. https://doi.org/10.1016/j.scitotenv.2019.135403.

Sollmann, R., Mohamed, A., Niedballa, J., Bender, J., Ambu, L., Lagan, P., Mannan, S., Ong, R.C., Langner, A., Gardner, B., Wilting, A., Regan, H., 2017. Quantifying mammal biodiversity co-benefits in certified tropical forests. Divers. Distrib. 23 (3), 317–328. https://doi.org/10.1111/ddi.2017.23.issue-310.1111/ddi.12530.

Stephenson, P.J., 2019. The Holy Grail of biodiversity conservation management: Monitoring impact in projects and project portfolios. Perspect. Ecol. Conserv. 17 (4), 182–192. https://doi.org/10.1016/j.pecon.2019.11.003.

Strindberg, S., Maisels, F., Williamson, E.A., Blake, S., Stokes, E.J., Aba'a, R., Abitsi, G., Agbor, A., Ambahe, R.D., Bakabana, P.C., Bechem, M., Berlemont, A., Bokoto de Semboli, B., Boundja, P.R., Bout, N., Breuer, T., Campbell, G., De Wachter, P., Ella Akou, M., Esono Mba, F., Feistner, A.T.C., Fosso, B., Fotso, R., Greer, D., Inkamba-Nkulu, C., Iyenguet, C.F., Jeffery, K.J., Kokangoye, M., Kühl, H.S., Latour, S., Madzoke, B., Makoumbou, C., Malanda, G.-A., Malonga, R., Mbolo, V., Morgan, D.B., Motsaba, P., Moukala, G., Mowawa, B.S., Murai, M., Ndzai, C., Nishihara, T., Nzooh, Z., Pintea, L., Pokempner, A., Rainey, H.J., Rayden, T., Ruffler, H., Sanz, C.M., Todd, A., Vanleeuwe, H., Vosper, A., Warren, Y., Wilkie, D.S., 2018. Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. Sci. Adv. 4 (4) https://doi.org/10.1126/sciadv.aar2964.

Stokes, E.J., Strindberg, S., Bakabana, P.C., Elkan, P.W., Iyenguet, F.C., Madzoké, B., Malanda, G.A.F., Mowawa, B.S., Moukoumbou, C., Ouakabadio, F.K., Rainey, H.J.,

Getz, W.M., 2010. Monitoring great Ape and elephant abundance at large spatial scales: Measuring effectiveness of a conservation landscape. PLoS ONE 5 (4), e10294. https://doi.org/10.1371/journal.pone.001029410.1371/journal.pone.0010294.s00110.1371/journal.pone.0010294.s00210.1371/journal.pone.0010294.s003.

Stowell, D., Sueur, J., 2020. Ecoacoustics: acoustic sensing for biodiversity monitoring at scale. Remote Sens. Ecol. Conserv. 6 (3), 217–219. https://doi.org/10.1002/rse2.v6.310.1002/rse2.174.

Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acustica United with Acustica 100 (4), 772–781. https://doi.org/10.3813/AAA.918757.

Sueur, J., Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. Biosemiotics 8 (3), 493–502.

Sugai, L.S.M., Silva, T.S.F., Ribeiro Jr, J.W., Llusia, D., 2019. Terrestrial passive acoustic monitoring: review and perspectives. Bioscience 69 (1), 15–25.

Takenoshita, Y., Yamagiwa, J., 2008. Estimating gorilla abundance by dung count in the northern part of Moukalaba-Doudou National Park, Gabon. African Study Monographs. Supplementary Issue. 39, 41–54.

Terborgh, J.W., 2015. Toward a trophic theory of species diversity. Proc. Natl. Acad. Sci. U. S. A., 112(37), 11415–11422. https://doi.org/10.1073/pnas.1501070112.

Towsey, M., Wimmer, J., Williamson, I., Roe, P., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. Ecol. Inf. 21, 110–119. https://doi.org/10.1016/j.ecoinf.2013.11.007.

Van Vliet, N., Nasi, R., 2008. Mammal distribution in a Central African logging concession area. Biodivers. Conserv. 17 (5), 1241–1249. https://doi.org/10.1007/s10531-007-9300-5.

Vokurková, J., Motombi, F.N., Ferenc, M., Hořák, D., Sedláček, O., 2018. Seasonality of vocal activity of a bird community in an Afrotropical lowland rain forest. J. Trop. Ecol. 34 (1), 53–64. https://doi.org/10.1017/S0266467418000056.

Warren, P.S., Katti, M., Ermann, M., Brazel, A., 2006. Urban bioacoustics: It's not just noise. In: Animal Behaviour, Vol. 71, Issue 3, pp. 491–502. Academic Press. https://doi.org/10.1016/j.anbehav.2005.07.014.

Welford, M.R., 2000. The importance of early successional habitats to rare, restricted-range, and endangered birds in the Ecuadorian Andes. Bird Conserv. Int. 10 (4), 351–359. https://doi.org/10.1017/S0959270900000307.

Zwerts, J.A., Stephenson, P.J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P.A., Waarde, J., Sterck, L.E.H.M., Verweij, P.A., Bruce, T., Brittain, S., Kuijk, M., 2021. Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. Conserv. Sci. Pract. 3 (12) https://doi.org/10.1111/csp2.v3.1210.1111/csp2.568.